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CONTENTS

Volume 70, Number 1, Pages 1–32, Issued March 28, 1980

Volume 70, Number 2, Pages 33–80, Issued June 30, 1980

Volume 70, Number 3, Pages 81–112, Issued September 29, 1980

Volume 70, Number 4, Pages 113–140, Issued December 30, 1980

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Intersectional Hybrids in Isoëtes[1]

BRIAN M. BOOM*

Engelmann (1886) and Campbell (1891) have described the simple procedure for germinating *Isoëtes* spores in the laboratory to obtain micro- and megagametophytes. Perhaps the absence of hybridization studies in this genus can be explained partly by the fact that sexually mature living plants of more than one species were rarely assembled at one time, or that when they were, the primary aim was comparative embryology (La Motte, 1937). The present study was undertaken to test for genetic compatibility among four selected *Isoëtes* species in three sections of the genus (*sensu* Pfeiffer, 1922). All crossing combinations produced progeny, and in at least one species apogamy may occur.

MATERIALS AND METHODS

Spores for the crosses were obtained from populations of plants as follows: *Isoëtes (Reticulatae) macrospora* Dur.—Monroe Co., TN, *Boom 318,* Shenandoah Co., VA, 8 Nov 1978, *Evans; I. (Reticulatae) engelmannii* A. Br.—Polk Co., TN, *Boom 317*, Putnam Co., TN, *Boom 267; I. (Tuberculatae) flaccida* Shuttlew.—Dixie Co., FL, *Boom 313,* Wakulla Co., FL, *Boom 314, 315; I. (Cristatae) riparia* Engelm.—Tyrrell Co., NC, *Boom 316*. Voucher specimens have been deposited in the Herbarium of the University of Tennessee (TENN). All plants were collected during the summer or autumn of 1978, and were grown in the greenhouse for a short time until the crosses were made in mid-January, 1979.

The crossing technique was quite simple, yet rigorously controlled. Forty-eight glass vials were filled with about 1 ml of sterilized fine sand and 10 ml of sterilized pond water. Each sporangium was dissected out of the sporophyll base, washed in a sterile water bath, and then teased apart to release the spores into a vial, taking great care to insure that the vials were not contaminated with unwanted spores. Since microsporangia and megasporangia are usually found on the same plant, spores were taken from completely intact sporangia to avoid the possibility of using megagametophytes which already had been fertilized.

The crosses among the eight populations were set up in such a way that the megaspores of each population were brought into contact with the microspores of every other population. To test for spore viability and self compatibility, one plant from each population was selfed. To provide controls for the crosses and to test for apogamy, one vial was set aside for each population in which only megaspores were placed. All vials were kept in the greenhouse at about 25° C, where they were exposed to normal ambient light fluctuations, and were not disturbed except for the occasional addition of sterile pond water.

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*Department of Botany, University of Tennessee, Knoxville, TN 37916.

[1] Contribution from the Botanical Laboratory, The University of Tennessee, N. Ser. no. 516.

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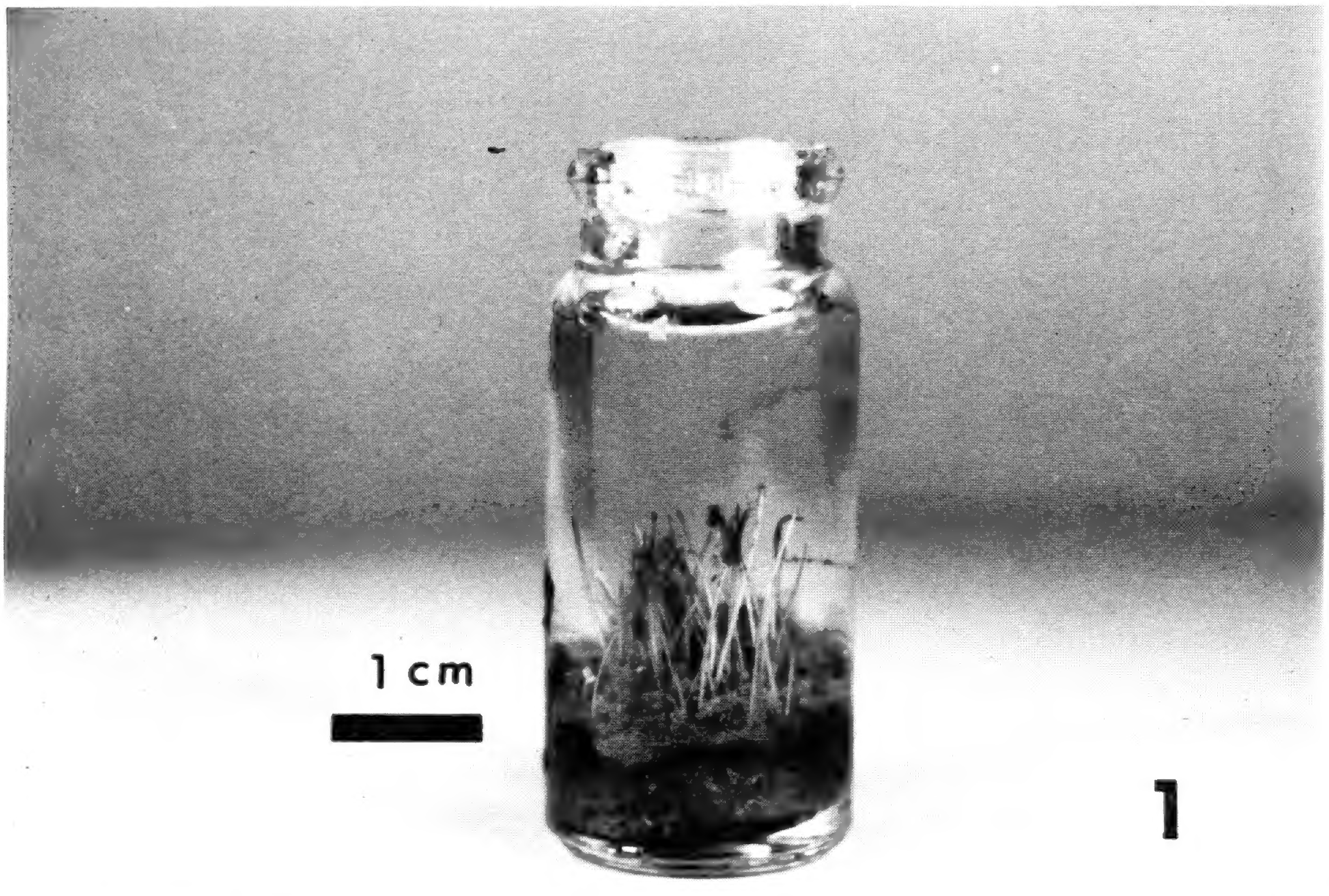

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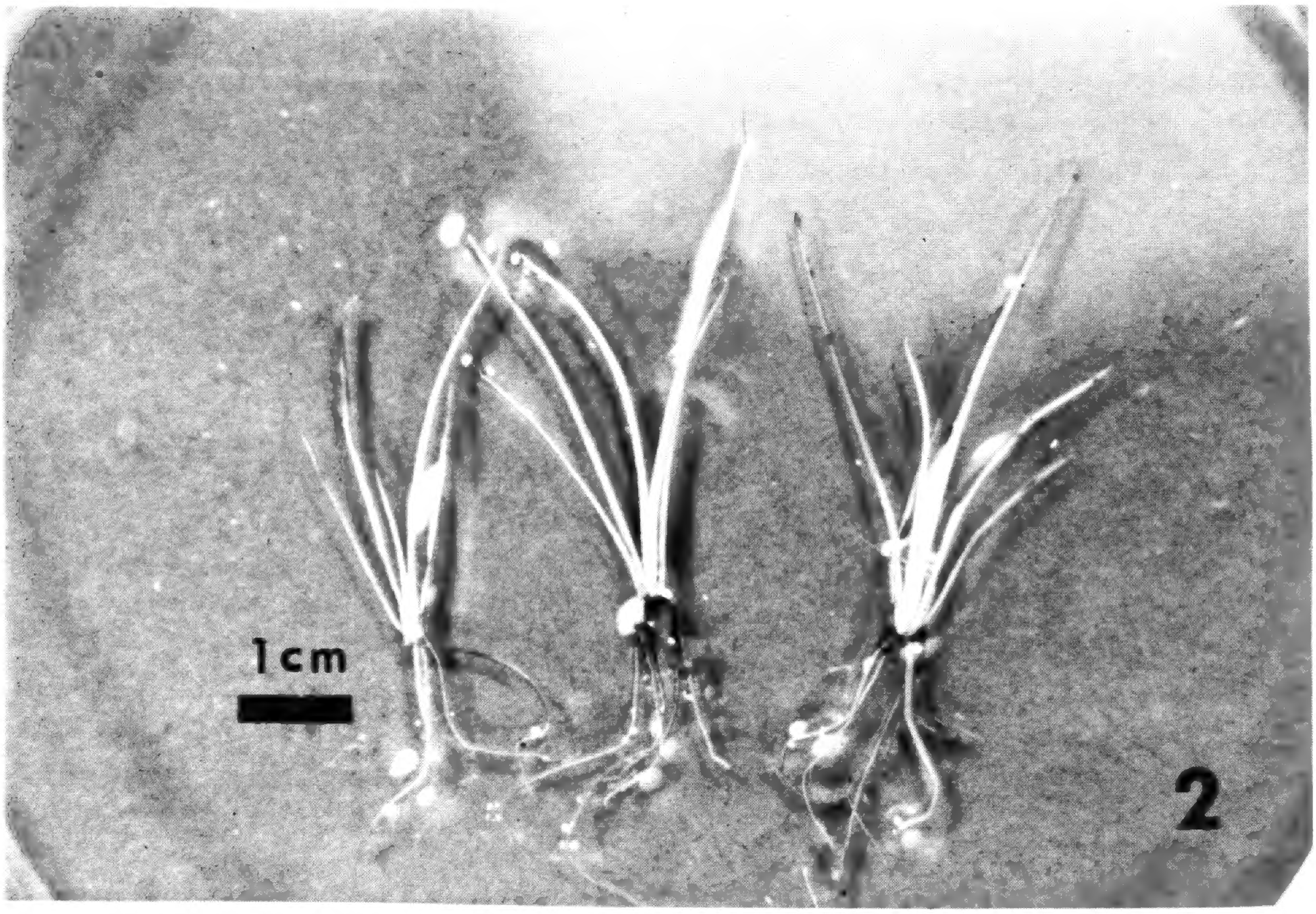

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FIGS. 1–2. Sporophytes resulting from a cross between *Isoëtes flaccida* and *I. macrospora*, two species thought to have had very different evolutionary histories. FIG. 1. Sporophytes in vial at two months after the cross was made. FIG. 2. Hybrid sporophytes at four months.

RESULTS AND DISCUSSION

About seven weeks after the crosses were made, the first green shoots of young *Isoëtes* sporophytes were observed in a number of the vials (*Figs. 1* and *2*). Although not every individual cross was successful, every possible crossing combination was successful within the first two months of the experiment. None of the control vials showed any signs of growth at that time, and the genetic compatibility of the four species presumedly has been demonstrated.

No new sporophytes were observed until 3.5 months after the experiment began, when a single sporophyte appeared in the *I. macrospora* control vial (*Boom 318*). Since no microspores had been introduced into this vial, either the megagametophyte had somehow become fertilized before it was introduced into the vial or the species is capable of reproducing apogamously. Considering the precautions taken by using only fully intact sporangia as a source of spores, apogamy seems more likely. Eight months after the crosses were made, no sporophytes had developed in any of the control vials of the other three species.

Easily hybridized species of *Isoëtes* means that hybridization followed by polyploidization may be a mode of evolution from time to time in the genus. The occurrence of facultatively apogamous taxa is consistent with such a process. If, as is suggested by the experimental observations, *I. macrospora* can be apogamous, this could help explain the Virginia and Tennessee populations disjunct from the typical northeastern range of this species (Dennis et. al., 1979). The reticulate distal face and the cristate proximal face of the megaspores of *I. macrospora* suggest a possible hybrid origin for this species.

Some *Isoëtes* populations on the Coastal Plain of the Carolinas have various characters, primarily megaspore ornamentation, which clearly are intermediate between typical *I. engelmannii* and *I. riparia*; supposedly these plants are hybrids between the two. Specimens from such populations occasionally have been annotated as *I. engelmannii* var. *georgiana* Engelm. or var. *caroliniana* Eaton.

The results of this study also support Matthews and Murdy's (1969) interpretation of the often confusing *Isoëtes* populations on the granite outcrops of the Piedmont of the southeastern United States. Introgression apparently is taking place in pools which are ecologically intermediate between the habitats typical of *I. piedmontana* (Pfeiffer) Reed and those of *I. melanospora* Engelm. For an alternate explanation, see Rury (1978), who suggests that intermediates represent developmental stages of one polymorphic species.

The naturalness of Pfeiffer's (1922) sections of the genus is suspect now more than ever in light of the artificial intersectional hybridizations. The infrageneric classification of *Isoëtes* should be reexamined by means of an extensive genetic, cytogenetic, and phytochemical survey, as well as by using traditional morphological characters.

This report of intersectional genetic compatibility need not necessarily affect *Isoëtes* taxonomy at the species level, however. In natural circumstances, the taxa generally are isolated by geographic, ecological, or phenological barriers, and they can be distinguished morphologically from one another. The amount of gene flow between the typically isolated populations must be relatively small. If this is not the case, it remains a challenge to explain why selection has not favored the establishment of reproductive barriers between species.

The present study was initiated to test the potential for genetic experimentation in *Isoëtes*. The preliminary results were very successful and indicate further and wider genetic studies would be beneficial. Such future hybridization research should take advantage of the artificial crossing technique recently described for *Selaginella* (Webster, 1979). The method appears to be well suited for *Isoëtes* crossing with little or no modification, and will permit more critical experimentation than ever could be possible with the non-sterile technique employed in the present study.

Appreciation is extended to Dr. A. Murray Evans for critically reviewing this paper. Field work was aided by a Grant-in-Aid of Research from Sigma Xi, The Scientific Research Society.

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REVIEW

"THE ECONOMIC USES AND ASSOCIATED FOLKLORE OF FERNS AND FERN ALLIES," by Lenore Wile May, Botanical Review 44:491–528. 1979—As stated by the author, this paper is not taxonomic in nature, but discusses fern folklore and to a lesser extent their economic history. It provides an easily read text for the generalist and a good bibliography for those persons interested in pursuing this topic further. Some of the section titles include: Folklore, Fern Dyes, Fern Fibers, Fern Foods, Medicinal Uses of Ferns, The Male Fern, and The Bracken Fern. The section on medicinal uses occupies forty percent of this article, with related medicinal notes in the folklore portion. The author mentions the following about *Ophioglossum vulgatum:* "This plant is called adder's tongue because out of every leaf it sendith forth a kind of pedestal like an adder's tongue, it cureth the biting of serpents."—*J. Scott Peterson, Dept. of Botany & Plant Pathology, Colorado State University, Ft. Collins, CO 80523.*

Notes on Some Pleopeltis and Polypodium Species of the Chihuahuan Desert Region

TOM WENDT[*,1]

In preparing a treatment of the Polypodiaceae *s. str.* for the forthcoming Chihuahuan Desert Flora (M. C. Johnston, et al.), I found several taxonomic changes to be necessary. A new variety of *Polypodium thyssanolepis* A. Br. ex Kl. is described, and *Pleopeltis erythrolepis* (Weath.) Pic. Ser. is lowered to varietal rank within *Pleopeltis polylepis* (Roem. ex Kunze) Moore. Material from GH, LL, NY, TEX, and US was consulted in preparation of the treatment.

POLYPODIUM

Polypodium thyssanolepis A. Br. ex Kl. is a species of lithophilic fern which ranges from the southwestern United States to South America and the West Indies. Originally described from Colombian material (Klotzsch, 1847), it was not reported from the United States until 1913, when Maxon noted it among the collections of L. N. Goodding from the Huachuca Mountains of southeastern Arizona. Maxon (1913) stated that Goodding's specimens were "perfectly typical of the species as it exists from Mexico to the Andes and in Jamaica." In his revision of several groups of squamate American polypodies (Maxon, 1916), the most recent revision in which *P. thyssanolepis* has been treated, he recognized no varieties within the species. However, in recording the species from Texas, Maxon (1923) noted that specimens from both Texas and Arizona "have fronds only scantily scaly beneath, in marked contrast to tropical material."

A number of characters are correlated with the sparser indument of the fronds of these northern populations. Material from western Texas, southeastern Arizona, northern Coahuila, and parts of Chihuahua appears to represent a strongly marked new variety of *P. thyssanolepis* (Fig. 1). None of the synonyms of *P. thyssanolepis* (see Maxon, 1916; Morton, 1973) refer to this new variety, which may be distinguished from the typical variety by the following key:

Stipes sparsley scaly, the scales mostly ovate or lance-ovate, suborbicular scales few or none; scaly indument of the lower lamina surface not so dense as to obscure the surface; venation mostly free, with fewer than 30%(40%) of the sori within areoles; basal lobes of the lamina distinctly alternate. .... *P. thyssanolepis* var. *riograndense*

Stipes densely scaly, the scales mostly suborbicular; scaly indument of the lower lamina surface dense, typically entirely obscuring the surface; venation mostly areolate, with more than 70% (usually nearly 100%) of the sori within areoles; basal lobes of the lamina opposite or subopposite. *P. thyssanolepis* var. *thyssanolepis*

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*Rama de Botánica, Colegio de Postgraduados, Chapingo, Edo. de México, México.

[1] Work accomplished at University of Texas at Austin and Gray Herbarium of Harvard University. I thank Alan R. Smith of the University of California at Berkeley for unpublished data.

Polypodium thyssanolepis var. riograndense Wendt, var. nov.

A var. *thyssanolepide* stipitibus multo minus squamatis squamis suborbicularis paucis vel absentibus, laminis minus squamatis, venatione libera pro parte maxima, et positione lobarum laminarum basilarium distincte alterna recedit.

Small lithophilic ferns. Rhizome slender, wide-creeping, 1.5–2.5 mm thick, densely scaly; rhizome scales subulate to lanceolate-acuminate, (1.0) 1.5–3.0 mm long, imbricate, light brown with a darker central stripe composed of dark-walled cells with clear lumina, the margins slightly erose to irregularly ciliate. Fronds distant or occasionally a few somewhat crowded, to 15(20) cm tall, usually much smaller; stipes usually slightly shorter than to slightly longer than the laminae, but varying from one-half to twice as long, sparsely scaly, the scales mostly subulate to lanceolate-acuminate, peltate, to 3 mm long, erose to fimbriate, the larger ones usually brown with a blackish central stripe, these scales often continuing into the lower part of the rachis, with nearly orbicular, irregular, peltate scales scattered or absent; laminae oblong or ovate to triangular-oblong to deltate, to 10 cm long, to 5.5 cm wide, acuminate or acute, deeply pinnatifid into up to 9(11) segments on each side (usually fewer), glabrous above, sparsely to moderately densely scaly below but the scales usually not completely obscuring the green of the surface, the lamina scales peltate, ovate to lanceolate, usually attenuate-acuminate, 0.8–2.0(3.0) mm long, light reddish-brown, darker at the point of attachment, weathering gray, the margin remotely toothed to lacinate, orbicular scales few or none, the lobes distant to fairly close, linear or spatulate to oblong, entire, obtuse to broadly acute, regular or irregular in length on the same frond, perpendicular or slightly ascending relative to rachis, the lowest pair distinctly alternate, venation mostly free, fewer than one-half of the sori (usually many fewer) within areoles; sori roundish, in a single row on each side of midvein of lobe, usually obscured by scales; spores 64 per sporangium.

TYPE: Uncommon in crevices of cliffs and boulders in sheltered canyon with *Quercus grisea, Juniperus* sp., *Ungnadia speciosa, Garrya ovata*, etc., lower Indian Cave Canyon (side canyon of Dead Horse Canyon), north side of Chinati Mountains, Presidio Co., Texas, 16 Oct 1977, *M. L. Butterwick & E. J. Lott 3897* (TEX; isotypes GH, MEXU).

Polypodium thyssanolepis has generally been characterized as having areolate venation and pinnatifid fronds (Maxon, 1916). A rare form of the species with bipinnatifid fronds is known to show partial loss of areolation; this form occurs with the normal form in Central America (Maxon, 1916), but is not known from northern Mexico or the United States. It agrees in density of indument and all other characters with typical var. *thyssanolepis*. On the other hand, the new variety differs strongly and consistently from var. *thyssanolepis* in venation (*Fig. 2*). These venation characters are constant regardless of size; occasional specimens of var. *thyssanolepis* from Chihuahua in which the fronds are much reduced (laminae as small as 0.5 cm long), with many fronds nearly entire, nevertheless display the areolate venation (and all other characters) typical of much larger tropical plants of the variety. South American material, including all specimens seen from Colombia (at GH), the type locality of the species, agrees with var. *thyssanolepis* as here circumscribed.

Fronds of var. *thyssanolepis* may reach much larger sizes (to 60 cm or more) than those of var. *riograndense*, but this probably is a direct environmental effect.

Specimens of var. *thyssanolepis* from northern Mexico are generally much smaller than tropical material; indeed, the reduction found in certain Chihuahuan specimens, noted above, is unparalleled in var. *riograndense*.

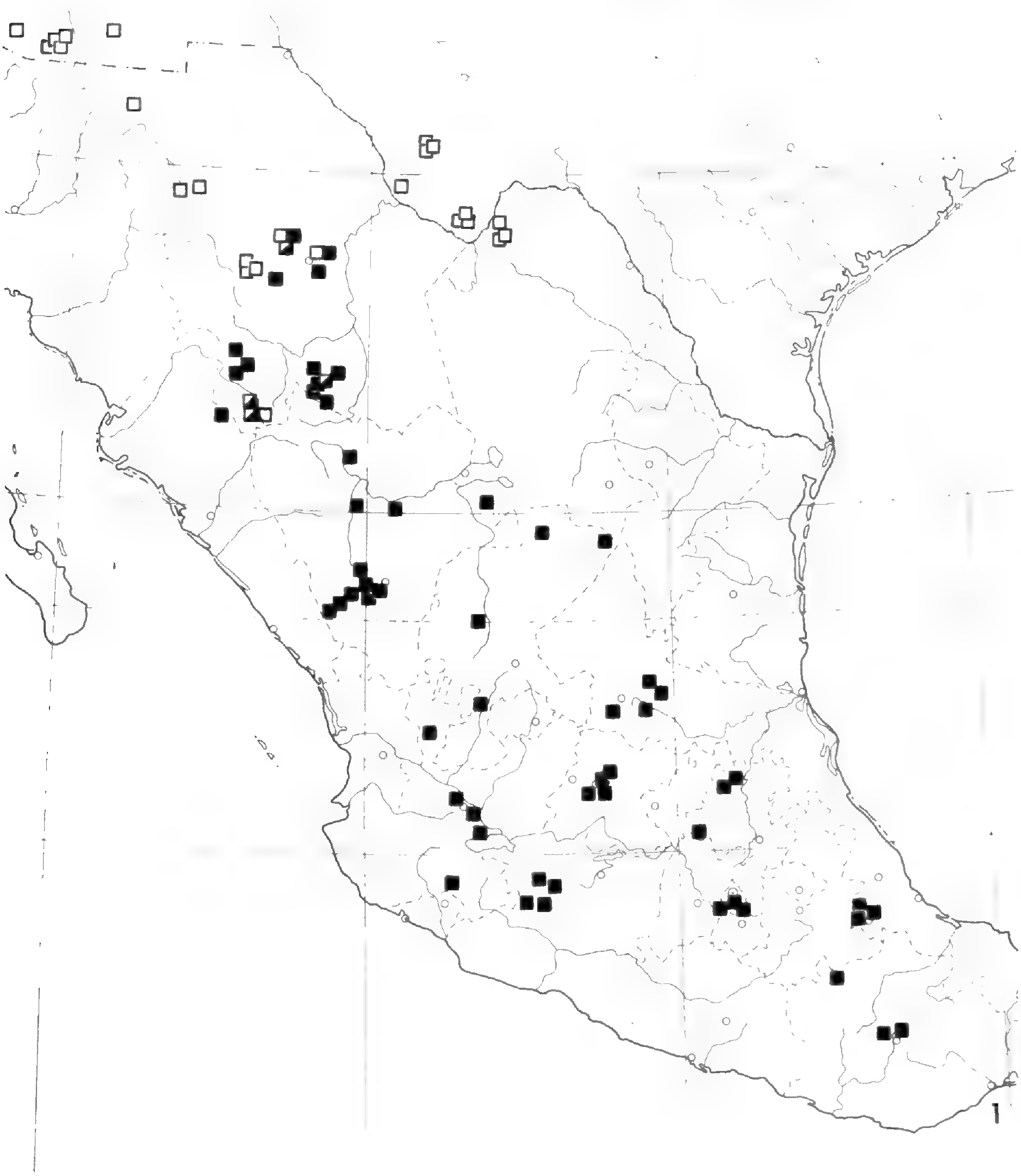
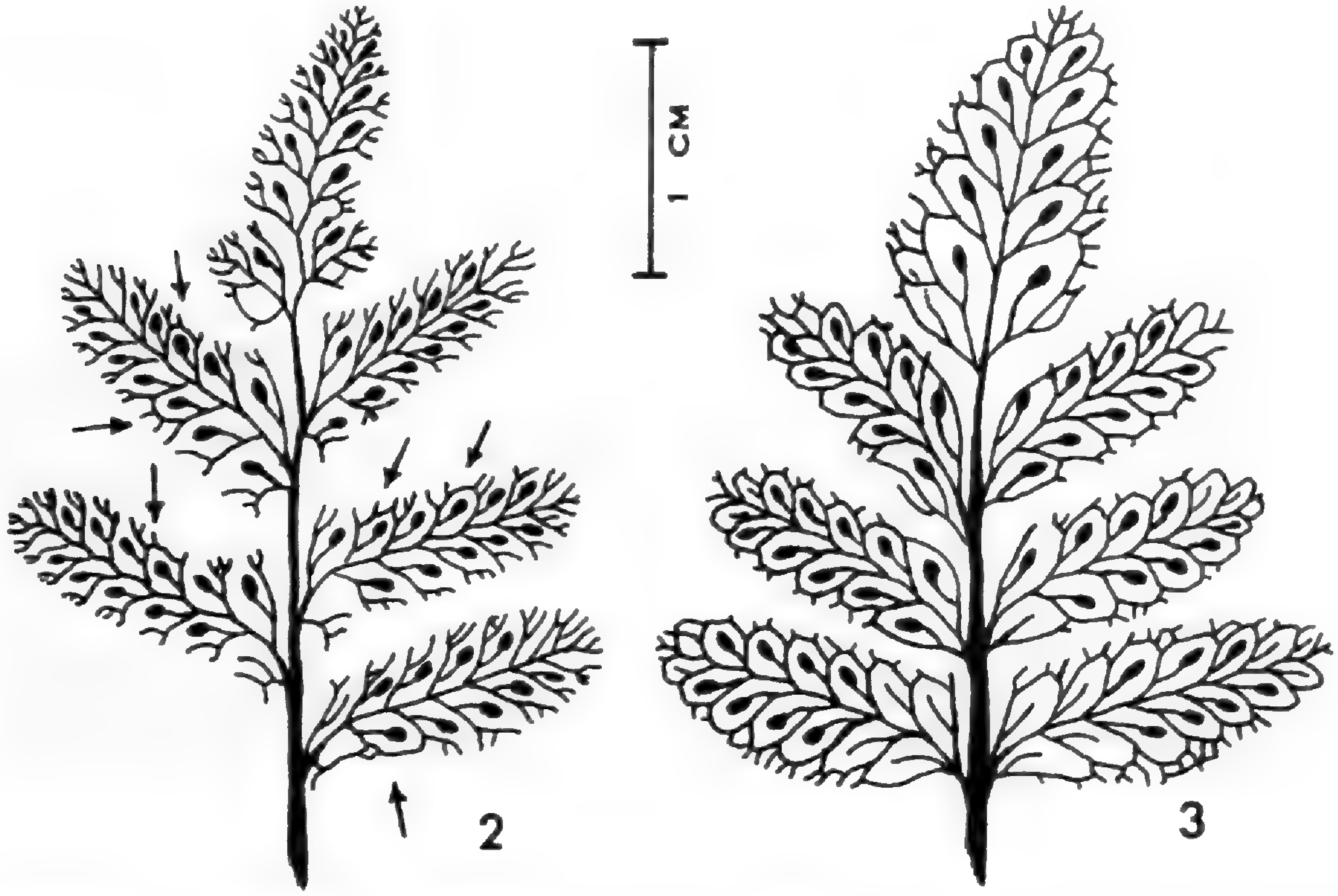


FIG. 1. Distribution of *Polypodium thyssanolepis* varieties in the United States and Mexico excluding Chiapas. Black squares = var. *thyssanolepis;* open squares = var. *riograndense;* half-squares = intermediates.

The chromosome number of *P. thyssanolepis* var. *thyssanolepis* has been reported as $n=37$ from South American material (Evans, 1963) and $n=74$ from a Jamaican population (Wagner & Wagner, 1975). *Polypodium thyssanolepis* (variety unknown) has been reported as n=ca. 72 from material from "Mexico" (Sorsa in Fabbri, 1965; Sorsa, 1966).

A limited number of varietal intermediates is found in Chihuahua (*Fig. 1*), but most specimens from this area are easily placed in one of the varieties. Several collections (e.g., *Pringle 443*) include fairly representative plants of both varieties. Further work, especially chromosomal, may reveal that var. *riograndense* would be better treated as a separate species.



FIGS. 2 and 3. Venation of *Polypodium thyssanolepis* varieties. FIG. 2. Type of var. *riograndense* (*Butterwick & Lott 3897*, TEX); arrows indicate scattered areoles. FIG. 3. Var. *thyssanolepis* from San Luis Potosí, Mexico (*Johnston, Chiang & Wendt 12275*, LL).

Figure 1 shows the geographical origin of the United States and Mexican specimens examined. All Chihuahuan material for the species, along with representative specimens of the new variety, is cited below.

Polypodium thyssanolepis var. riograndense:

MEXICO: Chihuahua: Mountains between Guadalupe y Calvo and Nabogame, 7200 ft, on large boulders in pine-oak forest, *Correll & Gentry 23052, p. p.* (GH, LL); 12 mi W of Cuauhtémoc, in crevices of cliff, *Correll & Johnston 21610* (LL); Between Yepomera and Babicora, in crevices of boulders in pine-oak-juniper open mountain forest, *Correll & Johnston 21624* (LL, US); Vicinity of village of Majalca, in crevices of boulders, *Correll & Johnston 21780* (LL); 12 mi W of Cuauhtémoc, steep, rocky (granitic) slope, in pinyon pine-scrub oak association, *Gould 8958* (LL); Río Negro and vicinity, *LeSueur 1273* (TEX); Rocky hills near Chihuahua, cold cliffs, *Pringle 443, p. p.* (GH, NY, US); 16 mi W of Cuauhtémoc, rolling terrain with scattered junipers, pinyons, and oaks, 7200 ft, in rocky crevices on a steep slope, *Reeder, Reeder, & Soderstrom 3477* (GH). **Coahuila:** Sierra del Jardín, Canyon Hundido on N side of Pico Centinela, 8 km E of Rancho El Jardín by winding road, 1500-2250 m, steep canyon through igneous sierra, *Johnston, Chiang, Wendt & Riskind 11803A* (LL). **Sonora:** Loop of the Río de Bavispe, S of Aribabi, Sierra de Huépari, 1495 m, *Harvey 1706* (US).

UNITED STATES: Arizona: Cochise Co.: Conservatory Canyon, Huachuca Mts., July–Sept 1882, *Lemmon s. n.* (GH, NY, US); Chiricahua Mts., *Peebles & Loomis 5415* (US). Pima Co.: Baboquivari Mts., *Gilman 15* (US). Santa Cruz Co.: Sycamore Canyon, Patagonia Mts., 2800 ft, *Ripley & Barneby 2822* (NY). **Texas:** Brewster Co.: Chisos Mts., Boot Spring, 30 June 1932, *Mueller s. n.* (GH, NY, TEX). Jeff Davis Co.: Near Fort Davis, in clefts and crevices of porphyritic rocks, *E. J. Palmer 32196* (TEX, US).

Polypodium thyssanolepis var. thyssanolepis:

MEXICO: Chihuahua: Minas Nuevas, ca. 8 mi NW of Parral, 6000 ft, *Correll & Gentry 22764* (GH, LL, US); Ca. 5.5 mi NW of Parral, 5800 ft, *Correll & Gentry 22723* (LL); Sierra de Santa Barbara, ca. 4 mi SW of Villa Matamoras, 6300 ft, *Correll & Gentry 22802* (NY, LL); Along old railroad W toward Rancho Ojito, *Correll & Johnston 21488* (LL, NY); 25 mi SE of Cuauhtémoc, *Correll & Johnston 21597* (LL); 11 mi S of Matamoras (Cuevas), 1950–2100 m, *Gentry & Arguelles 18037* (LL, US); Majalca (Pilares), 2075 m, *Harvey 1463* (GH, US); La Bufa, on Río Batopilas, *Knobloch 578* (US); Canyon E of Hidalgo de Parral, *Knobloch 751* (US); Cerocahui–Cuiteco Road, *Knobloch 882* (US); Barranca Guerachic, between Agua Blanca and Guerachic, *Knobloch 1849* (LL); Rocky hills near Chihuahua, cold cliffs, *Pringle 443, p. p.* (GH); Potrero Peak, *Pringle 977* (NY); Between San Francisco del Oro and Santa Barbara, near Arroyo de Granadeña, ca. 7000 ft, *Soderstrom 894* (LL).

Intermediates between var. thyssanolepis and var. riograndense:

MEXICO: Chihuahua: Small mountain on NE edge of Parral, *Correll 22688* (GH, LL); Mountains just SE of Nabogame, 6000 ft, *Correll & Gentry 23033* (LL); Mountains between Guadalupe y Calvo and Nabogame, 7200 ft, *Correll & Gentry 23052, p. p.* (GH, LL, US); Majalca, *Knobloch 329* (GH, US), *LeSueur 476* (US).

PLEOPELTIS

A study of material of *Pleopeltis erythrolepis* (Weath.) Pic. Ser. and *P. polylepis* (Roem. ex Kunze) Moore throughout their ranges in Mexico and the United States has led to the conclusion that they represent geographical varieties of the same species. The following new combination is necessary:

Pleopeltis polylepis var. erythrolepis (Weath.) Wendt, comb. & stat. nov.

Polypodium erythrolepis Weath. Contr. Gray Herb. 65:11. 1922. TYPE: Cold cliffs, Portrero [Potrero] Peak, Chihuahua, *Pringle 825* (GH!; isotypes, GH!, LL!, NY-2 sheets!, US-3 sheets!).

Phlebodium erythrolepis (Weath.) Conzatti, Fl. Tax. Mex. 1:95. 1946.

Pleopeltis erythrolepis (Weath.) Pic. Ser., Webbia 23:189. 1968.

Various characters have been used to distinguish the taxa. Weatherby (1922), in his description of *Polypodium erythrolepis*, emphasized the long stipe and imbricated, fimbriate-ciliate lamina scales of this "well-distinguished" species. However, in his treatment of the ferns of north-central Mexico (Weatherby, 1943) he states:

> [These new collections] go very far to break down the differences between *P. erythrolepis* and *P. peltatum* [*Pleopeltis polylepis*]. In them, the abundant, ovate, deeply lacerate-margined scales of the former, which seemed so distinctive when it was proposed, nearly disappear and are replaced by suborbicular ones. The surviving distinctions are: *P. erythrolepis*, stipe nearly as long as the blade, costa green on the lower surface; *P. peltatum*, stipe conspicuously shorter than the blade, costa black on lower surface. In addition, *P. erythrolepis* tends to have narrower rhizome-scales with narrower, more definitely erose-serrulate hyaline margins; but this is only a tendency. Furthermore, the collection here cited under *P. peltatum* . . . is also transitional . . . In all probability, *P. erythrolepis* would best be treated as a variety of *P. peltatum*.

Knobloch and Correll (1962) "more or less avoided the taxonomic issue by recognizing as *P. peltatum* those plants that have a distinctly blackish costa and placing those plants that lack this characteristic into *P. erythrolepis*," and in doing so recognized both species from Chihuahua.

In the present study it was found that both costa color and stipe length are too variable within both taxa to be taxonomically useful. The characters for distinguishing the varieties are given in the following key:

Scales of the lower surface of mature laminae entire or merely erose, mostly orbicular, usually not densely imbricate; rhizome scales ovate to broadly lanceolate..........*P. polylepis* var. *polylepis*

Scales of the lower surface of mature laminae fimbriate or ciliate and/or mostly acuminate, usually densely imbricate; rhizome scales lanceolate-acuminate to broadly lanceolate. *P. polylepis* var. *erythrolepis*

Populations from Sonora, Chihuahua, northern Durango, and Texas fit easily within var. *erythrolepis* as here circumscribed, and almost all central and southern Mexican populations (southern Durango and Guanajuato south to Oaxaca, also Baja California Sur) are "good" var. *polylepis*. However, a broad range of intergradation between the varieties occurs in the northern Sierra Madre Oriental of southern Coahuila, Nuevo León, and San Luis Potosí, where individuals referable to both varieties as well as a preponderance of intermediates occur. Furthermore, northern Coahuilan populations (Muzquiz to Sierra del Carmen) include many intermediate types in additon to those referable to var. *erythrolepis*.

The problem is compounded not only by intrapopulational variation in lamina scales, but also by the fact that scaliness of the fronds changes with age. Young fronds of all populations tend to have many acuminate scales; these are then apparently shed quite early in the case of var. *polylepis*, but are retained much longer in var. *erythrolepis*. Mature, preferably fertile fronds therefore are necessary for specimen identification.

Only one glaring exception to the above-mentioned geographical pattern was found in the material studied. A specimen from the state of Mexico (Parque Nacional de Laguna Zimpoala, *Barkley, Webster & Rowell 7420*, TEX) is referable by all characters to var. *erythrolepis*, although it is well south of the range of that variety.

There also appears to be some problem in the differentiation of *Pleopeltis polylepis* var. *polylepis* from *P. macrocarpa* var. *trichophora* (Weath.) Pic. Ser. in central Mexico, particularly in the general area of Mexico City. The taxonomic problems involving *P. polylepis* and *P. macrocarpa* are emphasized by the fact that a variety originally described by Weatherby (1944) within *P. polylepis* (as *Polypodium peltatum* var. *interjectum*) appears to belong closer to *Pleopeltis macrocarpa* (A. R. Smith, pers. comm.). Further studies are much needed in this complex.

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REVIEW

"THE EXPERIMENTAL BIOLOGY OF FERNS," by A. F. Dyer (ed.). Experimental Botany: An International Series of Monographs, vol. 14, 657 pp. 1979. Academic Press, London and New York, ISBN 0-12-226350-2. $79.00—Over the past forty years a significant amount of research has been devoted to the experimental biology of pteridophytes. Although information has accumulated and developmental and genetic problems have been better circumscribed, there has been no attempt to organize this into a fashion which would make the relevant ideas and literature easily available to experimental biologists and botanists. This volume attempts to review comprehensively nearly all of the significant studies in fern experimental biology in a context which stresses the controversies currently extant and the problems and avenues of approach which promise to provide the most productive and interesting rewards. In essence, it is a technical introduction to the literature, with over 2000 reference citations. The textual contents reflect accurately the current state of knowledge with heavy emphasis on morphogenetic studies of the gametophyte generation. The 16 chapters, contributed by 16 authors, detail our knowledge of meiosis; spore initiation, morphogenesis, and germination; structural, physiological, and biochemical aspects of the filamentous gametophytic stage; differentiation from one-dimensional to two-dimensional growth; antheridiogens; sporophyte development; apogamy, genetics, cytogenetics, and hybridization; and experimental ecology. Although many of the contributions are excellent, some are superficial, reflecting in my estimation the lack of experimental studies in those fields. However, because of the comprehensive literature surveys and the emphasis on ideas and problems, this volume will be a very valuable source book for experimental biologists and pteridologists for many years to come.—*Robert M. Lloyd, Department of Botany, Ohio University, Athens, OH 45701.*

The Deletion of Vittaria graminifolia from the Flora of Florida

GERALD J. GASTONY*

Interest in new state and national records, range extensions, and the status of rare or endangered species of ferns is probably nowhere more keen than in Florida. Critical field and herbarium work to upgrade our knowledge of the distribution and habitat requirements of ferns, especially in the subtropical southern region of the state, assumes political as well as scientific significance at a time when state and federal socio-economic decisions are influenced by the ecological status of species as humble as a lousewort or a snail darter. Efforts to increase the accuracy of our floristic records for Florida ferns have been quite evident in recent years, for example in the work of Messler (1974), Evans (1975), Ward and Hall (1976), Nauman and Austin (1978), Nauman (1978), Austin et al. (1979), Adams and Tomlinson (1979), and Nauman (1979a, 1979b). Such efforts, however, must include the deletion of erroneous records as well as the addition of new records. The deletion of one such erroneous record, the natural occurrence of *Vittaria graminifolia* Kaulf. in Collier County, Florida, is the subject of this report.

The belief that *V. graminifolia* occurs in Collier County, Florida, its only reported occurrence in the United States, is based on a statement appended to the discussion of *V. lineata* (L.) J. E. Smith in Wherry's (1964) Southern Fern Guide. Wherry stated that *V. filifolia* Fée was found in 1960 in Collier County, and he distinguished it from *V. lineata* by the weak iridescence and width of its scales. In another context, Tryon (1964a) showed that *V. filifolia* is an incorrect name for this species and that its correct name is *V. graminifolia*.

In an effort to bring cytological evidence to bear on the identity of the Appalachian gametophyte by counting its chromosomes and those of *V. lineata* and *V. graminifolia* (Gastony, 1977), I undertook a search for *V. graminifolia* in Collier County. Dr. Wherry responded to my request for more information relating to his 1964 report by noting (in litt., 15 Aug 1976) that at the age of ninety and a half he was no longer able to recall more specific locality data or whether an herbarium voucher documented his report. He did recall, however, that he had visited the living fern collection assembled by John Beckner in St. Petersburg, Florida and that Beckner had there "two *Vittarias*," one less winter hardy than the other. The less hardy one from Collier County was what Dr. Wherry took to be *V. graminifolia* (as *V. filifolia*).

Wherry's information enabled me to contact John Beckner, who agreed to take me to the site from which he had collected the *Vittaria* in question. In the company of Dr. Michael Madison of the Selby Botanical Garden and several others, we explored the swampy locality west of Copeland and Deep Lake where Beckner clearly remembered having made the original collection, and we eventually found several specimens of what Beckner said was *V. graminifolia* if anything in that

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*Department of Biology, Indiana University, Bloomington, IN 47401.

area was. These were immature, somewhat depauperate specimens epiphytic on the trunk of *Persea palustris*, unlike the usual *Sabal palmetto* epiphytism of *V. lineata*. They were not fertile and did not survive cultivation efforts in the Indiana University greenhouses.

Beckner was certain, however, that Wherry had taken a specimen of his original collection back to Pennsylvania and that a voucher specimen documenting Wherry's (1964) statement was to be found there. Subsequent inquiries led to a specimen (number 0925236) at the herbarium of the Academy of Natural Sciences in Philadelphia (PH) bearing the stamp of the herbarium of the University of Pennsylvania, which is on permanent loan to PH. The label identifies the specimen as *Vittaria filifolia* Fée and indicates that it had been cultivated from a plant collected by John Beckner west of Deep Lake in Collier County, Florida. The specimen was made on 3 January 1962, and has been annotated by Dr. Wherry as *V. filifolia*. Beckner (pers. comm.) has since assured me that the locality from which this specimen was taken is identical to the swampy locality we had visited west of Copeland and Deep Lake. On 4 January 1980, I returned to this site and established in a discussion there with Park Ranger Robert Goble that this locality is in the center of what is now the Fakahatchee Strand State Preserve protected by the Department of Natural Resources of the State of Florida.

I have analysed Wherry's specimen from PH, utilizing the characters employed by Tryon (1964b, pp. 212–215) in distinguishing *V. lineata* and *V. graminifolia* in the Ferns of Peru. Comparable or identical characters are used by Lellinger (pers. comm.) and by Stolze (pers. comm.) in distinguishing these species in their forthcoming treatments of the ferns of Costa Rica, Panama, and the Chocó and the ferns of Guatemala, respectively. Perhaps the most absolute criterion employed in the discriminatory sets of characters used in these three major floristic treatments is the incidence of tetrahedral-globose, trilete spores in *V. graminifolia*, as opposed to reniform, monolete spores in *V. lineata*. In this regard and in the other characters examined, the specimen upon which the record of *V. graminifolia* in Florida rests is surely *V. lineata*. I sent Beckner a photocopy of Wherry's herbarium specimen and he is certain (pers. comm.) that this specimen is the basis of Wherry's (1964) report.

It is interesting that Lakela and Craighead (1965), Long and Lakela (1971), and Lakela and Long (1976) discussed *V. lineata* in their treatments of the ferns of south Florida but made no reference whatever to *V. filifolia* or *V. graminifolia*. The reason for omitting *V. graminifolia* from these three works is unknown and is particularly curious since the work by Long and Lakela (1971) does cite Wherry's book (1964) as a selected reference on the ferns of Florida. Long is deceased and Craighead (pers. comm.) says that the decision as to what to include in their checklist was entirely that of Lakela. Lakela, now in retirement, does not recall the reason for this omission from any of these works (pers. comm.). There is no indication that any of these authors ever consulted the specimen at PH. Based on my experience with Beckner in revisiting the collection site of Wherry's specimen in the Fakahatchee Strand, I suspect that the difference in the cold-hardiness of the "two *Vittarias*" was most likely due to the sub-optimal substrate of the hardwood host tree and perhaps to a variant allelic constitution correlated with the occurrence of these individuals on this unusual host.

It is always possible that *V. graminifolia* or any other species common in tropical America may be carried into southern Florida by hurricane winds or other means of dispersal and that such adventives may become temporarily or permanently established in subtropical Florida. Because of Wherry's report, Austin and Nauman (pers. comm.) have searched extensively for *V. graminifolia* in the Fakahatchee Strand but have never found it and have concluded that it is not there. Critical examination of the morphology and ecology of the specimen discussed above indicates that there is no longer any reason to believe that *V. graminifolia* ever did or does now occur in Florida. It should therefore be deleted from the floristic record for Florida and thus from the flora of the United States.

I am grateful to Ross and Priscilla Stanley of Port Charlotte, Florida for their hospitality during the field work and manuscript preparation for this paper and to John Beckner for his aid in the field and in locating the specimen upon which Dr. Wherry's report was based. I thank Dr. Michael Madison for help in the field, Dr. Wherry for help in interpreting his report, the officers of the herbarium of the Academy of Natural Sciences (PH) for the loan of the specimen discussed, and Ranger Robert Gobel for aid in interpreting the specimen locality data in terms of the Fakahatchee Strand.

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New Taxa and Combinations of Pteridophytes from Chiapas, Mexico

ALAN R. SMITH*

This is the second and, it is intended, final report on new taxa and new combinations (beginning on p. 26) of pteridophytes in the state of Chiapas, Mexico. For the first report, see Proc. Calif. Acad. Sci., Ser. IV, 40:209–230. 1975. All of the taxa are to be included in the treatment of the pteridophytes of Chiapas, a part of the "Flora of Chiapas" project headed by Dennis Breedlove, California Academy of Sciences. English descriptions, fuller synonymies, and additional discussion will be found in the floristic account. Certain of the new names are also needed by Robert Stolze for his forthcoming treatment of the Polypodiaceae in the "Ferns and Fern Allies of Guatemala."

I thank Colleen Sudekum for preparation of the illustrations. Scanning electron micrographs of spores were made with a Coates and Welter 50 microscope, obtained by the Electron Microscope Laboratory at the University of California, Berkeley, under a grant from the National Science Foundation (GB-38359). Breedlove collections were made with the help of National Science Foundation grants GS-383, GS-1183, and GB-29483. I am grateful to A. M. Evans, who has collaborated in the description of *Polypodium chiapense*.

7.023 **Asplenium insolitum A. R. Smith, sp. nov.** **Figs. 1–2.**

Rhizomata suberecta, caudices ca. 1 cm diametro; frondes 35–45 cm longae, stipitibus laminas fere aequantibus; stipites brunnei vel griseo-brunnei, non lustrati, ca. 1.5 mm diametro, adaxialiter viridi-alati, glabri, basi paleis paucis atrobrunneis ovatis; paleae ca. 2 mm longae, obscure clathratae, parietibus crassis et luminibus congestis parvulis; laminae ovato-lanceolatae, 18–25 cm longae, bipinnatae, apice attenuatae sed nec flagelliformes nec proliferae; rhachides adaxialiter viridi-alatae, abaxialiter brunneolae, epaleatae; pinnae 15–20-jugae, usque 6 cm longae, 2.5 cm latae; pinnae infimae (1 vel 2 paria) aliquantum reductae, deflexae; pinnulae usque 8-jugae per pinnam, saepe lobo acroscopico, aliter dentatae vel bidentatae secus marginem, basi cuneatae, plerumque inaequilaterae (subdimidiatae), latere basiscopico exciso; pagina laminae et axes subter glabri vel pilis minutis (0.1 mm longis) adpressis capitatis; venae pinnatae, usque 4-jugae per pinnulam; sori 1.0–2.5 mm longi, indusia tenui albido.

✓TYPE: Terrestrial in montane rain forest, 11 km NW of junction of road to Motozintla along road to El Porvenir and Siltepec, southwest side of Cerro Mozotal, Munic. Motozintla de Mendoza, Chiapas, Mexico, 2100 m, 21 Nov 1976, *Breedlove 41653* (DS).

PARATYPE: Same locality, 27 Jun 1972, *Breedlove 25760* (DS).

Asplenium insolitum has no obvious close relatives. In dissection, it is similar to some of the more divided members of the *A. radicans* complex (e.g., *A. flabellulatum* Kunze var. *partitum* Klotzsch), but the blade apex is neither flagelliform nor budding and the stipes and rachises are not shining. A closer relative is perhaps *A. cuneatum* Lam., but that species differs in the flabellate venation of the segments, longer sori, and obviously clathrate scales. Another possible rela-

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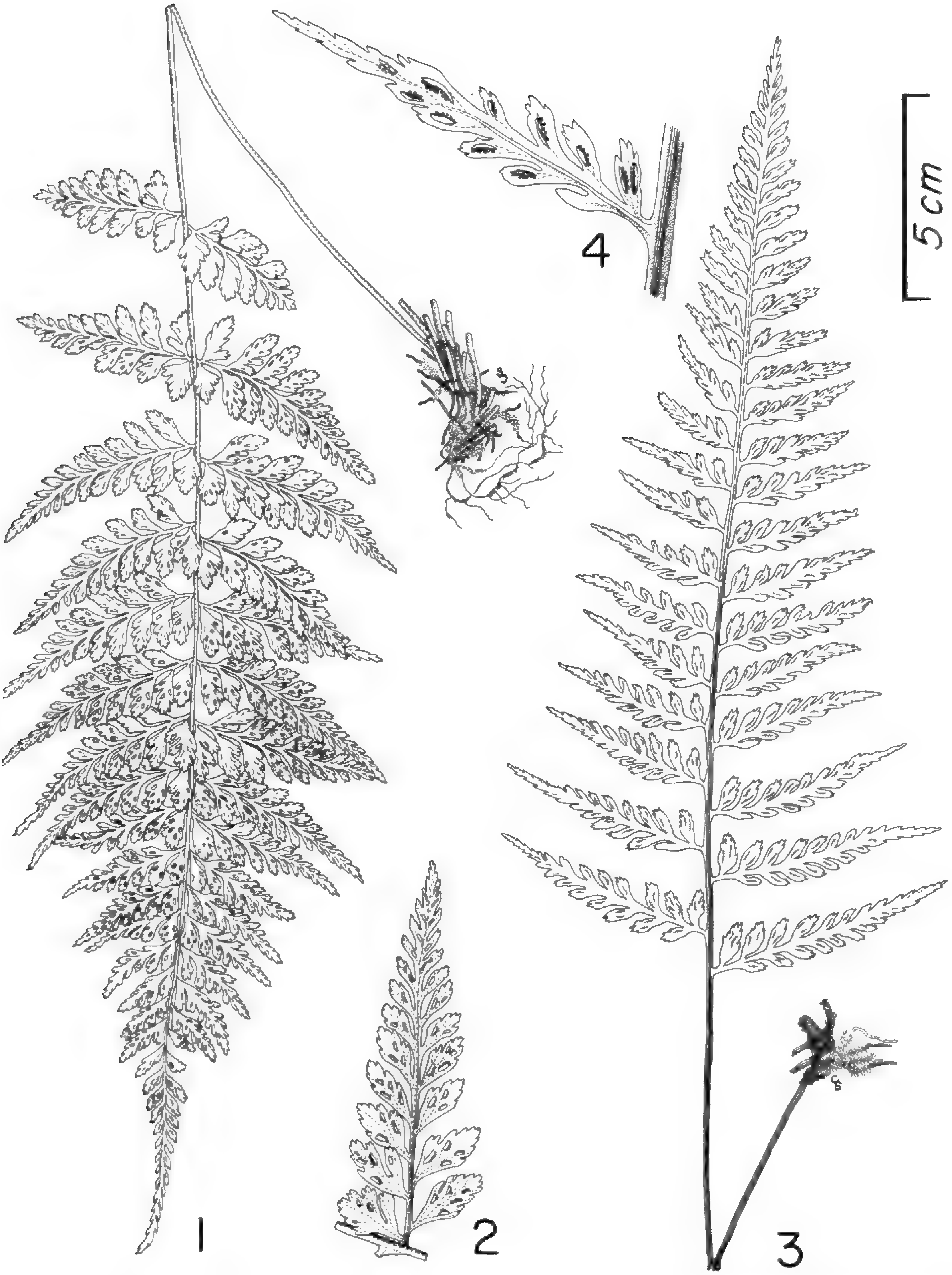
*University Herbarium, Department of Botany, University of California, Berkeley, CA 94720.



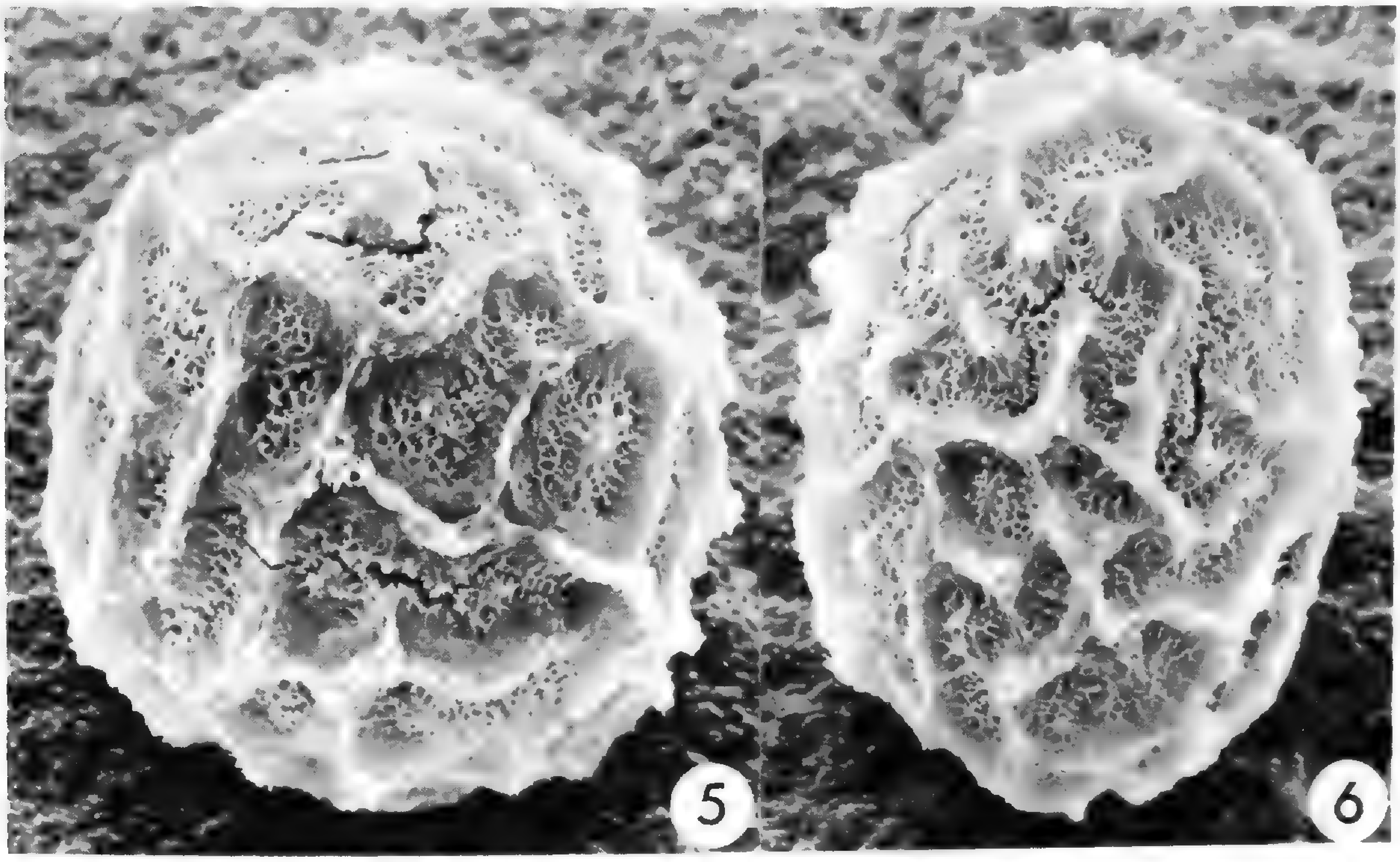
FIGS. 1–4. New *Asplenium* species. FIGS. 1–2. Type of *A. insolitum*, habit and lower pinna. *Breedlove 41653* (DS). FIGS. 3–4. Paratype of *A. sphaerosporum*, habit and lower pinna, *Breedlove 32512* (DS). Line scale for habit drawings.

tive is *A. solmsii* Baker ex Hemsl., but that species has tripinnatifid blades and often a few minute clathrate scales in the pinna axils.

7036 **Asplenium sphaerosporum A. R. Smith, sp. nov.** **Figs. 3–6.**

Rhizomata erecta; frondes plerumque 45–70 cm longae, usque 18 cm latae; stipites atri, ca. 2 mm diametro, glabri, longitudine 0.5–0.75 partes laminarum aequantes; rhachides atrae vel virides, distaliter viridi-alatae; laminae lanceolatae, ad apicem acuminatae; pinnae patentes, vulgo 25 vel plus, ad apicem acuminatae, paribus infimis plene bipinnatis, distaliter pinnis pinnatisectis, denique pinnis serrato-incisis; segmenta obovata, usque 1.3 cm longa, 5 mm lata, basi cuneata, apice dentata vel denticulata (dentibus 2–7), usque 12 paribus per pinnam, prope apices pinnarum segmentis adnatis et decurrentibus; paginae laminarum atrovirides vel aeruginosae, crassae, glabrae; sori usque 2–3 per segmentum; sporae grandes, globosae (interdum ellipsoideae), 32 per sporangium.

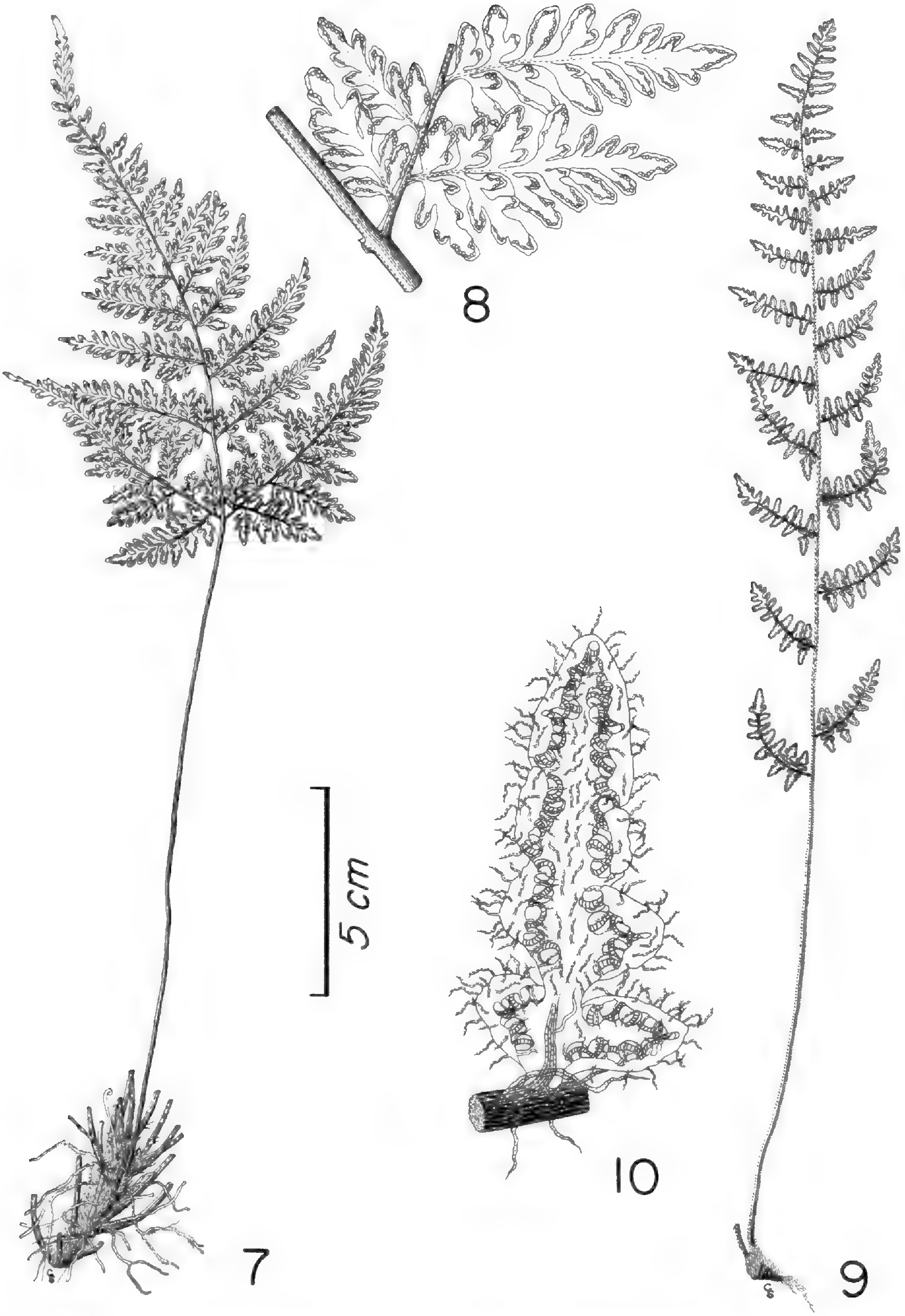
✓TYPE: SE side of Cerro Baul (16 km NW of Rizo de Oro), Chiapas, Mexico, *Breedlove 21805 with Smith* (DS).



FIGS. 5–6. Scanning electron micrographs of spores of *Asplenium sphaerosporum*, *Breedlove 28733* (DS), × 1500.

PARATYPES:

MEXICO: Chiapas: Lagos de Montebello, *Breedlove 22303 with Smith* (DS); Jct. of Tanaté River and river from Yochib, paraje Mahben Chauk, Munic. Tenejapa, *Breedlove 6368* (DS, US); SE of Cerro Baul (16 km NW of Rizo de Oro), *Breedlove 21810 with Smith* and *31338 with Smith* (both DS); 7 km NE of Bochil along road to Simojovel, Munic. Bochil, *Breedlove 28723*, *28733* (DS), *Breedlove 32311 with Smith* (DS); Near summit of Chuchil Ton, NE of Bochil, Munic. San Andres Larrainzar, *Breedlove 29244* (DS); 7 km NE of Jitotol–Pichucalco jct. on road from Bochil to Simojovel, Munic. El Bosque, *Breedlove 32512 with Smith* (DS); 6.5 km N of Jitotol, Munic. Jitotol, *Breedlove 32758 with Smith* (DS); Ocotepec, *Rovirosa 1049* (PH); 20 km S of Ocozocoautla, Munic. Ocozocoautla de Espinosa, *Breedlove 29138 p. p.* (DS), *Münch s.n.* (DS); *Ghiesbreght 404* (K, NY, PH). **Veracruz:** Techolo, *Sanchez 6* (UC, US); along Camino Real, near Jalapa, *Weatherwax 176* (UC). **State unknown:** *Schnee s.n.* (K); *Bourgeau 2365* (K). **GUATEMALA:** Fuego ?, *Salvin & Godman 368* (K); *Heyde & Lux* [*Donnell-Smith 3231*] (K, US).



FIGS. 7–10. New *Cheilanthes* taxa. FIGS. 7–8. Type of *C. complanata*, habit and base of lowermost pinna, *Breedlove 41747* (DS). FIGS. 9–10. Type of *C. microphylla* var. *fimbriata*, habit and pinnule, *Breedlove 39018* (DS). Line scale for habit drawings.

This species resembles somewhat *A. achilleifolium*, but I do not think that they are closely related. The affinity seems closest to *A. monodon* Liebm. and *A. cuspidatum* Lam. The former has large, globose spores, 32 per sporangium, like those of *A. sphaerosporum* (*Figs. 5–6*); all specimens of *A. cuspidatum* that I have looked at have small, reniform spores, 64 per sporangium. It is possible that *A. sphaerosporum* arose through hybridization between some member of the *A. auritum* group and *A. cuspidatum*. Alternatively, it could have speciated from *A. monodon*. Additional studies are needed to understand the evolutionary relationships within this complex group.

Asplenium auritum Swartz has often been applied in a broad sense, encompassing plants that are simply pinnate (sometimes with a basal auricle) to fully bipinnate. I would restrict the application of the name to those plants of the complex that are simply pinnate; such plants also have tan, reniform, relatively small spores, 64 sporangium. In Chiapas (and apparently elsewhere in the range), *A. auritum s. s.* occurs only at low elevations, 200–500 m.

Asplenium sphaerosporum occurs at higher elevations—(900)1250–2700 m—than any other member of the *A. auritum* complex in Chiapas, at elevations where *A. cuspidatum* can occur. The latter is chiefly from Montane Rain Forests, while *A. sphaerosporum* is most common in Pine-Oak-Liquidambar Forests.

7084 **Cheilanthes complanata A. R. Smith, sp. nov.** **Figs. 7–8.**

Differt a *C. hirsuta* Link paleis rhizomatis distincte bicoloris, ad marginem cinnamomeis, ad medium nigrescentibus; laminis pentagonis, latitudine longitudinem fere aequantibus, planis, segmentis ultimis non pendulis; segmentis ultimis obovatis vel anguste ellipticis, 2–4-plo longioribus quam latioribus; laminis atroviridibus, utrinque glabris; indusiis membranaceis, non valde dissimilibus laminae, integris (sine glandibus vel pilis), non vel leviter ad axe decurrentibus.

✓TYPE: North and west slope of Cerro Mozotal below microwave tower along road from Huixtla to El Porvenir and Siltepec, Munic. Motozintla de Mendoza, Chiapas, Mexico, 3000 m, *Breedlove 41747* (DS).

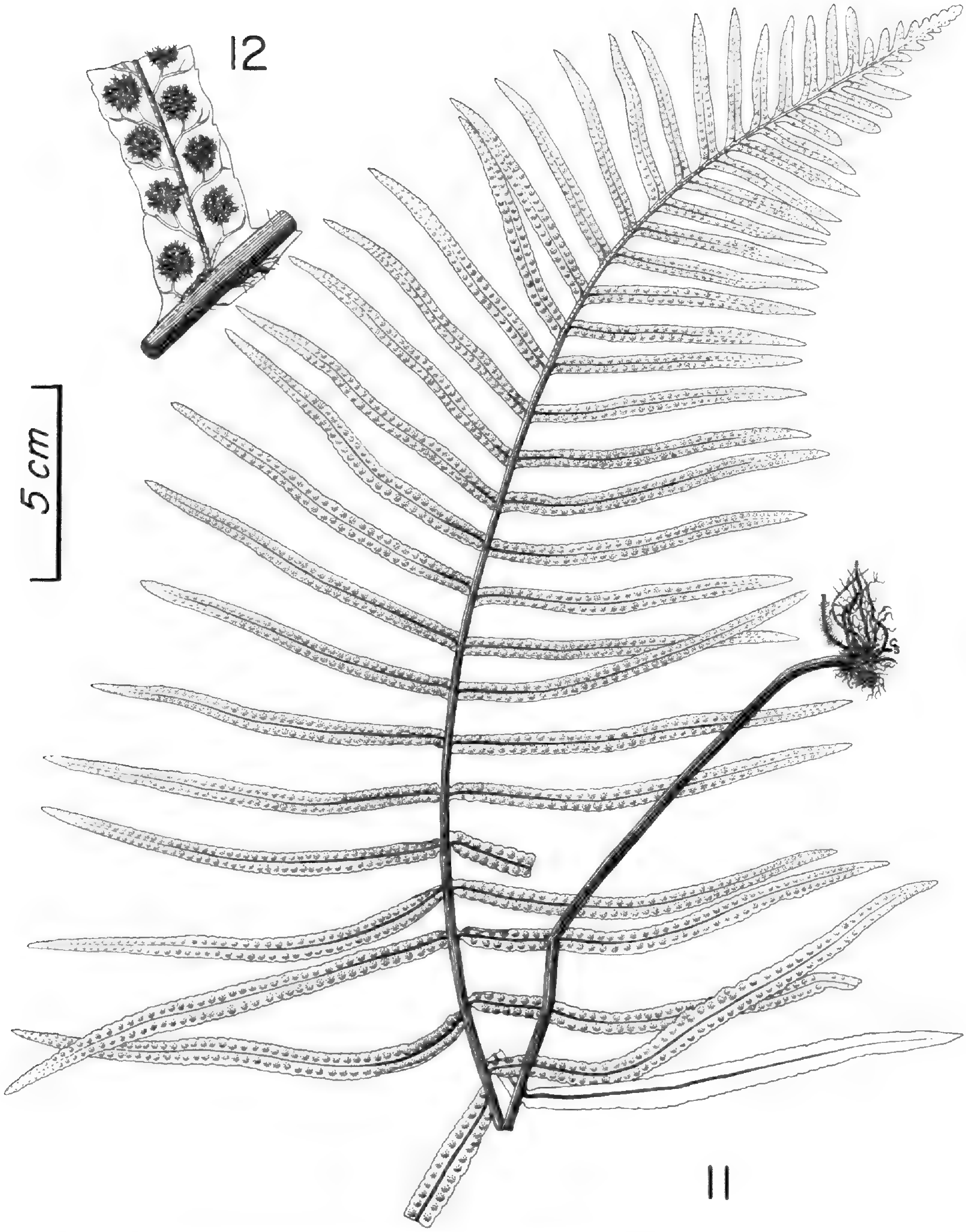
PARATYPE: Same locality, *Breedlove 40335* (DS).

The best characters for separating *C. complanata* from its nearest relatives, *C. marginata* H.B.K., *C. chaerophylla* (Mart. & Gal.) Kunze, and *C. hirsuta* (synonym of *C. pyramidalis* Fée), are the planar blades and the thin, entire indusia that completely lack trichomes or marginal papillae. Another relative may be *C. cuneata* Link, but that species has black or nearly black stipes and rachises, larger blades, darker, concolorous rhizome scales, and more sharply differentiated indusia.

7091 **Cheilanthes microphylla var. fimbriata A. R. Smith, var. nov.** **Figs. 9–10.**

Differt a var. *microphyllo* indusiis fimbriatis pilis usque 5 mm longis; trichomatibus numerosioribus albidis prope margines laminae supra; et laminis generaliter parvioribus bipinnatis subdimorphis.

✓TYPE: Along road to Ciudad Cuauhtemoc 6–8 km E of Frontera Comalapa, Munic. Frontera Comalapa, Chiapas, Mexico, *Breedlove 39018* (DS).



FIGS. 11–12. Type of *Polypodium alavae*, habit and base of pinna, *Alava 1287* (UC). Line scale for habit drawings.

PARATYPES:

GUATEMALA: Petén: Lake Petén Itza, NW of San Andres, *Contreras 3571* (US); Lake Petén Itza, along shore W of San Andres, *Lundell 17251* (US). **MEXICO: Chiapas:** El Carmen, *Münch 184* (DS); without locality, *Münch* (DS); Same locality as type, *Breedlove 26976* (DS); Munic. Ocozocoautla de Espinosa, Río de la Venta at the Chorreadero near Derna, *Breedlove 36556* (DS); Munic. Ocozocoautla de Espinosa, 13–18 km S of Ocozocoautla, *Breedlove 37838* (DS); Villa de Yajalón, *Rovirosa 971 p. p.* (PH). **Tamaulipas:** 2 mi S of Tres Palos and 1 mi down road to Loreto, *Johnston 4884* (TEX). **Yucatán:** San Anselmo, *Gaumer 1238bis* (US); Izamal, *Gaumer 534* (UC, US), *Gaumer 1409* (US); Chichankanab, *Gaumer 1473* (US), *P. Valdez 65* (US), *Gaumer 533* (US); Ruins of Nojpat, *Schott 686* (US); Mérida, *Schott 135* (US).

Variety *microphylla* is known from the Antilles, southeastern United States, and eastern and southern Mexico. I have not seen collections from the Yucatan peninsula, where var. *fimbriata* is common. In Chiapas, var. *fimbriata* seems to be more common than the type variety and does not grow with it.

7141 **Diplazium drepanolobium A. R. Smith, sp. nov.**

Differt a *D. lonchophyllo* Kunze segmentis pinnarum magis obliquis et falcatioribus; frondibus plerumque grandioribus, pinnis vulgo 20–25 cm longis, 3.5–6.0 cm latis.

TYPE: 10 km above Rayon, Chiapas, Mexico, *Breedlove 26122* (DS).

PARATYPES:

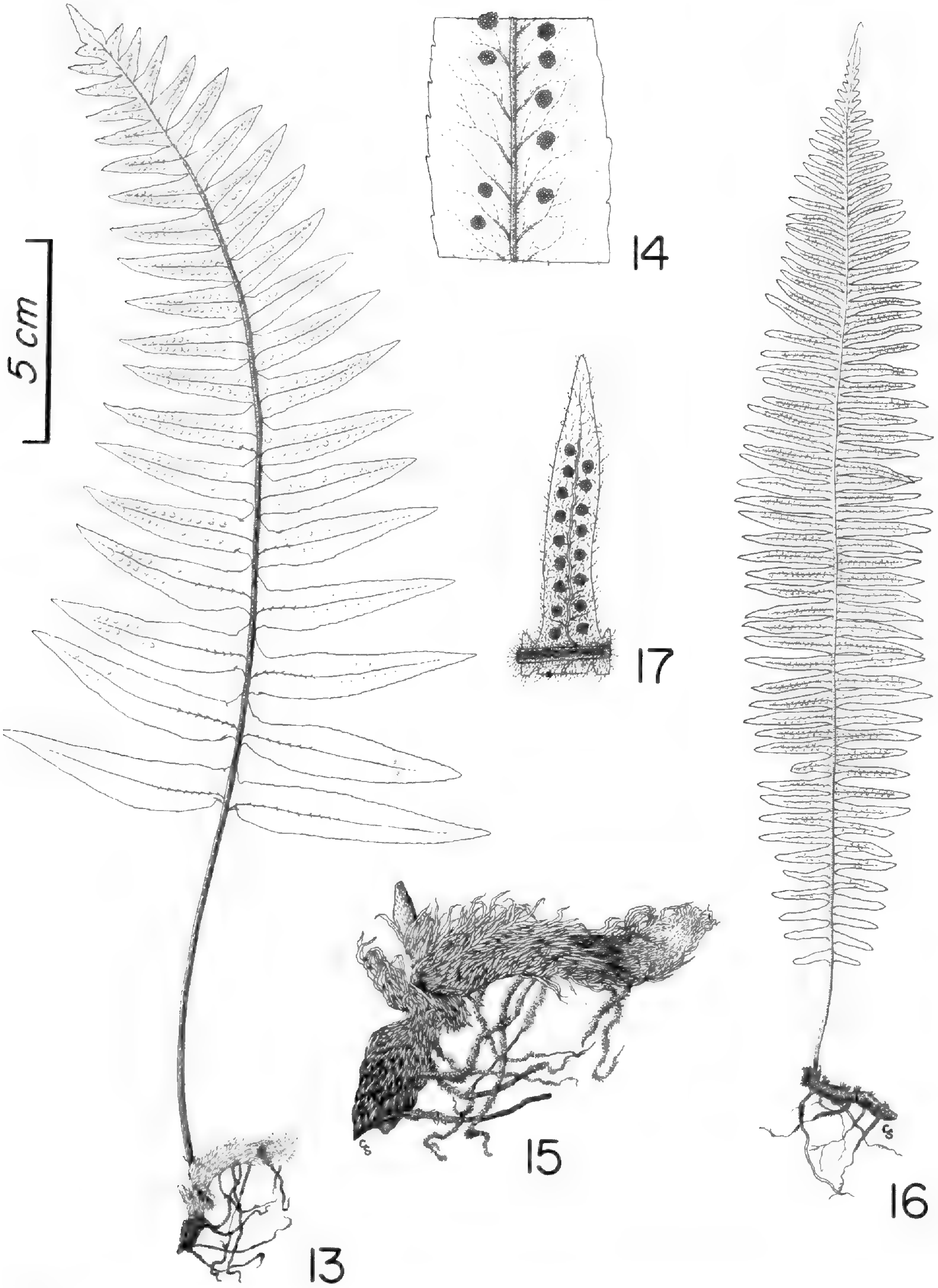
MEXICO: Chiapas: 26–28 km N of Ocozocoautla, *Breedlove 22451 with Smith* (DS); 45 km N of Ocozocoautla, *Breedlove 20760, 32852* (DS); 2–4 km below Ixhuatan, *Breedlove 24163* (DS); 32 km N of Ocozocoautla, *Breedlove 38162* (DS); 46 km N of Ocozocoautla, *Breedlove 38676* (DS); Without precise locality, *Ghiesbreght 361* (K); Arroyo de Ona, cerca Ixtacomitan, *Rovirosa 59* (K, PH). **Veracruz:** *Schaffner 470* (P).

It is possible that this is only an extreme variant of *D. lonchophyllum* Kunze, but *D. drepanolobium* has different blade dissection and seems at least as distinct as some other segregates of *D. lonchophyllum* (e.g., *D. prominulum* Maxon and *D. subsilvaticum* Christ). Relatively few specimens are intermediate between *D. drepanolobium* and *D. lonchophyllum*; one such specimen is *Breedlove 21624-A* (Chiapas, 13 km N of Berriozabal). This collection has abortive spores and may be a hybrid. More numerous are the intermediates between *D. drepanolobium* and a third species of the complex, *D. franconis* Liebm., which includes the following synonyms: *D. camptocarpon* Fée, *D. hahnii* (Fourn.) C. Chr., and *D. donnell-smithii* Christ. Several such intermediates from Chiapas are *22293*, *22484*, and *27480* (all DS). The best course in this difficult group seems to be to recognize all three species. The alternative is to recognize a single species, a treatment that has little merit.

On the basis of certain collections identified by Fée (e.g., *Schaffner 470*), formerly I applied the name *D. acutale* Fée to this species. However, the type of *D. acutale* is referable to *D. lonchophyllum*.

7362 **Polypodium alavae A. R. Smith, sp. nov.** **Figs. 11–12.**

Rhizomata repentia, 5–8 mm diametro, paleis aurantiaco-fulvis, aliquantum patentibus, concoloribus, glabris, ca. 5–10 mm longis; frondes (17)40–85 cm longae; stipites straminei vel brunneoli, parce pubescentes, longitudine 0.3–0.7 partes laminae aequantes, (1)3–5 mm diametro; laminae deltoideo-lanceolatae,



FIGS. 13–17. New *Polypodium* species. FIGS. 13–15. Type of *P. fuscopetiolatum*, habit, portion of pinna, and rhizome, *Breedlove 37155* (DS). FIGS. 16–17. Type of *P. chiapense*, habit and segment, *Breedlove 27453* (DS). Line scale for habit drawings.

(7)14–30 cm latae, basi latissimae, pinnatae praeter apicem, apice pinnatifido vel subconformi, confluenti; rhachides moderate vel conspicue pubescentes, sine paleis; pinnae plerumque 7–16 cm longae, 7–10 mm latae, integrae vel leviter crenulatae, ad apicem acutae, basi rotundatae, lateribus parallelis, pinnis sessilibus dimidio proximali laminae, adnatis dimidio distali laminae, nunquam dilatatis; venae (2)3-furcatae, liberae; paginae laminarum inter venas atrovirides vel olivaceae, subcoriaceae, utrinque glabrae vel sparse pubescentes; costae venaeque infra pilis dispersis vel numerosis, laxis, septatis, 0.4–0.8 mm longis; sori rotundati, mediales vel supramediales, vulgo ca. 2 mm diametro; sporangia pilis 0.2–0.3 mm longis, laxis, ca. 6 pilis per capsulam.

✓TYPE: About 3 mi from Jola along trail from Jola to Chanal, Chiapas, Mexico, *Alava 1287* (UC; isotype DS).

PARATYPES:

HONDURAS: Francisco Morazán: Km 24 on Tegucigalpa–Zamorano Rd., *Kimnach 449* (UC). **MEXICO: Chiapas:** Lagos de Montebello, *Breedlove 22337 with Smith* and *32126 with Smith* (both DS); same locality, *Breedlove 37005* (DS).

Polypodium alavae is related to *P. adelphum* Maxon, from which it differs in the narrower, more parallel-sided, mostly entire pinnae, long-hairy sporangia, and more coriaceous, dark-green leaf tissue. It is also related to *P. puberulum* Schlecht. & Cham., but it lacks the densely hairy leaf tissue on both surfaces and the lower pinnae are constricted at the base.

7355 **Polypodium chiapense Evans & Smith, sp. nov.** **Figs. 16–17.**

Rhizomata longe repentia, usque 10 cm longa, 3–5 mm diametro; paleae rhizomatis lanceolatae, basi interdum dilatatae, ferrugineae, acuminatae, inconspicue comosae, non clathratae, ad marginem interdum denticulatae; frondes 12–40 cm longae, distantes (ca. 7–10 mm), paucae, 1–2(3) per plantam; stipites longitudine 0.1–0.2 partes laminae aequantes, 0.5–1.0 mm diametro, straminei vel fulvi, pilis ca. 1 mm longis, mollibus, argenteis, laxis, septatis; laminae 11–35 cm longae, 2.5–7.0 cm latae, anguste ovatae vel lanceolatae, basi subtruncatae vel truncatae; rhachides sine paleis, utrinque laxe villosae pilis 1–2 mm longis; segmenta 13–40 mm longa, 3–6 mm lata, patentia, lineari-lanceolata, apice obtusa vel subacuta, basi pariter dilatata, integra vel versus apicem obscure undulata; venae 1-furcatae, liberae; paginae laminarum dilute virides, pilis numerosis, 1–2 mm longis, laxis, argenteis, secus costas densissimis; costae decurrentes ad rhachim; sori rotundati, inframediales; sporangia glabra.

✓TYPE: Selva del Ocote, 32 km NW of Ocozocoautla, Munic. Ocozocoautla de Espinosa, Chiapas, Mexico, *Breedlove 27453* (DS).

PARATYPES:

MEXICO: Chiapas: Finca Mexiquito, *Purpus 6754, p. p.* (UC, US); Finca Irlanda, *Purpus 7225* (UC, US); 13 km N of Berriozabal, *Breedlove 20281, 31231* (both DS); Same locality, *Breedlove 21671 with Smith, 31537 with Smith* (both DS).

Polypodium chiapense is similar to *P. hygrometricum* Splitg., but differs in the stramineous to tan stipes, these villose with soft, silvery, lax, septate hairs ca. 1 mm long; rachises stramineous with similar hairs 1–2 mm long; segments all perpendicular to the rachis; leaf tissue with numerous, lax, silvery, septate hairs 1–2 mm long, these densest along the costa; and in the glabrous sporangia.

7367 **Polypodium fuscopetiolatum A. R. Smith, sp. nov.** **Figs. 13–15.**

Rhizomata repentia, 3–6 mm diametro, brunneola, paleis arte adpressis, lanceolatis; paleae fulvae, in medio brunneo-vittatae, margine minute denticulatae vel papillatae, apice attenuato-filiformes; frondes (8)25–70 cm longae; stipites fulvi vel plerumque castanei (minimum infra), glabri vel glabrescentes, nitidi, longitudine 0.25–0.6 partes laminarum aequantes, (1)2–4 mm diametro; laminae ovato-deltoideae vel ovato-lanceolatae, (5)8–22 cm latae, profunde pinnatisectae vel paribus infimis fere liberis pinnarum, ad apicem segmento confluenti subconformi terminali usque 10 cm longo; rhachides pubescentes vel glabrescentes, plerumque castaneae, sine paleis; pinnae lanceolatae, apice acutae vel acuminatae, plerumque 9–15 mm latae; venae 3- vel 4-furcatae, anastomosantes, areolis 1-seriatis in quoque latere costae; pagina laminae utrinque pubescens vel glabrescens vel fere glabra; venae costaeque pubescentes; sori rotundi, ca. 1.0–1.5 mm diametro, mediales vel inframediales; sporangia glabra vel setosa, setis minus quam 0.1 mm longis.

✓TYPE: 6–8 km WNW of Soyalo, Chiapas, Mexico, *Breedlove 37155* (DS).

PARATYPES:

EL SALVADOR: San Salvador: Santa Tecla, *Jaurequi 67* (UC); Same locality, *Garcia 22* (UC). **GUATEMALA: Santa Rosa:** Jumaytepeque, *Heyde & Lux* [*Donn. Smith 4090*] (US). **Sololá**: Near Pueblo San Jorge, *Hatch & Wilson 317* (US). **Suchitepequez:** Cuyotenango, *Rojas 146* (US). **Guatemala:** Sapoti barranca, *Hayes* (US); Pinala, *Hayes* (US); San Gerónimo, *Salvin & Godman* (K). **MEXICO: Chiapas:** Salto de Agua, Escuintla, *Matuda 18397* (MEXU, DS); Cacaluta, Escuintla, *Matuda 17005* (MEXU, DS); Finca Mexiquito, *Purpus 6755, 6858* (UC, US); Huitla, *Purpus 7223* (UC); El Sumidero, 22 km N of Tuxtla Gutierrez, *Breedlove (all with Smith) 21584, 21593, 21595* (DS); 3 km N of Ocozocoautla, *Breedlove 21923 with Smith* (DS); 5–6 km W of Teopisca, *Breedlove 22867* (DS); NW side of Cerro Vernal, 25–30 km SE of Tonalá, *Breedlove 25616* (DS); 6–8 km E of Frontera Comalapa, *Breedlove 26978, 39083* (DS); 27 km NE of Huixtla, *Breedlove 28612, 28653* (DS); 65 km S of Hwy. 190 on rd. to Nuevo Concordia, *Breedlove 37784* (DS); Cerro Vernal, 21 km S of Tonalá, *Breedlove 38135* (DS). **Guerrero:** 25 mi S of Chilpancingo, *Storer 111* (US); Dist. Mina, Manchon, *Hinton et al. 9451* (K); Dist. Montes de Oca, Vallecitos, *Hinton et al. 11390* (K). **Jalisco:** Sierra del Halo, 7 mi SSW of Tecalitlán, *McVaugh 16189* (US). **México:** Dist. Temascaltepec, Rincón del Carmen, *Hinton 1737* (K, UC, US). **Michoacán:** Dist. Coalcoman, Pto. Zarzamora, *Hinton et al. 12249* (K).

This appears to be one of the more common species of *Polypodium* at lower elevations (500–1350 m in Chiapas) on the Pacific slope of southern Mexico and northern Central America. *Polypodium fuscopetiolatum* is closely related to *P. hispidulum* Bartlett, but it can be distinguished by the narrower rhizome scales that are denticulate or papillate on the margin and filiform at the tip and also by the stipes and rachises usually castaneous and shining. There is also a resemblance to *P. plesiosorum* Kunze, which has broader, ovate rhizome scales and grows at higher elevations. Specimens of *P. fuscopetiolatum* have often been identified as *P. plesiosorum* in herbaria.

Several Costa Rican collections are close to *P. fuscopetiolatum* but differ in having smaller, thicker-textured fronds, broader, squared sinuses, and broader and lighter-colored rhizome scales. I am not certain that they are conspecific with *P. fuscopetiolatum*, but they appear to be closely related: *Pittier 904, Tonduz 8796, Standley 41904, Tonduz 8804, Mickel 2394, Stork 2987,* and *Allen 547* (all US).

7392 **Polystichum mickelii A. R. Smith, sp. nov.**

Rhizomata erecta, caudices 1.5–3.0 cm diametro; frondes 45–110 cm longae; stipites longitudine 0.6–1.0 partes laminarum aequantes, basi paleis ovatis margine erosis usque denticulatis, usque 15 mm longis et 6 mm latis, bicoloribus, paleis fulvis in medio anguste brunneo-vittatis vel paleis concoloribus et uniformiter fulvis; laminae ovato-attenuatae, 12–35 cm latae; rhachides non proliferae, glabrescentes vel paleis capillaceis praesertim basi pinnarum; pinnae pinnatae, pinnulae lobo parvo deltoideo acroscopico, aliter integrae, vel in frondis grandis pinnulis crenulatis vel grosse dentatis et lobo fere libero elliptico acroscopico; costulae infra glabrescentes vel basi paleis fibrillosis; pagina laminarum et venarum infra plus minusve glabra, coriacea, supra nitida, atroviridis; sori parvi, ut videtur exindusiati, non confluentes.

TYPE: NE slope of Cerro Zempoaltepetl, trail from La Candelaria to Zacatepec, Dist. Mixes, Oaxaca, Mexico, *Mickel 4836 with Leonard* (NY).

PARATYPES:

GUATEMALA: San Marcos: Near Aldea Fraternidad, between San Rafael Pié de la Cuesta and Palo Gordo, *Williams et al. 26103 (F), 26299* (F, US). Above Finca El Porvenir, up Cerro de Mono, Volcán Tajumulco, *Steyermark 37397* (F). **HONDURAS: Intibuca:** Quebrada del Pelon de Guise, *Molina R. 6375* (F). **MEXICO: Chiapas:** SE side of Cerro Tres Picos, *Breedlove 25379, 34385* (DS); Without precise locality, *Ghiesbreght 401* (YU). **Oaxaca:** Type locality, *Mickel 4823 with Leonard* (NY); Dist. Mixes, vicinity of Zacatepec, *Mickel 1565* (NY); Dist. Choapan, Lovani to river toward La Selva, *Hallberg 1577* (NY); Dist. Tuxtepec, 24 km S of Valle Nacional, *Mickel 5929* (NY); Dist. Ixtlán, 5 km S of Vista Hermosa, *Mickel 7189* (NY, UC); Dist. Ixtlán, 29 km S of Valle Nacional, *Mickel 6363* (NY, UC). **Veracruz:** Munic. Yecuatla, El Haya, *Ventura A. 3431* (NY); Munic. Yecuatla, El Cajón, *Ventura A. 4812* (NY).

In Oaxaca and Veracruz this species grows at rather low elevations, 450–1450 m; the Chiapas collections were made at 2100–2500 m. At the lower elevations, the only other Polystichums encountered in Mexico are *P. platyphyllum* (Willd.) Presl and occasionally *P. muricatum* (L.) Fée. *Polystichum mickelii* appears to be without close relatives in Mexico and Central America. It is possibly of the group of *P. platyphyllum*, as indicated by the exindusiate sori. It resembles somewhat species from southern Brazil, e.g., *P. montevidense* (Spreng.) Rosenst.

7537 **Selaginella chiapensis A. R. Smith, sp. nov.**

Species heterophylla ex affinitate *S. idiosporae* Alston, sed foliis intermediis ovatis, acuminatis (nec aristatis), foliis argenteis subtus, rhizophoris gracilioribus, 0.2–0.4 mm diam. differt.

TYPE: 18–20 km N of Ocozocoautla, Munic. Ocozocoautla de Espinosa, Chiapas, Mexico, 800 m, *Breedlove 28159* (DS).

PARATYPE: Above Rancho San Luis, ca. 2 mi N of Ocozocoautla, Chiapas, Mexico, *Carlson 2127* (BM, US).

In addition to the differences between *S. chiapensis* and *S. idiospora* mentioned above, the new species seems to have the median leaves more obviously in two ranks adjacent to one another, the ranks scarcely or not at all overlapping. The paratype cited differs from the type in having acute median leaves, eciliate lateral leaves, and stouter rhizophores. It was originally annotated by Alston as "*S. idiospora* ined.", and presumably later in pencil, "sp. nov." In the sum of its characters, *S. chiapensis* seems more different from *S. idiospora* than the latter does from *S. guatemalensis* Baker.

6144

Diplopterigium bancroftii (Hook.) A. R. Smith, comb. nov.

6140 *Gleichenia bancroftii* Hook., Sp. Fil. 1:5, *t. 4A*. 1844. LECTOTYPE: Jamaica, *Bancroft* (K!; isolectotype BM!), chosen by Proctor in Howard (Fl. Less. Antill. 60. 1977). Hooker may never have seen the other syntype, which is Jamaica, *Swartz*.

Nakai (Bull. Natl. Sci. Mus. 29:50. 1950) regarded *Gleichenia bancroftii* as a synonym of *Diplopterigium farinosum* (Kaulf.) Nakai, but the original description and subsequent illustrations suggest that *Mertensia farinosa* Kaulf. is really a species of *Sticherus*. Löve, Löve, and Pichi Sermolli (Cytotax. Atlas Pterid., 1977), apparently following Nakai, also adopt the name *Diplopterigium farinosum* for *Gleichenia bancroftii*.

7261 Grammitis xiphopteroides (Liebm.) A. R. Smith, comb. nov.

7255 *Polypodium xiphopteroides* Liebm., Kongel. Danske Vidensk. Selsk. Skr., Naturvidensk. Afd., V. 1:196. 1849. LECTOTYPE (here chosen): Mexico, Veracruz, "Hac. de Mirador," *Liebmann* [*Pl. Mex. 2548, Fl. Mex. 189*] (C!).

I regard *Grammitis rigens* (Maxon) Proctor as a taxonomic synonym.

2367 Pellaea cordifolia (Sessé & Moc.) A. R. Smith, comb. nov.

7314 *Adiantum cordifolium* Sessé & Moc., Naturaleza (Mexico City), ser. II, 1(App.):182. 1890. TYPE: Mexico, Cuyuacan and San Agustín near Mexico City (MA?).

I regard *Pellaea cordata* (Cav.) J. Smith (*non* Fée, 1852), *P. cardiomorpha* Weath., and *P. sagittata* (Cav.) Link var. *cordata* (Cav.) A. Tryon as taxonomic synonyms.

Pellaea cordifolia differs from *P. sagittata* in having segments rotundate-cordate (vs. ovate-triangular to sagittate), rachis and segment stalks glabrous (vs. usually puberulous), and spores tetrahedral-globose, 64 per sporangium (vs. ellipsoidal, 32 per sporangium) (A. Tryon, Ann. Missouri Bot. Gard. 44:125–193. 1957). *Pellaea cordifolia* is a sexual diploid ($2n=29$ II), whereas *P. sagittata s. s.* is an apogamous triploid ($n=2n=87$). The two species are partially sympatric, but *P. cordifolia* has a much more restricted distribution than *P. sagittata*. The morphological, chromosomal, and chorological differences between the two taxa seem of a magnitude to justify recognition of two species.

7340 Pleopeltis macrocarpa var. interjecta (Weath.) A. R. Smith, comb. nov.

7342 *Polypodium peltatum* var. *interjectum* Weath. Amer. Fern J. 34:17. 1944. TYPE: Cerro de Tecpam near Santa Elena, Chimaltenango, Guatemala, *Standley 60957* (F).

As Weatherby stated, var. *interjectum* is closely related to var. *trichophora* (Weath.) Pic. Ser. and var. *macrocarpa* (Weatherby's var. *lanceolata*) on the one hand and *Pleopeltis polylepis* (Roem. ex Kunze) Moore (= *Polypodium peltatum* Cav., according to Christensen, Dansk. Bot. Ark. 9(3):11. 1937) on the other hand. It is quite possible that var. *interjectum* is an evolutionary link to *P. polylepis* from *P. macrocarpa*. My reason for placing it with the latter is that I find that scale size and number (large and numerous in *P. polylepis*, small and sparse in *P. macrocarpa* including var. *interjectum*) on the abaxial surface of the blade are more consistent than characters of scale margin (entire in *P. polylepis* and entire to erose to denticulate in *P. macrocarpa*). Weatherby used characters of the scale margin to distinguish between *P. macrocarpa* and *P. polylepis*.

7389 **Polystichum fournieri A. R. Smith, nom. nov.**

17120 *Polystichum muelleri* Fourn., Mex. Pl. 1:91. 1872 (*non* Schum., 1803). LECTOTYPE (here chosen): "In pinetis prov. Chiapas," Mexico, *Linden* (P!). The other syntypes (all from Mexico) are: "San Luis de Potosi," *Virlet d'Aost 46* (P–4 sheets!); "Orizaba," *F. Müller 1496* (not found at P); and "Prope ignovomum Río Frio," *Bourgeau* (P!). Of the syntypes I have seen, only the Linden specimen is fertile.

7414 **Sticherus brevipubis (Christ) A. R. Smith, comb. nov.**

7415 *Gleichenia brevipubis* Christ, Bull. Herb. Boissier, II. 6:280. 1906. LECTOTYPE: Valle del Río Navarro, Cartago, Costa Rica, *Wercklé* (P; isolectotype US), chosen by Lellinger, Proc. Biol. Soc. Wash. 89:713. 1977.

7427 **Tectaria transiens (Morton) A. R. Smith, comb. & stat. nov.**

7428 *Tectaria incisa* subsp. *transiens* Morton, Amer. Fern. J. 56:133. 1966. TYPE: Cordoba, Veracruz, Mexico, *Finck 57* (US).

In the sum of its characters, *T. transiens* is intermediate between *T. heracleifolia* (Willd.) Underw. and *T. incisa*, and it is possible that it has arisen through hybridization. However, in Chiapas it has been collected in areas where neither of the suspected parents have been found. It differs from *T. heracleifolia* in its nonpeltate indusia, greater number of lateral pinnae, shorter-stalked lower pinnae, and lack of strongly developed acroscopic lobes on lower pinnae. From *T. incisa*, it differs in the pinnae being serrately incised most of their length with two or three large basal basiscopic lobes. From both species (Chiapas material only), *T. transiens* differs in the presence of short, glandular hairs on the costae, veins, and leaf tissue below and also on the indusia. Spores of several collections appear well-formed. Throughout its range, *T. transiens* seems to grow at higher elevations than either *T. heracleifolia* or *T. incisa*.

Additional collections seen are *Sanchez 63* (UC) from Veracruz; *Tuerckheim 839* (UC) from Guatemala; and *Brade 47* (UC), *Stork 2107* (UC), and *Stork 1546* (UC) from Costa Rica. Similar collections have been seen from Ecuador and Peru.

SHORTER NOTES

A NEW COUNTY RECORD FOR PILULARIA AMERICANA IN TEXAS. — While collecting on the interesting granite outcrops of Central Texas on July 20, 1979 I came across a local, but extensive population of *Pilularia americana* A. Br. in a half-acre stock pond. The plants formed dense mats in mud at the margin of the pond, and in several places the mat extended onto the bare granite under the water surface. Livestock had uprooted many plants, and these were floating on the pond surface. Each rhizome measured 10–14 cm long. The plants were all in fruit, the sporocarps varying from olive-green to brown in color. Associated plants included *Eleocharis sp., Bacopa rotundifolia,* and *Lindernia anagallidea*. The pond in which the plants occurred had been enlarged from a previous vernal pool by means of an earth dam, which seems to have helped the *Pilularia* poplation. The population is the first known record for the species in Mason County. Other populations are known in Texas only from near Marble Falls, Burnet County, about 55 miles southeast, in similar habitats over granite. The Mason County outcrop is known locally as "Spy Rock" and is located on a private ranch 8.8 mi E on the north side of Ranch Road 1222 from the intersection with Hwy. 57, in Camp Air, near Fredonia. Specimens are being distributed to the following herbaria: B, F, GA, GH, K, MARY, MO, NCU, NY, SMU, TAES, TEX, US, VT.—*Steven R. Hill, Department of Botany, University of Maryland, College Park, MD 20742.*

ASPLENIUM ×GRAVESII DISCOVERED IN ARKANSAS.—In addition to serving as an addendum to the Pteridophytes of Arkansas by Taylor (Rhodora 81:503–548. 1979), this note is intended to document the value of the A.F.S. annual fern forays as a stimulus to discovery. One of us (Werth) went to Arkansas this past summer not only for the pure joy of a fern foray, but also with the ulterior motive of obtaining Ozarkian and Ouachitan materials for his studies on genetic variation in *Asplenium*. After a very successful foray, and at the suggestion of the other of us (Taylor) and David Johnson of the University of Michigan, Werth visited Hot Springs National Park in Garland County, Arkansas, on 13 August 1979.

It was known that *A. pinnatifidum* and *A. bradleyi* grew sympatrically in the park on the novaculite outcroppings of the Gulpha Gorge. This population was easily located, although fewer than thirty individuals of each species were found. (*Asplenium platyneuron* was also present and in much greater abundance.) Nonetheless a robust individual of *A.* × *gravesii* Maxon with leaves intermediate between the two parent species was discovered. Fronds and a portion of the rhizome were taken, and later examination of the spores showed them to be abortive. Comparison of the leaves with the drawings appearing in Wagner and Darling (Brittonia 9:57–63. 1957) confirmed that the plant was the hybrid.

This hybrid is quite rare, having been reported previously from only five states, apparently as a consequence of the limited concurrence of the uncommon parent species. It is likely that plants of *A. gravesii* have appeared sporadically in Gulpha Gorge and died, never having been observed until the arrival one summer of an unsated fern forayer. Voucher specimens of *Werth 39K8* have been deposited at MU and MIL.—*Charles R. Werth, Department of Botany, Miami University, Oxford, OH 45056* and *W. Carl Taylor, Department of Botany, Milwaukee Public Museum, 800 W. Wells St., Milwaukee, WI 53233.*

PILULARIA AMERICANA NEW TO TENNESSEE.—The Pillwort, *P. americana* A. Braun, a diminutive, aquatic pteriodophyte in the family Marsileaceae, was first collected near Fort Smith, Arkansas by Thomas Nuttall in 1819. Since that time, its known range in the United States has been slowly expanded.

Presently it is known in the United States from Crook (collected in 1894) and Lake Counties, Oregon; in California from Siskiyou and Modoc Counties southward to San Diego Co.; from Cherry Co., Nebraska; Reno and Harvey Counties, Kansas; Comanche Co., Oklahoma; Burnet Co., Texas; Conway, Faulkner, Garland, Logan, Sebastian, and Washington Counties, Arkansas; and Barrow, Walton, Washington, and Oglethorpe (9.3 mi NE of Lexington at Echols Mill, 11 Nov 1962, *D. Blake & F. Montgomery s. n.,* MO) Counties, Georgia. The range of *P. americana* has also been stated to include Louisiana by H. B. Correll (Amer. Fern. J. 57:31–32. 1967), but D. S. Correll (pers. comm. with D. B. Lellinger) has confirmed that this was an error.

On 12 Aug 1979, the second author discovered *P. americana* washed up on the shore of man-made Fall Creek Lake directly behind the Park Inn at Fall Creek Falls State Resort Park, Van Buren Co., Tennessee (*A. J. Petrik-Ott 1379 & F. D. Ott,* US). Following the initial discovery, we were amazed to find the shore line behind and ca. 100 yards to the east and west of the Inn literally covered with stranded plants of *P. americana,* and there were equally as many adrift in the water along the shore. These plants ranged from near perfect specimens to those in various stages of decay. In places along this shore, abundant stranded plants of *P. americana* formed drifts up to six inches wide and one inch deep. There were no rooted plants at this site.

The first author found rooted plants on the southeast side of the dam, growing in sand and about six inches of water (*A. J. Petrik-Ott 1380 & F. D. Ott,* US). A search of the northwest side of the dam yielded an unbelievably large plant of *P. americana* which was floating and caught among the stem bases of a cattail population (*A. J. Petrik-Ott 1381 & F. D. Ott,* US). This plant consisted of an extremely branched, continuous rhizome bearing numerous leaves (morphologically rachises and stipes) and tufts of roots. There was sufficient material from this one plant to make five rather crowded herbarium specimens. Other floating plants were caught among the rocks of the dam on the lake side in great quantity.

Rooted plants of *P. americana* (only 1 to 2 cm tall) were found to bear several sporocarps, but those found floating and stranded on shore (up to 6 cm tall) bore only occasional sporocarps. Before our collections were made, there had been a good deal of rain and the lake appeared to be up about a foot above normal. Many of the stranded and floating plants may have been washed free from their rooted places; indeed many still had sediment clinging to their roots. However, it is difficult to believe that the large, extremely rhizomatous plant found on the northwest side of the dam had been uprooted. Its rhizome was quite green, not whitish like the rhizomes of rooted plants, and its roots free of sediment. This plant certainly would have broken into many pieces had it previously been rooted in the soil.

This site for *P. americana* extends its known range by approximately 400 miles ENE from Faulkner County, Arkansas and 170 miles NW of Walton County, Georgia.—*Aleta Jo Petrik-Ott* and *Franklyn D. Ott, Department of Biology, Memphis State University, Memphis, TN 38152.*

NEW NAMES FOR POLYPODIUM CHNOODES AND P. DISSIMILE. —Among the species of *Polypodium* subg. *Goniophlebium,* few are more distinct than *P. chnoodes* Spreng. (Neue Entdeck. 3:6. 1822). Specimens of this species have very large (5–8 mm long), strongly clathrate, blackish, spreading rhizome scales and are weakly and evenly pilosulous on both lamina surfaces. The pinnae are fully to partially adnate to the rachis and, in the latter case, often have a conspicuous, basal auricle overlapping the rachis. Small, round sori are borne in 2 or 3 rows on each side of the pinna midrib. The veins anastomose in a typical goniophlebioid pattern. The species is found in the Antilles, on Trinidad, and from Guatemala to Venezuela and Colombia. In looking at type photographs and specimens of New World *Polypodium,* I was surprised to see that the type of *P. dissimile* L. (Syst. Nat. ed. 10, 2:1035. 1759), a specimen collected by Browne in Jamaica (LINN 1251.24), is exactly the same as *P. chnoodes.* Apparently everybody has adopted Sprengel's name; nevertheless it must be put in synonymy under *P. dissimile.*

The name *P. dissimile* has been applied consistently but incorrectly to a species of *Polypodium* subg. *Polypodium* which has small (2–4) mm long), non-clathrate, reddish-brown, appressed rhizome scales and which is glabrous on both lamina surfaces, except for minute hairs on the costae. Most pinnae are partially adnate to the rachis and are abruptly contracted at the base, often from a rather dilated supra-basal portion. Small to medium, slighty elongate sori are borne in a single row on each side of the pinna midrib. The veins are 2- or 3-forked and do not anastomose. The species is found over roughly the same range as "*P. chnoodes,*" and in addition extends to Mexico, Peru, and Suriname. Now that *P. dissimile* has to be used for what was called *P. chnoodes,* the next available name is *P. sororium* Humb. & Bonpl. ex Willd. (Sp. Pl. ed. 4, 5:191. 1810), based on a specimen collected by Humboldt and Bonpland near Caripe, Venezuela (B-Hb. Willd. 19684). The name *P. sororium* has been used occasionally in the past for some Venezuelan specimens, but generally has been thought to be a synonym of *P. dissimile.*—*David B. Lellinger, U.S. Nat'l. Herbarium NHB-166, Smithsonian Institution, Washington, DC 20560.*

A NEW RECORD FOR PELLAEA ATROPURPUREA IN MARYLAND. — While collecting specimens for the Herbarium at Towson State University, I discovered a small colony consisting of six plants of the Purple-stemmed Cliff-brake, *P. atropurpurea* (L.) Link, growing in east-facing crevices of an old railroad trestle at Rowlandsville, in Cecil County, Maryland. This is a new county record for Maryland, as well as the first record of this species for the Delmarva Peninsula. A voucher, *Redman 3698,* has been placed in the Towson State University Herbarium (BALT).—*Donn E. Redman, Herbarium, Towson State University, Towson, MD 21204.*

AN ATYPICAL ATHYRIUM FROM EASTERN TENNESSEE. — A recent botanical exploration of the Doe River gorge in Carter County, Tennessee has led to the discovery on 8 August 1979 of an unusual growth form of *Athyrium asplenioides* (Michx). A. A. Eaton. A single population consisting of several frond-bearing rhizomes occurs along a moist, northeast-facing rock face at Pardee Point, adjacent to the abandoned roadbed of the East Tennessee & Western North Carolina Railroad, 1.5 miles southeast of Hampton (*Wofford, Smith & Collins 79-222*, TENN, US). The identity of the specimen was confirmed by A. M. Evans.

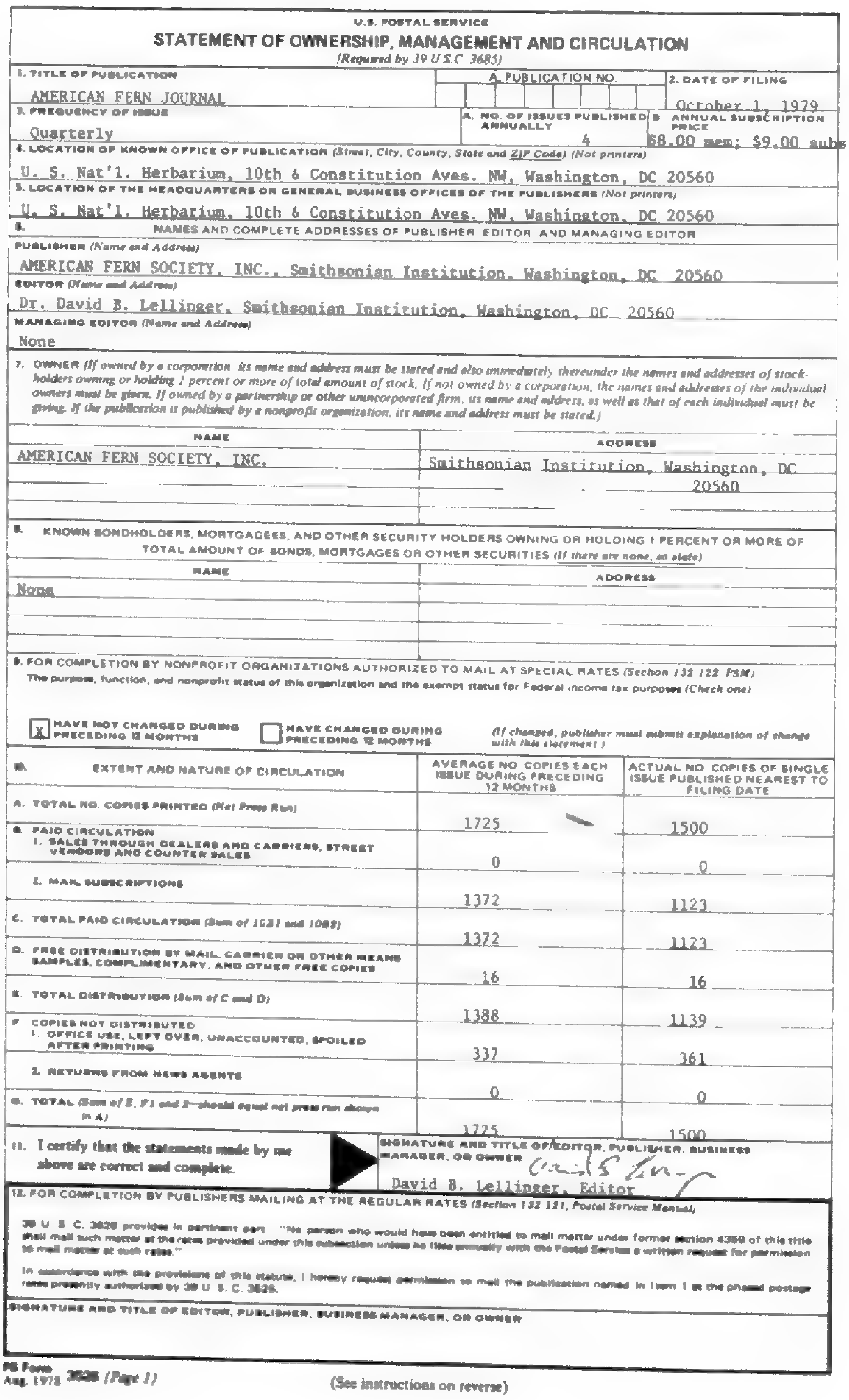
These plants resemble vigorously growing parsley and have crispate, fasciated pinnae crowded toward the lamina apex (*Fig. 1*). Although this is a dramatic departure from the usual frond morphology of *Athyrium*, the fragile, pale brown scales of the stipe base, the sparsely glandular indusia, and the paired vascular strands uniting above the stipe base into a U-shaped midvein are distinguishing characters of the genus. Sori are infrequent, are borne intramarginally, and have typical hammate-asplenioid indusia attached near the lateral vein. Examination of the sori reveals aborted sporangia and a complete absence of spores. The apparent adaptation to the rock face, atypical growth form, incomplete sporogenesis, and

FIG. 1. Specimens of *Athyrium asplenioides* mutant from Carter Co., Tennessee (*Wofford, Smith & Collins 79-222*).

the fact that typical *A. asplenioides* occurs in more mesic sites along the base of the same rock face favors the interpretation that these plants are morphological mutants, rather than of hybrid origin.

In addition to this unusual *Athyrium, Sanguisorba canadensis, Scirpus cespitosus, Paronychia argyrocoma,* and *Drosera rotundifolia* occur at the same locality. Except for *D. rotundifolia,* these species are of restricted occurrence in Tennessee and are included in the list of rare vascular plants of Tennessee (Committee for Tennessee Rare Plants. 1978. J. Tenn. Acad. Sci. 53(4):128–133).—*David K. Smith* and *B. Eugene Wofford, Department of Botany, University of Tennessee, Knoxville, TN 37916,* and *J. L. Collins, Division of Forestry, Fisheries and Wildlife Development, TVA, Norris, TN 37828.*

Contributions from the Botanical Laboratory, University of Tennessee, n. s. No. 520.



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Equisetum X litorale in Illinois, Iowa, Minnesota, and Wisconsin

JAMES H. PECK*

The cross between *Equisetum arvense* L. (Field Horsetail) and *E. fluviatile* L. (Water Horsetail) results in the hybrid *E.* × *litorale* Kuhl. (Shore Horsetail). It is distinguished from its parents by its abortive spores and intermediate anatomical and morphological traits (Hauke, 1978). The hybrid occurs less frequently in the Midwest than hybrids between unbranched species of *Equisetum*. The hybrid was reported from one county in Illinois (Mohlenbrock & Ladd, 1978) and four counties in Wisconsin (Hauke, 1965). It was not reported from Iowa (Peck, 1976) nor from Minnesota (Tryon, 1954), even though both parents occur together in those states. Its recent discovery in Minnesota (Peck & Swanson, 1978) initiated a field and herbarium search that uncovered a second locality in Illinois, first and second localities in Iowa, second, third, and fourth localities in Minnesota, and eight new localities in Wisconsin. Most of these new localities are on or adjacent to the flood-plain of the Mississippi River or its tributaries. The 2–3 ha stand located in Allamakee County, Iowa, is probably the largest stand of the hybrid in North America (pers. comm. with Drs. Hauke and Wagner). Consquently, efforts were made to study the habitat, stand dynamics, and reproductive biology of the hybrid at this locality to identify factors which clarify the origin, abundance, and persistence of the hybrid in this locality. Observations also were made at 16 of the 20 localities of the hybrid in these four states, but in less detail.

A summary of locality data is provided by *Fig. 1* and by citations from herbarium vouchers (new county records indicated by *). The original Illinois locality (Lee County) is accepted from the report by Mohlenbrock & Ladd (1978); voucher citation was not given and the specimen was not seen.

ILLINOIS: *Carroll Co.: Wet grounds near entrance to Mississippi Palisades State Park, N of Savannah, *Wunderlin 2668* (MWI).

IOWA: *Allamakee Co.: Lansing Twp.: Lansing Wildlife Refuge, 2–3 ha marsh, T99N R4W S12, *Peck 78-54* (ISTC, KIRI, MICH), *Farrar 78-6-3-1* (ISC), *Roosa 1759* (ISTC). Banks of Mississippi River, June 1900, *Orr s. n.* (EMNM). ***Des Moines Co.:** Huron Twp.: Near pumping station No. 4, Iowa Slough, adjacent to Mississippi River, T72N R1W S4, *Lammers 1542* and *2087* (IA, ISC, ISTC), *Peck 78-300* (ISTC, KIRI, MICH).

MINNESOTA: *Houston Co.: Mississippi River flood plain in wetlands of Crooked Creek at Reno, *Peck 79-734* (KIRI, MICH, MIN, UWL). **Washington Co.:** Confluence of Valley Branch Creek and St. Croix River in thicket of *Salix interior*, *Swanson 2878* (MIN, UWL). ***Wabasha Co.:** Weaver Bottoms, floodplain of Mississippi River, 2 mi N of Weaver, *Peck 79-709* (KIRI, MICH, MIN, UWL). ***Winona Co.:** On floodplain of Mississippi River, W of Red Oak Island in Lake Onalaska, *Peck 79-727* (KIRI, MICH, MIN, UWL).

WISCONSIN: *Buffalo Co.: Nelson Twp.: Nelson-Trevino Bottoms of Mississippi River floodplain, T22N R14W S36, *Peck 79-824* (KIRI, MICH, WIS, UWL). ***Crawford Co.:** Emergent along shore near bridge over Swamp Creek, 0.5 mi E of Lynxville on County Road B, T9N R6W S23, 8 Jul 1973, *Dawson s. n.* (UWL). **Grant Co.:** Wilderness area of Wyalusing State Park, T6N R6W S20/21, 19 June 1959, *Patman s. n.* (WIS). **Green Lake Co.:** Marsh shore on S side of Lake Puckaway, Marquette, *Fassett 8799* (WIS). ***La Crosse Co.:** Barre Twp.: Seepage area at roadside ditch along Swamp Road,

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*Department of Biology, University of Wisconsin-La Crosse, La Crosse, WI 54601.

T16N R6W S20, *Peck 79-803* (KIRI, MICH, UWL, WIS). ***Pierce Co.:** Clifton Twp.: Marshy thicket at mouth of Kinnicinick River under *Salix interior,* T27N R20W, *Peck 79-824* (KIRI, MICH, UWL, WIS). Isabella Twp.: Marshy slough, backwater of Mississippi River. 0.5 mi W of Bay City, T24N R17W S7, *Peck 79-838* (KIRI, MICH, UWL, WIS). **Richland Co.:** Shallow water springhole in slough of Wisconsin River, 3 mi E of Gotham, T8N R2E S4, *Hartley 5266* (IA, WIS). ***Rock Co.:** Marsh and lowlands east of cooling canal on Rock River near Beloit, *Rice 1649* (UWJ, WIS). *Trempealeau Twp.: Marshy edge of backwater area of Mississippi River floodplain in Delta Fish and Fur Farm, T18N R10W S11, *Peck 79-814* (KIRI, MICH, UWL, WIS). ***Vernon Co.:** Genoa Twp.: Shore to Bad Axe River near Mississippi River, T12N R7W S12, *Peck 79-813* (KIRI, MICH, UWL, WIS). **Winnebago Co.:** Springy shore of Fox River near Eureka, *Fassett 13243* (WIS).

The habitat of the hybrid is a shallow marsh or slough adjacent to a watercourse which has a fluctuating water level, periodically flooding or stranding the site where the hybrid occurs. The hybrid occurs in stands ranging from 1 m^2 to 2–3 ha, with many stands 0.05–0.1 ha in extent. Species diversity within the stand is very low compared to adjacent marshes. The most common associates are *Sagittaria latifolia, Salix interior,* and *Typha latifolia.* The parent species were found at the periphery of the hybrid's stand, but rarely within the stand. The hybrid appears to be quite aggressive in a habitat which is subjected to repeated disturbance by flooding and sediment deposition.

TABLE 1. CHANGES IN *EQUISETUM* × *LITORALE* STAND HEIGHT AND DENSITY IN ALLAMAKEE COUNTY, IOWA, DURING 1979.

Sample Date	*Stand height* ($\bar{x}$ ± sd)	*Stand density* (stems/m^2)	*Survivorship* (% of 21 April)
21 April	0.05 ± 0.012	2809 ± 61.8	100
12 May	0.49 ± 0.049	2560 ± 82.9	91
12 June	1.03 ± 0.101	1792 ± 133	64
30 July	1.52 ± 0.082	1324 ± 148	47
20 Aug[1]	0	0	0
15 Sep[2]	0.34 ± 0.031	32 ± 11.4	1

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[1] Stand lodged; all aerial parts senescent.
[2] Aerial stems newly arisen from subterranean stems.

Stand dynamics were monitored in 1979. A transect was established the length of the stand. Twenty-five 0.25 m^2 quadrats were selected at random points along the transect. Stand density was assessed by counting the number of stems per quadrat. Stand height was assessed by measuring the height of two corner plants per quadrat. Subsequent observations were made from a series of transects 5 m distant from and parallel to the previous transect. An average value for stand density (stems/m^2) and stem height was calculated for each transect. Survivorship of aerial stems through the growing season was calculated based upon the average stand density on April 21. Results are presented in *Table 1*. Stand density was greatest in spring and declined until summer, when only 47% of its initial stand density was present. Considering the initial stand density (2,809 stems/m^2), extensive self-thinning was expected. Stand height increased through time, resulting in mean stand height of 1.52 m, with some exceptionally tall specimens over 2 m.

The stand was flattened by a severe storm in early August 1979. Consequently, no measurements could be taken on August 20th. However, by September 15th, the stand had sprouted new aerial stems from subterranean stems. These new stems produced a comparatively sparse growth of limited stature. The new growth protruded through a 10–18 cm thick mat of senescent and decaying aerial stems that lodged following the storm. The stand also lodged in 1978 following a storm in July. The new growth that year attained a mean height of 1.2 m. The extent of recovery, therefore, is probably influenced by the time of lodging, with an earlier date favoring a stronger recovery.

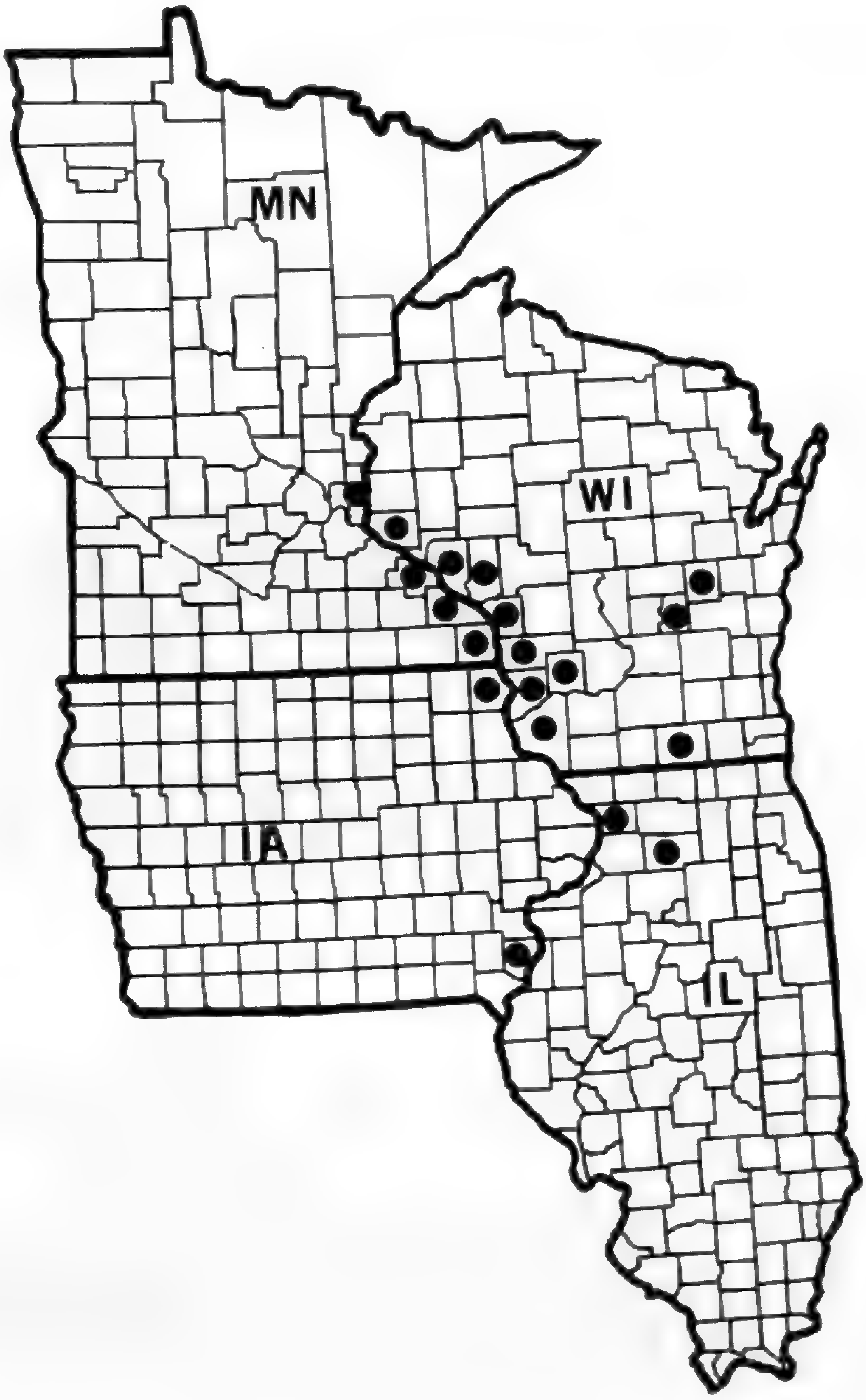

FIG. 1. Distribution of *Equisetum × litorale* in the four states of the upper Mississippi River Valley.

Observations on stand dynamics were also made on an adjacent pure stand of the parent species. Those stands were less densely stocked and did not recover following lodging to the extent the hybrid did. Whereas the hybrid occurs with stands of low species diversity, the parent species exist with many more species present within their stands. The lack of colonization or establishment within the hybrid's stands and the extensive colonization in parent stands in autumn suggests that the thick mat of lodged stems in the hybrid's stand physically prevents successful invasion. Consequently, the aggressive growth of aerial stems and capability to recover from mid-summer lodging contribute to the hybrid's ability to maintain stands of low species diversity.

In considering the reproductive biology of the hybrid, it should be noted at the outset that the hybrid's spores are unable to produce gametophytes and, thus, complete the sexual cycle. Furthermore, the general lack of strobilus production by the hybrid in the upper Mississippi River valley essentially precludes the rare event of production of an occasional viable spore. Consequently, sexual origin of the hybrid is restricted to hybridization between its parents. Frequent flooding along watercourses in the upper Mississippi River valley forms extensive sand and mud flats that provide suitable conditions for *Equisetum* gametophytes and ample opportunities for hybridization. The hybrid's occurrence in small, discrete stands, with uniform growth within a stand and readily demonstrated physical connections underground, suggests that each stand is the result of a single or a few successful hybridizations followed by establishment of a clone by vegetative growth. Therefore, the stand at each locality may represent an independent origin of the hybrid.

Once formed, a hybrid plant can persist indefinitely as long as it avoids catastrophic factors, such as desiccation during drought years. An indication of the longevity of the hybird is given by the continued presence of the hybrid in Allamakee Co., Iowa, for at least the last 80 years. Since 1900, when Ellison Orr first noted it on the flood plain of the Mississippi River, establishment of navigation lock and dams has changed the hydrology of the shoreline environment. The presence of the hybrid in that locality today suggests that its historical presence and persistence has not been eliminated by alterations to the shoreline.

Vegetative proliferation of hybrid stands, on the other hand, was suggested by the occurrence of small stands and isolated stems 50–350 m downstream from the 2–3 ha stand in Allamakee Co., Iowa. Fragmentation followed by water dispersal of stems and their subsequent establishment downstream would result in new stands from the same original plant. The propensity for vegetative proliferation of *Equisetum* was discussed by Hauke (1963) and experimentally investigated by Wagner & Hammitt (1970). In early August 1979, an experiment was conducted to verify the hybrid's ability to undergo vegetative proliferation and to contrast this ability with that of its parents. Aerial stems and subterranean stems of the hybrid and its parents were cut and either placed on mud or buried in the mud flat. Twenty-five stems were used per pecies per treatment. The plots were inspected in early September. The results (*Table 2*) indicate that burial increased the chance that a fragment would form a new plant, that subterranean parts withstood the stress of fragmentation, dispersal, and establishment better than aerial stems, and that the hybrid's ability is equal to or superior to that of its parents.

In summary, the origin, maintenance, and dispersal of the hybrid is favored by the physical results of flooding. Flooding can form mud flats where sexual formation of the hybrid can occur, lodge aerial stems into a mat that prevents invasion of the hybrid's stands by potential colonizers, and facilitate vegetative proliferation by physically breaking stems, dispersing them downstream and leaving them stranded or buried on mud flats where new stands can become established. Although vegetative proliferation probably has expanded the hybrid within its locality, evidence of long distance dispersal is lacking, in that both parents occur with the hybrid in these states.

TABLE 2. COMPARATIVE ABILITY OF *E.* × *LITORALE* AND ITS PARENT SPECIES TO REGENERATE PLANTS FROM AERIAL AND SUBTERRANEAN STEM FRAGMENTS AFTER BEING LODGED ON OR BURIED IN A MUD FLAT.

Species	*Cut and Lodged*		*Cut and Buried*	
	Aerial	*Subterranean*	*Aerial*	*Subterranean*
E. arvense	0%	20%	60%	68%
E. × *litorale*	0%	16%	40%	96%
E. fluviatile	0%	8%	0%	20%

These observations suggest that analysis and integration of habitat, stand dynamics, and reproductive ecology are feasible with *Equisetum*, and possibly with other pteridophytes. Additional observations are needed on changes in nutritional status (calories, macronutrients, and protein) of aerial and subterranean stems through the year. Additional measures on stand dynamics (height, density, biomass) are needed to contrast peripheral stands reported on here with stands to the north and east. Competitive experiments between the hybrid, parent species, and flowering plant associates would improve our understanding of *Equisetum* ecology.

Dr. Richard L. Hauke, University of Rhode Island, and Dr. Warren H. Wagner, Jr., University of Michigan, are thanked for verifying hybrid material and for comments on the ecology of *Equisetum*. Curators of the following herbaria are thanked for permission to examine specimens: Effigy Mounds National Monument, Marquette, IA (EMNM), Iowa State University (ISC), Mankato State University (MANK), University of Iowa (IA), University of Minnesota (MIN), University of Northern Iowa (ISTC), University of Western Illinois (MWI), University of Wisconsin-Janesville (UWJ), University of Wisconsin-La Crosse (UWL), and University of Wisconsin-Madison (WIS).

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REVIEW

"FLORA DE LA PROVINCIA DE JUJUY REPUBLICA ARGENTINA, PARTE II. PTERIDOPHYTA," by E. R. de la Sota. Angel L. Cabrera, general editor. Instituto Nacional de Tecnologĩa Agropecuária, Buenos Aires, Argentina, 1977. Ps. 22,000 (ca. $28.00).—INTA is publishing a series of very attractive Flora volumes for the provinces of Entre Rios and Jujuy (both in northern Argentina) and for the Patagonian region. This volume is the first on ferns for the three series. The endpapers have useful physiographic, phytogeographic, and political maps of the province. The book begins with a few pages concerning the morphology, cytology, reproduction, and systematics of the Pteridophyta. General keys lead to 23 families, which are used in a modern sense similar to that in Jermy and Mickel's classification. Each species treatment includes a synonymy, description, notes, and list of specimens. Each is illustrated with a nicely drawn habit sketch plus sketches of morphological details. Some 244 taxa are treated, judging by the index that concludes the volume. The printing is mostly of high quality, although a few plates had some light areas across them and a few typographical errors can be found. The weakest point of the book is the binding. This book will be highly useful to all who need to know the pteridophytes of northwestern Argentina and vicinity. Orders should be sent to INTA Publicaciones, Chile 460, 1098 Buenos Aires, Argentina.—*D.B.L.*

Gametophytes of Equisetum diffusum

RICHARD L. HAUKE*

Equisetum gametophytes have been studied for many years (Buchtien, 1887; Hauke, 1967, 1968, 1969, 1971, 1977; Duckett, 1970, 1972, 1973, 1977; and literature cited in these references). The gametophytes of all *Equisetum* species except *E. diffusum* Don have been described. In a recent monograph of *Equisetum* subg. *Equisetum* (Hauke, 1979), I presented an evolutionary sequence of species arranged according to gametophyte specialization which did not parallel the sequence based on sporophyte specialization. Subsequently I was able to obtain viable spores of *E. diffusum* and to culture them. The purpose of this paper is to describe gametophytes of *Equisetum diffusum* and to discuss their evolutionary implications.

MATERIALS AND METHODS

On 24 February 1974, I collected living rhizomes of *E. diffusum* along the road between Chail and Kandaghat, near Simla, Himachal Pradesh state, India. These flourished in pots in the greenhouse at the University of Rhode Island. In August 1978, I first noticed cones developing on the ends of unbranched, new stems in two pots. The plants in these pots apparently had died back and regrown. The first cone was removed before it expanded, surface sterilized with 50% commercial sodium hypochlorite bleach, rinsed with sterile distilled water, and dissected in sterile distilled water. Ten drops of the spore suspension were inoculated onto petri dishes containing Bold's Basal Medium (BBM) in 1.5% agar. Subsequent cones were allowed to open naturally, and the spores were shaken onto the surface of the solidified nutrient medium. The culture dishes were placed in a growth chamber on a 12 hr light/dark cycle at a temperature of 20/15°C under 40 watt cool white fluorescent tubes yielding 8000 ergs/cm^2/sec radiant energy at the surface of the cultures, as measured with a YSI radiometer.

Gametophytes were grown in isolation to determine crossability, self-compatibility, and the possible occurrence of apogamy. Spores that had begun to germinate in petri dishes were transferred aseptically into 15 mm diameter test tube slants of BBM agar capped with metal caps and placed in racks for incubation in the growth chamber. Initially the isolated gametophytes grew more slowly than those left in petri dishes, possibly because the test tube caps shaded the gametophytes; when the tubes were positioned to allow full light intensity on the agar surface, the growth rate accelerated.

RESULTS

The spores of *E. diffusum*, like those of all other species of *Equisetum*, are spherical, chlorophyllous, thin-walled, alete, and have two hygroscopic elaters attached at their middles, which form four strap-like arms with spoon-shaped tips. Under suitable conditions of moisture, temperature, and light, they germinate readily in 1–2 days by dividing eccentrically to produce a small rhizoid cell that

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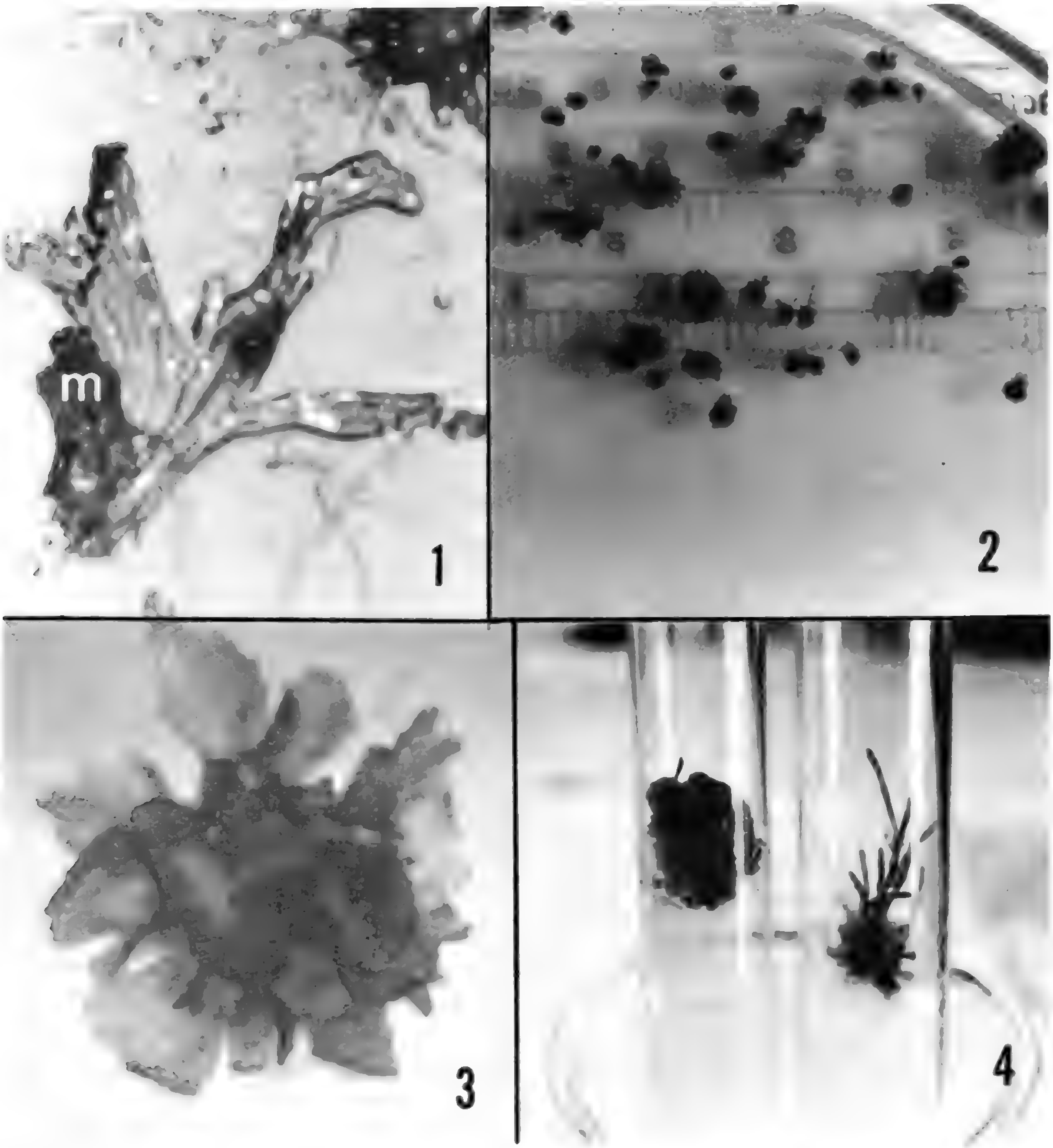
*Department of Botany, University of Rhode Island, Kingston, RI 02881.



FIGS. 1–4. Gametophytes of *Equisetum diffusum*. FIG. 1. Gametophyte 24 days old showing rhizoids, meristem (m), and plates, × 70. FIG. 2. Antheridial and archegonial gametophytes 64 days old, × 1.8. FIG. 3. Archegonial gametophyte 50 days old, showing broad plates with irregular margins, × 30. FIG. 4. Gametophytes 158 days old with sporophytes. Left = selfed bisexual gametophyte, sporophyte visible 20 days earlier. Right = crossed female gametophyte, sporophyte visible 55 days earlier. Note smaller size of gametophyte on right, × 1.

loses its chloroplasts and a large, green somatic cell. Further division of the latter produces a flattened, linear gametophyte which branches to form several plates of cells. Eventually a parenchymatous cushion bearing plates dorsally and rhizoids ventrally is established by a marginal meristem. (*Fig. 1*).

Sex organs begin to appear 35 days after inoculation on the basal cushion meristem of initially unisexual gametophytes. Young male and female gametophytes look alike, but with continued growth they become dimorphic (*Fig. 2*).

The female gametophytes become larger than the male, develop numerous plates, and assume a grass-green color (*Fig. 3*). The plates of *E. diffusum* are up to 2 mm broad and have irregular margins and thickened bases. Archegonia develop at the base of the plates and consist of three tiers of four neck cells each. The egg is embedded in the cushion. The terminal neck cells elongate to four times longer than broad and spread apart in an arching manner. Seen from above, the spread terminal necks cells resemble a pinwheel.

The male gametophytes remain smaller than the female, with only sparse plate development, and are yellowish to pinkish. Antheridia develop from the cushion and protrude somewhat at maturity, becoming twice as long as wide. They discharge sperm by two or four cap cells. The cap cells in this species are not so distinctive as in other species and apparently may divide anticlinally, so that at times there are three or five cap cells.

Female gametophytes that are not fertilized within a certain time begin to produce antheridia. The marginal meristem that has been producing archegonia grows out into an antheridial lobe. In petri dish cultures, where interaction between gametophytes is possible, the bisexual condition may become apparent within 50 days. In isolation tubes, where interaction is not possible, bisexuality is delayed to 90 days or later. Some isolated gametophytes 150 days old still appear only female. Gametophytes apparently cease growth when they begin bearing sporophytes (*Fig. 4*). If they are unisexual at that time, they never become bisexual. Unlike the situation usually seen in other pteridophytes, *Equisetum* gametophytes normally bear several sporophytes per gametophyte (*Fig. 4*).

Whereas more than 50% of the gametophytes in plate cultures are antheridial, in isolation tubes, in the absence of interaction between gametophytes (but presumably with better nutrition), only 5 out of 42 (12%) were male. The other 37 were female. One tube inadvertently received two gametophytes initially, one of which became male and the other female. Three of the male gametophytes were transferred to tubes with female gametophytes and flooded. The tube with two gametophytes was flooded (*Fig. 4*), as were 17 tubes with only female gametophytes. The four tubes with both male and female gametophytes all showed sporophytes a month later. None of those with only female gametophytes did. The tubes originally containing only female gametophytes were reflooded, and eventually they became bisexual and selfed (*Fig. 4*). At 158 days post inoculation the experiment was terminated and the tubes refrigerated to stop growth. Later they were examined and discarded, at which time 14 of the 17 selfed gametophytes had visible sporophytes. In two cases, the sporophytes all looked achlorophyllous.

Of the 17 tubes never flooded, one had a single visible sporophyte and another had four. In both cases, antheridial lobes had arched over to press antheridia against the archegonial meristem, and presumably sperm had been able to enter the archegonia in the absence of free water. The other 15 tubes showed no visible sporophytes. In general, flooded gametophytes grew slightly more than did unflooded ones.

DISCUSSION

The gametophytes of *E. diffusum* are similar to those of other species of *Equisetum* in basic form. They consist of a parenchymatous cushion bearing rhizoids ventrally and photosynthetic plates dorsally. In sexual condition, they produce separate antheridial and archegonial gametophytes, with the latter subsequently becoming bisexual if unfertilized. Sexual dimorphism, cessation of growth in sporophyte-bearing gametophytes, and production of numerous sporophytes per gametophyte are all seen in other species of *Equisetum*. The last character is rather uncommon in archegoniates, where gametophytes usually have several archegonia, but normally produce only one sporphyte per gametophyte. Bruce and Beitel (1979) tabulated 476 *Lycopodium* gametophytes, of which 17% had more than one sporophyte and one had 13 sporphytes. Mesler (1977) reported up to 27 sporophytes on a wild gametophyte of *Equisetum hyemale*. The increased percentage of archegonial gametophytes in isolation culture and the delay in their becoming bisexual also occurs in other species of *Equisetum* (Hauke, 1977).

Certain features of *E. diffusum* gametophytes indicate that they are relatively primitive and more closely allied to those of *E. telmateia* than to any other species. Their plates are broad, with irregular margins and thick bases. Their archegonia have terminal neck cells about four times longer than wide. Their antheridia have 2–4 cap cells and are about twice as long as wide. Plate development on antheridial gametophytes is more extensive than in other *Equisetum* species except *E. telmateia*.

Duckett (1973) carefully described the morphology of several species of subg. *Equisetum*; using that information plus my own observations (Hauke, 1968), I aligned the gametophytes of subg. *Equisetum* in a presumed evolutionary sequence (Hauke, 1979), with the most primitive species being *E. telmateia:*

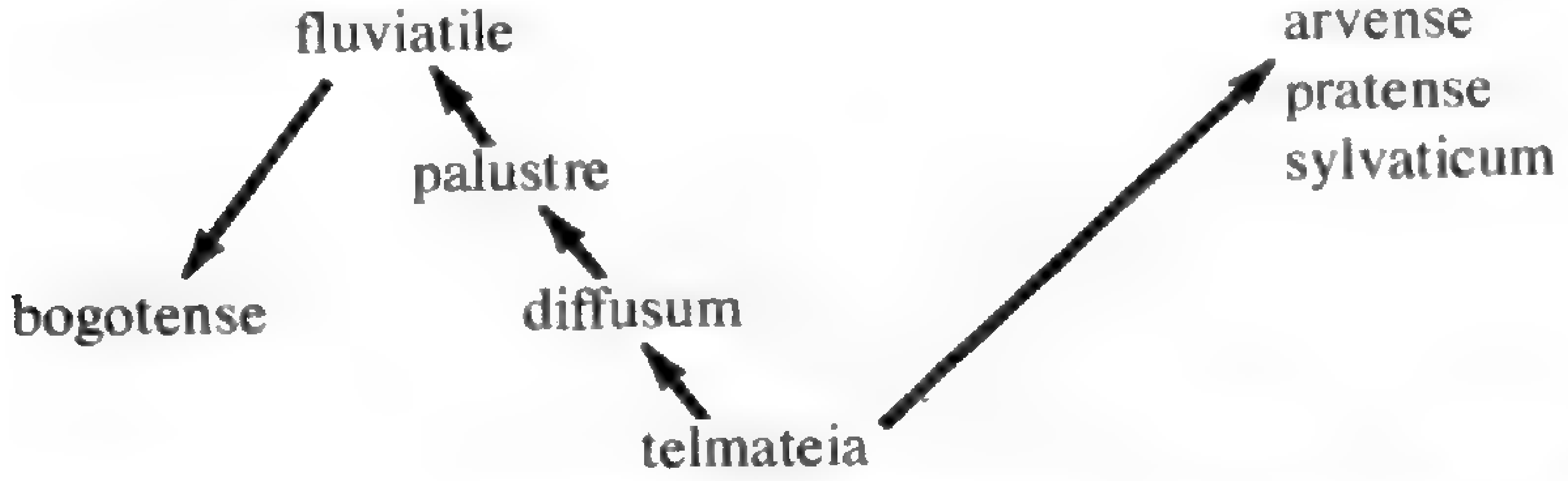
arvense
telmateia ⟶ pratense ⟶ palustre ⟶ fluviatile ⟶ bogotense
sylvaticum

From my current observations of *E. diffusum* gametophytes, it is now obvious that in an evolutionary scheme based on gametophytes, *E. diffusum* is intermediate between *E. telmateia* and the three species of sect. *Heterophyadica sensu* Hauke: *E. arvense, E. pratense,* and *E. sylvaticum*.

One problem raised by this sequence is that it does not correlate well with the apparent evolutionary sequence based on sporophyte character:

arvense
fluviatile ⟶ palustre ⟶ bogotense ⟶ diffusum ⟶ telmateia ⟶ pratense
sylvaticum

That sequence, it is true, placed *E. diffusum* and *E. telmateia* side by side, but it also considered *E. bogotense* to be most like *E. diffusum*. This is the greatest discrepancy between the schemes based on sporophyte and gametophyte evolution. Perhaps there is no reason why the two generations should be correlated evolutionarily, since they presumably evolve for different environmental fitness, but it seems appropriate to consider the whole plant in a single evolutionary scheme. In that case, one might expect the gametophyte to reflect more conservative traits, as the reproductive structures of other plants are assumed to do. For an example of independent selection for floral and vegetative fitness in flowering plants, however, see Wilken (1978). If taxonomy is intended to be phylogenetic, should it emphasize gametophyte or sporophyte? One factor which diminishes the usefulness of the gametophytic stage in pteridophyte taxonomy is the paucity of characters it possesses. A compromise scheme, utilizing characters of both gametophytes and sporophytes might be:



It injures my sense of the fitness of things to look at two species with sporophytes as similar as those of *E. bogotense* and *E. diffusum* and to separate them widely in a classification. Yet the gametophyte as well as the sporophyte must be considered in arriving at any taxonomy which claims to be phylogenetic. In fact, if it is more conservative in evolution, then it should be given greater emphasis in taxonomy.

Isolation experiments showed that the gametophytes of *E. diffusum* outcross readily. They also self readily in most cases, but the absence of any detectable sporophytes on three of 17 selfed gametophytes, and the chlorotic sporophytes on two others, indicates some lethal load (see Lloyd, 1974). The absence of sporophytes on individuals that were not flooded indicates the absence of apogamy in *E. diffusum*. Ease of selfing and absence of apogamy are also found in the other species of *Equisetum*.

I wish to thank Dr. Stoddard Malarky for helping me collect *E. diffusum* and Dr. Roger Goos for reading the manuscript.

ADDENDUM

In a paper which appeared while this article was awaiting publication, Duckett (1979) made several observations which are pertinent here. He reported that prolonged culture and numerous attempted fertilizations were required to obtain maximal sporophyte frequencies, and suspected "leaky lethals," but on the basis of crossing and selfing tests discounted that possibility. He noted that the initiation of sporophytes is accompanied by cessation of gametophyte growth, and attributed this to allelopathic substances from the sporophyte. He reported that polyembryony is present in all species, but is uncommon and occurs mostly in species with rapid sex change from female to bisexual, or with numerous archegonial lobes. I have observed polyembryony to be common in isolated, selfed gametophytes not only of *E. diffusum,* but also of *E. fluviatile, E. hyemale* var. *affine,* and *E. arvense,* and suspect that they were all larger and therefore with more receptive archegonia when flooded than were those of Duckett's experiments.

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A Double Spore Wall in Macroglossum

LUIS D. GÓMEZ P. and KERRY S. WALTER*

Since the original description of *Macroglossum alidae* by Copeland (1909a, p. 343; 1909b, p. 9), little has been learned about this strange and primitive member of the Marattiales. Campbell (1911, 1914a, 1914b) has dealt with the anatomical aspects of the gametophytes and sporophytes but, surprisingly, he gives no description of the spores. In Erdtman (1957, p. 79), the proximal and distal faces of *M. alidae* are illustrated both in surface view and in optical section; the spore is globose but distally flattened, with an irregular and sparsely tuberculate exine. Kremp & Kawasaki (1972, p. 4) described the spores from seven specimens as rounded-triangular (32.4 × 28.7 μm), trilete, and scabrate.

The observation of spores of *M. alidae (Molesworth-Allen 3197,* US) under the SEM shows a regularly and densely tuberculate-subbacillate perispore *(Fig. 1),* the shape and dimensions of which are in agreement with the foregoing authors. An unusual case of double-walled spores is shown in *Fig. 2,* a preparation from the same specimen. In it, the outer exine layer is cracked to reveal a smaller but morphologically perfect spore inside, one per "parent spore." This phenomenon is hitherto unreported in the fern literature but may not be rare, for we have observed a "parent spore" of *Botrychium* sp. containing four "daughter spores," and it is quite possible that such "angiospores" occur in other pteridophytes.

The biosystematic implications of angiospore production are, as yet, unknown. Research is needed to elucidate various questions that come to mind, including: (a) What, if any, percentage of angiospores is viable? (b) What is their genotype and resulting phenotype? (c) What is the ploidy level of angiospores in relation to "parent spores"? (d) Do angiospores represent a reduction mechanism for polyploidal pteridophytes? (e) Within a sporangium, what percentage of "parent spores" contain angiospores? (f) What effect would this ratio have on the population structures of the resulting gametophytic and sporophytic generations? (g) Does the smaller size the angiospores have any effect on the range and pattern of their dispersibility? (h) Is angiospory a primitive trait only to be found in eusporangiate pteridophytes?

Spore size and shape, of themselves, are not indicative of viability. Recent literature abounds with examples of the germination of supposedly non-viable abortive spores in hybrids and of larger than normal diplospores formed through ameiotic apogamy. At present, questions (b) and (d) are unanswerable due to the lack of appropriate materials. The fact that the cytology of *Macroglossum* has never been investigated prevents speculation on whether angiospores represent any change in ploidy level, be it reduction or augmentation. The Marattiales have high chromosome numbers as do the Ophioglossales, the only other instance in which we have as yet observed angiospory. Until a large enough quantity of both "parent spores" and angiospores are cultured, questions (e) and (f) also remain unanswerable.

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*Museo Nacional de Costa Rica, Apartado 749, San José, Costa Rica.

The Marattiales show a high degree of endemism; *Macroglossum*, for instance, is confined to Borneo. It is logical to assume that smaller spores, such as angiospores, might be more easily dispersed. On the other hand, smaller spores could be short-lived, reducing their dispersibility and enhancing endemism. The genus *Botrychium* is cosmopolitan, but throughout its range its species show complex patterns of geographically separated cytological races. This genetic variation may be partly responsible for the taxonomic chaos within the genus. It may be that angiospory is related to these races.

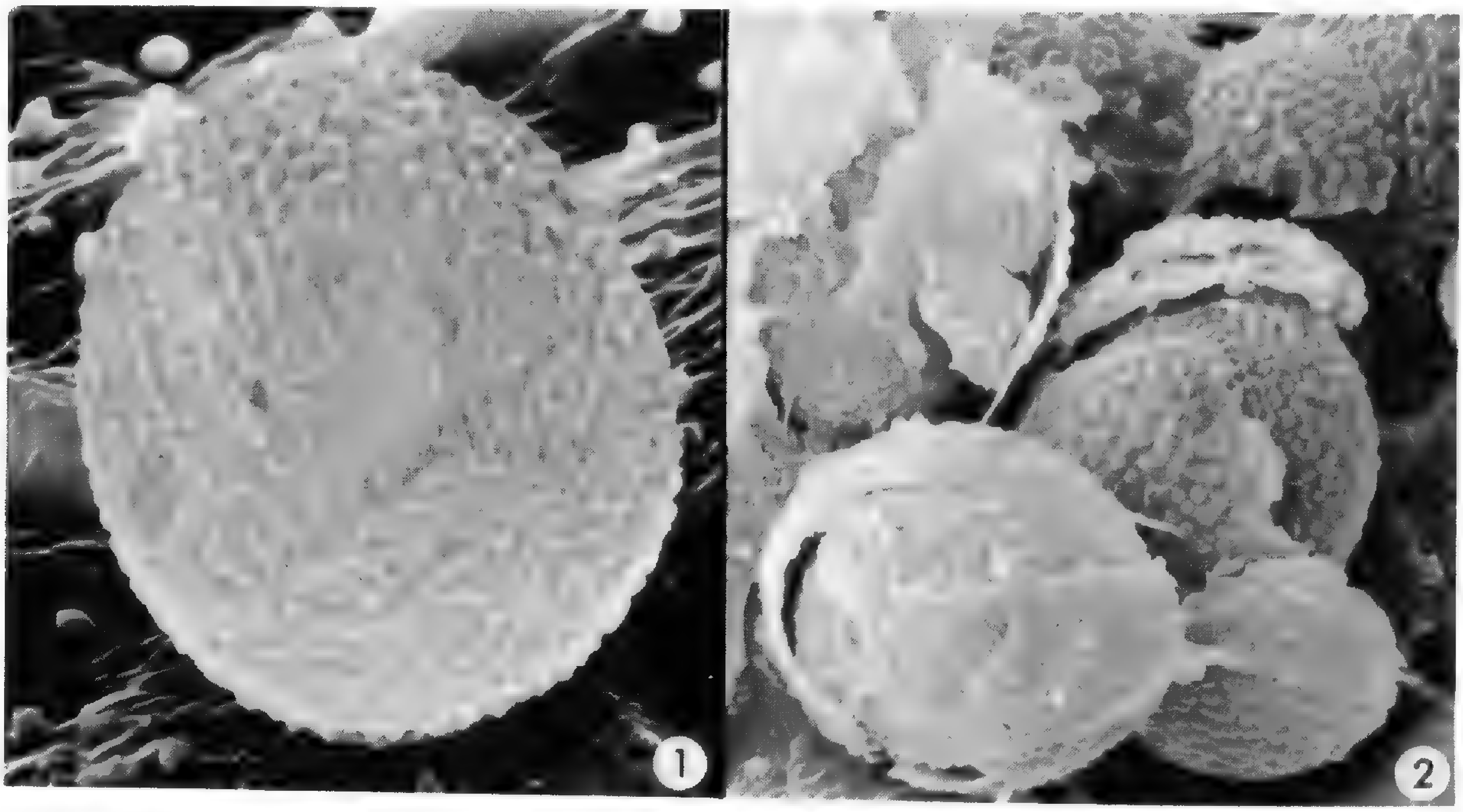

FIG. 1. Normal spore of *Macroglossum alidae*, × 3075. FIG. 2. Double-walled spore of *M. alidae*, × 1535.

The fact that angiospores have so far been observed only in the Marattiales and Ophioglossales might have one of three explanations: chance observation due to the much higher number of spores per sporangium; angiospores have been overlooked in the more advanced leptosporangiate pteridophytes; or within the pteridophytes, angiospory is a trait exclusive to the eusporangiate members.

The phenomenon of angiospory may well represent a new sub-pattern in the life cycle of pteridophytes.

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Subdivision of the Genus Elaphoglossum

JOHN T. MICKEL and LUCÍA ATEHORTÚA G.*

The genus *Elaphoglossum* is one of the largest and most complex of fern genera. It is composed of perhaps 600 species, which frequently are difficult to distinguish. The genus has not been afforded careful study in the past. As a result, some names have been misapplied and others not used at all, and sometimes new names have been made for old species. Consequently, much herbarium material is either misidentified or unidentified. "*Elaphoglossum* is more in need of a taxonomical revision than other fern genera, all the more so as many species are imperfectly known or badly delimited in comparison with their allies." (Pichi Sermolli, 1968).

Elaphoglossum is a remarkably uniform genus of mostly simple-bladed ferns with acrostichoid sori. The veins are free (with two exceptions), the rhizomes scaly, and the blades densely scaly to nearly glabrous. The taxonomy of the genus is based to some extent on frond form and rhizome habit, but more importantly on the scales of the rhizome and blade.

Until now there has not been a useful treatment that conveniently breaks the large number of species into smaller, more coherent units. Modern keys have been made for a few areas, such as tropical Africa (Schelpe, 1969), Brazil (Alston, 1956a), Guatemala (Mickel, 1980b), Malaysia (Holttum, 1978), and India (Sledge, 1967), but these do not provide insight into treatment of the genus as a whole. The purpose of this paper is to take the first step in revising the genus by breaking it into infrageneric units that subsequently can be monographed. Even so, this treatment is provisional because a complete understanding of the genus can be had only after the species are better known.

HISTORY OF THE GENUS

Linnaeus (1753) described *Elaphoglossum crinitum* under *Acrostichum*, which included all ferns with sporangia covering the dorsal blade surface. Schott (1834) first proposed the name *Elaphoglossum*, but it was not formally described until later by John Smith (1841, p. 148), and was not widely accepted until the end of the century.

The first broad treatment of the genus was prepared by Fée (1845) under *Acrostichum*. He divided the elaphoglossoids into two groups, Oligolepideae and Polylepideae. These in turn were subdivided on the basis of frond size and scale characters. Later, Fée (1852) used four primary groups without further subdivision: Oligolepideae, Polylepideae, Pilosellae, and Chromatolepideae.

Moore (1857–1862) was the first to use the genus name *Elaphoglossum* extensively; he made many new combinations under it. He utilized a generic breakdown of Oligolepidum ("fronds naked, or with but few scales") and Polylepidum ("fronds clothed with numerous scales"). Sodiro (1897, under *Acrostichum*) used more group names (Glabra, Setosa, Oligotrichia, Polytrichia, Squamosa, Oligolepidia, Laciniata, Polylepidia), but without designating nomenclatural rank.

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*New York Botanical Garden, Bronx, NY 10458.

Diels (1899) made two sections of the genus: *Eu-Elaphoglossum* for the bulk of the species and *Hymenodium* for the distinct, broad, net-veined *E. crinitum*. His informal subsectional groups largely followed those of Sodiro.

In the same year, Christ (1899) published his classic *Monographie des Genus Elaphoglossum*, which stands as the most detailed treatment of the genus, covering 142 species (and numerous synonyms) in 32 groups. The primary division was based on venation: ordo *Stenoneura* with veins running all the way to the margin without thickened vein ends and ordo *Condyloneura* with veins ending just short of the margin with swollen vein ends (hydathodes). Christ further subdivided these into sections, subsections, and divisions, using characters such as blade scales, frond size, stipe articulation, and rhizome habit and thickness. Basically, his species groups were natural and recognizable (nearly all of our ultimate divisions are based on them). Unfortunately he placed what we believe to be unrelated divisions and subsections together and did not provide a usable key to the groups. For example, Christ placed some of the species with black, marginal, subulate scales in each of the two ordos, when in fact they are very closely related and none shows the hydathodes of ordo *Condyloneura*. By the same token, his subsections *Dimorpha, Petiolosa, Pilosa*, and *Ovata* in *Condyloneura* show no signs of hydathodes and belong with close relatives in ordo *Stenoneura*. This is not to say that hydathodes are a poor character; we would have adopted Christ's two ordos as subgenera were it not for misgivings about possible convergent evolution of subulate scales and hydathodes or lack thereof.

As generally accepted, the species of *Elaphoglossum* have narrowly elliptic, undivided fronds, but several species of elaphoglossoid affinity with divided fronds are known. Several small, flabellately divided species were first generically segregated by Link (1841) as *Peltapteris* and pinnately divided plants by Presl (1851) as *Microstaphyla*. Although some of the American species had the pinnate form of *Microstaphyla* and had been placed in that genus, Gómez (1975) saw that their true relationship was with *Peltapteris*. He left only the type species (from St. Helena) in *Microstaphyla*. One large, pedately divided species, *E. cardenasii*, was described from Bolivia by Wagner (1954); strangely, no one has proposed a separate genus for it. Christ placed the species of *Peltapteris* (as *Rhipidopteris*) and *Microstaphyla* under *Elaphoglossum* and, after showing that frond architecture was the sole character for distinguishing these groups from species of *Elaphoglossum*, Mickel (1980a) concurred in keeping them all in *Elaphoglossum*.

RELATIONSHIPS OF THE GENUS

The relationships of the elaphoglossoid ferns to other ferns are unclear. *Elaphoglossum* is placed close to the lomariopsid genera by some authors because of the acrostichoid sori, largely epiphytic habitat, monolete spores, and chromosome number of $x=41$. Holttum (1947) placed it in the Lomariopsidoideae of his Dennstaedtiaceae, and Alston (1956b) placed it in the Lomariopsidaceae. Crabbe, Jermy, and Mickel (1975) placed it in the Elaphoglossoideae of the Aspleniaceae and close to the Lomariopsidoideae. Pichi Sermolli (1968) pointed out the distinctness of the group from the lomariopsids and erected a new family for it, the

Elaphoglossaceae, but placed this next to the Lomariopsidaceae. Christensen (1938) gave it its own subfamily Elaphoglossoideae in the Polypodiaceae, but could not determine its relationship with certainty.

Sporne (1975) and Holttum (1947) have suggested a davallioid relationship because of similarities of stele and chromosome number. We have found some spores which closely resemble those of *Bolbitis appendiculata* of the lomariopsids (Hennipman, 1977, pl. 4). Many other spores are similar to those of various species of *Oleandra* and *Arthropteris* (illustrated by Liew, 1977). This is especially interesting because *Oleandra*, like *Elaphoglossum*, has simple blades, straight, free veins, phyllopodia, hydathodes, and chromosome number of $x=41$.

MORPHOLOGICAL CHARACTERS

Rhizome habit.—Most species have short-creeping rhizomes, but they range from moderately to long-creeping and from ascending to erect, and are 1–12 mm in diameter. Members of a single subsection usually have a similar rhizome habit, but the entire spectrum can be found within subsection *Pachyglossa*.

Aerophores.—*Elaphoglossum* aerophores are pale, aerenchymatous outgrowths from the lenticel line on the stipe base or adjacent rhizome, one on each side of the stipe. They may appear as fleshy wings about 1 mm broad along the phyllopodia or as tongue-shaped emergences from the stipe base or adjacent rhizome. They are not conspicuous on dried specimens, especially in those species with fasciculate fronds, which makes a survey based on herbarium material difficult. Lloyd (1970) made a study of living specimens in Costa Rica and found aerophores in 92% of the species studied. More extensive systematic and morphological study of this structure is needed.

Phyllopodia.—These dark, sclerified stipe bases are not found in all species and are concentrated in a few subsections, particularly those with coriaceous, subglabrous fronds (esp. subsects. *Pachyglossa* and *Huacsaro* and sect. *Amygdalifolia*). Pichi Sermolli (1968) distinguished *Peltapteris* from *Elaphoglossum* on the basis of the former's lacking phyllopodia, but *Peltapteris'* closest relatives, which are in *Elaphoglossum* sect. *Squamipedia*, also lack them. Most sections or subsections either lack phyllopodia or have them only poorly developed.

Frond size.—Christ (1899) distinguished some of his glabrous sections by frond size. To some extent this is valid. Section or subsection members are consistently approximate in size. Subsections may have small and medium fronds or medium and large fronds, but generally not both small and large, although there are diminutive specimens of nearly all species. There are also very long individual specimens in groups with normally medium-sized fronds (e.g., *E. vestitum* to 1.7 m long and *E. herminieri* to 2 m long).

Blade shape.—Although the blades are basically simple and unlobed, there is some variation in form. They are fairly uniformly ovate-elliptic in the *E. lindenii* complex (subsect. *Setosa*), lanceolate with an obtuse apex in subsect. *Muscosa*, narrowly elliptic with an obtuse apex in subsect. *Huacsaro*, and linear-elliptic in subsect. *Eximia*. Blade shape seems to be more consistent in species groups or series than in sections or subsections.

Venation.—*Elaphoglossum* fronds are basically free-veined. *Elaphoglossum crinitum* has net venation and has been set aside as the genus *Hymenodium* by some authors, but *E. crassifolium*, which also has net venation, does not seem to be closely related. *Elaphoglossum decoratum* has an occasional anastomosis, and in several species the vein endings are laterally extended and even fused occasionally (e.g., *E. acutissimum*) to form a commissural vein. In most species the veins diverge from the midvein and go to the margin at an angle of 70–80°. In several sections (esp. *Undulata, Setosa, Eximia,* and *Amygdalifolia*), they diverge at a narrower angle (40–60°), are farther apart (ca. 2 mm), and terminate about 1 mm short of the margin, often ending in a round thickening or hydathode. Apparently in all species the veins end slightly short of the margin, but in many species the blade is coriaceous with slightly recurved margins, making the actual vein endings difficult to distinguish. Therefore, some authors (including Christ) have claimed that the veins go to the margin.

Hydathodes.—The veins in the blade generally end near the margin and are at least slightly swollen. In certain groups, the veins end 1–2 mm short of the margin and are greatly enlarged to form hydathodes. Whether these function differently from those not enlarged is not known. Hydathodes are found in all species of sects. *Setosa, Eximia, Undulata*, and *Amygdalifolia*, and are not known from any species of the other sections. These sections comprise what Christ designated ordo *Condyloneura*. We do not recognize these as subgenera here because it is unclear whether there are close relationships between members of the two ordos, as perhaps between sects. *Setosa* (with hydathodes) and *Polytrichia* (lacking them).

Blade texture.—Among members of a subsection and closely related groups, texture seems to be nearly uniform. Coriaceous fronds generally are nearly glabrous, but whether all species with such fronds are related is questionable. The absence of blade scales makes it difficult to assess relationships. Most species have herbaceous to firm laminae, but those with hydathodes are usually thin.

Rhizome scales.—The rhizomes are generally densely scaly, with linear, lanceolate, ovate, or rarely even round scales, which are attached at a cordate to peltate base. Scale color ranges from bright orange to maroon, brown, or black. Texture varies from thin to sclerotic. Scale margins in most species are entire or have weak teeth, but in sect. *Lepidoglossa* they often are fringed with slender, hair-like teeth. Differences in cell patterns have not yet been examined systematically, but probably will be helpful taxonomically. In some groups within sect. *Elaphoglossum,* the rhizome scales may be deciduous, leaving in some cases completely glabrous creeping rhizomes. In a few species the naked rhizome is black and glutinous.

Blade scales.—There is great diversity in scale morphology, but the blade scales are basically lanceolate. They may be erose-margined (*E. muscosum*), entire (*E. decoratum*), or deeply ciliolate-toothed (subsect. *Polylepidea*). Some are so deeply ciliolate-toothed there is barely any scale body (*E. vestitum*) or are reduced to stellate hairs (*E. pilosum*). In *E. tectum*, the stipe and upper blade scales are round-peltate with erose margins, whereas those of the lower blade surface are stellate hairs. In *E. petiolatum*, *E. huacsaro*, and their relatives, the blade scales are further reduced to resinous dots. Coriaceous, subglabrous groups often have reduced, minute, black, linear or stellate blade scales.

There are no multicellular hairs in *Elaphoglossum*; those thought to have hairs (sects. *Setosa* and *Polytrichia*) have in reality hair-like subulate scales which are linear-lanceolate with inrolled margins. It is not clear whether all groups with subulate scales are related or not. Although they have distinctive, minute, glandular hairs in common, they differ in their spores.

Stipe scales.—They are like those of the rhizome at the base and like those of the blade near the apex. Sometimes these are transitions from one to the other type, but in other cases, two distinct types are intermixed.

Glandular hairs.—Minute, erect, unicellular, gland-tipped hairs are located on the stipe in sects. *Polytrichia, Setosa*, and *Eximia*. Their presence seems to be correlated with the presence of subulate scales. In subsect. *Apoda,* these hairs also are found on the blade surface.

Fertile fronds.—In most species, the fertile fronds have narrower and shorter blades and proportionally longer stipes than the sterile ones. The fertile fronds may be longer, essentially equal, or noticeably shorter than the sterile ones. The relationship does not seem to be consistent in whole sections or subsections, but is so in species groups or occasionally in subsections (fertile longer in subsects. *Huacsaro* and *Pilosa*).

In some species, the fertile frond is folded in half lengthwise along the midvein until maturity. This conduplicate fertile blade is found in *E. lindenii* and *E. piloselloides* of sect. *Setosa*, but not in all species of the section; in subsect. *Petiolosa*, both species show this condition.

The indument of the fertile frond generally is the same on the upper surface as on that of the sterile blade. However, there are a few species that have scales on the lower surface among the sporangia, and their presence is especially noteworthy. It is not consistent with subsections, occurring in *E. villosum, E. muscosum, E. siliquoides*, all of different subsections, but seems to be common to all members of subsect. *Plumierana.*

In certain species, there seems to be a conspicuous sterile margin, that forms a pale border 1–2 mm wide outside the sporangial mass. It is especially noticeable in some thin-textured species such as *E. albomarginatum*. Although it is not readily apparent in most other species, close examination shows that the sterile margin is underrolled and thus concealed. Probably some sort of sterile margin exists in most or all species, which is to be expected since the veins do not reach the margin.

Spores.—*Elaphoglossum* spores usually have been described as having narrow crests with minute spicules on the surface (Erdtman, 1957, based on *E. vieillardii* from New Caledonia), but our survey of spores using the scanning electron microscope has shown considerable variation within the genus. We have examined 163 species, including representatives of all sections and subsections. *Figures 1–18* are based on specimens in the New York Botanical Garden herbarium.

Spores of most species have slender crests or low folds or ridges. Section *Squamipedia* (*Fig. 7*) also has low ridges, but the entire surface is densely ornamented with distinctive spicules found also in the flabellately or pinnately divided subsect. *Peltapteris*. High slender crests are found in sects. *Amygdalifolia*, *Decorata*, and in some members of sects. *Setosa* and *Elaphoglossum*. Subsection *Pachyglossa*, probably the largest in the genus, displays several different spore types: some species have tall, nearly spine-like, smooth or perforated crests, to highly fenestrated, lace-like crests; others have long, slender crests lacking holes; and others have low, broad ridges.

Spores with low, broad ridges are found in sects. *Lepidoglossa* (*Fig. 9*), *Polytrichia* (*Fig. 12*), and part of sect. *Elaphoglossum* subsect. *Pachyglossa* (*Fig. 3*). The ridges tend to be short (*Figs. 9* and *12*) rather than elongate, and often have small verrucae in the valleys between the ridges, which suggests a possible relationship among these groups. On the other hand, the lack of other ornamentation could indicate either a common or a primitive spore type or a condition arrived at independently. Correlations of additional characters are needed to resolve this.

Spores of subsect. *Muscosa* are unique in having verrucate surfaces (*Fig. 11*).

The spores of sects. *Eximia, Undulata*, and part of sect. *Setosa* subsect. *Setosa* lack ridges or crests of any sort. Instead, they have a dense covering of short spines which branch at the base to form a reticulum (*Figs. 14* and *16–18*). In sect. *Undulata*, the spines occasionally fuse to form small crests (*Fig. 18*). In *E. beaurepairii* (sect. *Eximia*, *Fig. 17*) the reticulum is very open, whereas in sect. *Setosa* subsect. *Setosa* (*E. crinipes et aff.*) the branches often fuse laterally to make a more dense covering on the spore surface (*Fig. 14*). Spores of some members of subsect. *Setosa* (*E. lindenii et aff.*) and *Alpestria* have low, slender crests which often have holes of various sizes in them (*Fig. 13*), somewhat like those mentioned for subsect. *Pachyglossa*. Holes also occur in the spore surface, which in some cases resembles somewhat the spore surface reticulum of sects. *Undulata* and *Eximia*. Perforations, at least in the body of the spore, also are found in some species of subsect. *Pachyglossa*, but whether this indicates a relationship has not yet been determined.

Not every species fits into the spore pattern for its group. Some species of subsect. *Pilosella* have holes in the surface and others do not. In subsect. *Plumierana*, *E. buchii* (*Fig. 15*) and *E. plumieri* have solid crests, whereas the morphologically similar *E. lanceum* has highly fenestrated crests. In general, however, spore morphology has been quite useful in confirming relationships presumed on other grounds and in suggesting new phyletic interpretations.

CONSPECTUS OF THE GENUS ELAPHOGLOSSUM (INCLUDING CHRIST'S INFRAGENERIC GROUPS IN PARENTHESES)

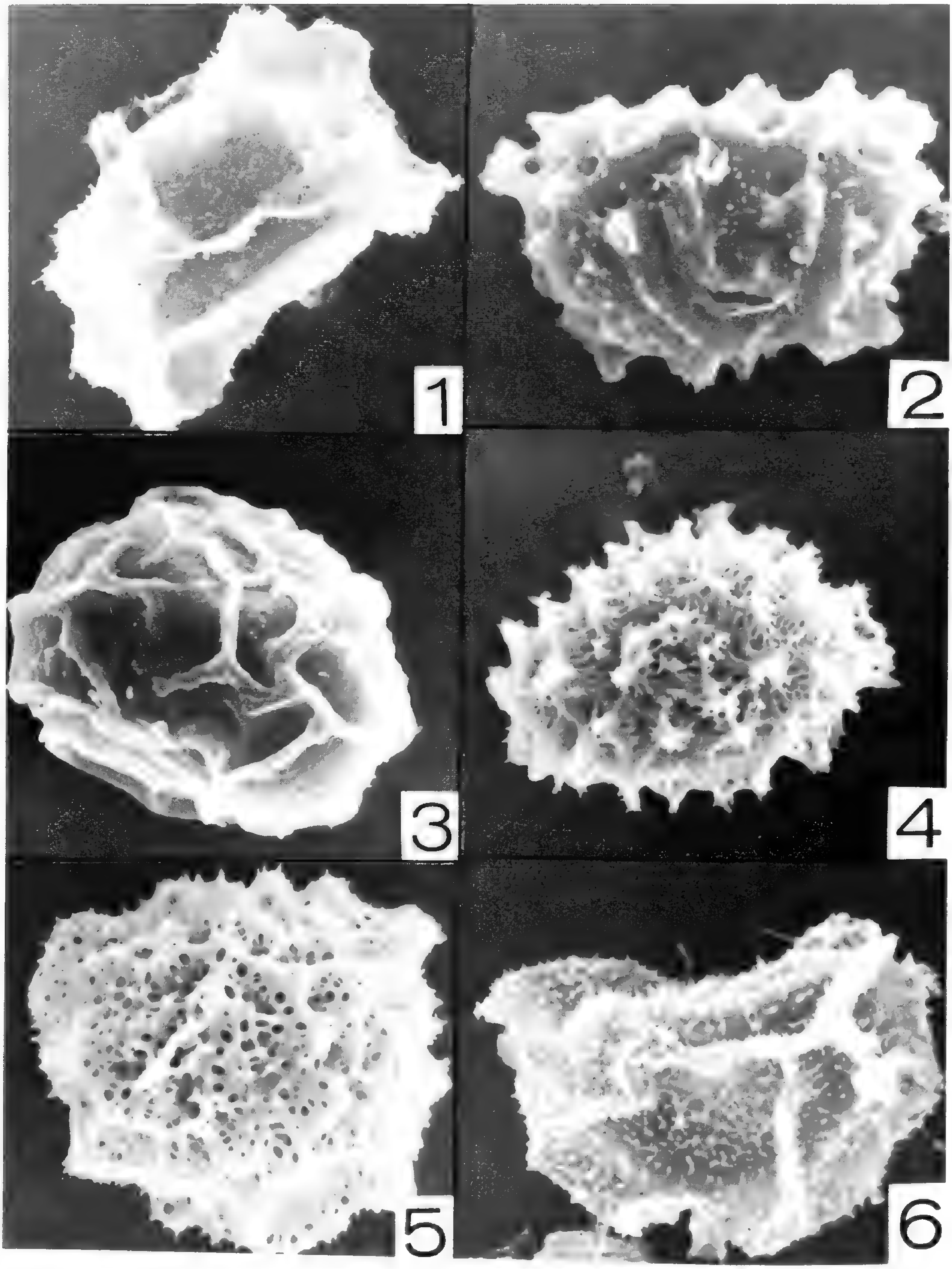
- sect. *Elaphoglossum* (sect. *Craspedoglossa*)
  - subsect. *Pachyglossa* Christ (subsect. *Pachyglossa* div. *Conformia*, including type of genus; subsect. *Platyglossa* div. *Latifolia*; subsect. *Flaccida* by type but not by description or other included species; subsect. *Herminieriana*)
  - subsect. *Tenuifolia* Mickel & Atehortúa (subsect. *Flaccida* by description and included species but not by type)

- sect. *Squamipedia* Mickel & Atehortúa
  - subsect. *Squamipedia* Mickel & Atehortúa (subsect. *Pachyglossa* div. *Squamipedia*)
  - subsect. *Peltapteris* (Link) Mickel & Atehortúa (subsect. *Pachyglossa* div. *Rhipidopteris*)
  - subsect. *Ovata* Christ
  - subsect. *Feeana* Christ
- sect. *Decorata* Mickel & Atehortúa (subsect. *Platyglossa* div. *Decorata*)
- sect. *Lepidoglossa* Christ (sect. *Gymnoglossa*)
  - subsect. *Polylepidea* Christ (subsect. *Polylepidea* div. *Auricoma*)
  - subsect. *Microlepidea* Christ (subsect. *Microlepidea* div. *Tecta*)
  - subsect. *Pilosa* Christ (subsect. *Pilosa* div. *Grata*; subsect. *Microlepidea* div. *Viscosa*; subsect. *Polylepidea* div. *Stipitata*; subsect. *Dimorpha*)
  - subsect. *Petiolosa* Christ
  - subsect. *Huacsaro* Mickel & Atehortúa
  - Subsect. *Muscosa* Mickel & Atehortúa (subsect. *Polylepidea* divs. *Muscosa* and *Bellermanniana*)
- sect. *Polytrichia* Christ
  - subsect. *Hymenodium* (Fée) Christ
  - subsect. *Hybrida* Christ (subsect. *Platyglossa* div. *Melanolepidea*; subsect. *Hybrida* by type and description but not by other included species)
  - subsect. *Apoda* Mickel & Atehortúa
- sect. *Setosa* (Christ) Mickel & Atehortúa
  - subsect. *Setosa* Christ
  - subsect. *Pilosella* Christ
  - subsect. *Alpestria* Mickel & Atehortúa
  - subsect. *Plumierana* Mickel & Atehortúa
- sect. *Eximia* Mickel & Atehortúa
  - subsect. *Eximia* Mickel & Atehortúa (subsect. *Hybrida* by included species but not by type or description)
  - subsect. *Cardenasiana* Mickel & Atehortúa
- sect. *Undulata* Christ
- sect. *Amygdalifolia* (Christ) Mickel & Atehortúa

The following of Christ's groups are of unknown relationship: subsect. *Glossoides*, subsect. *Coespitosa*, subsect. *Pachyglossa* div. *Micradenia*, subsect. *Polylepidea* div. *Argyrophylla*, subsect. *Polylepidea* div. *Fimbriata*, subsect. *Pilosa* div. *Boraginea*, and subsect. *Pilosa* div. *Gardneriana*.

KEY TO THE SECTIONS OF ELAPHOGLOSSUM

1. Veins ending short of the margin, enlarged at the tip to form generally conspicuous hydathodes.
  2. Rhizome long-creeping; blade glabrous; phyllopodia present, but short. ......sect. *Amygdalifolia*
  2. Rhizome short- to long-creeping; blade scaly, only rarely glabrous; phyllopodia lacking.
    3. Blade linear-elliptic or pedately divided; blade scales very small, dark, lanceolate, not subulate. sect. *Eximia*
    3. Blade narrowly elliptic or ovate-lanceolate; blade scales subulate or cordate-lanceolate, pale.
      4. Blade scales subulate. ....sect. *Setosa*
      4. Blade scales cordate-lanceolate, erose or toothed. ....sect. *Undulata*
1. Veins ending at or very close to the margin, not ending in hydathodes.
  5. Blade glabrous or subglabrous.
    6. Rhizome long-creeping, fronds very small (2–20 cm long), usually lacking phyllopodia; blade simple to finely dissected. ....sect. *Squamipedia*
    6. Rhizome erect or short- to long-creeping; fronds small to large (12–200 cm long), phyllopodia distinct or indistinct but always present. ....sect. *Elaphoglossum*



FIGS. 1–6. Spores of *Elaphoglossum* sect. *Elaphoglossum*. FIG. 1. *E. pteropus* (*Brade 19180*), × 1200. FIG. 2. *E. conforme* (*Murray s.n.*), × 1200. FIG. 3. *E. dussii* (*Broadway s.n.*), × 1200. FIG. 4. *E. acutifolium* (*Brade 5358*), × 1200. FIG. 5. *E. bicolor* (*Wacket 121*), × 1560. FIG. 6. *E. wacketii* (*Wacket 7849*), × 1080.

5. Blade scaly.
  7. Blade scales subulate. ....sect. *Polytrichia*
  7. Blade scales lanceolate, reniform, round-peltate, or stellate, not subulate.
    8. Blade scales only at frond margin and along midvein. ....sect. *Decorata*
    8. Blade scales not restricted to frond margin and midvein......................sect. *Lepidoglossa*

21586 Elaphoglossum sect. Elaphoglossum

25870 Sect. *Craspedoglossa* Christ, Monogr. Elaph. 20. 1899.

Rhizome long- to short-creeping or suberect; rhizome scales linear to lanceolate; phyllopodia distinct or indistinct; blade glabrous or subglabrous, coriaceous to very thin; hydathodes lacking; blade scales minute, laciniate-pectinate to stellate; spores with various forms of crests or low ridges.

TYPE SPECIES: *Acrostichum conforme* Swartz [≡ *Elaphoglossum conforme* (Swartz) Schott ex J. Smith].

KEY TO THE SUBSECTIONS OF SECT. ELAPHOGLOSSUM

1. Blade coriaceous; veins obscure; phyllopodia conspicuous........................subsect. *Pachyglossa*
1. Blade very thin, translucent; veins evident; phyllopodia inconspicuous...........subsect. *Tenuifolia*

21585 Elaphoglossum subsect. Pachyglossa Christ, Monogr. Elaph. 20. 1899. 7188

25871 Subsect. *Platyglossa* Christ, Monogr. Elaph. 20. 1899. LECTOTYPE (chosen here): *Acrostichum latifolium* Swartz [≡*Elaphoglossum latifolium* (Swartz) J. Smith]. Christ did not designate a type species for this subsection, but chose *E. latifolium* as the type of his first and most typical division, *Latifolia*.

25872 Subsect. *Flaccida* Christ, Monogr. Elaph. 20. 1899.

Subsect. *Herminieriana* Christ, Monogr. Elaph. 21. 1899.

Characters of the section, with the blade coriaceous and the phyllopodia especially distinct.

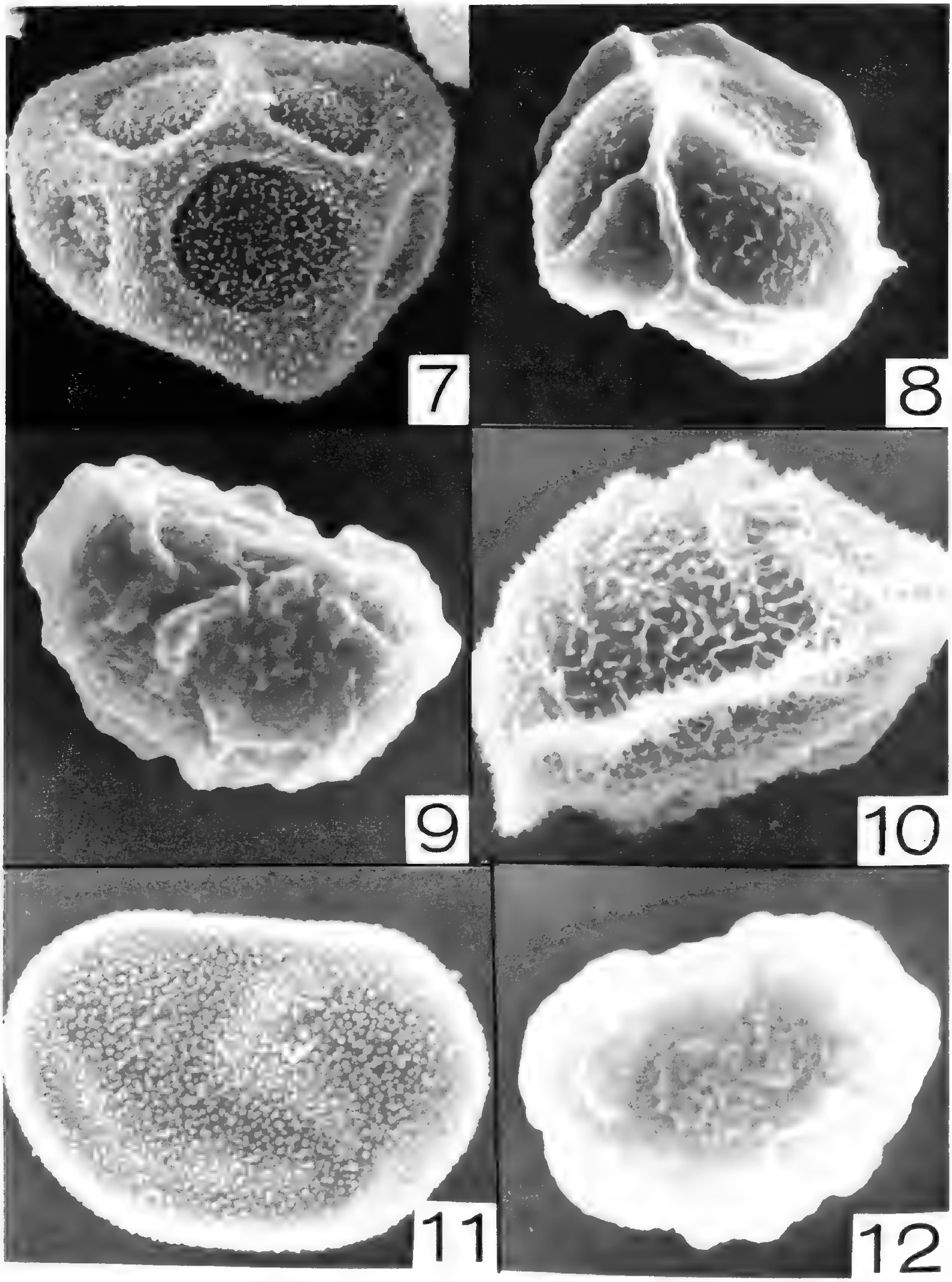
TYPE SPECIES: *Acrostichum conforme* Swartz [≡*Elaphoglossum conforme* (Swartz) Schott ex J. Smith]. 10930

SELECTED SPECIES EXAMINED:

Elaphoglossum acrostichoides (Hook.) Schelpe, *E. acutifolium* Rosenst., *E. affine* (Mart. & Gal.) Moore, *E. angulatum* (Blume) Moore, *E. angustatum* (Schrad.) Hieron, **E. bicolor* Rosenst., *E. callifolium* (Blume) Moore, *E. chartaceum* (Baker) C. Chr., *E. crassifolium* (Gaud.) Anderson & Crosby, *E. crassinerve* (Kunze) Moore, **E. funckii* (Fée) Moore, **E. gayanum* (Fée) Moore, *E. glabellum* J. Smith, *E. glaucescens* Rosenst., *E. glaucum* (Fée) Moore, **E. glossophyllum* Hieron., *E. guatemalense* Klotzsch, *E. herminieri* (Bory & Fée) Moore, *E. hoffmannii* (Mett.) Hieron, *E. hymenodiastrum* (Fée) Brade, *E. inaequalifolium* (Jenm.) C. Chr., *E. latifolium* (Swartz) J. Smith, *E. leptophyllum* (Fée) Moore, **E. lingua* (Presl) Brack., *E. longifolium* (Presl) J. Smith, *E. maxonii* Underw. ex Morton, *E. pteropus* C. Chr., *E. rigidum* (Aubl.) Urban, *E. schiffneri* Christ, *E. schomburgkii* (Fée) Moore, *E. simplex* (Swartz) J. Smith, *E. sporadolepis* (Kunze) Moore, *E. tenuifolium* (Liebm.) Moore, *E. tovarense* (Moritz ex D. C. Eat.) Moore, *E. tuckerheimii* Brause, **E. vagans* (Mett.) Hieron., and *E. wawrae* (Luerss.) C. Chr.

This is the largest and taxonomically most complex subsection of the genus. There are relatively few available diagnostic characters, and the variation within and between species is difficult to interpret. Several groups are vaguely discernible, but whether they are all closely allied or have evolved to the coriaceous, glabrous condition independently is still in question. We have refrained from distinguishing taxonomic groups until more information is gathered.

One group has very short to suberect, stout (4–12 mm diam.) rhizomes and spores with many short crests that resemble broad spines (*Fig. 2*). In some of



FIGS. 7–12. Spores of *Elaphoglossum*. Sect. *Squamipedia*. FIG. 7. *E. squamipes* (*Wurdack 692*), × 840). FIG. 8. *E. ovatum* (*Grubb 540*), × 1200). Sect. *Lepidoglossa*. FIG. 9. *E. paleaceum* (*MacBride 4301*), × 1560). FIG. 10. *E. huacsaro* (*Acosta-Artega 165*), × 1200). FIG. 11. *E. bellermannianum* (*Camp E 3938B*), × 960). FIG. 12. *E. auripilum* (*Mickel 2657*), × 1800).

these there are perforations in the crests and in the spore surface as well (*Figs. 4* and *5*). On the other hand, some species (e.g., *E. pteropus*) have spores with tall, slender, solid crests (*Fig. 1*).

Many species have more slender rhizomes (2–4 mm diam.) that have dark, sclerotic rhizome scales which may become deciduous, as in *E. guatemalense* and *E. glabellum*. These have spores with low, broad ridges (*Fig. 3*).

There is a species complex, including *E. affine*, *E. tenuifolium*, *E. leptophyllum*, and *E. schiffneri*, which has ovate-lanceolate, orange to tan rhizome scales with varying degrees of dark, sclerotic streaks in them. Their rhizomes range from short-creeping to rather long-creeping. Quite possibly this complex is related to what looks like a distinct group with very long-creeping, slender, cord-like rhizomes with black, ovate-lanceolate rhizome scales (species marked with an asterisk in the above list). *Elaphoglossum hoffmannii* has the most slender, nearly naked rhizomes and smallest fronds of the group and may not belong here.

Elaphoglossum subsect. Tenuifolia Mickel & Atehortúa, subsect. nov.

Rhizomata gracilia, saepe nuda; phyllopodia inconspicua; lamina angusta tenuissima; nervi visibiles; sporae dense spiculatae cristatae.

TYPE SPECIES: *Elaphoglossum acutissimum* Christ. - 7166

SELECTED SPECIES EXAMINED:

Elaphoglossum burchellii (Baker) C. Chr., *E. gramineum* (Jenm.) Urban, *E. praelongum* (Fée) C. Chr., *E. sherringii* (Baker) C. Chr., and *E. wacketii* Rosenst.

This group is distinct in its very thin-textured blades and often naked or even black and glutinous rhizome. The glabrousness of the blade induces us to place these species in sect. *Elaphoglossum*, but they may well belong elsewhere, perhaps nearer to subsect. *Pilosa*. At least one member of this group has resinous dots on the dorsal surface of the blade and spiculate spores (*Fig. 6*), such as are found in *E. huacsaro* (*Fig. 10*) in subsect. *Huacsaro* and in some members of subsect. *Pilosa*, but the naked rhizome and glabrous blade resemble subsect. *Pachyglossa*.

Elaphoglossum gramineum has a glabrescent rhizome and resin-dotted blade, but the blade is coriaceous, unlike that of other members of this subsection.

Subsection *Flaccida* was intended by Christ to include the thin-bladed species we treat as subsect. *Tenuifolia*, but unfortunately he selected as type *E. flaccidum*, which generally is regarded today as a synonym of *E. rigidum*, a member of the coriaceous subsect. *Pachyglossa*.

Elaphoglossum sect. Squamipedia Mickel & Atehortúa, sect. nov.[2]

Rhizomata gracillima longe repentia; rhizomatis stipitisque paleae ovato-lanceolatae peltatae, vel lacerato-pectinatae; phyllopodia rara; lamina parva; laminae paleae parvae fuscae reductae, saepe hastatae; nervi inconspicui; hydathodi nulli; sporae plerumque multispiculatae cristis demissis latis anastomosantibus ornatae.

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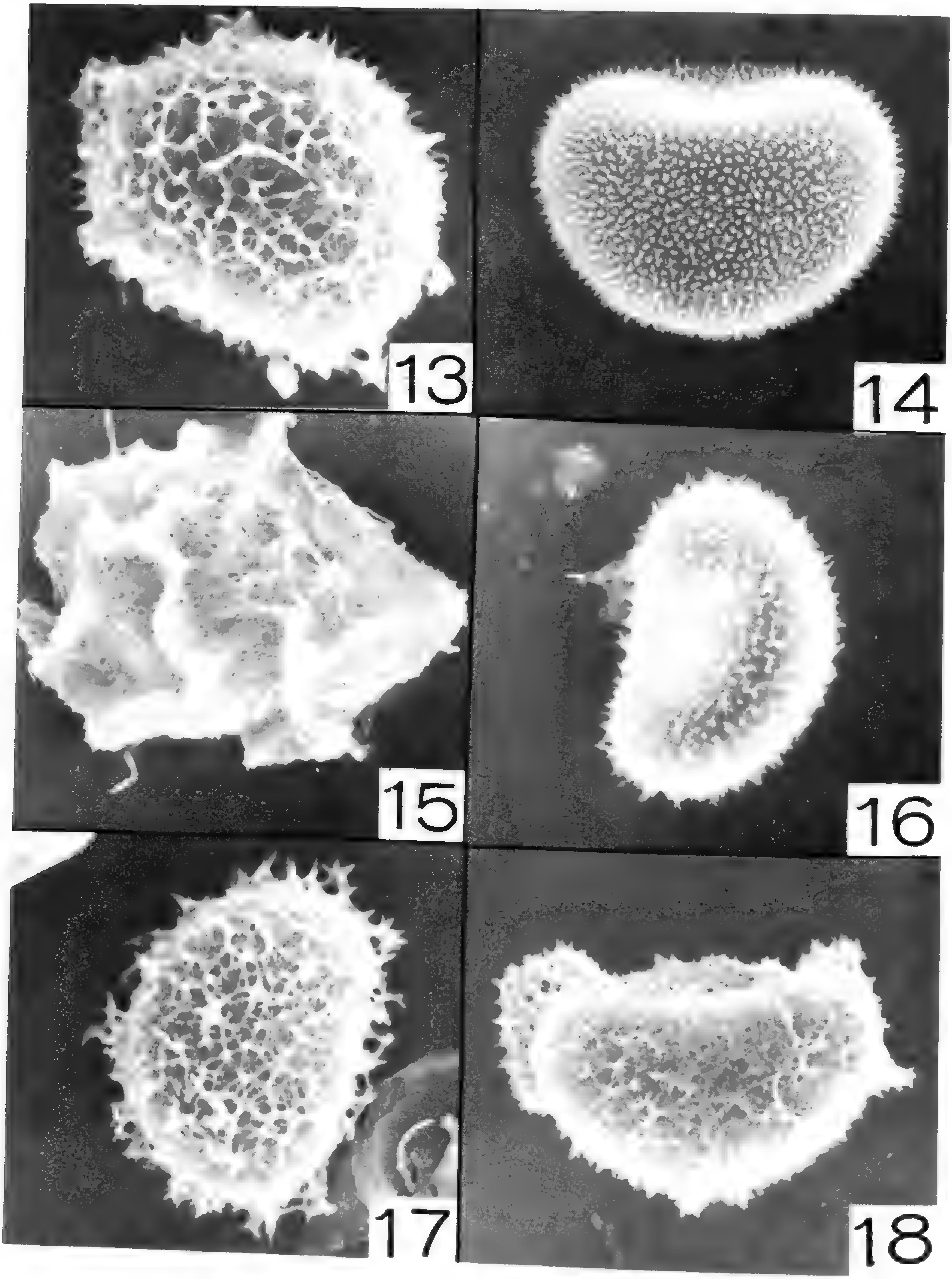
[2] Although the sectional names *Squamipedia*, *Setosa*, and *Eximia* repeat subsectional names, Latin diagnoses are given for both levels since at the subsectional level there are no automatic tautonyms nor type subsections, and some botanists might not construe the subsectional names as properly described without separate Latin diagnoses.



FIGS. 13–18. Spores of *Elaphoglossum*. Sect. *Setosa*. FIG. 13. *E. moritzianum* (*Fendler 362*), × 1440. FIG. 14. *E. crinipes* (*Standley 85982*), × 1200. FIG. 15. *E. buchii* (*Jenman. s.n.*), × 1200. Sect. *Eximia*. FIG. 16. *E. eximium* (*Mickel 3417*), × 1080. FIG. 17. *E. beaurepairei* (*Brade 20937*), × 1200. Sect. *Undulata*. FIG. 18. *E. hirtum* (*Mickel 2978*), ×1200.

7211

TYPE SPECIES: *Acrostichum squamipes* Hook. [≡*Elaphoglossum squamipes* (Hook.) Moore].

KEY TO THE SUBSECTIONS OF SECTION SQUAMIPEDIA

1. Stipe scales deeply lacerate-pectinate..subsect. *Ovata*
1. Stipe scales entire, ovate-lanceolate.
    2. Sterile blade pinnately or flabellately divided, rarely undivided but then broadly flabellate. subsect. *Peltapteris*
    2. Sterile blade entire, linear-elliptic or oblanceolate.
        3. Blade margin crenulate; blade thin; spores with narrow crests...................subsect. *Feeana*
        3. Blade margin entire; blade coriaceous; spores with low folds or ridges and many spicules. subsect. *Squamipedia*

25874 **Elaphoglossum subsect. Squamipedia Mickel & Atehortúa, subsect. nov.**[3]

Rhizomatis stipitisque paleae ovato-lanceolatae peltatae integrae; lamina simplex; sporae spiculatae (*Fig. 7*).

✓TYPE SPECIES: *Acrostichum squamipes* Hook. [≡*Elaphoglossum squamipes* (Hook.) Moore].

OTHER SPECIES EXAMINED:

Elaphoglossum cardiophyllum (Hook.) Moore, *E. craspedariiforme* (Fée) Brade ex Alston, *E. deltoideum* (Sod.) Christ, *E. lloense* (Hook.) Moore, and *E. revolutum* (Liebm.) Moore.

This is one of the most distinctive groups in the genus, with its small fronds, broadly ovate rhizome and stipe scales, and lack of phyllopodia. In blade form *E. cardiophyllum* seems to belong here, but phyllopodia are present and spore spicules are lacking. This subsection is extremely closely related to subsect. *Peltapteris* and agrees in all characters except frond architecture.

25877 **Elaphoglossum subsect. Peltapteris (Link) Mickel & Atehortúa, stat. nov.**

Peltapteris Link, Fil. Sp. Hort. Reg. Bot. Berol. Cult. 147. 1841.

Rhipidopteris Schott ex Fée, Mém. Fam. Foug. 2: 14. 1845, nom. illeg.

Similar to subsect. *Squamipedia*, but the sterile blade pinnately or flabellately divided, rarely undivided but flabellate.

TYPE SPECIES: *Osmunda peltata* Swartz [≡*Elaphoglossum peltatum* (Swartz) Urban].

OTHER SPECIES EXAMINED:

Elaphoglossum columbianum (Maxon) Mickel, *E. moorei* (E. Britt.) Christ, *E. peruvianum* (Gómez) Mickel, and *E. tripartitum* (Hook. & Grev.) Mickel.

This group is usually treated as a distinct genus (Gómez, 1975; Morton, 1955), but can be distinguished from species of subsect. *Squamipedia* only by the frond dissection.

25878 **Elaphoglossum subsect. Ovata Christ, Monogr. Elaph. 23. 1899.**

Similar to subsect. *Squamipedia*, but the scales of the blade, stipe, and rhizome deeply lacerate-pectinate; phyllopodia distinct; spores with broad folds or ridges but lacking spicules (*Fig. 8*).

TYPE AND SOLE SPECIES: *Acrostichum ovatum* Hook. & Grev. [≡*Elaphoglossum ovatum* (Hook. & Grev.) Moore]. - 22928

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[3] Although we are basing sect. *Decorata* and subsects. *Squamipedia* and *Muscosa* on Christ's divisions of the same names, some botanists would argue that the cited divisions must have been described in Latin to be valid. Since Christ's descriptions were in German, we here supply Latin descriptions to avoid any confusion.

In frond form and slender rhizome this looks strikingly like *E. squamipes*, but the deeply lacerated scales are quite distinct.

25879 **Elaphoglossum subsect. Feeana Christ, Monogr. Elaph. 22. 1899.**

Fronds linear-lanceolate or oblanceolate, thin, with crenulate margin; phyllopodia short but distinct; spores with crests and sparse to abundant spicules.

TYPE SPECIES: *Acrostichum feei* Bory [≡*Elaphoglossum feei* (Bory) Moore].
L 25884

OTHER SPECIES EXAMINED:

Elaphoglossum procurrens (Mett.) Moore and *E. wrightii* (Mett.) Moore.

These species are close to subsect. *Squamipedia* in the very slender, long-creeping rhizome and entire scales, but the thin blade with crenulate margin and spores with narrow ridges or crests distinguish them as a separate group.

25880 **Elaphoglossum sect. Decorata Mickel & Atehortúa, sect. nov.**[3]

Rhizomatis erecti crassi paleae lineares; phyllopodia brevia; stipitis paleae magnae patulae; laminae magnae ellipticae praeter costam marginesque paleis imbricatis aureis vestitas glaberrimae; nervi conspicui hinc inde anastomosantes; hydathodi nulli; sporae breviter cristatae.

TYPE AND SOLE SPECIES: *Acrostichum decoratum* Kunze [≡*Elaphoglossum decoratum* (Kunze) Moore].
L 2245

This species is remarkably distinct and without close relatives.

25881 **Elaphoglossum sect. Lepidoglossa Christ, Monogr. Elaph. 21. 1899.**

25882 Sect. *Gymnoglossa* Christ, Monogr. Elaph. 22. 1899. 9320 LECTOTYPE (chosen here): *Osmunda bifurcata* Jacq. [≡*Elaphoglossum bifurcatum* (Jacq.) Mickel]. Christ did not designate a type for sect. *Gymnoglossa*, but he did choose *E. furcatum* (syn. *E. bifurcatum*) as type of his subsect. *Dimorpha*, which is the first named and most typical subsection of sect. *Gymnoglossa*.

Rhizome short- to moderately creeping or ascending; rhizome scales mostly dark, lustrous, entire to toothed; phyllopodia indistinct to distinct; blade often densely scaly over both surfaces, rarely glabrous, scales often lanceolate and toothed, ciliolate or rarely entire, or round-peltate, or modified to stellate hairs; veins evident to obscure, free; hydathodes lacking; spores with low ridges, rarely crested, usually also with small verrucae between the ridges.

✓LECTOTYPE SPECIES: *Acrostichum paleaceum* Hook. & Grev. [≡*Elaphoglossum* paleaceum (Hook. & Grev.) Sledge] (syn. *Acrostichum squamosum* Swartz ≡*Elaphoglossum squamosum* J. Smith, *nom. superfl.*). Christ cited *E. squamosum* as the type of his division *Auricoma*, the first and most typical division of his subsect. *Polylepidea*, which in turn was the first and most typical subsect. of sect. *Lepidoglossa*. 7198

KEY TO THE SUBSECTIONS OF SECTION LEPIDOGLOSSA

1. Blade densely scaly; scales lanceolate, toothed, not stellate or reduced to resinous dots.
    2. Blade ovate-lanceolate, coriaceous, often obtuse at apex; blade scales erose; spores verruculate. subsect. *Muscosa*
    2. Blade linear-lanceolate or narrowly elliptic, acuminate at apex; blade scales lanceolate, ciliolate; spores with low, non-verruculate ridges. ....subsect. *Polylepidea*
1. Blade glabrous to scaly; blade scales often modified to stellate hairs and/or resinous dots.
    3. Stipe and adaxial blade scales round-peltate. ....subsect. *Microlepidea*
    3. Stipe and adaxial blade scales lanceolate or stellate or lacking.

4. Blade glabrous, elliptic with a caudate apex. ....subsect. *Petioloa*
4. Blade scaly to subglabrous, linear to lanceolate, acuminate to obtuse at apex.
   5. Rhizome short-creeping; blade acute to acuminate, rarely crenulate to pinnately divided. subsect. *Pilosa*
   5. Rhizome long, ascending; blade obtuse. ....subsect. *Huacsaro*

25883 Elaphoglossum subsect. Polylepidea Christ, Monogr. Elaph. 21. 1899.

Rhizome short-creeping to ascending; rhizome scales dark, ciliolate; blade scales long-ciliolate; blade narrowly elliptic, densely scaly; spores with low ridges, usually with small verrucae between the ridges (*Fig. 9*).

LECTOTYPE SPECIES (chosen here): *Acrostichum paleaceum* Hook. & Grev. [≡*Elaphoglossum paleaceum* (Hook. & Grev.) Sledge]. – 7198

SELECTED SPECIES EXAMINED:

Elaphoglossum acuminans C. Chr. ex Urban, *E. auricomum* (Kunze) Moore, *E. casanense* Rosenst., *E. deckenii* (Kuhn) C. Chr., *E. dombeyanum* Moore & Houlst., *E. eatonianum* (E. Britt.) C. Chr., *E. eggersii* (Baker) Christ, *E. fuertesii* Brause, *E. hyalinum* Christ, *E. kuhnii* Hieron., *E. laminarioides* (Bory) Moore, *E. langsdorfii* (Hook. & Grev.) Moore, *E. meridense* (Klotzsch) Moore, *E. orbignyanum* (Fée) Moore, *E. plumosum* (Fée) Moore, *E. rubescens* (Kuhn) Christ, *E. rufescens* (Liebm.) Moore, *E. vestitum* (Schlecht. & Cham.) Schott ex J. Smith, and *E. wagneri* (Kunze) Moore.

This is one of the two largest, most complex, and unmanageable groups in the genus. The toothed or ciliolate scales on the blade and usually also on the rhizome are the principal distinguishing features.

25884 Elaphoglossum subsect. Microlepidea Christ, Monogr. Elaph. 22. 1899.

Rhizome scales linear-lanceolate, entire; blade scales stellate below, round and peltate above; spores with low, smooth ridges.

LECTOTYPE SPECIES (chosen here): *Acrostichum tectum* Humb. & Bonpl. ex Willd. [≡*Elaphoglossum tectum* (Humb. & Bonpl. ex Willd.) Moore]. Christ selected this species as type of his div. *Tecta*, which is the first-named and most typical of the divisions under subsect. *Microlepidea*. 7213

OTHER SPECIES EXAMINED: *Elaphoglossum furfuraceum* (Mett.) Christ.

This subsection is very close to subsect. *Pilosa*, but the round, peltate scales are not found in any other group.

25885 Elaphoglossum subsect. Pilosa Christ, Monogr. Elaph. 23. 1899.

Microstaphyla Presl, Epim. Bot. 160. 1851.
25886 *Elaphoglossum* subsect. *Dimorpha* Christ, Monogr. Elaph. 22. 1899.

Rhizome short-creeping; rhizome scales usually dark, entire to pinnately divided; blade scales resembling stellate hairs or lanceolate-toothed; blade often with resinous dots; spores with low ridges or narrow crests.

LECTOTYPE SPECIES (chosen here): *Acrostichum pilosum* Humb. & Bonpl. ex Willd. [≡*Elaphoglossum pilosum* (Humb. & Bonpl. ex Willd.) Moore]. –7201 *Elaphoglossum pilosum* is the type species of Christ's div. *Grata*, which was the first and most typical division of subsect. *Pilosa*.

SELECTED SPECIES EXAMINED:

Elaphoglossum bifurcatum (Jacq.) Mickel, *E. dimorphum* (Hook. & Grev.) Moore, *E. gratum* (Fée) Moore, *E. lagesianum* Rosent., *E. lepidotum* J. Smith, *E. mathewsii* (Fée) Moore, *E. nervosum* (Bory) Christ, *E. petiolatum* (Swartz) Urban, *E. rosenstockii* Christ, *E. salicifolium* (Willd. ex Kaulf.) Alston, and *E. viscosum* (Swartz) J. Smith.

The degree of scaliness and variation from scales to resinous dots within one species is not well understood. This subsection is very closely allied to subsects. *Huacsaro* and *Microlepidea*, and the demarcation between them is not clear.

Elaphoglossum dimorphum displays an intermediate frond morphology between simple fronds, such as those of *E. nervosum*, and the pinnately dissected fronds of *E. bifurcatum*. All three species occur on St. Helena, and Mickel (1980a) has shown that they differ essentially only in dissection. Whether these are in fact three distinct species or all forms of one species is still a question.

25891 **Elaphoglossum subsect. Petiolosa Christ, Monogr. Elaph. 23. 1899.**

Rhizome short-creeping; rhizome scales dark, linear, bristle-like; blade elliptic with caudate tip; fertile blade folded; blade scales lanceolate or lacking, occasionally with resinous dots; spores with low ridges. — 11606

✓TYPE SPECIES: *Acrostichum petiolosum* Desv. [≡*Elaphoglossum petiolosum* (Desv.) Moore].

OTHER SPECIES EXAMINED: *Elaphoglossum trianae* Christ.

The relationships of this subsection are not clear. The resinous dots are reminiscent of those of subsects. *Pilosa* and *Huacsaro*, the bristle-like rhizome scales are similar to those of some members of subsect. *Hybrida*, and the conduplicate fertile blades are similar to those found in some members of subsect. *Setosa*. The blade shape and spore details are unique.

25892 **Elaphoglossum subsect. Huacsaro Mickel & Atehortúa, subsect. nov.**

Rhizomata adscendentia longa; rhizomatis paleae fuscae integrae; lamina elliptica, apice obtusa; laminae saepe resinoso-punctatae; paleae lanceolatae denticulatae vel pilis stellatis conspersae; sporae dense spiculatae late cristatae.

✓TYPE SPECIES: *Acrostichum huacsaro* Ruiz [≡*Elaphoglossum huacsaro* (Ruiz) Christ]. 7185

SELECTED SPECIES EXAMINED:

Elaphoglossum alfredii Rosenst., *E. calaguala* (Klotzsch) Moore, *E. ciliatum* (Presl) Moore, *E. dendricola* (Baker) Christ, *E. tenax* Rosenst., and *E. vulcanicum* Christ.

This group probably is closely related to subsect. *Pilosa*, as shown by the scales and resinous dots, but the long ascending rhizome, obtuse blade apex, and the highly spiculate spores are distinctive (*Fig. 10*).

25893 **Elaphoglossum subsect. Muscosa Mickel & Atehortúa, subsect. nov.**[3]

Rhizomata breviter repentia; phyllopodia nulla; stipites laminaeque dense paleaceae; stipitis paleae latae patulae; lamina anguste elliptica ad lanceolata vel ovato-lanceolata, coriacea, apice plerumque obtusa; paleae saepe cum sporangiis mixtae; sporae verrucosae ecristatae.

✓TYPE SPECIES: *Acrostichum muscosum* Swartz [≡*Elaphoglossum muscosum* (Swartz) Moore]. 7197

SELECTED SPECIES EXAMINED:

Elaphoglossum aschersonii Hieron., *E. bellermannianum* (Klotzsch) Moore, *E. blandum* Rosenst., *E. corderoanum* (Sod.) Christ, *E. decipiens* Hieron., *E. engelii* (Karst.) Christ, *E. lehmannianum* Christ, and *E. plicatum* (Cav.) C. Chr.

Although the scales of *E. engelii* approach those of the subsect. *Polylepidea*, the spores are unique in the genus in having verruculae covering the surface (*Fig. 11*).

25894 **Elaphoglossum sect. Polytrichia Christ, Monogr. Elaph. 22. 1899.**

Rhizome short-creeping to erect; rhizome scales linear to linear-lanceolate; phyllopodia inconspicuous or lacking; stipe and blade, especially blade midvein and margin, with subulate scales and also bearing minute glandular hairs; hydathodes lacking; spores with low ridges and often small verrucae between them.

LECTOTYPE SPECIES (chosen here): *Acrostichum crinitum* L. [≡*Elaphoglossum crinitum* (L.) Christ]. This was the type of Christ's first-named and most typical subsection, *Hymenodium*. – 2244

KEY TO THE SUBSECTIONS OF SECTION POLYTRICHIA

1. Blade broadly elliptic and fleshy; veins netted, obscure.......................... subsect. *Hymenodium*
1. Blade linear-elliptic, narrowly elliptic, or ovate-lanceolate, subcoriaceous or papyraceous; veins free, usually evident.
    2. Stipe short to long; blade scales dark brown to black, located mostly on the margin and midvein. subsect. *Hybrida*
    2. Stipe nearly lacking; blade scales orange, distributed subuniformly over the blade surfaces. subsect. *Apoda*

25895 **Elaphoglossum subsect. Hymenodium (Fée) Christ, Monogr. Elaph. 23. 1899.**

Hymenodium Fée, Mém. Fam. Foug. 2: 20. 1845.

Fronds large, fleshy, broadly elliptic; veins obscure, netted; spores with low ridges. – 7853

TYPE AND SOLE SPECIES: *Acrostichum crinitum* L. [≡*Elaphoglossum crinitum* (L.) Christ].

Although this is occasionally distinguished as a separate genus, it agrees very closely with subsect. *Hybrida*.

25896 **Elaphoglossum subsect. Hybrida Christ, Monogr. Elaph. 23. 1899.**

Rhizome short-creeping or ascending; stipe long; blade usually papyraceous; blade scales especially on the margin and midvein, black or dark brown; spores with low ridges (*Fig. 12*). – 1584

TYPE SPECIES: *Acrostichum hybridum* Bory [≡*Elaphoglossum hybridum* (Bory) Moore].

SELECTED SPECIES EXAMINED:

Elaphoglossum albomarginatum A. Reid Smith, *E. auripilum* Christ, *E. cordifolium* Rosenst., *E. denudatum* (Jenm.) Maxon ex Morton, *E. erinaceum* (Fée) Moore, *E. lindbergii* (Mett.) Rosenst., *E. melanopus* (Kunze) Moore, *E. prestonii* J. Smith, *E. scolopendrifolium* (Raddi) J. Smith, *E. spannagelii* Rosenst., and *E. tambillense* (Hook.) Moore.

This subsection is very complex, and the species limits are not well understood. The variation in rhizome scales is especially perplexing. Most species have linear, orange rhizome scales, and others have bristle-like, maroon scales, but the differences are not always clear-cut. At least two species have a glabrous or subglabrous blade.

This subsection is composed mostly of Christ's "divisio *Melanolepidea*" of ordo *Stenoneura*, since they lack hydathodes. Christ referred subsect. *Hybrida* to ordo *Condyloneura*, although *E. hybridum*, the type species, lacks hydathodes and belongs to div. *Melanolepidea*. All other species Christ included in subsect. *Hybrida* have hydathodes and make up our subsect. *Eximia*.

25897

Elaphoglossum subsect. Apoda Mickel & Atehortúa, subsect. nov.

Stipites fere nulli; laminae paleae aurantiacae subulatae, per laminae superficiem regulariter conspersae; sporae breviter cristatae. 2241

TYPE SPECIES: *Acrostichum apodum* Kaulf. [≡*Elaphoglossum apodum* (Kaulf.) Schott ex J. Smith].

OTHER SPECIES EXAMINED:

Elaphoglossum cubense (Mett. ex Kuhn) C. Chr. and *E. siliquoides* (Jenm.) C. Chr.

Members of this subsection closely resemble those of subsect. *Setosa* in their orange to brown subulate blade scales, but seem to belong to sect. *Polytrichia* on the basis of no hydathodes and spores with low ridges and perforated crests. They also differ from sect. *Setosa* in their very short stipes.

25899

Elaphoglossum sect. Setosa (Christ) Mickel & Atehortúa, stat. nov.[2]

25899 *Elaphoglossum* subsect. *Setosa* Christ, Monogr. Elaph. 23. 1899.

Rhizome short- to long-creeping or erect; rhizome scales linear; phyllopodia lacking; stipes with minute, erect, glandular hairs; plants mostly small; veins evident, spaced well apart, ending well short of the margin in distinct hydathodes; scales subulate, orange to brown; spores with many low crests and usually with a perforate surface, or not crested and the surface echinate-reticulate. 25581

TYPE SPECIES: *Acrostichum villosum* Swartz [≡*Elaphoglossum villosum* (Swartz) J. Smith].

KEY TO THE SUBSECTIONS OF SECTION SETOSA

1. Rhizome long-creeping; rhizome scales dark brown to black .... subsect. *Alpestria*
1. Rhizome ascending to erect; rhizome scales pale to dark brown.
   2. Blade margin usually crenulate. .... subsect. *Plumierana*
   2. Blade margin entire.
      3. Plants very small (2–15 cm tall); blade spatulate, rarely sublinear; hydathodes inconspicuous. subsect. *Pilosella*
      3. Plants small to medium-sized (5–40 cm tall); blade narrowly elliptic to linear-lanceolate; veins and hydathodes evident. .... subsect. *Setosa*

25899

Elaphoglossum subsect. Setosa Christ, Monogr. Elaph. 23. 1899.

Rhizome ascending to erect; blade narrowly elliptic to linear-lanceolate; veins and hydathodes evident; spores with low crests (*Fig. 13*) or spines (*Fig. 14*).

TYPE SPECIES: *Acrostichum villosum* Swartz [≡*Elaphoglossum villosum* (Swartz) J. Smith]. 25581

SELECTED SPECIES EXAMINED:

Elaphoglossum costaricense Christ, *E. lindenii* (Bory ex Fée) Moore, *E. moritzianum* (Klotzsch) Moore, *E. ocoense* C. Chr., *E. omphalodes* (Fée) Brade, *E. palorense* Rosenst., and *E. setosum* (Liebm.) Moore.

Some other species, such as *E. crinipes* C. Chr., *E. oblanceolatum C. Chr.*, *E. papillosum* (Baker) Christ, and *E. setigerum* (Sod.) Diels, are included here because they look like species of subsect. *Setosa* in their external morphological characters, but they differ significantly in spore architecture. Rather than having crests, their spores are densely covered with short spines whose bases branch to form a reticulum (*Fig. 14*). *Elaphoglossum fluminense* Brade may belong here also. It looks like a slender member of subsect. *Pilosella*, but has perforate spores with very low crests like those of most members of subsect. *Setosa*.

25900

Elaphoglossum subsect. Pilosella Christ, Monogr. Elaph. 23. 1899.

Rhizome erect; scales subulate; hydathodes inconspicuous; plants especially small (2–15 cm tall); spores non-perforate with the ridges low and broad, usually lacking spicules.

7200

TYPE SPECIES: *Acrostichum piloselloides* Presl [≡*Elaphoglossum piloselloides* (Presl) Moore].

OTHER SPECIES EXAMINED:

Elaphoglossum hayesii (Mett.) Maxon, *E. horridulum* J. Smith, *E. jamesonii* (Hook. & Grev.) Moore, *E. pusillum* (Mett.) C. Chr., and *E. spatulatum* (Bory) Moore.

Elaphoglossum horridulum and *E. jamesonii* look like they belong here, but are different in their spores having spicules. This subsection is close to subsect. *Setosa*, although its spores have ridges rather than crests and hardly any are perforate, while the hydathodes are less conspicuous than in subsect. *Setosa*.

25901

Elaphoglossum subsect. Alpestria Mickel & Atehortúa, subsect. nov.

Rhizomata longe repentia; rhizomatis paleae fuscae; phyllopodia inconspicua; nervi raro furcati; hydathodi conspicui; stipitis laminaeque paleae subulatae, raro lanceolatae; paleae inter sporangia nullae; sporae perforatae spiculatae breviter cristatae.

25904

TYPE SPECIES: *Acrostichum alpestre* Gardn. [≡*Elaphoglossum alpestre* (Gardn.) Moore].

OTHER SPECIES EXAMINED:

Elaphoglossum barbae Rosenst., *E. chiapense* A. Reid Smith, *E. hirtipes* (Fée) Brade, and *E. leptophlebium* (Baker) C. Chr.

This subsection is close to subsect. *Setosa* in the subulate scales and perforate spores, but differs in the rhizome scales and habit. *Elaphoglossum yatesii* (Sod.) Christ seems to fit here, except that its blade is densely clothed with lanceolate scales.

25902

Elaphoglossum subsect. Plumierana Mickel & Atehortúa, subsect. nov.

Rhizomata breviter repentia usque erecta; lamina margine crenulata; laminae paleae subulatae aurantiacae; sporae cristatae (*Fig. 15*).

TYPE SPECIES: *Elaphoglossum plumieri* Moore. — 17328

OTHER SPECIES EXAMINED:

Elaphoglossum buchii C. Chr., *E. lanceum* Mickel, and *E. smithii* (Baker) Christ.

In their thin, crenulate blades these species resemble somewhat the species of subsect. *Feeana*, but are distinct in rhizome habit, rhizome and blade scales, phyllopodia, and hydathodes. There is considerable spore variation within the few species of this group. *Elaphoglossum lanceum* has highly perforate, lace-like crests, whereas the other species have solid, slender, nonperforate crests.

25903

Elaphoglossum sect. Eximia Mickel & Atehortúa, sect. nov.[2]

Rhizomata breviter repentia vel adscendentia; phyllopodia nulla; stipitis paleae lanceolatae minimae vel saepe subulatae; nervi distantes, angulo 40–60° abeuntes; hydathodi conspicui; laminae paleae sparsae minimae, non subulatae; sporae reticulato-echinatae ecristatae.

TYPE SPECIES: *Acrostichum eximium* Mett. [≡*Elaphoglossum eximium* (Mett.) Christ].

7178

KEY TO THE SUBSECTIONS OF SECTION EXIMIA

1. Blade entire, linear to linear-elliptic; stipe scales subulate. ....subsect. *Eximia*
1. Blade pedately divided; stipe and rhizome scales small, lanceolate. ....subsect. *Cardenasiana*

25907 **Elaphoglossum subsect. Eximia Mickel & Atehortúa, subsect. nov.**

Lamina integra, linearis vel lineari-elliptica; stipitis paleae subulatae; laminae paleae sparsae minusculae.

7128

✓TYPE SPECIES: *Acrostichum eximium* Mett. [≡*Elaphoglossum eximium* (Mett.) Christ].

OTHER SPECIES EXAMINED:

Elaphoglossum aubertii (Desv.) Moore, *E. beaurepairii* (Fée) Brade, *E. brachyneuron* (Fée) J. Smith, *E. gracile* (Fée) Christ, *E. lineare* (Fée) Moore, and *E. stenopteris* (Klotzsch) Moore.

In the subulate scales, hydathodes, and reticulate-echinate spores (*Figs. 16* and *17*), this group is similar to some members of subsect. *Setosa* and to some extent to sect. *Undulata*.

25908 **Elaphoglossum subsect. Cardenasiana Mickel & Atehortúa, subsect. nov.**

A subsect. *Eximia* paleis stipitis rhizomatisque minoribus, rhizomate magis carnoso, laminaque pedatim divisa diversa.

9675

✓TYPE AND SOLE SPECIES: *Elaphoglossum cardenasii* Wagner.

This species is unique in the genus in its pedately divided fronds, but in other characters shows close relationship to subsect. *Eximia*.

25909 **Elaphoglossum sect. Undulata Christ, Monogr. Elaph. 24. 1899.**

Rhizome short-creeping to erect; phyllopodia lacking; blade ovate-lanceolate; blade scales subulate to deltate-lanceolate, erose or toothed; hydathodes conspicuous; spores without ridges, openly reticulate-echinate, the spine bases diverging and forming a reticulum occasionally with irregular verrucae or perforated crests (*Fig. 18*).

TYPE SPECIES: *Acrostichum hirtum* Swartz [≡*Elaphoglossum hirtum* (Swartz) C. Chr.] (*syn. E. undulatum* (Willd.) Moore).

OTHER SPECIES EXAMINED:

Elaphoglossum bakeri (Sod.) Christ, *E. boryanum* (Fée) Moore, and *E. proliferans* Maxon & Morton ex Morton.

This subsection is closely related to subsect. *Setosa* and possibly to subsect. *Eximia*, with which it has subulate scales and echinate spores in common.

Elaphoglossum castaneum (Baker) Diels is similar to *E. hirtum* in size and shape and in spores with very small, crest-like projections perforate at the base (*Fig. 18*). This could represent a condition intermediate between sects. *Undulata* and *Setosa*, but the rhizome is longer-creeping, the rhizome scales are small, sclerotic, and resinous, and blade scales are lacking.

25910 **Elaphoglossum sect. Amygdalifolia (Christ) Mickel & Atehortúa, stat. nov.**

25911 *Elaphoglossum* subsect. *Amygdalifolia* Christ, Monogr. Elaph. 22. 1899.

Rhizome very long-creeping, slender; phyllopodia short; rhizome scales round to ovate, peltate; blades linear-lanceolate; veins evident; hydathodes conspicuous; blade subglabrous with minute stellate hairs; spores with narrow crests with minute spicules.

TYPE AND SOLE SPECIES: *Acrostichum amygdalifolium* Mett. [≡*Elaphoglossum amygdalifolium* (Mett.) Christ]. — 7349

This species is quite distinct and has no close relatives.

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REVIEW

"HOW TO KNOW THE FERNS AND FERN ALLIES," by John T. Mickel, 1979. Wm. C. Brown Company Publishers, Dubuque, Iowa. $7.95 hardcover, $5.95 wire coil bound.—In the standard format of the Pictured Key Nature Series, this book provides the information needed to identify North American ferns and fern allies. Introductory chapters on structure, life history, hybridization, cultivation, collection, and nomenclature provide a basic understanding of ferns and fern allies and the terminology needed to identify these plants successfully. This also makes the work useful as a textbook or handbook for amateur pteridologists.

The greatest part of the volume consists of bracketed keys which lead the user to the appropriate genus and species. Diagnostic characters for each species, provided in the annotated keys, are supplemented by a brief description, habitat preference, frequency of occurrence, and distribution map, as well as an illustration for nearly every species. Limited synonymy is also included. Hybrids and infraspecific taxa are mentioned with related species. Problems in taxonomy are explained so that the basis for confusion can be understood. The genera are listed alphabetically, enabling the experienced pteridologist to turn to the appropriate genus and begin keying at that point. The uninitiated can begin with the generic key that is found near the beginning of the book. Edgar Paulton's line drawings are quite good and in general capture the distinguishing characteristics of each species. The book concludes with a listing of state and regional identification manuals, a checklist of North American (United States and Canada) ferns and fern allies, and an index which includes a glossary.

The information contained in this volume is presented in a clear and concise manner using currently accepted taxonomy and nomenclature. Anyone who has an interest in North American ferns or fern allies should have a copy of this book. Dr. Mickel is to be congratulated for condensing and synthesizing a great amount of information into the kind of reasonably priced book amateur and professional pteridologists alike have long awaited.—*W. Carl Taylor, Department of Botany, Milwaukee Public Museum, Milwaukee, WI 53233.*

Notes on the Natural History of Stylites gemmifera

ERIC E. KARRFALT and DALE M. HUNTER*

Several unexpected observations were made recently while collecting plants of *Stylites* E. Amstutz for anatomical study. The plants were collected near the end of the growing season (18–19 April 1979) so as to obtain young plants which had just completed various numbers of growing seasons. In the type locality, *Stylites* is described as forming pure colonies which stand just above the water level in the lacustrine bog in which they are found (Rauh & Falk, 1959); but the plants we collected at 4100 m altitude (*Karrfalt & Hunter* 22, NY) near Lago Junín, 14 km north of Junín, Peru, were invariably growing in association with various flowering plants (*Figs. 1* and *2*) and were frequently submerged. The colonies at the Junín locality were generally in the form of radially symmetrical, dome-shaped hummocks (*Fig. 1*), but various other rounded shapes occurred as well. The hummocks ranged in diameter from 20 to about 200 cm. The larger hummocks generally were found to contain a larger proportion of other plants in addition to *Stylites* than did the smaller ones. The plants in the hummocks were extremely densely packed and usually stood above the water level, but some hummocks were partially or completely submerged. The submerged portions of these hummocks were populated nearly exclusively by *Stylites*, but the emergent portions included other plants as well (*Fig. 5*). These plants usually were rather small (with stems a few millimeters in length), but some were quite good-sized (stems 2–4 cm long) and bore about 40 leaves up to 7 cm long, as well as numerous gemmae. Their leaves did not have the typical flattened form with deflexed tips, but rather were subtriangular to terete in cross section and ascending. All intermediate forms between these atypical leaves and those described by Rauh and Falk (1959) were also seen; the variation in leaf morphology will be described in detail in a subsequent report. The plants with the atypical leaf form always were submerged and not densely crowded. On the other hand, plants bearing typical leaves occurred both above and below the water level in the bog, but these plants always were densely crowded. Leaf form correlates with population density rather than with emergence or submergence. The nature of this correlation is not certain, but experiments in progress suggest that it is largely or entirely environmental.

In contrast to its very limited geographical range, *Stylites* is extremely vigorous and abundant where appropriate conditions for its growth exist. The Junín locality is a bog which has been used as a pasture for many years. It is heavily grazed by sheep and llamas, as indicated by the cropped herbage (*Figs. 1* and *4*) and abundant llama dung. The *Stylites* plants, however, very rarely show any evidence of even accidental damage by the animals. The Junín locality occupies at least several acres; we were unable to determine its full extent due to our anoxemia and consequent lack of energy.

The leaves of *Stylites* are coated with considerable quantities of mucilage, as are the basal parts of the leaves of all *Isoëtes* species of which we have seen living

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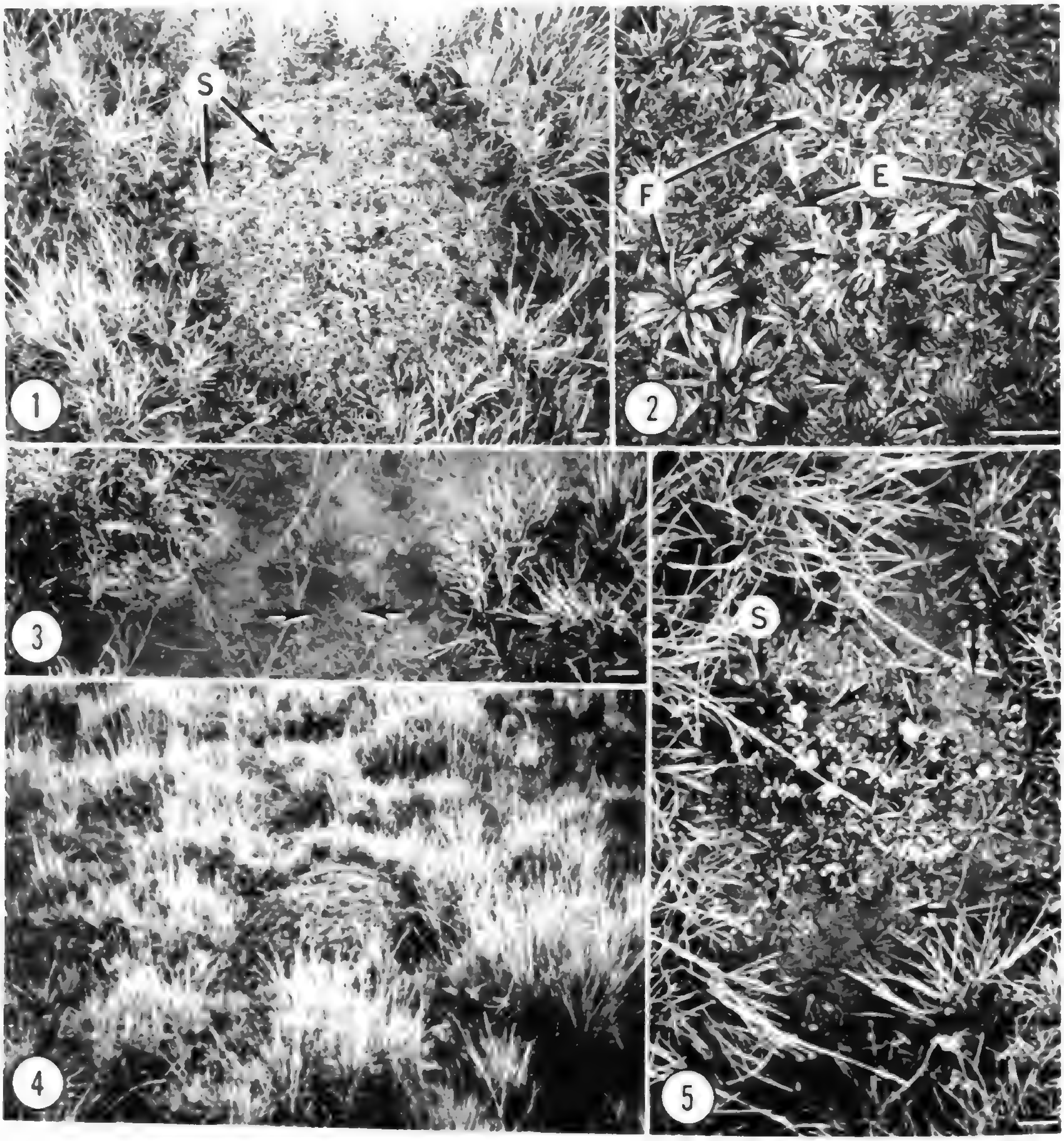
*Department of Biology, Brooklyn College, Brooklyn, NY 11210.

material. Also as in *Isoëtes*, the leaves are replaced annually (Rauh & Falk, 1959). As the new leaves grow and expand within the hummock, the dead, mucilage-coated leaves of the largest plants are extruded *en masse* onto the surface of the hummock (*Fig. 2*, E). Once out on the surface of the hummocks, the individual dead sporophylls become separated from one another (*Figs. 1, 5*, S). The extrusion of the old sporophylls would seem to be advantageous for spore dispersal. Indeed, an analogous process has been shown to be involved in spore dispersal in



FIGS. 1–5. *Stylites gemmifera*. FIG. 1. A typical hummock. FIG. 2. Close up of part of the hummock shown in FIG. 1. FIG. 3. Submerged plants with atypical leaves. FIG. 4. A hummock and surrounding vegetation. FIG. 5. A partially submerged hummock. Unlabelled arrows = *Stylites* plants; E = partially extruded masses of dead sporophylls; F = various flowering plants; S = separated extruded sporophylls; bar = 4 cm.

Isoëtes drummondii (Osborn, 1922). However, examination of large numbers of extruded sporophylls of *Stylites* never revealed any discernible evidence of the establishment of gametophytes by the spores carried with the extruded sporophylls. Field observations of gametophytes were necessarily limited to those which could be made with a hand lens; that is, only megaspores were examined and these only for the opening of the trilete scar. Any megagametophytes which were contained within unopened spore walls were not distinguished from ungerminated spores.

Rauh and Falk (1959) found very few megagametophytes and no microgametophytes of *Stylites*. In our material, gametophytes were likewise very infrequently encountered. Only megagametophytes were identified in the field and these were found only in association with adult sporophytes which showed some evidence of recent damage or injury, such as relatively few leaves or a reduced stem diameter near the apex. Six gametophytes were found, all of which bore sporophytes with one or two leaves and roots. The occurrence of the rare megametophytes only in association with the rare, injured sporophytes suggests that the absence of gametophytes from other locations is the result of unequal competition between the gametophytes and the much larger, densely crowded adult sporophytes and gemmae.

It was not possible to determine the specific source of the spores which gave rise to the gametophytes we collected. Our gametophytes were probably derived from the massive quantities of spores produced by the immediately adjacent sporophytes, but the possibility cannot be excluded that the successful spores may be have been transported with old sporophylls which had been extruded onto the surface of the same or some other hummock.

Many of the plants which we collected bore abundant gemmae and therefore must be assigned to *S. gemmifera* W. Rauh, inasmuch as *S. andicola* E. Amstutz has no vegetative reproduction. The other criteria by which Rauh and Falk (1959) distinguished the sporophytes of *S. andicola* from those of *S. gemmifera* are merely quantitative and are of questionable value. For example, the leaves of *S. andicola* are said to be 5–7 cm long, whereas those of *S. gemmifera* are said to be 3.5–5 cm long, but as noted above some gemma-bearing plants in our collection had leaves as long as 7 cm. Although these longest leaves did not have the morphology typical of *Stylites*, the leaves of plants collected from hummocks invariably had the typical form, and some of these were as long as 5.5 cm. According to Rauh and Falk, the stem of *S. andicola* is mostly unbranched and up to 20 cm long, whereas that of *S. gemmifera* is frequently branched and not more than 8 cm long; obviously these characters would be of no use in identifying an unbranched plant whose stem was not more than 8 cm long. Also, *S. andicola* is supposed to form hummocks in which all individuals are the same age, whereas colonies of *S. gemmifera* contain both old and young plants. Although they did not explicitly state their method, Rauh and Falk seem to have used size as an indicator of relative age. In any case, the hummocks which contain unbranched plants of a uniform large size and no gemmae (i.e., hummocks of "*S. andicola*") may simply be relatively old colonies in which the intense competition for space has been resolved in favor of the largest and most vigorous individuals which neither branch nor produce gemmae. The only qualitative distinction between the sporophytes of the two species of *Stylites* is the presence of gemmae in *S. gemmifera* and their absence in *S. andicola*. However, the number of gemmae on a plant is highly variable. In our material, from one to eight were seen, and many plants had no gemmae at all. According to the criteria given by Rauh and Falk, sporophytic specimens without gemmae and with stems shorter than 8 cm may be distinguished as to species only by the length of their leaves. Unfortunately, as noted above, we have gemma-bearing plants, obviously assignable to *S. gemmifera*, which have leaves longer than 5 cm. Thus it appears to us that the distinctness of the two species of *Stylites* is in sufficient doubt that a critical reexamination of these two taxa is in order. Moreover, inasmuch as the separation of *Stylites* from *Isoëtes* already has been questioned (Kubitzki & Borchert, 1964; Bierhorst, 1971), this reexamination also should review the generic assignment of these species.

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Reciprocal Allelopathy Between the Gametophytes of Osmunda cinnamomea and Dryopteris intermedia

RAYMOND L. PETERSEN* and DAVID E. FAIRBROTHERS**

Allelopathy is the chemical inhibition of growth and/or development of one organism by another. The literature on allelopathy is very extensive and has been summarized in several reviews (Muller, 1970; Pickett & Baskin, 1973; Rice, 1974). See also Swain (1977) for a synoptic review of secondary compounds as allelopathic agents.

In the life cycle of any species, one portion, designated by Petersen & Fairbrothers (1973) as the weakest link, is likely to be the most vulnerable to allelopathic interactions. As an evolutionary strategem, allelopathy would be developed most effectively against the weakest link in an organism's life cycle, such as germinating spores and developing prothalli of ferns or germinating seeds and seedlings of higher plants. Furthermore, it is at these critical points that one ought to be able to best detect allelopathy.

Intra- and interspecific allelopathic interactions occur in four ways: (1) sporophytes acting on sporophytes; (2) sporophytes acting on gametophytes; (3) gametophytes acting on sporophytes; and (4) gametophytes acting on gametophytes. Seed plants reduce gametophytic vulnerability structurally by enclosing the gametophyte and ovule and functionally by pollination and fertilization. Therefore, the weakest link in seed plants is shifted from their gametophytes to their germinating seeds and seedlings. In pteridophytes, presumably the gametophyte generation—spore, prothallus and gametes—is the most vulnerable portion of the fern life cycle with regard to interspecific interactions for habitat maintenance (allelopathy and competition), for a smaller amount of chemicals would be required to eliminate a gametophyte from effective competition than a sporophyte.

Of the four interactions, gametophytes acting on gametophytes of different species permits study of the weakest link hypothesis in an experimental design where interspecific competition is minimal. Fern gametophytes were selected as experimental organisms because they are easily cultured and amenable to the experiments' requirements of control, replication, manipulation, and minimization of competition. Six fern species usually found growing in similar natural habitats were selected for the initial survey experiment which was conducted to determine if allelopathic effects were detectable between any of the species. By similar natural habitats we mean that, among the species selected, there is some overlap between their respective ecological amplitudes so that it is possible that they would be in competition for the same space.

The literature on fern allelopathy is limited but increasing. Froeschel (1953) reported that water extracts of *Polypodium aureum* and *Lycopodium clavatum*

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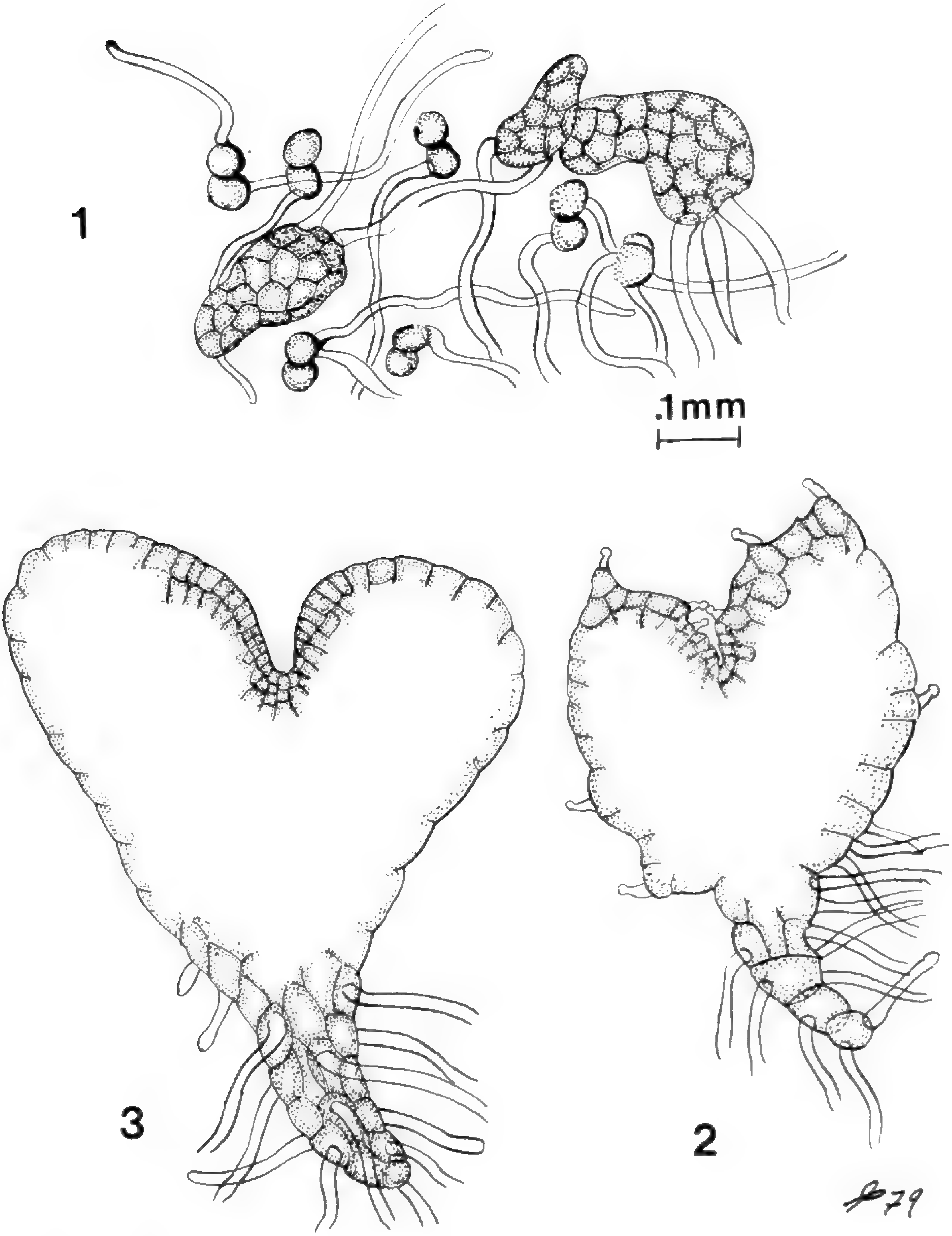
*Department of Botany, Howard University, Washington, D.C. 20059.

**Department of Botany, Rutgers University, New Brunswick, NJ 08903.



FIGS. 1–3. Gametophytes of *Dryopteris intermedia* and *Osmunda cinnamomea* after 30 days of growth. FIG. 1. Gametophytes of *D. intermedia* (2 prothallial cell stage) and *O. cinnamomea* (multicellular prothalli). FIG. 2. Typical *D. intermedia* gametophyte from a control monoculture. FIG. 3. Typical *O. cinnamomea* gametophyte from a control monoculture.

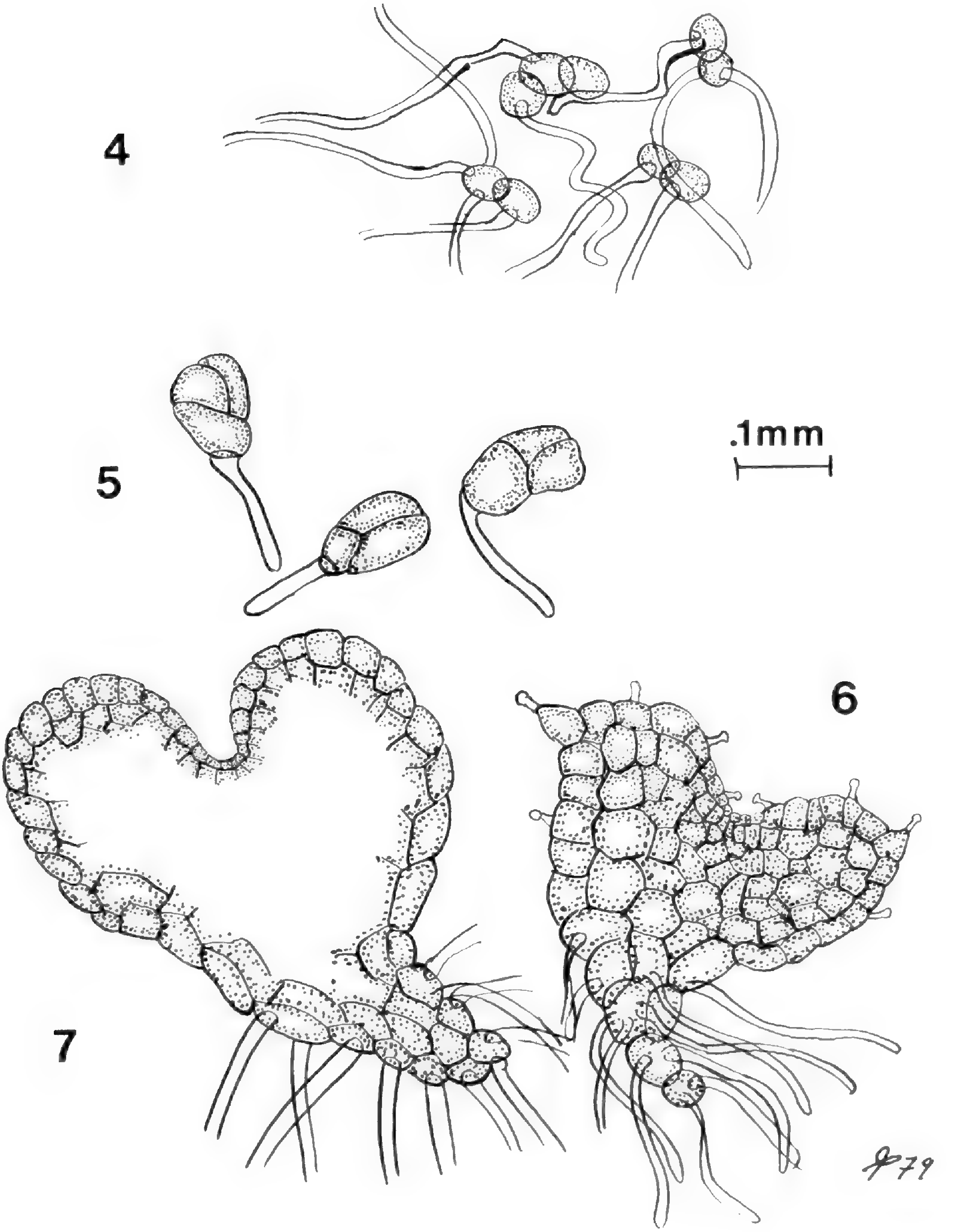
decreased the growth rates of gametophytes of four fern species. Bell (1958) found that an aqueous extract of *Dryopteris filix-mas* gametophytes stimulated spore germination and prothallium growth in *D. borreri*, but that the gametophytic debris of *D. filix-mas*, when incorporated into agar medium, prevented *D. borreri* spore germination, an example of gametophyte–gametophyte allelopathy. Fukuzumi (1971) reported allelopathic effects from *Pteris japonica* frond extracts on *Impatiens balsamina* root growth. Gliessman and Muller (1972) investigated the phytotoxic effects of compounds from *Pteridium aquilinum* on the surrounding vegetation. (See Miller, 1968 for an excellent, though now dated, comprehensive review of fern gametophyte literature.)

Davidonis and Ruddat (1973, 1974) reported sporophyte–gametophyte allelopathy in ferns. The roots and fronds of *Thelypteris normalis* produce two allelopathic chemicals, thelypterin A and B, which inhibit cell division in the gametophytes of *T. normalis*, *Pteris longifolia*, and *Phlebodium aureum*. Thelypterin A has been tentatively identified as an indole derivative. Davidonis (1976) found that *T. normalis* gametophytes produce thelypterin A; the sporophytes of other ferns also contain these compounds: thelypterin A and B in *T. dentata* roots, thelypterin A in *T. noveboracensis* leaves, and thelypterin B in the roots of two *Pteris* species. Davidonis (1976) also reported the presence of an unidentified growth inhibitor in the leaves of *Osmunda cinnamomea*. Star and Weber (1978) reported that sporophyte exudates from *Pityrogramma* species inhibit spore germination and gametophyte development in *P. calomelanos*. Inhibitors were identified as a dihydrochalcone and a flavonol. Munther and Fairbrothers (1980), testing leaf leachates and extracts of *Dennstaedtia punctilobula*, *Osmunda cinnamomea*, and *Osmunda claytoniana* obtained from New Jersey and Vermont populations, demonstrated geographic differences in allelopathic and autotoxic responses among these species based on the amount of spore germination.

MATERIALS AND METHODS

Mature spores were collected from the following species: *Osmunda cinnamomea*, *O. claytoniana*, *O. regalis*, *Matteuccia struthiopteris*, *Onoclea sensibilis*, and *Dryopteris intermedia*. White's minimal nutrient medium at one-half strength at pH 5.5 was used to culture the gametophytes. Both liquid and 1% agar cultures were used. Spore density was approximately 1,000 spores per 90 mm diam. plate. All cultures were grown under axenic conditions (Steeves, 1955), in a growth chamber with fluorescent light (300 ft-c) at 20° C under a diurnal cycle of 12/12 hr.

In the initial survey experiment, spores of the six species were sown on agar plates in paired strips adjacent to one another in all possible combinations. Control plates containing spores from one species also were sown. Plates were examined daily at the interfaces of adjacent species for symptoms of allelopathy or competition such as decreases from the control plates in percent germination or growth.



FIGS. 4–7. Gametophytes of *Dryopteris intermedia* and *Osmunda cinnamomea* after 20 days of growth. FIG. 4. *D. intermedia* gametophytes from a plate sprayed with *O. cinnamomea* supernatant. FIG. 5. *O. cinnamomea* gametophytes from a plate sprayed with *D. intermedia* supernatant. FIG. 6. Typical *D. intermedia* gametophyte from a plate sprayed with *D. intermedia* supernatant. FIG. 7. Typical *O. cinnamomea* gametophyte from a plate sprayed with *O. cinnamomea* supernatant.

On the basis of this experiment, *D. intermedia* and *O. cinnamomea* were selected as the most promising taxa for further experimentation because the gametophytes of these species appeared to inhibit each other's growth. A minimum of 10 replicates was run for each experiment. Initially, control plates and experimental plates containing a mixture of *Dryopteris* and *Osmunda* spores were prepared. The next phase was designed to eliminate the possibility of competition. Separate liquid cultures of *D. intermedia* and *O. cinnamomea* gametophytes (0.5g spores/liter of half-strength White's Medium at pH 5.5) were initiated and grown for two weeks. The gametophytes were then filtered off and the supernatants were conserved. Agar plates were prepared as above. Control plates consisted of spores of one species sprayed with one ml of the supernatant of the same species; experimental plates contained spores of one species sprayed with one ml of the supernatant of the other. This experimental design eliminates the possibility of interspecific competition (e.g., differential nutrient assimilation by one species over the other).

RESULTS AND DISCUSSION

In the survey of six species for allelopathic symptoms, a clear area was detected on the plates at the interface between *O. cinnamomea* and *D. intermedia* gametophytes. This was the result of progressive inhibition of *D. intermedia* gametophyte growth, which was proportional to the proximity of *Osmunda* gametophytes.

In the first phase of the *Dryopteris–Osmunda* growth rate analyses, *Dryopteris* spore germination was initially lower on the experimental plates (60% germination after 7 days) compared to the control plates (90% germination after 7 days). But after 10 days, 90% germination was reached on the experimental plates. Post-germination rate data was discontinued because it soon became apparent that the gametophytes of both species on the experimental plates were growing very slowly (*Fig. 1*) and no longer had significantly different growth rates. In contrast, the control plate gametophytes developed normally (*Figs. 2* and *3*).

The gametophytes of *D. intermedia* and *O. cinnamomea* inhibit the growth and development of one another, but one cannot distinguish from these results whether the inhibition is the result of allelopathy or competition, and so a set of supernatant experiments was designed to do so. These experiments essentially reproduced the results of the preceeding set of experiments. Control plates sprayed with supernatant from the same species produced normally developed gametophytes (*Figs. 4* and *5*). But experimental plates sprayed with supernatant from the other species yielded gametophytes having a severely retarded growth rate; after germination and a few cell divisions, development essentially ceased (*Figs. 6* and *7*).

This reciprocal supernatant experiment proves that the gametophytes of each species were suppressing cell division of the gametophytes of the other species and that this was done through the release of inhibitory compounds, rather than by competition.

This is the first recorded example in ferns of reciprocal allelopathy, in which two antagonistic species act on one another, that has been demonstrated *in vitro* between gametophytes.

Previous investigators working with ferns have demonstrated unidirectional allelopathy in the following systems: sporophyte acting on gametophyte (Froeschel, 1953; Davidonis & Ruddat, 1973, 1974; Star & Weber, 1978; Munther & Fairbrothers, 1980) and gametophyte acting on gametophyte (Bell, 1958).

We wish to acknowledge financial aid from NSF Grant GB-13202 and a Rutgers Research Council Grant awarded to D. E. Fairbrothers.

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REVIEW

"FLORA DEL AVILA" by Julian A. Steyermark and Otto Huber. Publication Especial de la Sociedad Venezolana de Ciencias Naturales, Caracas. 1978. 971 pp. + 308 plates. Bs. 150 (ca. $35.00).—This is a flora of the Parque Nacional 'El Avila,' part of a small mountain range lying between the city of Caracas and the Caribbean Sea. The area is about 130 square kilometers and the major peaks reach an altitude of 2000 to 2700 meters.

Introductory chapters describe the history of botanical exploration of the region, the soils, geology, climate, principal vegetation types, and the geographic relations of the flora. There is also a series of color photographs of flowers, the vegetation, and three pteridophytes.

The flora consists of 127 families of flowering plants, 809 genera, and 1741 species. Each family treatment has an illustrated key to the species and a list of them with ecological notes. There are also line drawings of a selection of species. The "Flora of Avila" is a major addition to neotropical floras, and its utility extends well beyond the region covered.

The ferns and fern-allies are all treated under the Pteridophyta, rather than by families, with 52 genera and 151 species included. The key to these is rather long, but it is well organized and accurate. Marginal illustrations of characters aid in the use of the headings. Following the list of species, there are excellent drawings of 99 species. The largest genus is *Polypodium (sens. lat.)* with 19 species, followed by *Elaphoglossum* with 15 and Asplenium with 13. About a third of the genera are represented by a single species.

The fern flora consists mostly of rather common and widely distributed species of the montane forest and cloud forest of northern South America. There are no ednemics, but about 25 species are of restricted distribution or are otherwise of geographic interest. For example, the rare *Lycopodium caracasicum,* restricted to the coastal Cordillera, reaches its easternmost station here, and both *Phanerophlebia juglandifolia* and *Pellaea ovata* are represented by disjunct stations at the eastern limit of their range. About two-thirds of the species grow in the cloud forest zone and some are restricted to it, for example the five species of Cyatheaceae and several species of *Elaphoglossum* and *Polypodium.* There is a subparamo zone on the highest parts of the mountains, and it is here that the strongest relations with the flora of the high Andes are found. *Asplenium monanthes* and *Lycopodium vestitum* are examples among the pteriodphytes.

The "Flora de Avila" may be obtained from: Sociedad Venezolana de Ciencias Naturales, Calle Arichuna, Apartado de Correos 76771, Urb. El Marques, Caracas 107, Venezuela. The price if 150 bolivares (ca. $35.00).—*Rolla Tryon, Gray Herbarium, Harvard University, Cambridge, MA 02138.*

SHORTER NOTE

THELYPTERIS TORRESIANA IN VENEZULEA. — For several years, the senior author has been intrigued by the sudden appearance and persistence in his Caracas garden of a terrestrial, acaulescent fern, most attractive with its pale green, large, gracefully thrice-cut fronds. Specimens sent to Dr. John Mickel were identified as *Thelypteris torresiana* (Gaud.) Alston, a species originally described from Guam and found native elsewhere in the Asian tropics. In the New World, this species has become introduced and naturalized in the southeastern United States, Cuba, Jamaica, the Lesser Antilles, Trinidad, Tobago, Honduras, Venezuela, Brazil, and Argentina.

Vareschi in Lasser (Fl. Venez. 1:439. 1969) treats this species under the invalidly published name "Lastrea setigera." Morton (Amer. Fern J. 52:27–29. 1962) gives a correct synonymy and has shown that the species should not be confused with the rare Old World *T. setigera* (Blume) Ching.

Leonard (Amer. Fern J. 62:97–99. 1972) observed the preference of *T. torresiana* for moist ravines and stream banks in the southeastern United States. It occurs in similar habitats in Venezuela, in such places as moist forests along roads and trails at 400–1400 m altitude. It is common in cool cloud forests, but also grows in warmer zones, both in deciduous and evergreen tropical forests. In the senior author's garden in Caracas, it is aggressive, weedy, and often invasive, characteristics which have facilitated its spread in natural habitats. In the localities where it has become naturalized, it appears to be part of the native vegetation.

According to specimens in the Herbario Nacional de Venezuela (VEN), *T. torresiana* was first found in Venezuela in 1943 in the Parque Nacional Pittier, Estado Aragua *(Killip & Lasser 37797,* US, VEN). Since then it has spread in the Coastal Cordillera throughout northeastern Venezuela to the states of Portuguesa, Yaracuy, Carabobo, Guarico, Miranda, Sucre, and Monagas, and to the Distrito Federal.—*Julian A. Steyermark, Instituto Botánico, Apartado 2156, Caracas, Venezuela* and *Francisco Ortega, Estación Biológica "Pozo Blanco," Apartado 116, Acarigua, Edo. Portuguesa, Venezuela.*

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The Distribution and Ecology of Phyllitis scolopendrium in Michigan

RICHARD P. FUTYMA*

The Hart's-tongue, *Phyllitis scolopendrium*, has been noted for its circumboreal and North American disjunct distributions (Fernald, 1935; Wagner, 1972). On this continent *P. scolopendrium* var. *americana* Fern. is known to occur in Ontario (Soper, 1954), Michigan (Hagenah, 1954, 1956), New York, Tennessee, and Alabama (Short, 1979). By far the majority of the Hart's-tongue sites are associated with the limestones and dolomites of the Niagara escarpment. This geological formation can be traced from central New York westward into Ontario, where it turns northwestward near the head of Lake Ontario, and through the Bruce Peninsula and Manitoulin Island in Lake Huron, into the upper peninsula of Michigan. From there it arcs southwestward through Wisconsin's Door Peninsula to the east of Green Bay and disappears to the south.

This paper will deal principally with the northernmost American Hart's-tongue colonies, those in upper Michigan, and with some ideas concerning the factors determining its distribution in that region.

A NEW LOCALITY IN MICHIGAN

On 3 August 1978, I discovered a previously unreported locality for *P. scolopendrium* in Mackinac County, Michigan, while I was botanizing along the slopes of a bedrock knob on the Niagara escarpment. The site is strewn with low, moss-covered dolomite boulders under a tree canopy almost completely dominated by *Acer saccharum*, with only minor numbers of other hardwood species (*Fig. 1*).

At the time of the discovery of the site, two fronds of *P. scolopendrium* were collected as a voucher specimen and deposited in the herbarium of the University of Michigan Biological Station (UMBS). Also found were *Polystichum lonchitis* and *Geranium robertianum* (*Fig. 2*), two plants frequently associated with *Phyllitis scolopendrium* (Hagenah, 1956). Walking Fern, *Camptosorus rhizophyllus*, occurs locally at the site, densely covering large boulders at least 1.5 m above the ground surface. Dr. W. H. Wagner, Jr. was among those visiting the site shortly after its discovery. He compiled the following list of pteridophytes on 29 August 1978: *Asplenium trichomanes, Botrychium virginianum, Camptosorus rhizophyllus, Cystopteris bulbifera, C. fragilis, Dryopteris filix-mas, D. intermedia, D. spinulosa, Equisetum arvense, E. scirpoides, E. sylvaticum, Matteuccia struthiopteris, Onoclea sensibilis, Polypodium virginianum, Polystichum braunii,* and *P. lonchitis*. All were found within 50 m of the *Phyllitis* colony. *Asplenium viride* also has been reported at the site (D. Henson, pers. comm.)

This new Hart's-tongue site is situated within the Hiawatha National Forest, and will be referred to here as the "East Lake station." In the Fall of 1978, the U.S. Forest Service decided to survey and map the extent of the *Phyllitis* colony.

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*Department of Botany, University of Michigan, Ann Arbor, MI 48109.

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FIG. 1. General view of part of the East Lake station of *Phyllitis scolopendrium*, Mackinac Co., Michigan. A group of the ferns is growing on the side of the boulder in the central foreground. The map tube (horizontal) in the right foreground is 65 cm long. FIG. 2. *Phyllitis scolopendrium* growing on a low boulder, along with *Polystichum lonchitis* and *Geranium robertianum* on top of boulder.

In all, 64 individuals were counted, their locations mapped, and the tree nearest to each group of individuals was marked. In combination with long-term observation, this information has potential for use in studying the population ecology of this rare fern.

During the summer of 1979, the U.S. Forest Service undertook an inventory of all prospective localities within the borders of the Hiawatha National Forest in hopes of uncovering other unreported Hart's-tongue sites. Unfortunately, no success was reported.

DISTRIBUTION IN UPPER MICHIGAN

Hagenah (1954, 1956) reported on the first two upper Michigan sites for *P. scolopendrium*. The East Lake station is situated between these two, which are 30 km. apart (*Fig. 3*). The population at the Trout Lake station in Chippewa County apparently is extinct. The easternmost station, known as the Hagenah site, has recently been acquired by the Michigan Nature Association as a plant preserve. The location of these sites and the major North American concentration of *P. scolopendrium* in Ontario, south of Lake Huron, are shown in *Figure 3*.

All three Michigan localities are similarly located on prominent hills that are part of the Niagara escarpment. Along much of its length in Mackinac and Chippewa counties, the escarpment is obscured by thick deposits of glacial drift. The position of the escarpment is manifested mainly by a series of bedrock knobs scattered from east to west across the region. These hills rise 30–100 m above the surrounding plain and range in area from 150 to over 3000 hectares. It is highly unlikely that they were ice-free nunataks during the Wisconsinan glaciation, as suggested by Fernald (1935) in explaining the occurrence of Hart's-tongue on the highest outcrops of the same escarpment in Ontario.

Another similarity shared by the three localities is that the Hart's-tongue colonies are situated at elevations near or above that of the ancient shoreline of Lake Algonquin. In fact, the East Lake station was discovered in the course of floristic reconnaissance along one such shoreline. The plants are growing on boulders uncovered by wave action. Lake Algonquin, a precursor of lakes Huron and Michigan, covered much of upper Michigan immediately upon retreat of the continental ice sheet about 11,000 years ago. At that time the bedrock hills that define the Niagara escarpment formed an archipelago in the lake. By about 10,400 years ago Lake Algonquin ended when the waters fell to lower levels and more of the present land area was uncovered.

The fact that *P. scolopendrium* has been found in upper Michigan only in places that were islands in Lake Algonquin may have some special significance. Throughout Mackinac and parts of Chippewa counties, there is a large area which was inundated by Lake Algonquin but now is covered by deciduous forests of the sort preferred by the fern, in which there are limestone and dolomite outcrops (e.g., Drummond Island) or concentrations of glacially-transported boulders. Although actively sought, Hart's-tongue has not been seen in those places. This distribution pattern may be explained in several ways; here we will consider three hypotheses.

Hypothesis 1.—*Phyllitis scolopendrium* was dispersed to upper Michigan, presumably from the south, at the time of the existence of Lake Algonquin, ca. 10,500 years ago. These rocky islands with their depauperate flora may have offered suitable substrates and conditions of low competition favorable to the establishment of this fern. When more land area was uncovered by the recession of lake levels and closed forests covered the region, *P. scolopendrium* may not have been a sufficiently aggressive colonizer to spread from its territory acquired earlier.

FIG. 3. Distribution of *Phyllitis scolopendrium* in the upper Great Lakes region. The three stations of the fern in upper Michigan are indicated by dots. The general area where the fern occurs in Ontario is shown by stippling. (modified from Soper, 1954).

Hypothesis 2.—Confinement of *P. scolopendrium* to the former islands may be a result of environmental differences between hilltop rock outcrops and those at lower elevations. The hills along the escarpment have thin soils with more outcrops, and the fact that they were high enough to escape submergence under Lake Algonquin may be only a coincidence. Fewer favorable sites for the fern exist at lower elevations because thicker deposits of glacial till and lake sediments cover the bedrock. At those lowland sites where rock surfaces are available, other environmental factors may be unfavorable.

Hypothesis 3.—*P. scolopendrium* had (or has) a wider distribution in upper Michigan than is known at present. Logging of forests may have opened the vegetation at many former localities of the fern, making the sites unsuitable and leading to its extinction. Therefore, the original distribution of the Hart's-tongue in upper Michigan prior to European settlement had little to do with the geography of Lake Algonquin.

DISCUSSION

The suggestion that *P. scolopendrium* first reached upper Michigan during the existence of Lake Algonquin has some appeal. Such an hypothesis could explain why extensive areas of limestone outcrops which are situated between the Michigan stations and the main North American concentration of Hart's-tongue in Ontario, and which were inundated by Lake Algonquin, such as Manitoulin Island and Drummond Island, are devoid of the fern. The Bruce Peninsula, where many of the Ontario stations are located, also was completely submerged at that time, but one may propose that its connection to the mainland at a point where many non-submerged Hart's-tongue localities exist facilitated its colonization at a later date.

However, fossil pollen studies by the present author and others (Brubaker, 1975; Saarnisto, 1974) indicate that the late-glacial forests of the region, during and after the existence of Lake Algonquin, comprised mainly spruce (*Picea* spp.) and jack pine (*Pinus banksiana*). A salient feature of the ecology of *Phyllitis scolopendrium* var. *americana* is that it is never found in coniferous forests, even when adjacent tracts of deciduous forests contain the fern. In Ontario it is seen under deciduous canopies ranging from successional poplar stands to climax maple-beech forest, but never under conifers (A. Reznicek, pers. comm.). If the Hart's-tongue is a strict associate of the northern hardwoods forest, then it might have reached northern Michigan only within the past 5000 years, which is when this vegetation type became most widespread in the region. Thus, unless the ecology of this species was different 10,500 years ago from what it is today, we should be safe in rejecting the first hypothesis.

The effect of forest clearance on populations of *P. sclopendrium* is poorly known. Most of the localities in Ontario and Michigan have been logged at one time or another. In the case of the East Lake station, logging did take place, but perhaps not to the extent of clearcutting. The example of the Ontario Hart's-tongue colonies found in early successional *Populus* woods shows that it can be an aggressive colonizer little affected by logging, provided that spore sources exist nearby. There is still the possibility that small, isolated colonies could become extinct and not be recolonized after logging and forest regrowth.

Most North American *P. scolopendrium* sites appear to be associated with moist slopes or hillsides, such as bouldery talus slopes and crests of escarpments (Soper, 1954) and sinkholes (Short, 1979). Along the Michigan outcrops of the Niagara escarpment, there are very few places where there is a high, steep cliff below which a rocky talus has accumulated. The Michigan Hart's-tongue colonies are found where bedrock just breaks through the surface on a moderately steep hillside or on slopes with a high concentration of low boulders that are separate from the bedrock. At the East Lake station, and possibly the second, easternmost locality described by Hagenah (1956), the boulders on which the ferns are growing represent a lag deposit formed by the removal of the surrounding sandy till by the action of the waters of Lake Algonquin. The boulders themselves had been quarried from nearby outcrops by the glacier and carried only a short distance before being deposited.

Extensive flat areas with limestone bedrock near or outcropping at the surface, such as Manitoulin and Drummond islands, do not appear to be suitable. Possibly these present too dry a habitat (Hagenah, 1956) or the forests are too open for the Hart's-tongue.

Another indicator of this fern's requirement for moist conditions is its preference for growing on low boulders no more than 30 or 40 cm above the forest leaf litter *(Fig. 2)* or in crevices of limestone pavement. The plants would be more exposed and subject to desiccation on sheer cliff faces or higher on boulders. Low position may also be a consequence of insulation and protection from desiccation provided by winter snow at northern localities.

Large, glacially transported dolomite and limestone boulders exposed above the soil are scattered throughout much of Mackinac County south of the Niagara escarpment. Most are close to 1 m in diameter, but individuals 2–3 m in diameter are not unusual. Seldom do these boulders occur in concentrations similar to those seen in typical Hart's-tongue habitat. Although the overall forest setting may seem suitable, these boulders may present desiccation problems and may be too few at any given location to provide a sufficient number of microsites for a viable colony of *P. scolopendrium* to become established.

CONCLUSIONS

Phyllitis scolopendrium has now been reported from three localities on the Niagara escarpment in upper Michigan. All three stations are similar in that they are situated on hills that were islands in Lake Algonquin, which existed ca. 10,500 years ago. Despite assiduous searching by botanists, *P. scolopendrium* has never been found in this region on ground that had been inundated by Lake Algonquin.

This interesting distribution pattern probably does not indicate that *P. scolopendrium* first reached these sites while Lake Algonquin was in existence, for the late-glacial vegetation was coniferous forest, a vegetation type at present not associated with this fern. A more likely explanation is that these hillside sites fulfill the fern's environmental requirements in terms of topography, moisture, and microsite abundance more adequately than other sites where limestone outcrops and boulders are available.

We can never be certain that *P. scolopendrium* did not occur in a greater number of localities in upper Michigan at some time in the last 10,000 years. More intensive botanical exploration in the region may eventually confirm or refute the apparent correspondence between Hart's-tongue fern localities and island areas in Lake Algonquin. In this regard it may be productive to pay particular attention to boulder concentrations along the ancient shorelines of this glacial lake.

With respect to determining the time of immigration of *P. scolopendrium* to upper Michigan, we can only say that it arrived less than 10,000 years ago and possibly only within the last 5000 years. There is little hope of being able to pinpoint this date more exactly, for it is unlikely that the spores or other parts of this rare plant will be found in the fossil condition.

Therefore, the first hypothesis is the least likely and the second is the most plausible explanation for the distribution of Hart's-tongue in Michigan. We do not have sufficient information to reject the third hypothesis.

In order to understand the factors determining the geographic distribution of rare plant species such as *P. scolopendrium*, we must take into account the vegetational history of the region, as well as the ecological relationships between rare species and the biotic and abiotic components of their immediate environment. Further contributions in this regard can be made by studying the population dynamics of known colonies of *P. scolopendrium*. Such a study will be possible at the East Lake station, where an entire Hart's-tongue colony has been counted and mapped.

I would like to thank the following people for their help in providing information at various times during my research and for their comments and criticisms of the manuscript: Joseph Beitel, William S. Benninghoff, Don C. Henson, Anton Reznicek, Charlotte Taylor, Edward G. Voss, and Warren H. Wagner, Jr. The work was supported in part by a National Science Foundation Doctoral Dissertation Improvement Grant.

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Supplemental Notes on Lesser Antillean Pteridophytes

GEORGE R. PROCTOR*

During the several years since publication of the author's pteridophyte volume in R. A. Howard's "Flora of the Lesser Antilles" (vol. 2, 1977), a number of errors and a few omissions have come to light. For the convenience of persons interested in the ferns of this geographic area, it seems desirable to bring together and make available the more important corrections and augmented facts. I am indebted to Dr. David Lellinger of the Smithsonian Institution for placing many of these data at my disposal. The information is presented according to the page-numbers of the volume. Emendations of geographic range, minor corrections of spelling, etc., are omitted.

p. 7.—In citing collectors for the various islands, the name of Stehlé, 1953–1954, was unfortunately omitted from the lists for Guadeloupe, Les Saintes, and Martinique. My apologies to Dr. Stehlé!

p. 16.—The correct citation for this plant is **Psilotum nudum** (L.) Beauv., Prodr. Fam. Aethéog. 112. 1805. Also, the correct date of J. Bot. Schrader 1800(2) should be 1802, not 1801. This correction should be made at numerous places where it appears throughout the volume.

p. 18.—H. & M. Stehlé (Mém. Soc. Bot. France 1953–54, p. 45) reported *Psilotum complanatum* Swartz from Martinique on the basis of unpublished reports by Fée and Urban. No specimens were cited. The Urban record (Symb. Ant. 9:391. 1925) merely cites the Fée reference. Fée's record (Mém. Foug. 11:133. 1866) cites a collection by *Mlle. Rivoire*, "sur un *carapa*, près de Saint-Pierre." This report should be considered doubtful unless it can be substantiated by an authentic specimen.

pp. 75-78.—In subgenus *Mecodium*, two possible additional species should be noted. One of these, known only from Guadeloupe, was given the illegitimate name *Hymenophyllum caespitosum* by Fée (1866, *non* Gaud., 1825) and an unpublished one by Maxon and Morton. This entity, based on a L'Herminier specimen at Paris, can perhaps be considered a diminutive form of *H. undulatum*, but requires further study.

The other species is *Hymenophyllum l'herminieri* Mett. (Linnaea 35:392. 1868). This plant has the frond shape of *H. fucoides* (subg. *Hymenophyllum*), but its entire margins place it in subg. *Mecodium*. Although the original L'Herminier specimens were found in Guadeloupe, more recently similar material was collected in Dominica (*G. Proctor Cooper 106*, US, collected Jan. 31, 1933, "on rocks"). This may well be a valid species.

pp. 132–133.—The correct generic name of this plant is **Lonchitis** L., Sp. Pl. 2:1078. 1753, and the correct species citation is **Lonchitis hirsuta** L., loc. cit. The name *Anisosorus* falls into synonymy, but the relevant typification remains the same.

p. 136.—the correct citation for the *Pteridium* is **P. aquilinum** var. **arachnoideum** (Kaulf.) Brade (Zeitschr. Deutsch. Ver. Wiss. Kunst. S. Paulo 1:56. 1920).

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*Arnold Arboretum Herbarium, 22 Divinity Avenue, Cambridge, MA 02138.

pp. 136–138.—The plant described and illustrated here should bear the generic name **Blotiella** R. Tyron (Contr. Gray Herb. 191:96. 1962), and the species should be known as **Blotiella lindeniana** (Hook.) R. Tyron, based on a type from Venezuela. The name *Lonchitis* should not be associated with this taxon. As the only record of this species from the Lesser Antilles has been shown by Lellinger (Taxon 26:578–580. 1977) to be based on a misidentification, the genus *Blotiella* cannot be listed as occurring in the Lesser Antilles, and this entire entry should be deleted from the book.

p. 176.—The type species of *Cheilanthes*, by conservation, is *C. micropteris* Swartz, of South America.

p. 183.—The correct authority of **Adiantum lucidum** is "(Cav.) Sw.", with the basionym *Pteris lucida* Cav., based on a specimen collected by Née in Ecuador; this was cited by R. Tryon (Contr. Gray Herb. 194:148. 1964). The phrase "not *Pteris lucida* Cav." on line 1 should therefore be deleted.

p. 194.—The correct name of this plant is **Oleandra articulata** (Swartz) C. Presl, Tent. Pterid. 78. 1836, based on the same type cited for *O. nodosa*. The latter name should be considered illegitimate. This question was thoroughly discussed by G. J. de Joncheere (Taxon 18:538–541. 1969).

p. 219.—**Bolbitis aliena** (Swartz) Alston (Kew Bull. 1932:310. 1932) was recorded from the Lesser Antilles by Hennipman (Leiden Bot. Ser. 2:135. 1977). He cited the following specimens: **St. Eustatius:** *Boldingh 44B* (U); **Guadeloupe:** *L'Herminier 21* (CAL); and "Leeward Is.," *Holme s. n.* (K).

This species can be distinguished from *B. nicotianifolia* by the lobed pinnae and the absence of a separate terminal pinna. From *B. portoricensis* it is distinguished by the vein-areoles lacking (or nearly lacking) included free veinlets and by the sterile blades being neither elongate nor proliferous.

p. 288.—The correct citation for the species on this page should be **Nephrolepis rivularis** (Vahl.) Mett. ex Krug in Urban (Engl. Bot. Jahrb. 24:122. 1897).

p. 265. Species 8, listed as *Diplazium limbatum*, should be removed from *Diplazium* and restored to the monotypic genus *Hemidictyum*. The correct name of this species is therefore **Hemidictyum marginatum** (L.) C. Presl, based on *Asplenium marginatum* L.

p. 292.—The correct name of species no. 20 is **Thelypteris opulenta** (Kaulf.) Fosberg (Smiths. Contr. Bot. 8:3. 1972), based on *Aspidium opulentum* Kaulf. The type is *Chamisso s. n.* (LE), from Guam.

p. 295.—The correct name of species no. 22 is **Thelypteris kunthii** (Desv.) Morton (Contr. U. S. Natl. Herb. 38:53. 1967), based on *Nephrodium kunthii* Desv. The type is a Venezuelan specimen without stated collector, *ex. herb. Desvaux* (P.)

p. 296.—The correct name of species no. 24 is **Thelypteris hispidula** (Dcne.) Reed (Phytologia 17:283. 1968), based on *Aspidium hispidulum* Dcne. (Nouv. Ann. Mus. Hist. Nat. 3:346. 1835). The type is said to be a *Riedlé* or *Guichenot* specimen from Timor (P.)

p. 297.—Note 24a, **Thelypteris hispidula** var. **hispidula** and 24b, **Thelypteris hispidula** var. **inconstans** (C. Chr.) Proctor, comb. nov., based on *Dryopteris dentata* var. *inconstans* C. Chr. (Kungl. Sv. Vet. Akad. Handl. 16(2):27. 1936). The lectotype of the latter is *Ekman H 10524* (S, isolectotype US), selected by A. R. Smith (Univ. Calif. Publ. Bot. 59:67. 1971).

p. 329.—The correct name of species no. 3. is **Polypodium sororium** Humb. & Bonpl. ex Willd. in L. (Sp. Pl. 5:191. 1810). The type is *Humboldt 424* (B–*Herb. Willd. 19684-1*) from near Caripe, Venezuela.

p. 331.—The correct name of species no. 6 is **Polypodium dissimile** L., the type being *P. Browne* (LINN *1252.24*) from Jamaica.

p. 338 or 339. **Polypodium palmeri** Maxon (Contr. U. S. Natl. Herb. 17(7):600. 1916) should be added to the Lesser Antilles list. The type is *Palmer 308* (US 572544 from Mexico. This member of subg. *Microgramma* was collected long ago in Barbados by *Jenman* (NY, US), unfortunately without further data. This species is largely Central American in distribution, but also has been found once in Jamaica.

This species is somewhat similar to *P. lycopodioides*, but differs in its larger size (sterile fronds 5–20 cm long, 2–4 cm broad) and thicker texture, and in the thicker, rope-like, whitish-scaly rhizomes.

p. 344.—*Polypodium decurrens* Raddi (Opusc. Sci. Bol. 3:287. 1819; Pl. Bras. 1:23, *t. 33*. 1825), based on material from Brazil, has been confirmed as occurring in the Lesser Antilles. There is a good Martinique specimen of *Duss 1568* at US, whose label says, "Terrestre, rare. Piton Marcel, entre la montagne Pelée et le Precheur; tres rare dans les pitons de Fort de France," collected July 1885. The Plumier plate cited on p. 344 (Tr. Foug. 99, *t. 114*) unquestionably belongs to the same species.

Polypodium decurrens is referred to subg. *Campyloneurum*, and is unique among the lesser Antillean species of this subgenus in having pinnate instead of simple fronds. The individual pinnae are not unlike the entire blade of *P. repens* in shape, texture, and venation.

p. 344.—*Polypodium recurvatum* Kaulf. can definitely be excluded from the Lesser Antilles list; the record was based on *Duss 4093*, which was referred to *P. plumula* Humb. & Bonpl. ex Willd. by A. M. Evans (Ann. Mo. Bot. Gard. 55(3): 231. 1969).

p. 361.—In the caption for Figure 60b, the name for "e" should be **G. taxifolia** (not *G. taenifolia*).

p. 366. A recently described species of *Cochlidium* from the Lesser Antilles is **C. jungens** L. E. Bishop (Amer. Fern J. 68:84. 1978), based on *Nicolson 1975* (US) from Morne Micotrin, St. George Parish, Dominica. Among the Lesser Antillean species of *Cochlidium*, *C. jungens* is distinguished from *C. seminudum* by the smaller size of the fronds (2–8 cm long vs. 8–20 cm), but also by the non-contracted and non-acuminate fertile fronds; the sterile blades are also narrower, being mostly less than 3 mm wide. From *C. rostratum* it is distinguished by the superficial sori, not immersed in a deep central groove.

p. 368.—The name of species no. 2. should be **Cochlidium rostratum** (Hook.) Maxon ex C. Chr. (Dansk. Bot. Ark. 6(3):23. 1929), based on *Wright s. n.* (K., isotype US) from Omotepe Island, Nicaragua. Additional Lesser Antillean records of this species include *Stehlé 341* and *1096* (both US) from Guadeloupe.

p. 374. The correct citation for *Vittaria lineata* is (L.) J. E. Smith (Mém. Acad. Turin 10:421, *t. 9, f. 5*. 1793).

Additions to the Pteridophyte Flora of the Great Plains

RALPH E. BROOKS*

Recent herbarium studies made while preparing manuscript for the forthcoming manual of the Great Plains flora have led to the discovery of several specimens representing new state records or significant range extensions apparently overlooked by Petrik-Ott in "The Pteridophytes of Kansas, Nebraska, South Dakota and North Dakota" (Beih. Nova Hedwigia 61:1–332. 1979).

Botrychium lunaria (L.) Swartz var. lunaria.—This taxon has been reported previously for the Great Plains from North Dakota by Petrik-Ott (1979, p. 37); however, that specimen is *B. minganense* Vict. The South Dakota collection represents a southern range extension for this circumboreal species.

SOUTH DAKOTA: Lawrence County: Northern Black Hills: Old Balmoral Mine, NW from Crown Hill, shrubby glade on plateau at old mine, 6100 ft alt., June 1930, *Mrs. F. L. Bennett s.n.* (BHSC).

Botrychium lunaria var. onondagense (Underw.) House.—This plant previously was known from scattered localities in the northwestern and northeastern United States.

NORTH DAKOTA: Burke County: 12 mi SE of Lignite, N-exposed wooded ravine, 11 June 1971, *G. D. Hegstad 7855* (NDA).

Botrychium matricariifolium A. Braun.—Petrik-Ott (1979, p. 294) stated that she had seen no collections of this species from South Dakota, and so she excluded it from the Great Plains flora. In 1978 I visited the U.S. National Herbarium and found the specimen cited by Clausen (Mem. Torrey Bot. Club 19:87. 1938) to be determined correctly. This was verified by Dr. David Lellinger (pers. comm., 1980), and so *B. matricariifolium* must remain a part of the Great Plains flora.

SOUTH DAKOTA: Custer County: Black Hills: Custer, 5500 ft alt., 15 Aug 1892, *P. A. Rydberg 1186* (US).

Botrychium minganense Vict.—Petrik-Ott (1979, pp. 34–36) annotated, described, and illustrated this specimen as typical *B. lunaria*. Of the five plants on the cited sheet, two are immature. The remaining three are typical *B. minganense*; they have distinctly pinnatifid or pinnate lower pinnae, with only the uppermost pinnae flabellate. This determination was kindly verified by Dr. Warren Wagner, Jr. (pers. comm., 1979). The collection represents a slight southern range extension since the species previously was known from Labrador west to Alaska and south to Michigan, Minnesota, Colorado, Nevada, and California.

NORTH DAKOTA: McHenry County: Towner, sandy prairie, 11 June 1955, *O. A. Stevens 1530* (NDA).

Ophioglossum vulgatum var. pseudopodum (Blake) Farw.—This specimen was first reported as *O. vulgatum* L. by Clausen (1938, p. 126), who did not recognize any infraspecific taxa within this species. Petrik-Ott (1979, p. 295) listed

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*Herbarium, University of Kansas, Lawrence, KS 66044.

the record as unverified since she had not examined the specimen. I examined it in 1978, and found it to be the northern var. *pseudopodum*. The collection was made at the southernmost limit of the range in our region. The variety previously was reported from southern Canada south to Virginia, Indiana, Illinois, Nebraska, and California. I have visited the Kansas locality in recent years and, although the habitat is suitable for this plant, the chances are that it is now extirpated. Road construction and housing developments have drastically altered the area since 1929.

KANSAS: Crawford County: Pittsburg, 1 mi W of Broadway, in woods on low, rich slopes and in draws, rare clusters, 15 June 1929, *F. A. Riedel s.n.* (NY).

Polystichum lonchitis (L.) Roth.—This collection is a slight southern and eastern range extension from northeastern Wyoming. Both the South Dakota and northeastern Wyoming sites are disjunct from the primary range of this circumboreal species, which lies more than 150 miles to the west and many more miles to the north.

SOUTH DAKOTA: Lawrence County: Black Hills, SW1/4, Sec. 36, T5N, R1E, S of Roughlock Falls, mossy loam underwoods, over talus below limestone bluff, N-facing slope, 22 July 1971, *C. A. Taylor, W. Casper & A. Glynn 10918* (SDC).

I wish to thank the following curators for the loan of specimens and for aid in various other ways: Dr. William T. Barker, North Dakota State University (NDA); Dr. Gary Larson, South Dakota State University (SDC); Dr. John Mickel, New York Botanical Garden (NY); and Dr. Joseph Thomasson, Black Hills State College (BHSC).

REVIEW

"**DAS BUCH DER FREILANDFARNE**," by R. Maatsch. 196pp. illustr. Paul Parey, Berlin and Hamburg. 1980. ISBN 3-489-61422-4. DM. 68. (ca. $40.00).—This book is intended for serious hardy fern growers. An introductory portion contains notes on nomenclature, taxonomy, morphology, and fern habitats illustrated with black-and-white photographs and line drawings. About half the book is a useful alphabetical list of fern species and cultivars, concentrating on those grown in Europe, and giving Latin and common names, a brief description of the plant, and other useful notes. The last quarter of the book concerns fern culture. Unusual and helpful information on flowering plants suitable for growing with ferns is included. I hope the publisher will prepare an English edition so that Prof. Maatsch's book receives the wide circulation it deserves in the English-speaking world.—*D.B.L.*

Flavonoid Synthesis and Antheridium Initiation in Dryopteris Gametophytes

RAYMOND L. PETERSEN* and DAVID E. FAIRBROTHERS**

There is now a fairly extensive vascular crytogam flavonoid literature and there are a number of researchers actively engaged in this research field (Swain & Cooper-Driver, 1973). All vascular crytogam flavonoid work has been done on the sporophyte generation, with one exception: Laurent (1966) determined that *Blechnum brasiliense* gametophytes produced the flavonoid kaempferol, which is one of the flavonoids produced by the *B. brasiliense* sporophyte. Reasons for the paucity of information on fern gametophyte flavonoids include the easy accessibility of sporophytes and the now disreputed opinion that flavonoids, being associated with lignin synthesis, are exclusive to vascularized plant bodies. This exclusivity has been lost because flavonoids have been isolated and identified in various non-vascular plant groups: certain algal divisions, bryophytes (Swain, 1974), and fern gametophytes (Laurent, 1966).

Initially our investigation was undertaken to determine if *Dryopteris intermedia* A. Gray and *D. marginalis* A. Gray gametophytes produce flavonoids and, if so, were these the same flavonoids produced by their sporophytic counterparts (Petersen, 1976). Because of the unusual results of this first portion of the research, the inquiry was amplified to include an analysis of flavonoid content along a developmental profile of the gametophytes.

Half-strength White's minimum nutrient medium adjusted to pH 6.0 was used to culture the gametophytes. Liquid cultures were prepared by placing 0.25 g of spores in a 4 l flask and adding 2 l of nutrient solution. Separate cultures of *D. intermedia* and *D. marginalis* were grown at 22°C under 300 ft-c of illumination from cool-white fluorescent lights in a 12/12 hr diurnal cycle.

Gametophytes were harvested and assayed for flavonoids at three developmental stages: (1) pre-antheridial initiation (0 antheridia/gametophyte), (2) antheridial initiation (0 or 1 antheridia/gametophyte), and (3) post-antheridial initiation (4–6 antheridia/gametophyte).

Ten-gram samples of harvested gametophytes were immediately extracted in methanol and re-extracted repeatedly until a colorless supernatant was obtained. Concentrated extracts were spotted onto Whatman 3MM chromatography paper (42 × 55 cm). Chromatograms were developed in two dimensions employing the two standard solvent systems for the separation of flavonoids: t-butanol, acetic acid, water (3:1:1) for the first dimension and 15% acetic acid, water for the second dimension. Completed chromatograms were inspected under UV light, both in the presence and absence of NH_3. Spot color changes under both conditions were noted and R_f values determined. Spots were excised, eluted in spectral grade methanol, and UV spectral data obtained using standard procedures (Mabry

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*Department of Botany, Howard University, Washington, D.C. 20059.
**Department of Botany, Rutgers University, New Brunswick, New Jersey 08903.

et al., 1970). Positive determinations of isolated flavonoid aglycones were done by co-chromatographing them against authentic compounds. Quantitative scoring for flavonoid content was done by comparative visual inspection of spot intensity and size.

In the initial experiment, *D. marginalis* gametophytes were cultured for 30 days and then harvested. Because of extreme crowding, most of the gametophytes formed filaments rather than plates, and most bore a number of antheridia laterally. Flavonoids were detected in these gametophytes, and they were the same ones that occur in *D. marginalis* sporophytes *(Table 1)*.

TABLE 1. IDENTIFICATION DATA FOR FLAVONOID GLYCOSIDES OF QUERCETIN AND KAEMPFEROL FOUND IN *DRYOPTERIS INTERMEDIA* AND *D. MARGINALIS* GAMETOPHYTES AND SPOROPHYTES.

	Quercetin (A)	*Kaempferol* (B)	*Kaempferol* (C)
	CHROMATOGRAM SPOT APPEARANCE		
UV	Violet	Violet	Violet
UV/NH_3	Yellow	Yellow	Yellow
	CHROMATOGRAM SPOT R_f VALUES		
TAB	0.50	0.60	0.63
HOAc	0.44	0.56	0.45
	UV SPECTRAL DATA (λ max., nm)		
MeOH	256, 282, 306, 357	266, 292, 347	265, 302, 349
NaOMe	271, 323, 412	274, 324, 401	275, 325, 401
$AlCl_3$	270, 302sh, 362sh, 403	274, 302, 349, 395	273, 302, 348, 394
$AlCl_3$/HCl	268, 300sh, 358,	273, 302, 343, 392	273, 298, 343, 392
NaOAc	273, 415	273, 302, 381	273, 301, 375

Because of inadequate material for spectrometric analysis, new cultures of *D. marginalis* were started, and cultures of *D. intermedia* were begun to determine if they likewise produced the same flavonoids as *D. intermedia* sporophytes. After three weeks, the cultures were harvested and assayed for flavonoids. No flavonoids were detected on the chromatograms, and examination showed that the gametophytes had not produced antheridia. Therefore, more gametophytes were cultured so that flavonoid content could be analyzed at three developmental stages *(Table 2)*.

The last experiments showed that the same flavonoids are produced by the gametophytes of these two species as are produced by their respective sporophytes *(Table 1)*. They are quercetin and kaempferol glycosides. (See Mabry et al., 1970, for data comparisons and structural details.) *Dryopteris intermedia* sporophytes and gametophytes produced two flavonoids: a quercetin glycoside (Compound A) and a kaempferol glycoside (Compound B). *Dryopteris marginalis* produced these two compounds, as well as an additional kaempferol glycoside (Compound C).

The experiments *(Table 2)* also show flavonoids to be absent (−) during the pre-antheridial stage. They were first detected as faint spots (+) at the onset of antheridium formation. Flavonoid concentration is much higher (++) in the post-antheridium initiation stage than at the onset of antheridium formation, as revealed by greater intensities of spot fluorescence. Antheridium formation and flavonoid synthesis clearly are associated, but whether the two events are interrelated (cause and effect) or merely a coincidence remains to be determined. Although nothing comparable has been discovered in flowering plants, Barber (1956) identified a glucose-rhamnose glycoside of quercetin in staminate squash flowers that was absent from the pistillate flowers.

TABLE 2. FLAVONOID CONTENT OF *DRYOPTERIS* GAMETOPHYTES AT THREE DEVELOPMENTAL STAGES.

	Pre-antheridial initiation			*Antheridial initiation*			*Post-antheridial initiation*		
COMPOUNDS	*(A)*	*(B)*	*(C)*	*(A)*	*(B)*	*(C)*	*(A)*	*(B)*	*(C)*
D. intermedia	−	−	−	+	+	−	++	++	−
D. marginalis	−	−	−	+	+	+	++	++	++

− = compound not detected; + = compound detected but at a low concentration relative to ++.

We wish to acknowledge financial aid from NSF Grant GB-13202 and a Rutgers Research Council Grant awarded to D. E. Fairbrothers.

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SWAIN, T. 1974. Biochemical evolution in plants (Chapter II). *In* M. Florkin and E. H. Stotz, eds. Comprehensive Biochemistry, vol. 29A. Elsevier, Amsterdam.

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Date of Publication of Sodiro's "Sertula Florae Ecuadorensis"

DAVID B. LELLINGER*

Several years ago, Morton (Amer. Fern J. 62:57–64. 1972) published on the dates of original publication of the parts of Father Luis Sodiro's "Cryptogamae Vasculares Quitenses." In that case, original publication in periodicals antedated the reprint "Cryptogamae," sometimes by several years. Sodiro's "Sertula Florae Ecuadorensis" exhibits similar, but shorter differences between original and reprint publication dates. The portions concerning ferns first were published in four parts in the "Anales de la Universidad Central" in Quito, Ecuador. These parts were reprinted a few months later with changes of pagination in two parts under the general title "Sertula Florae Ecuadorensis." The details are presented in *Table 1*. Some pages apparently were not reset to produce the reprint, but others obviously were. For instance, the bottom line of page 191 of the first part of the "Anales" ends "linea-", but in the repaged reprint this is six lines from the bottom and has been misspelled "ilnea-"! This might lead one to think that the reprint actually is a preprint. However, the "Anales" issue is dated January 1905 and the reprint 1905 with no indication of month, and so it is unlikely that the reprint was issued before the "Anales."

TABLE 1. DATES OF PUBLICATION OF "SERTULA FLORAE ECUADORENSIS" PARTS CONTAINING FERNS.

Original publication in Anal. Univ. Central	*Repaged and reprint publication as Sert. Fl. Ecuad.*
19(135)191–200. Jan 1905.	I. Acrosticha. pp. 1–12, *t. I.* 1905.
22(158–159):21–30. Jan/Feb 1908.	II. Pteridophyta. pp. 1–12(part). June 1908.
22(160):89–104. Mar 1908.	II. Pteridophyta. pp. 12(part)–27(part). June 1908.
22(161):161–176. Apr 1908.	II. Pteridophyta. pp. 27(part)–42. June 1908.

Fortunately, not much time elapsed between the original and reprint publication dates; probably no botanical names will be affected by the adoption of the earlier dates. Many authors, including Christensen in his "Index Filicum," have cited pages and dates from the reprints, rather than from the original publication, as should be done. Because the original publication is rare, the names and bibliographic data for correct citation of new fern names and taxa are given in *Table 2*.

I am indebted to Dr. Dan Nicolson and Mr. James Zarrucci for calling this problem to my attention and for obtaining xerocopies of the original "Anales" articles.

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*U. S. Nat'l. Herbarium, Smithsonian Institution, Washington, DC 20560.

TABLE 2. NEW FERN SPECIES AND VARIETIES PUBLISHED BY SODIRO IN THE "ANALES DE LA UNIVERSIDAD CENTRAL."

Acrostichum actinolepis Sodiro, op. cit. 19(135):199. Jan 1905.
A. angamarcanum Sodiro, op. cit. 19(135):193. Jan 1905.
A. antisanae Sodiro, op. cit. 22(161):164. Apr 1908.
A. chodatii Sodiro, op. cit. 22(161):174. Apr 1908.
A. christii Sodiro, op. cit. 19(135):192. Jan 1905.
A. cinereum Sodiro, op. cit. 22(161):172. Apr 1908.
A. cladotrichum Sodiro, op. cit. 19(135):197. Jan 1905.
A. diversifolium Sodiro, op. cit. 22(161):166. Apr 1908.
A. ellipsoideum Sodiro, op. cit. 22(161):164. Apr 1908.
A. engleri Sodiro, op. cit. 22(161):167. Apr 1908.
A. fulvum Sodiro, op. cit. 22(161):168. Apr 1908.
A. gossypinum Sodiro, op. cit. 22(161):172. Apr 1908.
A. guamanianum Sodiro, op. cit. 22(161):169. Apr 1908.
A. hieronymi Sodiro, op. cit. 19(135):199. Jan 1905.
A. hikenii Sodiro, op. cit. 22(161):169. Apr 1908.
A. litanum Sodiro, op. cit. 19(135):198. Jan 1905.
A. longissimum Sodiro, op. cit. 19(135):191. Jan 1905.
A. molle Sodiro, op. cit. 22(161):171. Apr 1908.
A. muriculatum Sodiro, op. cit. 22(161):174. Apr 1908.
A. oleandropsis Sodiro, op. cit. 19(135):195. Jan 1905.
A. pangoanum Sodiro, op. cit. 19(135):194. Jan 1905.
A. pellucidum Sodiro, op cit. 19(135):195. Jan 1905.
A. pichinchae Sodiro, op. cit. 22(161):173. Apr 1908.
A. pruinosum Sodiro, op. cit. 22(161):166. Apr 1908.
A. pteropodum Sodiro, op. cit. 19(135):196. Jan 1905.
A. rupicola Sodiro, op. cit. 22(161):175. Apr 1908, as "rupicolum."
A. subsessile Sodiro, op. cit. 19(135):194. Jan 1905.
A. trichophorum Sodiro, op. cit. 19(135):198. Jan 1905.
A. urbani Sodiro, op. cit. 22(161):170. Apr 1908.
A. viscidulum Sodiro, op. cit. 22(161):165. Apr 1908.
Alsophila bilineata Sodiro, op. cit. 22(160):90. Mar 1908.
A. christii Sodiro, op. cit. 22(160):89. Mar 1908.
Asplenium anomalum Sodiro, op. cit. 22(160):95. Mar 1908.
A. chimboanum Sodiro, op. cit. 22(160):102. Mar 1908.
A. costale Sodiro, op. cit. 22(160):95. Mar 1908.
A. crassifolium Sodiro, op. cit. 22(160):97. Mar 1908.
A. heterolobum Sodiro, op. cit. 22(160):98. Mar 1908.
A. hieronymi Sodiro, op. cit. 22(160):99. Mar 1908.
A. humile Sodiro, op. cit. 22(160):99. Mar 1908.
A. melanosorum Sodiro, op. cit. 22(160):101. Mar 1908.
A. oxylobum Sodiro, op. cit. 22(160):96. Mar 1908.
A. procerum Sodiro, op. cit. 22(160):96. Mar 1908.
A. tungurahuae Sodiro, op. cit. 22(160):97. Mar 1908.

A. vesiculosum Sodiro, op. cit. 22(160):100. Mar 1908.
Cyathea asperata Sodiro, op. cit. 22(158-159):27. Jan/Feb 1908.
C. asperata var. minor Sodiro, op. cit. 22(158-159):28. Jan/Feb 1908.
C. brachypoda Sodiro, op. cit. 22(158-159):26. Jan/Feb 1908.
C. canescens Sodiro, op. cit. 22(158-159):22. Jan/Feb 1908.
C. furfuracea Sodiro, op. cit. 22(158-159):25. Jan/Feb 1908.
C. muriculata Sodiro, op. cit. 22(158-159):28. Jan/Feb 1908.
C. nitens Sodiro, op. cit. 22(158-159):21. Jan/Feb 1908.
C. ochroleuca Sodiro, op. cit. 22(158-159):29. Jan/Feb 1908.
C. oxyacantha Sodiro, op. cit. 22(158-159):24. Jan/Feb 1908.
C. parvifolia Sodiro, op. cit. 22(158-159):25. Jan/Feb 1908.
C. subinermis Sodiro, op. cit. 22(158-159):28. Jan/Feb 1908.
C. tungurahuae Sodiro, op. cit. 22(158-159):30. Jan/Feb 1908.
Nephrodium cinereum Sodiro, op. cit. 22(160):103. Mar 1908.
N. cinereum var. intermedium, Sodiro, op. cit. 22(160):104. Mar 1908.
N. longipilosum Sodiro, op. cit. 22(160):103. Mar 1908.
Polypodium scutulatum Sodiro, op. cit. 22(161):163. Apr 1908.
Pteris aspidioides Sodiro, op. cit. 22(160):91. Mar 1908.
P. biternata Sodiro, op. cit. 22(160):94. Mar 1908.
P. esmeraldensis Sodiro, op. cit. 22(160):92. Mar 1908.
P. falcata Sodiro, op. cit. 22(160):93. Mar 1908.
P. procera Sodiro, op. cit. 22(160):94. Mar 1908.
P. rigida Sodiro, op. cit. 22(160):92. Mar 1908.
P. rimbachii Sodiro, op. cit. 22(160):91. Mar 1908.
P. robusta Sodiro, op. cit. 22(160):93. Mar 1908.

REVIEW

"**TAXONOMY OF THELYPTERIS SUBGENUS STEIROPTERIS, INCLUDING GLAPHYROPTERIS (PTERIDOPHYTA),** by Alan R. Smith, Univ. Calif. Publ. Bot. 76:1-38, t. 1-4. 1980.—Among the large neotropical fern genera, none is more complex than *Thelypteris*. Even though subg. *Steiropteris* is but a small portion of the genus (22 species, some divided into varieties), this monograph is very welcome. Over half the taxa are new species or required a new name or combination, which is a measure of the confusion which the author has resolved. Spores and some details of morphology are illustrated with photographs, and distributions are shown by means of maps. The author has seen many type specimens, and so the synonymies are doubtless accurate. A list of exsiccatae is included but, unfortunately, an index to scientific names is not. The work is available for $5.00 from University of California Press, 2223 Fulton St., Berkeley, CA 94720.—*D.B.L.*

Reproductive Biology and Gametophyte Morphology of New World Populations of Acrostichum aureum

ROBERT M. LLOYD*

The majority of homosporous ferns are characterized by a life-cycle which permits the production of a genetically homozygous zygote following self-fertilization of a single gametophyte (intragametophytic selfing). This homozygosity leads to the expression of recessive deleterious or lethal genes (genetic load, as defined here) present in the genotype, unless this expression is buffered by the polyploid system. Sporophytes expressing such genes will be eliminated rapidly and the spore genotypes produced individually by the remaining viable sporophytes will be genetically uniform, barring mutation and meiotic irregularities (e.g., homeologous pairing; Klekowski, 1979). In species which regularly undergo selfing, genetic load will be absent or will be expressed at low levels (Klekowski, 1979). Thus, analysis of genotypes for genetic load allows for an estimate of the genetic variability in a population.

The fern life-cycle also permits reproduction which is genetically analogous to inbreeding and outbreeding in angiosperms, the latter facilitating the storage of recessive deleterious and lethal genes (Wallace, 1970). Although none of the above patterns of reproduction are mutually exclusive, work of the past decade has led to the hypothesis that specific morphological and developmental features of the gametophyte generation will increase the probability of selfing or crossing (intergametophytic mating) and that these probabilities can be correlated with estimates of heterozygosity in the form of genetic load (Lloyd, 1974). However, more recent work with *Ceratopteris* (Lloyd & Warne, 1978) and *Acrostichum* (Lloyd & Gregg, 1975) suggests that the past hypotheses are insufficient to explain the genetic diversity expressed in these species and that other factors are involved. This paper summarizes our most recent work on the gametophyte morphology, reproductive biology, and genetic diversity in a number of populations of *Acrostichum aureum* distributed from Florida to the northern coast of South America and attempts to circumscribe the current problems in this field.

The genus *Acrostichum* consists of at least three species: *A. danaeifolium* Langsd. & Fisch., a New World endemic which is widely distributed in fresh water and slightly saline swamps (Adams & Tomlinson, 1979); *A. aureum* L., circumtropical in distribution and usually most abundant in mangrove habitats where it can withstand partial tidal immersion (Holttum, 1954; Small, 1938); and *A. speciosum* Willd., a species of tropical Asia and Australia which is abundant in mangroves through Malaya in areas frequently inundated by tides (Holttum, 1954). These types of habitats are extreme; few species of plants have evolved the necessary physiological and morphological features to successfully colonize them. Previous work on the gametophyte generation in *Acrostichum* includes mor-

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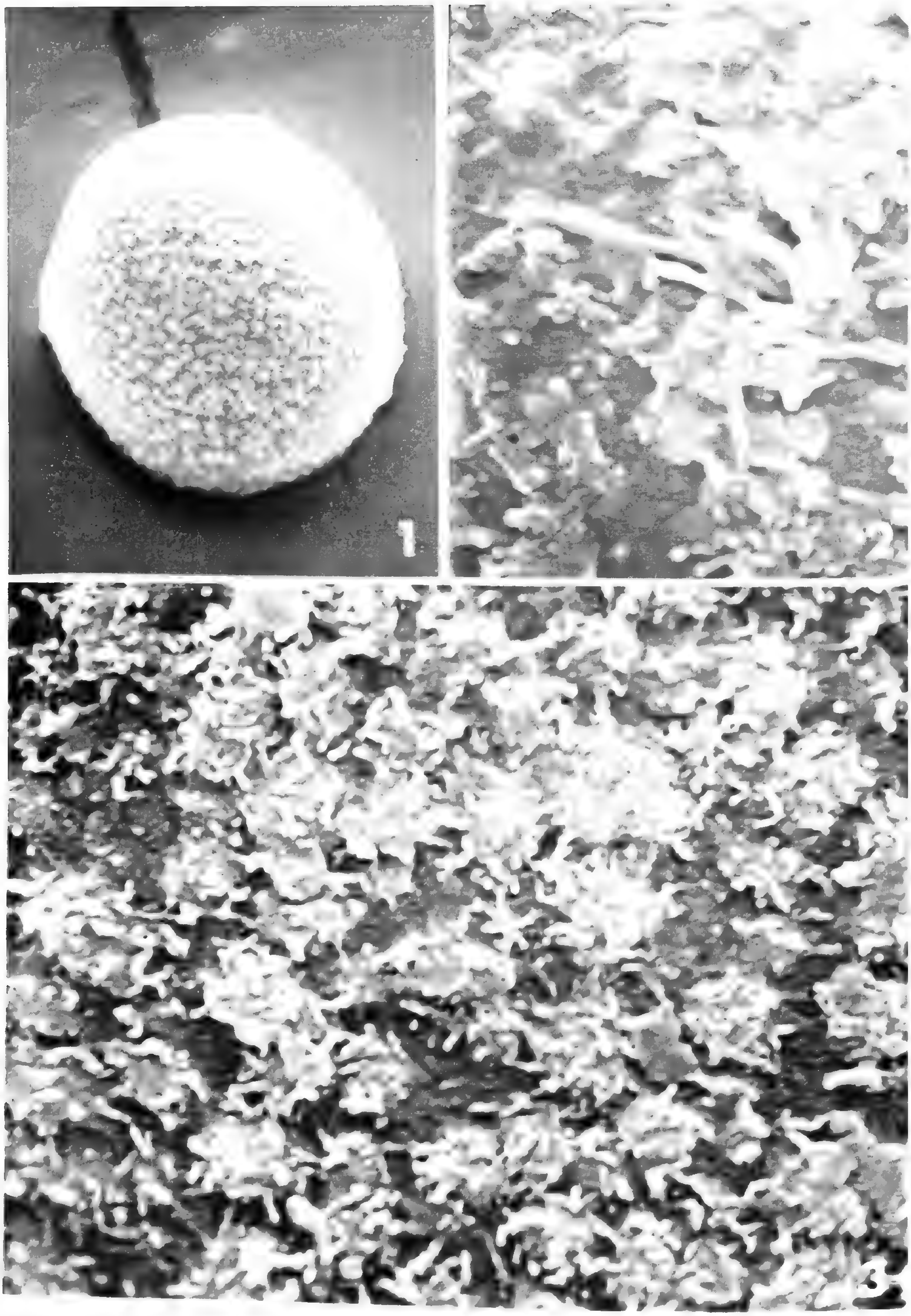
*Department of Botany, Ohio University, Athens, OH 45701.



FIGS. 1–3. Spores of *A. aureum*. FIG. 1. Papua, *Brass 518* (UC), × 1000. FIG. 2. Florida, *Curtiss 5463* (UC), × 10000. FIG. 3. Papua, *Brass 518* (UC), × 8000.

phological studies of *A. speciosum* by Stokey & Atkinson (1952) and a study of the morphology and reproductive biology of Mexican populations of *A. danaeifolium* by Lloyd & Gregg (1975).

MATERIALS AND METHODS

Spores of *A. aureum* were collected from 39 plants from eight populations as follows:

Culture No. *146:* 1.1 mi W of U. S. Highway 41 on State Highway 92, Collier Co., Florida. *148:* 2.1 mi W of Westlake on State Highway 27, Everglades National Park, Dade Co., Florida. *150:* 30.5 mi SW of entrance station on State Highway 27 at road to Westlake, Everglades National Park, Monroe Co., Florida. *190:* 0.25 mi E of Negril on road to Savana la Mar, Westmoreland Parish, Jamaica. *191:* Mile post 57, 57 mi E of Georgetown on Public Road East, Guyana. *192:* 8 km N of Governor's Palace, Parimaribo, near end of road to Leonsburg, Suriname. *193:* 0.2 mi from road to Colón on road to Coco Solo, Canal Zone, Panama. *194:* Lowland area near Pacific Ocean at N end of the Bridge of the Americas, Canal Zone, Panama.

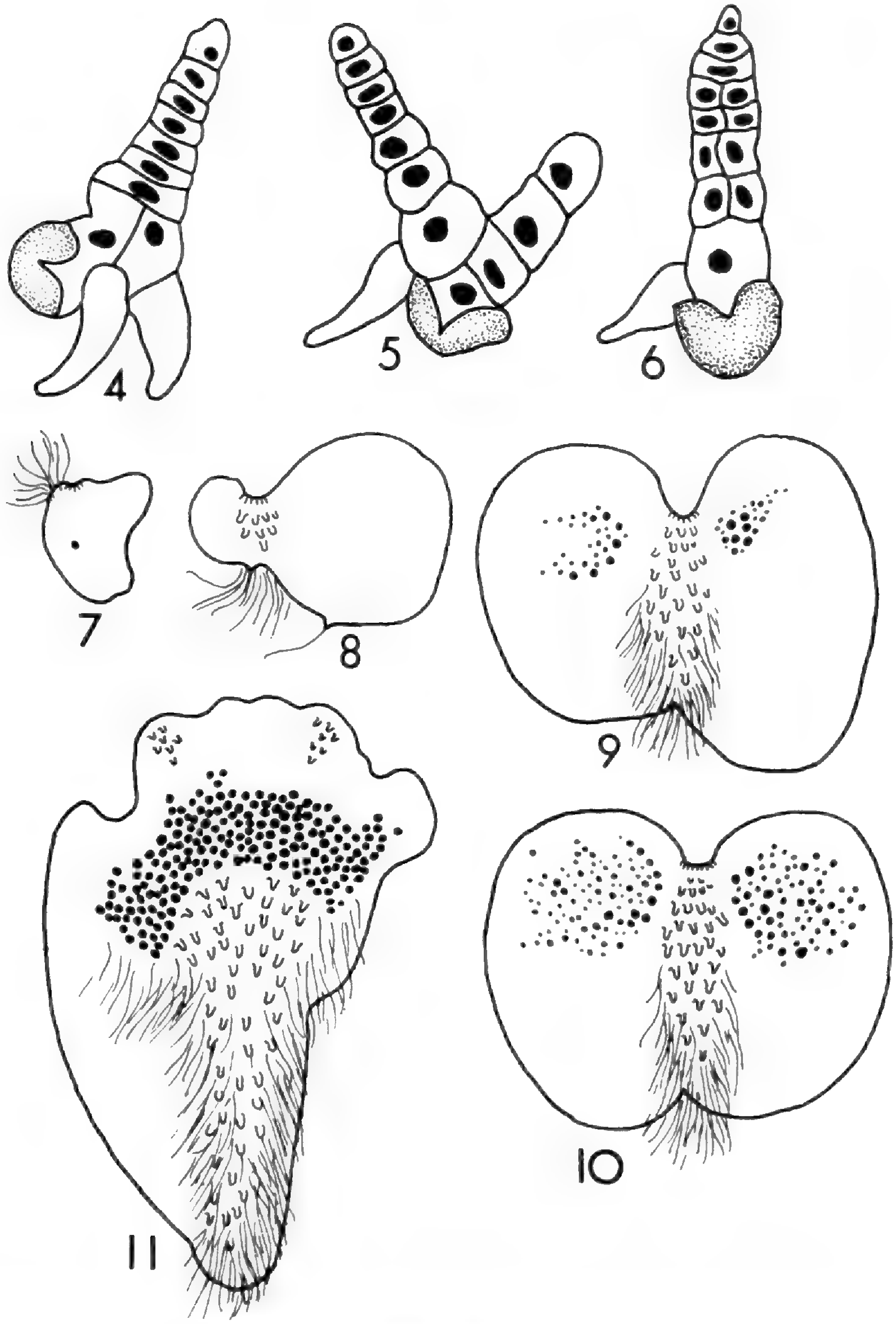
Spores were sown and gametophytes grown aseptically on sterile inorganic nutrient medium solidified with 1% agar (for composition see Klekowski, 1969) in 100 × 15 mm petri dishes. Gametophytes were grown under continuous illumination by fluorescent and incandescent lamps at an intensity of 210 to 290 ft-c at temperatures of 19–24° C. Prothallial morphology was studied using living material as well as that mounted in Hoyer's medium mixed with acetocarmine. Spore sizes were determined by mounting spores in diaphane and calculating their equatorial diameters with a calibrated ocular micrometer. Other methods utilized in specific experiments are described below.

Spores observed by the scanning electron microscope were dry-mounted on double-stick tape, coated with gold ca. 10 nm thick, and observed at 20 kv accelerating voltage with a Hitachi HHS-2R scanning electron microscope.

RESULTS

Spores of *A. aureum* are tetrahedral and are (37)45–72 (mean ± s.d. = 56.7 ± 4.58) μm in diameter. The spore surface is minutely tuberculate (*Fig. 1*). The tubercle-like structures on the surface bear varying numbers of projecting papillae. Spores from plants from Papua (*Figs. 1, 3*) and Fiji exhibit numerous but somewhat irregularly shaped and oriented papillae. Spores from Florida plants (*Fig. 2*) and other Fijian plants appear to have more numerous papillae as well as other types of superficial deposits. In contrast, spores examined from plants from Australia and Trinidad are tuberculate but appear either to lack papillae or to have thickened superficial deposits which more or less obscure their presence. Spores examined of *A. speciosum* from Papua exhibit surface features highly similar to those from Florida plants of *A. aureum*.

Spore germination is usually initiated by the emergence of a rhizoid five days following sowing. Gametophytes produce a one-dimensional filament up to 10 cells in length before initiation of two-dimensional growth (*Fig. 4*). In some instances, cells near the base of the filament will divide, producing a second one-dimensional filament (*Fig. 5*).



FIGS. 4–11. Stages in gametophyte development and sexually mature gametophytes of *A. aureum*. FIG. 4. One-dimensional filament with initiation of two-dimensional growth in basal cell, 185 μm long, 10 days after sowing. FIG. 5. Branched gametophyte with two filaments, 196 μm long, 10 days after sowing. FIG. 6. Two-dimensional filament with two-ranked cells, 208 μm long, 10 days after sowing. FIG. 7. Male prothallus with single antheridium, 1.3 mm long, 29 days after sowing. FIG. 8. Female prothallus with asymmetrical wings, 1.5 mm long, 29 days after sowing. FIG. 9. Young hermaphroditic gametophyte with numerous immature antheridial initials and few mature antheridia, 3.4 mm long, 51 days after sowing. FIG. 10. Young hermaphroditic prothallus with numerous gametangia, 4.0 mm long, 51 days after sowing. FIG. 11. Mature gametophyte showing sequential pattern of archegonial-antheridial-archegonial production and branched meristem, 7.5 mm long, 96 days after sowing.

Two-dimensional growth is initiated by a longitudinal division in a central or more basal cell of the one-dimensional filament. Further longitudinal divisions in the filament may follow one or more patterns: cells throughout the filament, except for the terminal and basal cells, may divide longitudinally and produce a two-dimensional filament two cells wide (*Fig. 6*); less frequently, central cells of the 1-dimensional filament may divide sequentially, producing an area up to four or more cells in width before further divisions occur in the more basal and terminal cells of the filament. In both pathways, 2-dimensional growth ultimately results in a broadly linear or spatulate gametophyte four to six cells wide. Further divisions of cells along one of the lateral margins of these prothalli will produce a lateral meristematic region located near the basal region of the gametophyte. Subsequent growth produces an asymmetrical ovate prothallus with different sized wings (*Fig. 8*). In older gametophytes, growth frequently produces more or less symmetrical wing tissue on both sides of the lateral meristem, resulting in a mature prothallus which appears to have an apical meristematic notch (*Figs. 9* and *10*)). This notch area remains shallow in most prothalli observed; in some, however, the meristem exceeds the wing tissue and no notch is evident. In some older gametophytes, the meristematic region becomes quite broad, and, rarely, may divide into two separate regions (*Fig. 11*) with non-meristematic tissue between.

Gametangia initiation in culture was rapid. All cultures, except 193-K[1], exhibited a female to hermaphroditic gametangial sequence of development (*Fig. 8*) with the exception of occasional gametophytes which precociously initiated antheridia (*Fig. 7*). Of the 20 cultures studied in detail, seven produced some male gametophytes, but the percentage of such gametophytes in culture (except 193-K) was less than 6.0 (*Tables 1* and *2*). In all cases these prothalli rapidly became hermaphroditic.

The length of the unisexual female gametophytic stage varied from culture to culture. In one culture (190-D), hermaphroditic prothalli were produced simultaneously with female prothalli. In other cultures (150-I, 193-E, 193-L), gametophytes remained unisexual and female throughout the culture period. In the remaining cultures, hermaphroditic prothalli were produced (2)6–28 (mean ± s.d. = 15.6 ± 5.8) days following appearance of female prothalli (*Table 1*).

Gametangial sequences of individual gametophytes are diverse, but the vast majority of gametophytes exhibited a female to hermaphroditic sequence. Archegonia were initiated on the cushion immediately behind the young lateral meristem and were produced continuously until the gametophytes were fully cordate with a pronounced elongate cushion with numerous senescent gametangia (*Fig. 8*). Antheridia were initiated on wing tissue near the apical notch, initially along the margin of the cushion and later outward toward the wing margins (*Figs. 9* and *10*). Fully mature hermaphroditic gametophytes exhibited antheridia covering both wing surfaces near the apical region of the prothallus (*Fig. 10*). Antheridia have not been observed in the distal portions of the prothallus. In culture 190-A, sam-

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[1] Here and elsewhere in this paper the letter following the culture number designates a gametophyte population originating from a specific sporophyte.

ples of gametophytes 46 days after sowing indicated that some of them had produced up to 90 antheridial initials. These prothalli exhibited up to 28 or more senescent, 8 mature, and 50 immature archegonia. Six days later (52 days following sowing), fully mature hermaphroditic prothalli were present, exhibiting up to 60 senescent, 10 mature, and 35 immature archegonia, and over 325 antheridia per wing of which about 12% contained mature spermatozoids.

Gametophytes which were initially male produced only one or two antheridia prior to the initiation of archegonia. In most cases, following maturation and dehiscence of these antheridia, gametophytes became functionally unisexual and female and their subsequent ontogeny paralleled that described above.

TABLE 1. DAYS FROM SOWING TO APPEARANCE OF GAMETOPHYTE-TYPES IN CULTURES OF *A. AUREUM*.

Culture number	*Density/cm^2*	*Days to appearance of*		
		Male	*Female*	*Hermaphroditic*
146-C	27.7	28	21	38
146-G	6.5	35	29	(35)50
146-L	6.9		35	50
146-M	21.3		28	46
148-B	27.7		28	44
150-A	18.0	51	33	(35)56
150-B	29.7		33	44
150-C	28.2		33	56
150-E	3.9		35	50
150-I	8.1		33	–[1]
150-K	14.1		33	44
190-A	6.1		37	49
190-C	5.2		33	49
190-D	12.6	37	33	(33)46
190-F	31.5	59	33	53
193-A	17.6		28	56
193-B	98.3	44	32	–[2]
193-E	45.7		29	–[3]
193-K	79.1	29	29	39
193-L	1.5		29	–[3]

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[1] sampled up to 76 days
[2] sampled up to 85 days
[3] sampled up to 90 days

Some of the gametophytes expressed sequential patterns of functional unisexuality. In 146-C, about 15% of the sampled gametophytes expressed a sequence of archegonial initiation, maturation, and senescence, followed by initiation and maturation of antheridia. Other gametophytes appear to have gone through functional stages in sexual ontogeny from archegoniate to hermaphroditic to antheridiate to archegoniate. This sequence was noted in several older prothalli in 193-A (*Fig. 11*) and in one gametophyte of 150-K. In gametophytes producing proliferations near the base, such as those with two 1-dimensional filaments arising from the single basal cell, some of the proliferations were covered with antheridia, whereas others were only archegoniate.

Culture 193-K was unique among those studied in its expression of large numbers of male prothalli (*Table 2*). The initial ratio of male to female prothalli, excluding asexual prothalli, was 1:1. As the culture developed, male gametophytes increased in frequency to a 3:1 ratio; this; in turn, was followed by an increase in both female and hermaphroditic gametophytes. It is of interest to note that at the end of the observation period, there was a 1.1:1 ratio of male and hermaphroditic prothalli to female prothalli. Male gametophytes in this culture frequently were highly elongate and irregularly formed. Many of them initiated antheridia in the early ontogenetic stages following the attainment of a 2-dimensional morphology. In contrast, female prothalli were larger and appeared to be similar in all respects to the female prothalli of the other cultures.

TABLE 2. SEXUAL ONTOGENY IN AGAR CULTURES OF *A. AUREUM*.

	Sexual expression (%)			
Days from sowing	*Neuter*	*Male*	*Female*	*Hermaphroditic*
	Culture No. 146-C			
21	97.5		2.5	
28	48.6	5.4	45.9	
35	26.4		74.6	
38	8.7		78.3	13.0
44	10.5	2.6	68.4	18.0
47	20.0	5.7	40.0	34.2
	Culture No. 190-A			
33	100.0			
37	64.7		35.3	
43	22.2		77.8	
49	29.4		47.1	23.5
52	28.6		31.4	40.0
55	11.1		40.7	48.1
58	6.7		33.3	60.1
76			14.3	85.7
87				100.0
	Culture No. 193-K			
30–33	38.3	29.8	31.9	
39–45	21.7	56.7	19.1	2.5
48–54	15.9	32.9	50.0	1.2
63		24.4	46.3	29.3
	Culture No. 193-L			
30	71.4		28.6	
40	58.3		41.7	
42	38.5		61.5	
48			100.0	
90			100.0	

Parameters of gametophyte morphology and ontogeny discussed above suggest that intergametophytic mating should be prevalent in gametophyte populations of *Acrostichum aureum*. Specific factors exhibited by the gametophyte generation which increase the probability for intergametophyte mating include the female to hermaphroditic gametangial sequence in most gametophytes studied, the dioecious condition expressed in some populations, and the sequential functional unisexuality expressed in some gametophytes of some populations. Additional support for this assessment comes from observations on sporophyte production in composite cultures and in timing of the appearance of sporophytes in isolate vs. composite cultures. For example, in culture 146-M, after 83 days 90.9% of the prothalli were unisexual female and 9.1% were hermaphroditic. Examination of sampled prothalli indicated that all of the unisexual female gametophytes had produced one or two young embryos, which would only be possible through intergametophytic mating. In addition, in nearly all cultures sampled sporophyte production in composite culture occurred between 17 and 31 days earlier than in isolate culture. As the gametangial sequence is from female to hermaphroditic in these prothalli, in composite cultures spermatozoids produced by the early hermaphroditic gametophytes will fertilize many of the unisexual female prothalli. In contrast, in isolate culture, each of the gametophytes must become hermaphroditic prior to sporophyte production. This sequence of events has been well documented in studies on *Ceratopteris* by Klekowski (1970a).

TABLE 3. FREQUENCY OF DELETERIOUS SPOROPHYTIC GENOTYPES IN INTRAGAMETOPHYTICALLY SELFED, ISOLATED HERMAPHRODITIC GAMETOPHYTES OF *A. AUREUM*.

Culture number	*Number tested prothalli*	*No. (%) normal*	*No. (%) zygotic lethals*	*No. (%) embryonic lethals*	*No. (%) late sporophytic lethals*	*No. (%) leaky lethals*
146-N	19	18(94.7)	1(5.3)			
148-B	20	19(95.0)	1(5.0)			
150-A	20	19(95.0)	1(5.0)			
150-B	20	17(85.0)		1(5.0)		2(10.0)
150-I	18	17(94.4)	1(5.6)			
190-F	19	15(78.9)	3(15.8)	1(5.3)		
191-B	19	17(89.5)	1(5.2)		1(5.2)	
192-A	40	39(97.5)	1(2.5)			
193-C	20	17(85.0)	1(5.0)			2(10.0)
193-E	20	11(55.0)	9(45.0)			
193-F	8	7(87.5)	1(12.5)			
193-M	20	19(95.0)				1(5.0)
All others:[1]	511	511(100.0)				
Totals:	754	726(96.3)	20(2.65)	2(0.26)	1(0.13)	5(0.66)

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[1] Includes 27 cultures: 146-C, 146-G, 146-I, 146-J, 146-L, 146-M, 146-O, 150-C, 150-E, 150-H, 150-K, 190-A, 190-C, 190-D, 190-I, 191-D, 192-C, 193-A, 193-B, 193-D, 193-G, 193-H, 193-I, 193-K, 193-L, 193-N, 194.

Additional information relative to reproductive biology can be obtained by analyzing frequency of deleterious or lethal genes (genetic load) expressed in sporophytes (Klekowski, 1979). To analyze genetic load in *A. aureum*, from 20 to 40 gametophytes per sporophyte (= a gametophyte family), prior to the attainment of sexual maturity, were selected at random from stock cultures and individually isolated in 60 × 20 mm petri dishes containing nutrient agar. Following growth, cultures were watered twice weekly to facilitate fertilization, and the resultant sporophytes were allowed to develop to the third frond stage. Results of these studies are given in *Table 3*.

Genetic load was determined as the percentage of the hermaphroditic gametophytes per gametophyte family which failed to yield normal sporophytes. Families exhibiting genetic load in a portion of the gametophytes tested are considered to be expressing heterozygosity in their gametophytic genotypes. Expressions of genetic load were in the form of zygotic lethals (in 2.65% of the 754 gametophytes tested), embryonic lethals (in 0.26%), late sporophytic lethals (in 0.13%) and leaky lethals (in 0.66%) (see Klekowski, 1970b, 1979, for complete discussion of these genetic expressions). It is significant to note that 96.3% of the tested prothalli did not exhibit any deleterious or lethal genotypes. Of the 39 sporophytes tested, 27 (69.2%) were devoid of genetic load (*Table 4*). In the 12 sporophytes expressing load, it varied from 5.0% (cultures 148-B, 150-A, 193-M) to 45.0% (culture 193-E). The mean genetic load for all plants tested was 3.7%.

TABLE 4. GENETIC LOAD IN *A. AUREUM* RELATIVE TO SIZE AND LOCATION OF THE POPULATION.

Population culture number	*Location*	*Size (est. no. plants)*	*Range ($\bar{x}$) % genetic load*	*No. plants tested*	*No. (%) plants with genetic load*
193	Panama	3000	0–45.0 (5.96)	13	4(30.8)
190	Jamaica	1000	0–21.1 (4.22)	5	1(20.0)
191	Guyana	400	0–10.4 (5.2)	2	1(50.0)
150	Florida	75–100	0–15.0 (3.65)	7	3(42.8)
146	Florida	25–50	0–5.3 (0.66)	8	1(12.5)
148	Florida	20	5.0	1	1(100.0)
194	Panama	15	0	1	0(00.0)
192	Surinam	8	0–2.5 (1.25)	2	1(50.0)
Total:			0–45.0 (3.24)	39	12(30.8)

Although the number of plants tested from each population is insufficient for statistical comparison, it is of interest to note that those sporophytes exhibiting the higher genetic load values are found in the larger populations and that the small populations (with 50 or fewer individuals) have very low levels of recessive deleterious or lethal genes (*Table 4*).

Leaky lethal expression (Klekowski, 1970b) was noted in three gametophyte families. In 150-B, normal sporophytes appeared on the two prothalli 165 days after sowing and 38 days following normal sporophyte production of the remaining prothalli tested. Each of these two prothalli exhibited several abortive embryos, indicating that previous selfing had occurred involving lethal genetic combinations. In 193-M, the first sporophyte which appeared was abnormal and exhibited a long, cylindrical, tubular growth with ruffled margins. Subsequent sporophytes from other fertilizations produced normal fronds.

Apomictic proliferations were noted on only one gametophyte in 147-L. Ninety days after sowing, this prothallus proliferated a blade of tissue bearing rhizoids on one margin and small epidermal cells similar to those found on young sporophytes. Irregularly organized vascular tissue was present near the base of this blade, but no roots or stomata were noted.

DISCUSSION

Gametophyte Morphology.—The gametophyte morphology and ontogeny of *A. aureum* is remarkably similar to that of *A. danaeifolium* (Lloyd & Gregg, 1975) and agrees in most respects with that of *A. speciosum* Willd. (Stokey & Atkinson, 1952). Spores of *A. aureum* are almost identical in size and shape to those of *A. danaeifolium*; however, there are minute differences in spore surface markings, especially the more pronounced tuberculate pattern exhibited by *A. aureum*. Other gametophyte features which are qualitatively similar between the two species are formation of the 1-dimensional filament, the lateral meristematic region of the 2-dimensional prothallus, the relatively shallow apical notch region (however, protruding beyond the wing tissue in some prothalli of *A. aureum*), the female to hermaphroditic gametangial sequence, and the sexual expression in gametophyte families grown in composite culture.

The major difference between gametophytes of the two species is the distribution of antheridia, which are mostly restricted to the apical wing and meristem region of *A. aureum*, but also are found in more basal regions along the cushion margins and among the rhizoids in *A. danaeifolium*. In addition, the sequential production of archegonia-antheridia-archegonia in some prothalli of *A. aureum* is unknown in the other species.

It is apparent from both sporophyte and gametophyte studies that these two species are closely related. Further evidence in support of this is their ability to freely hybridize in culture and to produce normal viable F_1 sporophytes, although these sporophytes have not yet been grown to maturity to measure chromosome homology (Lloyd, unpubl.).

Reproductive Biology.—Sex ontogeny in most cultures of *Acrostichum aureum* sampled in this study is female to hermaphroditic or initially dioecious. The length of the unisexual stage prior to the attainment of bisexuality is sufficient to facilitate intergametophytic mating. The facility for such mating is also evidenced in culture by the rapidity of embryo formation in unisexual prothalli following the initiation of antheridia on just one gametophyte in a composite culture. Thus, the gametophytic developmental pathway must be considered as one which has a higher probability of intergametophytic mating than of intragametophytic selfing. However, correlative heterozygosity in the form of genetic load is insufficient in naturally occurring sporophytes to suggest that outbreeding is a normal occurrence. For example, of the tested plants 69% exhibited no heterozygosity for recessive deleterious genes and 15% exhibited such genes in less than 6% of the genotypes sampled. As intergametophytic mating is strongly suggested by the culture experiments, if the assumption is made that these plants are genetically homozygous due to the lack of genetic load expression, other factors must be superimposed upon the hypothesized mating system which are more significant in determining the genetic composition of the populations as a whole.

First and foremost, the culture methodology as used in these experiments may be insufficient to document with accuracy the gametangial sequences as they are realized in nature. In parallel experiments on *A. danaeifolium*, gametophytes grown on soil exhibit greater antheridial production (Lloyd & Gregg, 1975). Although some of these gametophytes undergo a male to hermaphroditic gametangial ontogeny, dioecism in cultures was still highly prevalent, suggesting that soil grown gametophyte populations in nature would have higher probabilities of intergametophytic mating. As gametophytic ontogenies on agar cultures of *A. aureum* and *A. danaeifolium* are highly similar, it is reasonable to assume that the gametophytes of *A. aureum* would present similar responses to soil culture. However, the habitat of *A. aureum* is at least partially inundated by tides, suggesting that the soil component for gametophyte populations will contain higher levels of salts. Brief experiments by Stokey & Atkinson (1952) using dilute sea water as part of the culture medium induced restricted growth of gametophytes of *A. speciosum.* This type of reduced growth under less than optimal conditions frequently leads to the initial production of antheridia and can prevent formation of viable archegonia (Page, 1979). Thus, it is possible that the gametophytic ontogenies in the culture experiments reported here do not represent gametophytic ontogenies as realized in nature.

Other factors which undoubtedly have a significant influence are population size, spore output per plant, the influence of the specific aquatic habitat, and the genetic system. It is of interest to note that the highest levels of genetic load were found in the larger populations, suggesting that the frequency and success of recombinants increases with number of individuals as well as age of the population. As spore production by each individual of *A. aureum* is massive, it is probable that inbreeding (in this case, intergametophytic selfing) will occur until such time as there is sufficient spore intermixing to increase the likelihood of outbreeding.

The influence of the aquatic habitat may play an important role in the selection of specific genotypes, perhaps perpetuated by intragametophytic selfing. It is significant to note that work to date on other aquatic species, including *Acrostichum danaeifolium, Ceratopteris thalictroides* and *C. pteridoides,* has provided highly similar results. These species are all characterized by a gametophyte ontogeny which favors intergametophytic mating (including an antheridogen in *Ceratopteris* spp.), but the vast majority of individuals tested express little or no heterozygosity in the form of genetic load. In this regard, Baker (1965) cites seashores and the margins of salt marshes as open habitats where species which are inbreeding with "general purpose genotypes" may be advantageous. Angiosperms which occupy these open and disturbed types of habitats are generally found to be autogamous or apomictic and so are unable to build up recombinants in the population rapidly.

Lastly, the genetic system of pteridophytes must be considered. We still have little understanding of the polyploid system and the maintenance and expression of heterozygosity in these organisms. It is possible that most of them are highly heterozygous and that genetic load is effectively screened from expression. If so, our current methodology for analysis for heterozygosity is insufficient.

It is obvious from these studies that we have little understanding of fern mating systems as they operate in nature and much further work, especially that oriented toward the genetic system and natural populations of gametophytes and sporophytes, is required before we will be able to circumscribe adequately these phenomena as they operate in nature.

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SHORTER NOTES

DIPLAZIUM JAPONICUM NEW TO ALABAMA.—In the summer of 1977 while I was a student at Auburn University, J. I. Glick, another student, asked me to confirm his identification of a fern frond he had collected from a plant growing in a steep-sided, wooded ditch on the Auburn campus in an area that had been allowed to remain wild by the university groundskeepers. Glick had identified the frond as *Athyrium thelypteroides*. However, Auburn is in Lee County of east-central Alabama, far south of the range of that fern, and the fern did not look exactly like *A. thelypteroides*. I identified the frond as *Diplazium japonicum* (Thunb.) Bedd., a native of eastern Asia (*Glick s.n., Short 979*, both AUA). According to Wherry (Southern Fern Guide, 1964), this fern had been found previously in one Florida locality. Wherry was doubtful whether the fern was cultivated locally and did not know the source of the spores which produced the plants. The species is not known to be in cultivation in the Auburn area, and the source of these plants is equally unknown. To my knowledge, *D. japonicum* has not been reported from any other localities in the southeastern United States. The Auburn population consisted of two mature, spore-bearing plants and several juveniles. The plants seem to be established well enough to be considered naturalized. The winters previous to and subsequent to the plants' discovery were among the most severe on record, but they had no adverse effect on the plants. Other ferns found in the ditch include *Asplenium platyneuron* and the naturalized *Lygodium japonicum*, *Pteris multifida*, and *Thelypteris torresiana*.—*John W. Short, 905 McKinley Ave., Auburn, AL 36830.*

MOTHS AND FERNS.—In a previous paper (Amer. Fern J. 61:166-170. 1971), I reported on a nymphalid-like moth that oviposits on *Cyathea holdridgeana* in such a fashion that the eggs mimic the immature sori of the fern. Recently, I have found the larvae of a microlepidopteron predating the laminar tissue of *Cnemidaria mutica, C. choricarpa,* and *Sphaeropteris brunei,* of the family Cyatheaceae. In their last stages, the caterpillars weave cocoons with silk, spores, and sporangia. The adults obtained from the three ferns are the same species of moth, a species yet to be determined. Another moth lays eggs on the fronds of *Botrychium dissectum*. The larval stages feed on it and later spin a cocoon by sewing together two segments or pinnules.

The most interesting relationship between moths and ferns I have encountered so far is that of *Hymenophyllum myriocarpum* and a microlepidopteron whose larvae feed on the filmy fern and pupate in a case made up of the folded segments, which then resemble mature involucres in their size, color, and position. It is surprising to find that the insects only use the basal, lower, and middle pinnae of the fern fronds to build their cocoons, perhaps to guarantee themselves an appropriate relative humidity among the mosses or a more efficient camouflage. Certainly, a careful survey of tropical ferns will reveal that they are not so impervious to insect attack as they commonly are thought to be.—*Luis D. Gómez P., Herbario Nacional, Museo Nacional de Costa Rica, Apartado 749, San Jose, Costa Rica.*

THREE ADDITIONS TO THE PTERIDOPHYTE FLORA OF ESCAMBIA COUNTY, FLORIDA. — In 1978 a number of students from the University of West Florida conducted a field survey of the pteridophytes of Escambia County, Florida, concentrating on the botanically largely unexplored northern part. Just north of where Florida Highway 4 crosses Canoe Creek (R31W, T5N, Sec. 8), eight fern species were found along the west bank, including two which we had not observed previously in the county: *Thelypteris torresiana* (Gaud.) Alston (*Burkhalter & Booker 5844, 5912*) and *Athyrium asplenioides* (Michx.) A. A. Eaton (*Burkhalter & Booker 5845, 5913*). Vouchers have been deposited at the University of Florida, Gainesville (FLAS), and the University of West Florida, Pensacola (UWFP). Dr. Daniel B. Ward (pers. comm., 26 Feb. 1979) verified that these species had not been collected previously in Escambia County.

The collection site is an open area with mostly clay and sand soil. In addition to a number of weedy flowering plants like *Carex* spp. and *Boehmeria cylindrica*, the following ferns were found: *Asplenium platyneuron, Lygodium japonicum, Osmunda regalis, O. cinnamomea, Thelypteris normalis*, and *Woodwardia areolata*. *Thelypteris torresiana* and *A. asplenioides* are not found in the shaded swamp forest understory somewhat to the north of the collection site; they were, however, observed at a few other scattered locations in northern Escambia County.

Later, a small, spontaneous colony of *Nephrolepis cordifolia* (L.) Presl was discovered in downtown Pensacola on an old, brick building at the northeast corner of Palafox and Main Streets. The plants were securely anchored in the brickwork about seven feet above the sidewalk, and were situated below the broken end of a raingutter downspout, from which they received plentiful water. This is not an unusual habitat for certain ferns in urban areas like New Orleans and Mobile, and the colony appeared to be quite old and healthy. Clifton Nauman (pers. comm., 31 Aug 1978) commented that the specimen (*Burkhalter 5919*, UWFP) constituted a new record for Escambia County.—*James R. Burkhalter, 3703A W. Brainerd St., Pensacola, FL 32504.*

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A Range Extension for Dryopteris filix-mas

ERWIN F. EVERT*

On 14 December 1979, I collected *Dryopteris filix-mas* (L.) Schott in a mesic ravine in Glencoe, Cook County, Illinois. Two large plants and a smaller one were growing within a few feet of each other on a steep, relatively undisturbed northwest-facing slope of the ravine, about 400 feet west of Lake Michigan in T42N, R13E, SE1/4, Sec. 6. Associates were *Acer saccharum, Aralia nudicaulis, Hamamelis virginiana, Quercus rubra,* and *Trillium grandiflorum*. A search of other ravines in the vicinity failed to reveal any other plants of *D. filix-mas*.

This fern has not been reported previously for Illinois (Mohlenbrock & Ladd, 1978). It is newly reported for Wisconsin (Brown County) by Peck and Taylor (1980). The nearest stations appear to be in Marquette County, Michigan (Billington, 1952, p. 177) and in Brown County, Wisconsin, about 270 and 160 miles distant.

Are these plants spontaneous on this site or is their occurrence due to the actions of man? Although this question cannot be answered with absolute certainty, the following points support natural occurrence:

(1) The plants grow in an environment typical for the species, in a relatively undisturbed area with autochthonous associates.

(2) Pepoon (1927), Moran (1978), Swink and Wilhelm (1979), and personal observation document the presence of many other uncommon plants for this area in the ravines along Lake Michigan. Some of these are: *Dryopteris intermedia, D. marginalis, Equisetum scirpoides, Fagus grandifolia, Lycopodium lucidulum, Mitchella repens, Pinus resinosa, Polystichum acrostichoides, Shepherdia canadensis,* and *Thelypteris hexagonoptera*.

(3) Personal observation indicates that *D. filix-mas* is not commonly cultivated in this area at present. Therefore, it is not likely that these plants have escaped from cultivation. Although the Male Fern formerly was grown for its medicinal properties, the colony does not appear to have been established for a long time, and so it is unlikely to have originated from plants that were cultivated in the past. It is also unlikely that plants on such a steep and inaccessible site were deliberately planted.

(4) Single plants or small colonies of other ferns with northern distributions are known to occur widely disjunct in southern Michigan (Wagner, 1972, p. 205 and pers. comm.). Examples include *Botrychium minganense, Gymnocarpium dryopteris,* and *Polystichum braunii*.

(5) *Dryopteris filix-mas*, a homosporous pteridophyte, apparently is capable of intra-gametophytic selfing (W. H. Wagner, pers. comm.), and so one wind-borne spore could produce a new, disjunct colony.

(6) The distribution pattern of *D. filix-mas* (Hultén, 1962, p. 119), with its widely disjunct stations in California, Mexico, South America, Hawaii, Greenland, Iceland, and Africa, indicates that this species is capable of wide dispersal.

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*1476 Tyrell St., Park Ridge, IL 60068.

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Specimens of *Evert 1651* have been deposited at the Morton Arboretum Herbarium (MOR) and the University of Michigan Herbarium (MICH).

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Differential Germination of Fern and Moss Spores in Response to Mercuric Chloride

RAYMOND L. PETERSEN and PATRICK C. FRANCIS*

The pervasive use of toxic substances and the synthesis of myriad new such compounds requires that toxic substance limits be set and that environmental monitoring be maintained in order to insure the health and integrity of the biosphere. Bioassays are the primary mechanism for meeting these two requirements. A bioassay designed to determine the environmental impact of a particular toxic substance, for example divalent mercury, should have the following attributes: ease of performance, low cost, brevity, sensitivity, and high overall reflectivity of environmental stress induced by the presence of the toxic substance. The appropriateness of a bioassay is based on the selection of its two primary components—the living system employed and the parameter measured.

Petersen et al. (1980) have demonstrated the feasibility of using the germination of *Onoclea sensibilis* spores to gauge the toxicity of various heavy metal ions. It was found that for the three metal ions tested, toxicity was directly proportional to atomic weight. Hg^{++} is twice as toxic as Cd^{++} and four times as toxic as Co^{++}. The present study is a comparison of the germination responses of different fern and moss spores to divalent mercury.

There are few investigations on the effects of metal ions and other potential pollutants on fern spores and gametophytes that yield data pertinent to pollution research and control. Nakazawa and Tsusaki (1959) determined that the fern spore cytoplasm associated with rhizoid differentiation has a marked affinity for metal ions. Nakazawa and Otaki (1962) demonstrated the affinity of developed rhizoids for metal ions. Fern rhizoids apparently function like the root hairs of vascular plants in absorbing water and minerals from the soil. Therefore, their affinity for metal ions is not surprising. Co^{++} and Ni^{++} were shown to prolong filamentous (one-dimensional) growth in *Lygodium smithianum* gametophytes (Parés, 1958) resulting in a retardation of their development sequence. LiCl caused a precocious differentiation of terminal papillae (gland-like hair cells produced by some fern gametophytes) in *Dryopteris varia* (Nakazawa, 1960a, b). Several metal chlorides at concentrations of 0.005–0.08M decreased the period of fern sperm motility (Igura, 1958).

A few papers on ferns with direct application to pollution monitoring have been published. Klekowski (1976), Klekowski and Berger (1976), and Klekowski and Poppel (1976) found that meiotic chromosome behavior during fern sporogenesis was correlated with the presence of toxic substances in the environment. Howard and Haigh (1972) studied the effects of increasing doses of X-radiation on the first mitotic division of *Osmunda regalis* spores. Edwards and Miller (1970, 1972a, b) studied the quantitative effects of ethylene on *Onoclea sensibilis* spore germination and gametophyte growth. Fern gametophytes also have been successfully employed in bioassay procedures for the plant hormones kinetin, gibberelic acid, and antheridogen (Bopp, 1968; Brandes, 1973).

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*Department of Botany, Howard University, Washington, DC 20059.

Mosses are especially adapted to absorb and concentrate substances present in the atmosphere, and so moss gametophytes have proven to be sensitive indicators of airborne pollutants (Huckabee, 1973; Skaar et al., 1973; Little & Martin, 1974). Francis and Petersen (1980) reported on the synergistic effects that metal ion combinations had on the germination of *Polytrichum commune* spores.

Spores of *Onoclea sensibilis, Osmunda cinnamomea,* and *Osmunda claytoniana* and the moss *Polytrichum commune* were selected for investigation because they are of wide distribution and frequent occurrence and all produce copious quantities of easily collected spores. In addition, *O. sensibilis* had been employed in the development of the fern spore heavy metal bioassay (Petersen, et al., 1980). The two *Osmunda* species represented a fern family distinct from that of *Onoclea* and would yield data on intrageneric differences in response to heavy metal ions. *Polytrichum commune* was selected to compare its heavy metal response with those of the ferns.

TABLE 1. SPORE GERMINATION IN VARIOUS Hg^{++} CONCENTRATIONS EXPRESSED AS A PERCENTAGE OF CONTROL GERMINATION.[1]

Hg^{++} ppm	*O. sensibilis*	*O. cinnamomea*	*O. claytoniana*	*P. commune*
0.0	100	100	100	100
0.2	101	98	96	77
0.4	98	91	89	30
0.6	98	77	33	8
0.8	88	60	20	0
1.0	85	13	14	0
1.5	75	8	-	0
2.0	68	1	1	-
3.0	55	0	0	-
4.0	30	-	-	-
6.0	9	-	-	-
8.0	1	-	-	-
10.0	0	-	-	-
20.0	0	-	-	-

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[1] Tests were not run, or the experiment was lost, where no numerical value is given.

MATERIAL AND METHODS

Approximately 10,000 spores of each species were cultured in a petri dish 60mm diam. in 8 ml of full strength liquid Knudson's medium at a pH 5.5 with 0–20 ppm of divalent mercury ion (Hg^{++}) added as $HgCl_2$. The dishes were sealed in clear plastic sandwich bags and cultured in a Sherer Growth Chamber at 20°C in 300 ft-c of continuous light from cool-white fluorescent lamps. Spore germination was considered to have occurred when the spores produced a rhizoid or the first prothallial cell divided. After eight days, 500 spores were examined per plate. Three replicates were run for each species tested at each Hg^{++} concentration.

RESULTS AND DISCUSSION

The germination of the controls (0 ppm HG^{++}) was uniformly high; *O. sensibilis* had 88%, *O. cinnamomea* 92%, *O. claytoniana* 96%, and *P. commune* 94%. Spore germination at each Hg^{++} concentration except one was lower than in the controls. Germination was expressed as a percentage of each species' control germination (*Table 1*). These results are summarized in terms of the standard bioassay toxicity values of LC_{50} and LC_{100}, which are presented both in terms of ppm and µM (*Table 2*). LC_{50} is the concentration of a toxic substance necessary to kill 50% of the organisms from a control value, and LC_{100} is the minimum concentration necessary to kill 100%.

TABLE 2. Hg^{++} LC_{50} AND LC_{100} VALUES FOR FOUR TAXA.

Toxicity value	*O. sensibilis*	*O. cinnamomea*	*O. claytoniana*	*P. commune*
LC_{50}				
ppm	3.2	0.82	0.53	0.30
µM	16	4.1	2.6	1.5
LC_{100}				
ppm	10	3.0	3.0	0.8
µM	50	15	15	4.0

A comparison of spore germination responses shows that *P. commune* is the taxon most susceptible to HG^{++} and is ten times more sensitive than *O. sensibilis*, which is the least susceptible. The two *Osmunda* species have intermediate and similar HG^{++} toxicity values. They are approximately four times more sensitive to HG^{++} than is *O. sensibilis* (*Table 2*). Therefore, based on the sensitivity of response, *P. commune* would be the species of choice in a mercury ion bioassay.

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Differences in the Apparent Permeability of Spore Walls and Prothallial Cell Walls in Onoclea sensibilis

JOHN H. MILLER

The spores of *Onoclea sensibilis* L. undergo marked changes in their apparent permeability during germination. For example, spores do not stain with an acetocarmine-chloral hydrate mixture until germination has proceeded for about 20 hr (Towill & Ikuma, 1975; Fisher & Miller, 1978), whereas after that time stain is absorbed readily. During the early stages of germination, the spores of *Onoclea*, *Matteuccia struthiopteris* (L.) Tod., and other species are difficult to prepare for electron microscopy because embedding resins fail to penetrate adequately (Marengo, 1973; Gantt & Arnott, 1976; Raghavan, 1976). Spores in later stages can be processed with no difficulty. This impermeability seems to be associated with the inner spore coat (intine). Fisher and Miller (1978) noted that when the intine of *Onoclea* spores was artificially ruptured during the early stages of germination and the protoplast was directly exposed to acetocarmine-chloral hydrate, the protoplast stained rapidly, whereas no intact spores could be stained. The time at which *Matteuccia* and *Onoclea* spores normally become penetrable by embedding resins coincides with the time the intine ruptures naturally during germination (Gantt & Arnott, 1965; Marengo, 1973). If the intine of *Onoclea* is caused to open by treatment with sodium hypochlorite, even dormant spores and those in early stages of germination may be infiltrated readily with embedding resin (Bassel, Kuehnert & Miller, 1981).

Dormant spores of both *Onoclea* and *Matteuccia* have a loose outer spore coat and a thick intine, along which there is a longitudinal seam, the raphe (laesura), on the flattened, proximal face of the spore; the spore protoplast is naked within the intine (Gantt & Arnott, 1965; Bassel, Kuehnert & Miller, 1981). Germinating spores synthesize a new wall around the protoplast inside the intine between 8 and 16 hr. At the time the intine ruptures and is cast off, this new wall becomes the bounding wall of the young protonema. Clearly there is a difference in which materials will penetrate the spore intine and which will cross the normal prothallial cell wall. Carpita et al. (1979) published a method for obtaining quantitative information about the apparent capillary pore size of plant cell walls, which limits the passage of solutes. The cells are placed in a solution of a non-ionic solute having a water potential lower than that of the cells, which causes water to leave the cells. If the solute can pass through the wall, and thus the solution can be in contact with the plasma membrane, one observes plasmolysis (retraction of the protoplast from the cell wall). If, however, the solute particles are too large to penetrate the wall, exit of water from the cell causes cytorrhysis (collapse of the cell wall around the protoplast as it shrinks). I applied this technique to spores and young gametophytes of *Onoclea* and observed differences in the apparent capillary pore sizes of the spore intine, prothallial cell walls, and rhizoid walls.

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*Department of Biology, Syracuse University, Syracuse, NY 13210.

MATERIALS AND METHODS

Sporophylls of *Onoclea sensibilis* were collected in the vicinity of Syracuse, NY in the fall of 1978. They were stored in plastic bags and refrigerated until needed. The methods by which spores were isolated from the fertile fronds and general cultural methods are described in Miller and Greany (1974). An additional step was taken in which the outer spore coat was removed from the dry spores by brief treatment with sodium hypochlorite, following which the spores were redried and stored (Vogelmann & Miller, unpubl.). Removal of the brown outer spore coat made it easier to observe plasmolysis or cytorrhysis. Dormant spores were hydrated before they were used by floating them on the surface of distilled water for three hours. Young gametophytes were grown by floating spores on the surface of Knop's solution for three days in an air-conditioned growth chamber where the temperature was 26 ± 1°C and the light intensity was about 800 ft-c of continuous cool-white fluorescent illumination. After three days, the gametophytes had 3–5 vegetative cells and one primary rhizoid.

The solutes tested included NaCl, ethylene gylcol, glycerol, glucose, sucrose, polyethylene glycol-600 (PEG-600) and PEG-1000 (all chemicals from Fisher Scientific Co.). All compounds were dissolved in distilled water. The concentrations of the solutions, which are given in *Table 1*, were selected in preliminary experiments so that responses were observed within 1–5 min. Spores or prothallia were mounted directly in a drop of solution on a microscope slide and were covered with a cover slip. Observations were made with a microscope at a magnification of approximately 300 ×. Photographs were made of representative cells.

TABLE 1. INDUCTION OF PLASMOLYSIS (P) OR CYTORRHYSIS (C) BY DIFFERENT SOLUTES.

Substance and Concentration[1]	*Molecular diameter* (nm)[2]	*Spores*	*Prothallial cells*	*Rhizoids*
Ethylene glycol (50, 15)	0.45	P	P	P
Glycerol (50, 15)	0.55	P	P	P
Glucose (50, 20)	0.88	C	P	P
Sucrose (50, 20)	1.03	C	P	P
PEG-600 (50, 20)	2.9	C	P and C	P
PEG-1000 (—, 40)	3.5	—	C	C

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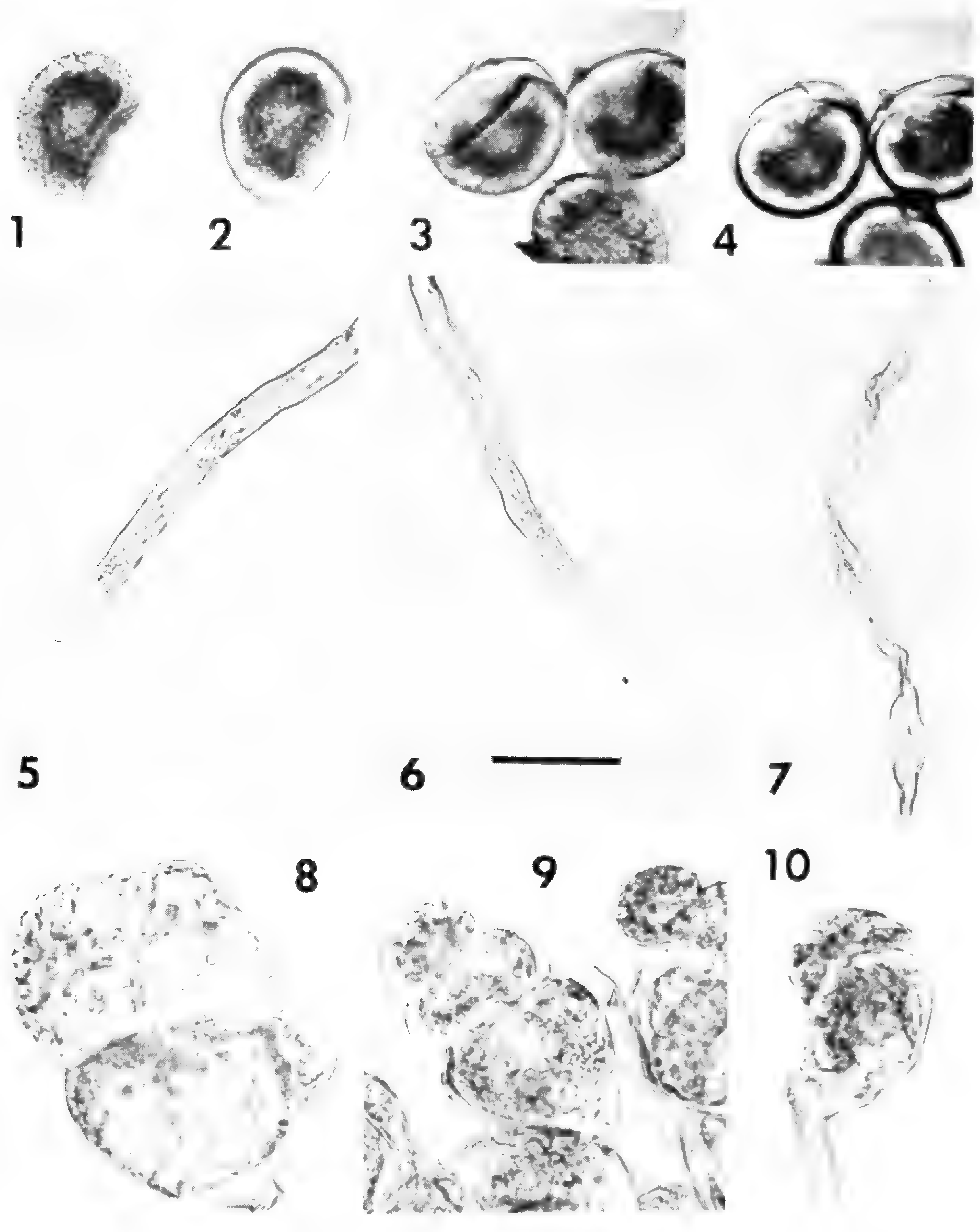
[1] % concentration (w/v). First concentration in parenthesis is for spores; second concentration is for prothallia and rhizoids.

[2] Values for ethylene glycol and glycerol from Goldstein and Solomon (1960); for glucose and sucrose from Durbin (1960); for PEG-600 and PEG-1000 from Carpita, et al. (1979).

RESULTS AND DISCUSSION

The phenomena of plasmolysis and cytorrhysis occurred in *Onoclea* spores, prothallial cells, and rhizoids *(Table 1)*. Collapse of the spore wall through cytorrhysis was demonstrated in 50% sucrose (*Figs. 1* and *2* show two views of a spore at different focal levels). Typically the spores became indented and bowl-shaped; the indentation always occurred on the proximal face (*Fig. 1*). No plasmolytic retraction of the protoplast took place at any point; even at the rim of the



Figs. 1–10. Examples of plasmolysis and cytorrhysis in spores, rhizoids, and prothallial cells of *O. sensibilis*; 50 μm scale is the same for all photographs. FIGS. 1 and 2. Cytorrhysis in a spore shown at different focal levels. FIGS. 3 and 4. Plasmolysis in spores shown at different focal levels. FIG. 5. Control rhizoid. FIG. 6. Plasmolysed rhizoid. FIG. 7. Ribbon-like rhizoid, collapsed as a result of cytorrhysis. FIG. 8. Control prothallus. FIG. 9. Plasmolysed prothallus. FIG. 10. Cytorrhysis in prothallus.

bowl the granular cytoplasm was in contact with the intine (*Fig. 2*). A 15% NaCl solution clearly induced plasmolysis (*Fig. 4*). Spore plasmolysis also was accompanied by an indentation of the proximal spore face (*Fig. 3*), since there appeared to be a firm adhesion of the protoplast to the intine in the area of the raphe, and when the protoplast became plasmolysed, the intine was drawn in at that point. A control rhizoid is shown in *Fig. 5*, and plasmolysis in 20% glucose is illustrated in *Fig. 6*. Cytorrhysis in a rhizoid in 40% PEG-1000 resulted in the collapse of the cell into a ribbon form (*Fig. 7*). The vegetative portion of a normal prothallus is pictured in *Fig. 8*. Plasmolysis gave the appearance shown in *Fig. 9*, whereas the collapse and crumpling of the cells through cytorrhysis is shown in *Fig. 10*. The figures give the pictorial definition of the terms plasmolysis and cytorrhysis as they are used in this paper.

The main results are summarized in *Table 1*. Prothallial cells showed only plasmolysis with compounds up to the size of sucrose. PEG-600 caused both cytorrhysis and plasmolysis, whereas PEG-1000 produced pure cytorrhysis. Following the reasoning of Carpita, et al. (1979), the limiting pore size of prothallial cell walls appears to be between 2.9 and 3.5 nm. This is somewhat smaller than the values found by Carpita, et al. (1979) for the cells of several species of angiosperms. Rhizoids appear to have a slightly larger wall pore size than prothallial cells, since PEG-600, which caused both cytorrhysis and plasmolysis in prothallial cells, caused only plasmolysis without cell collapse in rhizoids. The overall permeability of rhizoids was shown by Smith (1972) to be greater than the permeability of prothallial cells of *Polypodium vulgare*. His measurements were made by following the uptake of a vital dye into the protoplast, and thus reflect the permeability of the plasma membrane. The results of the present study indicate that some of the difference between the permeability of rhizoids and prothallial cells may be caused by differences in the permeabilities of their walls. The spore intine clearly was much more impermeable than the cell walls of the gametophyte. Glycerol was the largest molecule which caused plasmolysis of the spore protoplast; glucose induced pure cytorrhysis. The capillary pore size of the intine appeared to be less than 0.8 nm.

Spores were visibly affected only by higher concentrations of each of the substances than were required to produce effects in rhizoids or prothallial cells. This may reflect the fact that the spore cytoplasm is very dense and non-vacuolate, as seen in electron micrographs (Bassel, Kuehnert & Miller, 1981). More of the water of the spore may be bound in the hydration of proteins, for example, and relatively little available for free osmotic exchange. The same concentrations of osmotic solutions which plasmolysed or collapsed prothallial cells within 1–5 min acted much more rapidly on rhizoids. In each test, rhizoids were affected in less than 30 sec, the time necessary to prepare the sample and make the first observation. This rapidity is probably another reflection of the greater permeability of rhizoids. When young gametophytes were placed in plasmolysing solutions, the basal cell of the plant was affected first, followed by the intermediate and more apical cells. Deplasmolysis occurred in prothallial cells and rhizoids which were plasmolysed in certain of the solutions. Both cell types deplasmolysed completely within 15 min after immersion in ethylene glycol. Prothallial cells were deplasmolysed completely in two hr in glycerol and were partially deplasmolysed in the same time in glucose.

Rhizoids showed only a partial recovery in either of these two compounds. Plasmolysis appeared to be permanent in solutions of any of the large substances. The instances of deplasmolysis indicate that the plasma membranes of the cells were permeable to the plasmolysing solute, and enough was taken up eventually to reverse the flow and cause an influx of water into the protoplasts.

The results which are presented in this paper support the idea that the low permeability of *Onoclea* spores results from the permeability properties of the intine. The estimated capillary pore size of the intine is only about one quarter that of prothallial cells and rhizoids. The intine should play a major role in determining the entry and exit of materials into and from the spore during the first stages of germination before the intine is ruptured. Some aspects of permeability seem not to be explicable on this basis. Vogelmann (1980), for example, showed that colchicine, griseofulvin, and isopropyl N-chlorophenyl carbamate produce striking effects on spore germination, and each appears to enter the spore before the time of intine rupture, although one would expect them to be excluded on the basis of their size. One possible explanation for this type of anomaly is the suggestion by Carpita, et al. (1979) that a small number of larger pores might provide access to the protoplast by larger molecules, whereas osmotic effects may be governed by the more abundant smaller pores.

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Allelopathy and Autotoxicity in Three Eastern North American Ferns

WILLIAM E. MUNTHER and DAVID E. FAIRBROTHERS*

Undoubtedly gametophytes are the most vulnerable stage in the fern life cycle. Although individual sporophytes produce from 50 to 100 million haploid spores (Shaver, 1954), few of the small, delicate gametophytes, which in most ferns are less than 1.25 cm wide, survive and produce sporophytes. Conditions governing spore germination are critical to gametophyte establishment. Conway (1953) found that, in Scotland, few gametophytes or young sporophytes of *Pteridium aquilinum* occurred under field conditions, despite heavy spore production by mature plants. This suggests that the gametophyte and young sporophyte stages may be limiting in the establishment of this species. Many studies (cited in Hill, 1971) suggest that fern gametophytes and sporophytes can possess quite different habitat requirements and that one stage of the life cycle can be more sensitive than the other to physical and biological conditions, and so limit the success of the species.

Although environmental (abiotic) conditions are extremely important, biotic conditions, particularly those created by the sporophytes or gametophytes, may also be of critical importance in the establishment of new individuals of the same or another species. Therefore, these factors may regulate both population density and community composition. Chemical inhibition of one plant by another, or allelopathy, has been known for over a century (Muller, 1966) and has been much studied in flowering plants and conifers. The phenomenon of antibiosis is also well known to microbiologists. However, relatively little research has been devoted to plant inhibitors produced by non-seed plants, other than microorganisms (Rice, 1967).

Bohm and Tryon (1967) reported that many species of ferns produce phenolic compounds. They examined 46 species for the presence of hydroxylated cinnamic and benzoic acids and found a basic complement of cinnamic acids (p-coumaric, caffeic, and ferulic) in the ferns they tested. Also generally present were p-hydroxybenzoic, protocatechuic, and vanillic acids. Sinapic, syringic, and o-coumaric acids were reported to be less common. In a follow-up study, Glass and Bohm (1969) found similar phenolic compounds in 46 additional species. The presence of a basic complement suggests that the well established pathways of phenolic metabolism in the seed plants also function in ferns.

Many of the phenolic compounds found in ferns are known to be allelopathic in many species of higher plants, either directly or indirectly, such as after microbial decomposition (Rice, 1974). Most phenolic acids are at least slightly soluble in water. With the increasingly acidic rainfall in the northeastern United States (Likens et al., 1970; Bormann & Likens, 1977), weak organic acids such as the phenolics may be leached quite readily either from the leaves during the growing season or from senescent plants. A wide variety of organic and inorganic sub-

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*Department of Botany, Rutgers University, New Brunswick, NJ 08903.

stances known to be allelopathic are capable of being leached from the leaves of a number of species of higher plants (Tukey, 1966, 1969; Rice, 1974).

Of the few allelopathic studies concerned with ferns, most have involved *Pteridium aquilinum*. Del Moral and Cates (1971) reported that aqueous leaf extracts and litter extracts of *P. aquilinum* inhibit seeds of *Hordeum vulgare*, *Bromus tectorum*, and *Pseudotsuga menziesii*. Gliessman and Muller (1972) found that *P. aquilinum* inhibited germination and subsequent radicle growth of seeds of *Bromus rigida* and *Avena fatua*. The toxic principle was detected in the fern leaf leachates. Because the toxic principle was transported by some form of precipitation, water-soluble phenolic acids were suspect, and cinnamic acid was tentatively identified. In another study, Stewart (1975) found that water-soluble extracts from Western Bracken (*P. aquilinum* var. *pubescens*) delayed germination of *Rubus spectabilis* seeds and inhibited germination of *R. parviflorus* seeds, but had no effect on the seeds of *Pseudotsuga menziesii*.

Glass (1976) prepared a solution of phenolic acids having the same composition as was detected in the soil associated with the roots of *P. aquilinum* and tested its effect on the growth of barley, wheat, oats, rye, rye-grass, barley grass (*Hordeum murinum*), clover, and *Agropyron repens*. Growth was inhibited in all species investigated except *A. repens*. Whether *P. aquilinum* sporophytes in some way inhibit the germination of their own spores or those of another species of fern was not investigated in Glass's or any other study reported in the literature.

Davidonis and Ruddat (1973) found that *Thelypteris normalis* sporophytes inhibit the growth of *T. normalis* gametophytes, as well as those of *Pteris* and *Phlebodium*. The inhibitors, which they termed thelypterins a and b, were similar in many ways to indoleacetic acid (IAA) and were found to be exuded from sporophyte roots. Davidonis and Ruddat (1974) also reported that gametophytes grown in the immediate vicinity of a mature sporophyte of *T. normalis* had a reduced number of cells and an altered gross morphology. They observed the greatest inhibition of *T. normalis* gametophytes when the thelypterins were added before spore germination had occurred.

Davidonis (1976) reported that *T. noveboracensis*, *Pteris multifida*, and *P. vittata* also contained thelypterins. Since the thelypterins were detected in leaf diffusates of *T. normalis* and *T. noveboracensis*, she postulated that foliar leaching may be one mechanism by which these inhibitors are released into the environment.

Petersen (1976) found that *Dryopteris intermedia* and *Osmunda cinnamomea* gametophytes inhibited each other's development when grown together in culture. He also reported that gametophytes of these two species "lock" each other into perpetual juvenility. Petersen was unable to isolate and indentify the inhibitory substances since they occurred in very small amounts or were highly volatile.

Horsley (1977) reported that the presence of *Dennstaedtia punctilobula* and *T. noveboracensis* sporophytes were correlated with reduced numbers of *Prunus serotina*, *Acer rubrum*, and *A. saccharum* seedlings under field conditions.

Very limited research has been conducted either to detect possible allelopathic interactions between species of ferns or to demonstrate the inhibition of one generation by the other within a species (autotoxicity). It is not known whether allelopathy and autotoxicity are widespread in natural fern communities. Davidonis and Ruddat (1973, 1974) and Davidonis (1976) examined a small number of species for inhibitors, but in many instances the species tested for allelopathic interactions were those that are maintained in greenhouses, and not those which occur together in natural situations. Petersen (1976) has shown that fern gametophytes of one species produce substances that inhibit gametophytes of others, the classic allelopathic inhibition of one species by another. Under field conditions, however, the dominant and normally perennial sporophytes probably produce much greater quantities of allelopathic compounds capable of affecting spore germination or gametophyte growth than would the much smaller gametophytes. Petersen's research suggests that sporophytes might also inhibit gametophytes, as they were found to have produced the same flavonoids, but no experimental evidence to support such a hypothesis was presented.

There are reports suggesting allelopathy between fern generations in both natural populations and the greenhouse. In greenhouses, potted ferns often produce large numbers of spores, but gametophytes are seldom found growing on the soil surface directly underneath the sporophytes. It is also unusual to find gametophytes growing underneath or even near mature sporophytes under field conditions, even when spore production is heavy.

In this research, aqueous leaf extracts, leaf leachates, and leaf litter infusions from *Osmunda cinnamomea, O. claytoniana*, and *Dennstaedtia punctilobula* were examined for their allelopathic and autotoxic potential. Leaves of all three species were also tested for the production of volatile inhibitors.

All three species occupy much the same habitat, although *O. cinnamomea* is often found in moister areas than the other two. The geographical ranges of all three species also are approximately the same, and all are native and common in the northeastern United States. Although these three species occupy almost identical habitats, they seldom occur in close proximity to one another within a given area.

MATERIALS AND METHODS

Mature spores of *O. cinnamomea, O. claytoniana*, and *D. punctilobula* were collected in 1976 and 1977 from wild populations which were located in Sandystone Township, Sussex County, New Jersey, and in the Town of Goshen, Addison County, Vermont.

Spore-bearing leaves of both species of *Osmunda* were collected during the first two weeks of May from New Jersey populations and during the last week of May and first week of June from Vermont populations. Sporangia were allowed to dehisce at room temperature. Spores were refrigerated at 4.4° C as soon as possible after they were shed from the sporangia. Although *Osmunda* spores contain chlorophyll and remain viable for only a few days at room temperature (Cobb, 1963), they will retain their viability for over a year if refrigerated (Stokey, 1951).

Spore-bearing leaves of *D. punctilobula* were collected during the last two weeks of July from the New Jersey populations and during the first week of

August from Vermont populations. After dehiscence of the sporangia, spores were stored dry and at room temperature. The spores of *D. punctilobula* lack chlorophyll and have a thicker, more resistant spore wall than *Osmunda* spores, and so require no refrigeration to remain viable.

Fresh fronds from all three species were used to prepare aqueous extracts and leachates. They were collected from both Vermont and New Jersey populations throughout the growing season. Fronds were refrigerated immediately after collection and were then stored at 4.4° C. The extracts and leachates were prepared from the fronds within three or four days after collection.

All aqueous leaf extracts were prepared by first cutting into pieces 5 g of leaves (fresh weight) and then placing the pieces in 80 ml of distilled water. The leaves were boiled briefly (3 min) to stop enzyme activity and, it was hoped, to destroy some of the microorganisms which might later contaminate cultures. After boiling, the leaves were ground in a Virtis blender for 5 min. The ground mixture was then vacuum filtered and the resulting aqueous extract was brought to volume with distilled water (100 ml distilled water for each 5 g of ground leaves). Extracts were stored at 4.4° C until they were used to prepare cultures, usually within 3–5 days.

Leaf leachates for each species were prepared by placing fronds (2 thick) on 1.5 mm mesh screen which was placed on top of a rectangular plastic box. Fronds having an area of ca. 630 cm^2 were then misted with 300 ml of distilled water. The droplets of water falling from the leaves were collected in the large plastic box. Leachates were stored at 4.4° C until used.

Litter infusions were prepared by placing 10 g of chopped dry frond litter in a 500 ml beaker. Weekly additions of 100 ml of distilled water were made for a period of 3 weeks. Beakers were placed in direct light in the greenhouse. Filter paper was placed on top of each beaker to prevent external contamination. After 3 weeks, the aqueous portion of the infusion was decanted and vacuum filtered. The filtered liquid was used to prepare the experimental cultures.

The methods used to prepare cultures were based on those reported by Munther (1975). All cultures using extracts, leachates, and infusions were prepared as follows: plastic seed germinators (clear plastic boxes measuring 11 × 11 × 3 cm) were filled with 0.138 l (dry) of autoclaved horticultural grade (medium) vermiculite, and various treatment solutions were added to the vermiculite. The treatment solutions contained two parts of extract, leachate, or infusion and one part of 2X Hoagland's no. 1 solution plus trace elements (Hoshizaki, 1975). Fern spores generally require only moisture to germinate (Miller, 1968), but a nutrient solution was added because the cultures were examined over an extended time, and nutrients are necessary after the first few cell divisions of germinating spores. A total of 75 ml of solution was added to each experimental box. In controls, distilled water was mixed with Hoagland's solution instead of the extracts, leachates, or infusions. Fern spores were sown on the upper surface of pieces of unglazed clay pots placed on top of the vermiculite, 3 per germinator. New pots were used, and all were from the same manufacturer's lot. The pots, broken into pieces of approximately equal size, were boiled vigorously in water for 15 min three separate times, using fresh water for each boiling to remove the impurities.

Cultures were placed under 285–315 ft-c of illumination provided by alternately placed 40-watt plant grow (G.E.) and cool white fluorescent tubes with a photoperiod of 14 hrs. The light intensity used was based on field observations obtained with a light meter and on a recommendation reported by Miller and Miller (1961). Temperature was maintained at 22–24° C.

Each culture was checked daily after sowing until the first spores began to germinate. At that time, a count was made to determine percent germination and then repeated every other day for thirteen days. Since experimental data indicated that the last two counts were not appreciably different, the time was later reduced to 11 days. The criterion used to determine when spore germination had occurred was the appearance of the rhizoid following the first division of the spore, not just the uptake of water as shown by swelling. All counts were made under low power (100×) of a light microscope, and a mechanical counter was used to record the number of germinated and non-germinated spores within a randomly selected microscopic field. One count was taken from each chip in the box. All experiments were conducted in triplicate, using three germinator boxes for each replicate.

To test for the production of volatile compounds by the fronds of each of the three species, 30 g of fresh fronds were placed in a 16 × 31 cm plastic box. Also within this plastic box were 9-cm petri dish bottoms containing culture medium similar to that used in the other experiments. Each plate contained 0.091 l (dry) of vermiculite plus 50 ml of control solution on top of which were the pieces of clay pot with spores. The box was sealed with clear plastic tape. For controls, 30 g of cotton moistened with water was used in place of the fresh fronds. This method was similar in principle to that described by Muller (1966), and allowed any volatile compounds produced by the fronds to concentrate in the closed atmosphere of the box. The only contact between the fronds and the spores was through the air. The sealed boxes were placed under 300 ft-c of light for 14 days, after which counts were taken to calculate percent germination. All experiments were conducted in tripicate.

The replicated means of percent germination resulting from treatment with leaf leachates and extracts were compared statistically using Duncan's multiple range test (Duncan, 1955; Steele & Torrie, 1960), with replicated control means, for every possible autotoxic and allelopathic interaction (Munther, 1978). Separate comparisons to controls were made using the litter infusion treatment means. Only the means from the first (day 1) and last (day 11 or 13) counts were used for statistical analysis. These statistical comparisons were therefore based on a minimum (the presence of any germinated spores in any replicate of a species and treatment) and a maximum (all spores capable of germination from a variable population) level of germination for every possible interaction. Replicated volatile treatment means were compared to the controls in a similar manner; however, only one series of means representing the maximum level of germination was used in these comparisons, since it was not possible to obtain a minimum level due to the design of the experiments.

RESULTS AND DISCUSSION

In the following discussion, compounds produced in the leaves of a species which inhibit the germination of spores of the same species will be termed "autotoxic." The inhibitory effects on spores of another species will be termed "allelopathic."

Spores of both *Osmunda* species began to germinate in five or six days in Vermont and New Jersey populations. *Dennstaedtia* spores generally took longer to begin germination. Those from Vermont required at least 11 days, and those from New Jersey required at least 8 days.

TABLE 1. EFFECTS OF AQUEOUS LEAF EXTRACTS AND LEACHATES ON SPORE GERMINATION AND EARLY GAMETOPHYTE GROWTH IN *DENNSTAEDTIA* AND *OSMUNDA*.

Species		*Vermont*				*New Jersey*			
Spores	*Leaves*	*Leachate*		*Extract*		*Leachate*		*Extract*	
		FC	LC	FC	LC	FC	LC	FC	LC
		Autotoxic Interactions							
O. cinn.	O. cinn.	+	+	+	+	–	–	–	–
O. clay.	O. clay.	–	–	–	+	–	–	–	–
D. punc.	D. punc.	–	–	+	+	–	–	+	+
		Allelopathic Interactions							
O. cinn.	O. clay.	–	–	+	+	–	–	–	+
O. cinn.	D. punc.	–	–	+	+	+	+	+	+
O. clay.	O. cinn.	–	–	–	–	–	–	–	–
O. clay.	D. punc.	–	–	–	–	–	–	–	–
D. punc.	O. cinn.	–	–	+	+	–	–	–	–
D. punc.	O. clay.	–	–	+	+	–	–	–	–

FC = first count; LC = last count
+ = statistically significant inhibition (0.05 level); – = no significant inhibition

In the Vermont populations, all species exhibited some degree of autotoxicity (*Table 1*). In each species, the leaf extract was found to inhibit germination significantly, particularly in the last count. In *O. cinnamomea,* leaf leachates also significantly inhibited spore germination, and the inhibition was nearly as great as that caused by the extracts (*Table 3*). This differed considerably from the results obtained from the New Jersey populations, where only one species, *D. punctilobula*, was found to be significantly autotoxic (*Table 1*). In this case, the inhibition was caused by the extract.

Significant allelopathic interactions also were found in the Vermont populations. Leaf extracts of both *O. claytoniana* and *D. punctilobula* inhibited spores of *O. cinnamomea*, significantly lowering percent germination (*Table 1*). Inhibition of germination was quite severe, particularly as revealed in the final counts (*Tables 4* and *5*). Spores of *D. punctilobula* were inhibited by leaf extracts of *O. cinnamomea* and *O. claytoniana* (*Table 1*). Inhibition in this case also was quite marked, especially by extracts of *O. claytoniana* (*Table 4*). Aqueous leaf extracts of *O. claytoniana* often severely inhibited spores of the other two species, but extracts of both *O. cinnamomea* and *D. punctilobula* had little effect on *O. claytoniana* spore germination (*Table 1*). Leaf leachates of the three species tested produced no significant allelopathic inhibition of spore germination.

The number of significant allelopathic interactions was lower in the New Jersey populations than in the Vermont populations (*Table 1*). Spores of *O. cinnamomea* were inhibited by leaf leachates of *D. punctilobula*, which was the only significant allelopathic inhibition by leaf leachates in either the New Jersey or Vermont populations (*Tables 1* and *5*). The inhibition produced by the leachates was not so severe as that produced by the extracts (*Table 5*). Also in New Jersey, germination of *O. cinnamomea* spores was inhibited by leaf extracts of both *O. claytoniana* and *D. punctilobula* (*Table 1*). *Osmunda cinnamomea* and *O. claytoniana* leaf extracts had little effect on germination of *D. punctilobula* spores (*Table 1*). This result is quite different from that obtained for the Vermont populations (*Table 1*). However, as in the Vermont populations, spores of *O. claytoniana* were unaffected by leaf extracts (or leachates) of both *O. cinnamomea* and *D. punctilobula* (*Table 1*). Nevertheless, in the majority of cases, the Vermont and New Jersey populations reacted quite differently in terms of the number and type of allelopathic and autotoxic interactions.

TABLE 2. EFFECT OF LEAF LITTER INFUSIONS ON SPORE GERMINATION AND EARLY GAMETOPHYTE GROWTH IN NEW JERSEY POPULATIONS OF *DENNSTAEDTIA* AND *OSMUNDA*.

Species		*Effect of litter infusion*	
Spores	*Leaves*	*FC*	*LC*
	Autotoxic Interactions		
O. cinn.	O. cinn.	+	−
O. clay.	O. clay.	−	−
D. punc.	D. punc.	−	−
	Allelopathic Interactions		
O. cinn.	O. clay.	−	−
O. cinn.	D. punc.	−	−
O. clay.	O. cinn.	−	−
O. clay.	D. punc.	−	−
D. punc.	O. cinn.	−	+
D. punc.	O. clay.	−	−

FC = first count; LC = last count
\+ = statistically significant inhibition (0.05 level); − = no significant effect

Leaf litter infusions of New Jersey material did not inhibit germination greatly (*Table 2*). *Dennstaedtia punctilobula* spores were inhibited by *O. cinnamomea* leaf litter infusions, the only allelopathic inhibition caused by treatment with litter infusions. The only species exhibiting autotoxicity was *O. cinnamomea* (*Table 2*), in which the litter infusion merely delayed germination, since there was no inhibition in the last count.

Two types of inhibition were observed in spores treated with extracts and leachates. Spores of all three species imbibed water readily when treated with leachates or extracts, but spores treated with extracts often did not divide. This indicates that the inhibitor was able to enter the spore through the wall and to prevent the first division. This type of inhibition causes a low percentage of spores to germinate, is evident in the first count when compared to the controls, and continues through the last count (*Table 1*). This was the most common type of inhibition. In the second type, several divisions occurred and percent germination was not affected in the first count (see *O. claytoniana*, autotoxicity, *Table 1*). The inhibitor in this instance did not affect germination, but acted on the several-celled stage (young gametophyte). In the later counts, if a spore had germinated but had died (chlorophyll lost) at the several-celled stage, it was counted as not germinated. Therefore, the last count measures the inhibitor's effect on early gametophyte growth and development. The presence of this type of inhibition can be recognized only at the last count.

When leaf extracts caused significant inhibition of germination, gametophyte development from spores which germinated usually was affected, with the gametophyte usually arrested in the filamentous stage and little or no further growth occurring. Leaf leachates usually did not cause this type of response. Gametophytes resulting from spores which did germinate underwent normal development, but often exhibited somewhat slower growth than did the controls.

TABLE 3. AUTOTOXIC EFFECTS OF LEAF LEACHATES AND EXTRACTS EXPRESSED AS A PERCENTAGE OF SPORE GERMINATION AND EARLY GAMETOPHYTE GROWTH IN VERMONT POPULATIONS OF *O. CINNAMOMEA*. STATISTICAL ANALYSIS USING DUNCAN'S MULTIPLE RANGE TEST WITH A 0.05 SIGNIFICANCE LEVEL. (ALL EXTRACT AND LEACHATE MEANS SIGNIFICANTLY DIFFERENT FROM ALL CONTROL MEANS.)

First count ($s_{\bar{x}} = 5.421$)

Means	E1	L1	E3	L3	E2	L2	C1	C3	C2
s=	4.7	2.4	4.3	4.8	4.0	10.3	19.9	14.2	2.7
$\bar{x}$=	14.7	15.6	16.8	17.2	17.8	18.1	52.1	58.2	65.5

Last count ($s_{\bar{x}} = 5.034$)

Means	E3	E1	E2	L2	L3	L1	C1	C3	C2
s=	7.1	4.4	5.3	14.4	11.4	5.5	8.1	10.2	7.0
$\bar{x}$=	9.1	10.1	14.0	23.6	26.3	48.8	76.8	80.5	81.3

$s_{\bar{x}}$ = standard error (of the mean); s = standard deviation; $\bar{x}$ = mean percent germination
C1–3 = control means; L1–3 = leachate treatment means; E1–3 = extract treatment means

Phenolic compounds are known to inhibit ion uptake in flowering plants through reversible alterations in membrane permeability (Glass, 1973, 1974) and may affect IAA metabolism. The spore wall may prevent the phenolic inhibitor from entering the spore, with the first divisions of the spore occurring on stored reserves. By the time the gametophyte reaches the several-celled stage, the phenolic inhibitor may prevent ion uptake sufficiently to inhibit growth or further cell division.

The effects of the extracts on spore germination and on early gametophyte stages were much greater than the effects of the leachates in almost every experiment. While experimental effects of the leachates may be easily extrapolated to field conditions, the extracts present an enigma. While nothing directly paralleling an extraction procedure exists in nature, experimental results obtained using extracts do possess some validity in determining the phytotoxic potential of plants under laboratory conditions. Extracts may concentrate compounds which are leachable and concentrated in the soil under field conditions. However, some compounds present in an extract may not be leached from healthy, growing tissue, and many substances can be altered by the extraction procedure itself. On the other hand, substances that are not normally leached from such tissue can be released by senescent tissue quite readily (Gliessman & Muller, 1972; Stewart, 1975). Various forms of stress, such as temperature extremes, drought, attack by pathogens, or mechanical injury also increase the leachability of metabolites from foliage (Tukey, 1966, 1969; Rice, 1974). Soils also vary in their composition, structure, moisture content, pH, and the kinds of microorganisms present. Thus, they would have different affinities for various inhibitors, or may even render them inactive or increase their activity due to microbial decomposition (del Moral & Cates, 1971; Rice, 1967, 1969; Wang et al., 1967).

TABLE 4. ALLELOPATHIC EFFECTS OF *O. CLAYTONIANA* LEAF EXTRACTS AND LEACHATES EXPRESSED AS A PERCENTAGE OF SPORE GERMINATION AND EARLY GAMETOPHYTE GROWTH IN VERMONT POPULATIONS OF *O. CINNAMOMEA* AND *D. PUNCTILOBULA*. STATISTICAL ANALYSIS USING DUNCAN'S MULTIPLE RANGE TEST WITH A 0.05 SIGNIFICANCE LEVEL. (ALL EXTRACT (NOT LEACHATE) MEANS SIGNIFICANTLY DIFFERENT FROM ALL CONTROL MEANS.)

O. cinnamomea

Last count ($s_{\bar{x}}$ = 8.450)

Means	E2	E3	E1	L2	L1	L3	C1	C3	C2
s=	14.1	18.0	27.2	19.0	8.7	3.5	8.1	10.2	7.0
$\bar{x}$=	12.2	22.1	39.4	43.6	54.8	58.4	76.8	80.5	81.3

D. punctilobula

First count ($s_{\bar{x}}$ = 4.618)

Means	E1	E3	E2	L1	L2	C1	C3	L3	C2
s=	3.8	5.8	3.3	13.7	3.8	9.1	14.5	4.5	1.3
$\bar{x}$=	15.1	18.5	28.0	36.0	41.9	47.5	49.7	52.7	54.5

Last count ($s_{\bar{x}}$ = 4.965)

Means	E1	E3	E2	L1	L2	L3	C3	C1	C2
s=	5.1	12.5	15.6	2.3	10.9	5.3	6.4	2.9	6.2
$\bar{x}$=	11.0	26.0	32.8	64.0	65.1	67.3	74.9	75.7	76.2

$s_{\bar{x}}$ = standard error (of the mean); s = standard deviation; $\bar{x}$ = mean percent germination
C1–3 = control means; L1–3 = leachate treatment means; E1–3 = extract treatment means

In all samples except one of *D. punctilobula* from New Jersey, the pH of the extracts was lower than that of the leachates (*Table 5*). The pH of the extracts and leachates from New Jersey populations did not differ greatly from that obtained from the Vermont material (*Table 6*). Although in all samples the pH of the leachates from Vermont populations was higher than in leachates from New Jersey, the difference probably is not enough to be significant. It can be deduced from *Table 6* that allelopathy is not strictly a low pH phenomenon. For example, the leaf leachates and extracts from *O. cinnamomea* (New Jersey) exhibited very little phytotoxicity, yet they possessed the lowest pH.

As already mentioned, litter infusions of *O. cinnamomea* were found to be autotoxic (*Table 2*) only in the first count, indicating delayed germination. Such a delay could be important under field conditions, however, increasing the chances of attack by microbial pathogens which could cause damping off of the young prothalli, as is often the case with seeds.

Within the species studied in New Jersey, the pH values obtained for leaf-litter infusions were higher than expected when compared with those obtained for leaf leachates and extracts (*Table 6*).

TABLE 5. ALLELOPATHIC EFFECTS OF *D. PUNCTILOBULA* LEAF EXTRACTS AND LEACHATES EXPRESSED AS A PERCENTAGE OF SPORE GERMINATION AND EARLY GAMETOPHYTE GROWTH IN VERMONT AND NEW JERSEY POPULATIONS OF *O. CINNAMOMEA*. STATISTICAL ANALYSIS USING DUNCAN'S MULTIPLE RANGE TEST WITH A 0.05 SIGNIFICANCE LEVEL. (ALL EXTRACT (NOT LEACHATE) MEANS SIGNIFICANTLY DIFFERENT FROM ALL CONTROL MEANS IN VERMONT; ALL MEANS SIGNIFICANTLY DIFFERENT FROM ALL CONTROL MEANS IN NEW JERSEY.)

Vermont

Last count ($s_{\bar{x}}$ = 5.488)

Means	E2	E3	E1	L1	L2	L3	C1	C3	C2
s =	2.7	3.5	9.5	15.8	14.7	7.2	8.1	10.2	7.0
$\bar{x}$ =	27.8	33.2	38.8	47.2	53.6	67.6	76.8	80.5	81.3

New Jersey

First count ($s_{\bar{x}}$ = 4.569)

Means	E1	E3	E2	L2	L3	L1	C1	C2	C3
s =	10.4	8.1	10.6	7.4	4.2	8.8	7.9	7.5	3.0
$\bar{x}$ =	29.9	36.7	37.1	51.7	53.4	53.7	78.8	79.3	85.9

Last count ($s_{\bar{x}}$ = 4.608)

Means	E1	E2	E3	L3	L1	L2	C2	C3	C1
s =	12.2	12.3	5.3	3.9	6.1	4.4	8.3	6.1	8.2
$\bar{x}$ =	30.9	32.6	39.7	46.2	48.3	56.8	72.8	79.8	81.7

$s_{\bar{x}}$ = standard error (of the mean); s = standard deviation; $\bar{x}$ = mean per cent germination
C1–3 = control means; L1–3 = leachate treatment means; E1–3 = extract treatment means.

Frond litter was collected while the fronds were still standing, following the first killing frost in 1976. It is unknown whether or not it rained between the time of the first frost and the time of collection. If it did, this may account for the apparent lack of phytotoxicity in the infusions, since any water soluble phytotoxins could have been removed by the rainfall. The importance of the first rainfall after frond senescence already has been cited by Gliessman and Muller (1972), who studied the effects of *P. aquilinum* leaf litter extracts on *Avena fatua* and *Bromus rigida* radicle growth, and by Stewart (1975), who examined the effects of *P. aquilinum* litter extracts on seeds of *Rubus* sp. and Douglas-fir.

No inhibitory volatile compounds were detected in biologically significant levels from leaves removed from New Jersey or Vermont populations. *Dennstaedtia punctilobula* leaves are quite fragrant, particularly when crushed, but the substance producing this fragrance, presumably coumarin, had no apparent effect on spore germination.

Water-soluble inhibitors predominate in more humid or wet environments, according to the hypothesis developed by Whittaker (1970) relating toxin production to climate. Since the Vermont populations exist in a wetter environment than do the New Jersey ones (Climatological Data, U. S. Dept. of Commerce, NOAA, 1976–1977), this may partially explain the increased number of allelopathic and autotoxic interactions caused by water-soluble leachates and extracts. Volatile inhibitors, according to Whittaker (1970) and Muller (1970), would be most common in a hot, arid environment. The fact that none were found in either Vermont or New Jersey populations would also lend support to their theory relating toxin production to climate, as both areas are relatively moist. Summer temperatures in the study areas in Vermont and New Jersey were nearly identical (Climatological Data, NOAA, 1976–1977).

TABLE 6. pH VALUES OBTAINED FROM AQUEOUS LEAF EXTRACTS AND LEACHATES FOR NEW JERSEY AND VERMONT POPULATIONS, AND LITTER INFUSIONS FOR NEW JERSEY POPULATIONS.

	pH	
Species	NJ	VT
Osmunda cinnamomea		
leaf extract	5.40	5.20
leaf leachate	6.00	6.60
litter infusion	6.50	—
soil (5/77)	5.20	—
Osmunda claytoniana		
leaf extract	5.60	5.80
leaf leachate	6.20	6.65
litter infusion	6.75	—
soil (5/77)	6.40	—
Dennstaedtia punctilobula		
leaf extract	5.70	5.80
leaf leachate	5.50	6.00
litter infusion	5.95	—
soil (5/77)	5.90	—

We express our appreciation to R. W. Willemsen for his help during a portion of this research, and to B. F. Palser and J. A. Quinn for their helpful suggestions and comments.

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SHORTER NOTES

SANDSTONE ROCK CREVICES, AN EXCEPTIONAL NEW HABITAT FOR THELYPTERIS SIMULATA.—The Massachusetts or Bog Fern, *Thelypteris simulata* (Davenp.) Niewl., is a common wetland fern in the New England states. Most manuals give its typical habitat as very acid, shaded bogs and swamps, frequently in association with sphagnum moss. In some New England cranberry bogs, the fern is so abundant as to be a weed. Hartley (Rhodora 67:399– 404. 1965) reported for the first time *T. simulata* from Wisconsin, a disjunction of approximately 600 miles from the nearest station in West Virginia. Since the original discovery, twelve other stations have been found for *T. simulata* in west-central Wisconsin. The Wisconsin habitats are all flat, low-lying woods with a moist layer of peat about one foot thick overlying sand. The dominant trees usually are *Pinus strobus* and *Acer rubrum*, and the most common understory species *Alnus rugosa* and *Ilex verticillata*. The most abundant herbaceous plant at most sites is *Osmunda cinnamomea*. Other characteristic ground layer associates include *Carex brunnescens, C. folliculata, C. trisperma, Dryopteris intermedia, D. spinulosa, D.* × *triploidea, Maianthemum canadense, Mitchella repens, Osmunda regalis, Rubus hispidus, Sphagnum* spp., and *Viola incognita*. It seems likely that in presettlement times, before the natural character of central Wisconsin was vastly changed by drainage ditches, peat fires, farming, etc., *T. simulata* was a common member of the low, wet-acid woods flora that once covered much of the sandy plain of extinct glacial Lake Wisconsin.

In mid-August 1979, I found a single plant of *T. simulata* growing one foot above the ground in the crevice of a sandstone cliff at Castle Mound, Castle Mound State Park, Jackson County, Wisconsin (T21N, R4W, SW¼SW¼ sec. 23). To my knowledge, there are no reports in the literature of *T. simulata* occurring on rock cliffs. The plant consisted of only eight sterile fronds, one of which was taken as a voucher (*Moran 995, MIL*). Two more fronds were taken on 13 Aug 1980 and checked by Dr. W. H. Wagner, Jr. for correct identity (*Moran 1267, MICH*). One of the fronds was soriferous, although all the sporangia were still white and immature; maturation was late compared with several other Wisconsin populations that were already actively sporulating.

Castle Mound is composed of Cambrian sandstone that rises 180 feet above the surrounding lake plain of extinct glacial Lake Wisconsin. It is typical of many weathered, castellated mounds found in the central Wisconsin sand plains. The *T. simulata* cliff habitat on Castle Mound faces north and is shaded by *Pinus resinosa, P. strobus,* and *Quercus rubra*. The soil reaction in the crevice where *T. simulata* was growing was pH 5.0. No other vascular plants were growing in the crevice with *T. simulata*. The cliff face immediately surrounding the plant was barren, except for one plant of *Dryopteris spinulosa* growing in a crevice about one foot above *T. simulata*. About ten feet above the plant was a ledge with numerous individuals of *Polypodium virginianum*, along with *Aquilegia canadensis, Athyrium filix-femina*, and *Betula papyrifera*.

Although it seems odd that *T. simulata* should occupy a dry sandstone cliff when its typical habitat is wet, acid bogs, usually in association with sphagnum moss, the two habitats are similar in certain respects. The wet, cold acid conditions of a bog make it physiologically difficult for roots to absorb water and mineral nutrients. Such a state of "physiological drought" simulates the dry, nutrient-poor crevices of a sandstone cliff. This type of habitat switch is known to experienced field botanists from other examples of swamp or bog plants growing on rocks, and vice-versa. A few such examples are: *Cystopteris bulbifera, Dryopteris marginalis, D. spinulosa, Ledum groenlandicum, Lorinseria areolata, Matteuccia struthiopteris, Osmunda cinnamomea, Phegopteris connectilis, Sphagnum* spp., and *Thelypteris palustris.*

Although *T. simulata* may have been common in the low wooded acid swamps that surrounded Castle Mound in presettlement times, the nearest presently known locality is two miles away. The Castle Mound individual certainly is the result of relatively wide-range spore dispersal. It is important to point out that, in view of Klewkowski's (Science 153:305–307. 1966) ideas on the adaptive value of polyploidy in homosporous pteridophytes, the Castle Mound individual is most probably the result of single spore establishment and intragametophytic selfing.—*Robbin C. Moran, Wisconsin Scientific Areas Preservation Council, Department of Natural Resources, P.O. Box 7921, Madison, WI 53707.*

A SECOND ALABAMA LOCALITY FOR THE HART'S TONGUE.—The discovery of the Hart's-tongue, *Phyllitis scolopendrium* (L.) Newm., in a sinkhole in Jackson County, Alabama (Amer. Fern J. 69:47–48. 1979) generated interest in further searches for this fern among members of the Huntsville Grotto of the National Speleological Society who had participated in the find. According to Eric Bachelder, my guide to the Jackson County locality, these spelunkers found a second, larger population in a sinkhole in Morgan County soon after the original discovery (Huntsville Grotto Newsletter 20:49–50. 1979). On 31 May 1980, I visited the new locality with Mr. Bachelder again as my guide. The population is in a deep sinkhole in the area known as Newsome Sinks, a large sink-valley in northeastern Morgan County about 25 miles southwest of the Jackson County locality and 65 miles southwest of the one in Marion County, Tennessee. The sinkhole is about 70 feet deep and has sheer walls. A small stream falls into the sink, making the air very misty and humid, unlike the dry Jackson County sink. Also unlike the Jackson County sinkhole, it is necessary to rappel down to a wide ledge about half-way down, where most of the *Phyllitis* plants are. Fifty-three plants occur on the ledge, along with luxuriant *Cystopteris bulbifera* and Wood Nettle *(Laportea canadensis),* which may have obscured more *Phyllitis* plants. At least 20 Hart's-tongues were mature adults; the juveniles ranged from sporelings to almost adults. The ledge is partially overhung by the cliffs above, and the *Phyllitis* plants grow in a narrow strip beneath the overhang. The left end of the strip contains mostly adults and large juveniles; the plants toward the right are gradually reduced in size, age, and density. Apparently the population is spreading towards the right. Four fairly large Hart's-tongues also were seen at the bottom of the sinkhole. A number of fronds were collected as a voucher (*Short 1195*, AUA and duplicates to be distributed).—*John W. Short, 905 McKinley Ave., Auburn, AL 36830.*

AMERICAN FERN JOURNAL

Manuscripts submitted to the JOURNAL are reviewed for scientific content by one or more of the editors, and, often, by one or more outside reviewers as well. During the past year we have received the kind assistance of J. Beitel, B. M. Boom, M. I. Cousens, A. M. Evans, L. G. Hickok, A. C. Jermy, J. H. Miller, J. D. Montgomery, D. H. Nicolson, H. E. Robinson, J. Skog, A. R. Smith, A. Star, R. G. Stolze, W. C. Taylor, R. A. White, D. P. Whittier, and J. J. Wurdack, to whom we are deeply indebted. We welcome suggestions of other reviewers.—*D.B.L.*

INDEX TO VOLUME 70

ERRATA

Page 52, line 22: For "*beaurepairii*" read "*beaurepairei*."
Page 55, line 39: For "*tuckerheimii*" read "*tuerckheimii*."
Page 61, line 1: For "*Petioloa*" read "*Petiolosa*."
Page 66, line 10: "For *beaurepairii*" read "*beaurepairei*."

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CONTENTS

Volume 71, Number 1, Pages 1—32, Issued March 30, 1981

Volume 71, Number 2, Pages 33—64, Issued June 29, 1981

Volume 71, Number 3, Pages 65—96, Issued September 30, 1981

Volume 71, Number 4, Pages 97—124, Issued December 30, 1981

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Equisetum variegatum and E. × trachyodon in New Jersey

JAMES D. MONTGOMERY*

Equisetum variegatum Schleich., the Variegated Scouring-rush, occurs northward from the northern tier of states of the United States into Canada, on damp sand or shores, often on calcareous substrate (Fernald, 1950; Wherry, 1961). This paper reports the first verified record of *E. variegatum* from New Jersey and discusses a dubious record from that state. The hybrid *E.* × *trachyodon* A. Br. is also reported for New Jersey.

Equisetum variegatum was listed for New Jersey by Taylor (1915) and Fernald (1950), but not by Chrysler and Edwards (1947), Wherry (1961), or Hauke (1963). The record for New Jersey was apparently based on an undated specimen collected by C. F. Austin, labeled "Closter, Bergen Co." Chrysler and Edwards (1947) disallowed this record, indicating that *E. variegatum* and *E. pratense* were mounted on one sheet and concluding that *E. variegatum* was mounted by mistake with *E. pratense*. Further investigation by the author showed that there are specimens of many pteridophytes from New Jersey collected by C. F. Austin, usually labeled only "Closter, Bergen Co." and without dates or specific locality. A total of 36 species of the more common northeastern ferns and fern allies are represented at CHRB or NY by such collections. It is interesting that specimens of plants known to be difficult to grow or transplant (e.g., *Lycopodium* spp., *Botrychium* spp. other than *B. dissectum*) are lacking. I suggest, therefore, that at least some of these C. F. Austin collections represent garden plants which were originally collected at various places in western New Jersey and probably elsewhere. This conclusion is supported by the fact that, in addition to the mixed collection of *E. variegatum* and *E. pratense*, there is a sheet of *E. fluviatile* at NY with labels from both "Closter, Bergen Co." and "St. Lawrence Co., NY," and another undated sheet of *E. pratense* labeled "Closter and Sparta." I agree with Chrysler and Edwards that the record for *E. variegatum* from Closter, Bergen Co. is highly suspect. Other Closter records by this collector without specific location or date are likewise dubious.

A hybrid involving *E. variegatum* has been known from New Jersey since at least 1950: *E.* × *trachyodon* is the hybrid between *E. variegatum* and *E. hyemale* L. As far as is known from herbarium records, this hybrid was first collected by J. L. Edwards along the Delaware River, near Flatbrookville, Sussex Co., 28 October 1950 (CHRB, NY).

On 19 August 1977, Vincent Abraitys collected plants of *E. variegatum* near Marksboro, Warren Co. I came across this material in connection with a project to revise the Chrysler and Edwards book. Material was sent to Dr. Richard Hauke, who verified the identification.

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*Ichthyological Associates, Inc., R. D. 1, Berwick, PA 18603.

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The discovery of *E. variegatum* in Warren County, New Jersey, represents a southward range extension for this species. The plant is known in New York from a collection made in 1960 along the Hudson River in southern Ulster Co. (NYS), and from central Columbia and Greene Cos. (NYS). The plant is more common in central New York, and there are many records from the edges of the Adirondacks (New York State Botanist's Office, pers. comm.). The distance from the Ulster Co. site is about 100 km (60 mi); other locations in eastern and central New York are more than 160 km (100 mi) distant. The only location for *E. variegatum* in Pennsylvania is from Presque Isle, Erie Co., in the extreme northwestern corner of the state (Wherry, Fogg, & Wahl, 1979).

Equisetum variegatum occurs on the damp shore of a lake underlain by limestone, a habitat similar to that recorded in herbarium records from New York and Pennsylvania.

Mr. Abraitys reports that it is unlikely that plants were present about 1960, so this probably represents a recently established colony. The source of the plants and means of introduction are unknown, although cultivation can be ruled out. It is interesting that both *E. variegatum* and *E.* × *trachyodon* should appear recently in New Jersey. The localities are separated by approximately 15 km (9 mi). The appearance of *E.* × *trachyodon* is more easily explained since the colony is on the shore of the Delaware River which extends northward into the range of *E. variegatum* in New York. Herbarium records (and observation of the *E. variegatum* site) indicate that the hybrid became established separately from and earlier than the species in New Jersey.

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Comparative Ecology of Woodsia scopulina Sporophytes and Gametophytes

PAUL J. WATSON and MARGARITA VAZQUEZ*

Woodsia scopulina D. C. Eaton, an obligate rock fern, is widespread in the Rocky Mountains and has a few disjunct populations in eastern North America. This report concerns the ecology of *W. scopulina* gametophytes and sporophytes.

An understanding of the life history of any fern is incomplete as long as the functioning of its gametophytes remains obscure. Yet, the study of gametophyte ecology is in its infancy. Adaptations of gametophytes to cold and dessication have been explored by Pickett (1914). Hill (1971) compared the habitat requirements for spore germination and gametophyte development for three ferns in Michigan. Gametophyte population divergence and general ecology have been studied by Cousens (1979).

Wagner and Sharp (1963) found that free-living *Vittaria* prothalli occurred in areas far north of their sporophytes. Since this discovery, several other genera of tropical ferns have been found to possess gametophytes with geographic ranges much more extensive than the sporophyte (Wagner & Evers, 1963; Farrar, 1967; McAlpin & Farrar, 1978). Page (1979) sums up much of the research on fern gametophyte ecology.

Gametophyte ecology is, of course, microecology. We find this a fascinating and unusual level at which to study plant ecology, a science in which investigation of systems at the macro level is the norm.

PROCEDURES

Our study areas consisted of xeromesic to xeric talus slopes and rock outcrops in the immediate vicinity of Bigfork, Montana. These rocky sites represent typical *Woodsia scopulina* habitat, and many hundreds of sporophytes as well as thousands of gametophytes are found there. *Cystopteris fragilis* (L.) Bernh. also occurs at the sites; however, it is only a minor contaminant of the nearly pure *W. scopulina* fern communities. Other herbaceous plants are only sparsely distributed on the sites. Shrubs such as Mountain Spray (*Holodiscus discolor* (Pursh) Maxim.), Serviceberry (*Amelanchier alnifolia* Nutt.), and Rocky Mountain Maple (*Acer glabrum* Torr.) occur, especially on the less disturbed sections of the talus slopes. Douglas-fir (*Pseudotsuga menziesii* (Mirbel) Franco.) also occurs sparingly. A rich moss flora is present on the talus and the rock outcrops.

We explored the microhabitats of numerous *W. scopulina* gametophytes, gametophytes harboring juvenile sporophytes (in which the sporophytes' leaves were still dichotomous, not yet resembling those of the mature sporophyte), young, sterile sporophytes, and fully-developed, fertile sporophytes. For each of these life cycle phases, we noted such environmental factors as substrate composition and pH, sunlight exposure, and nearby plant associates. Consistently occurring differences in the habitat of each of the four phases were recorded.

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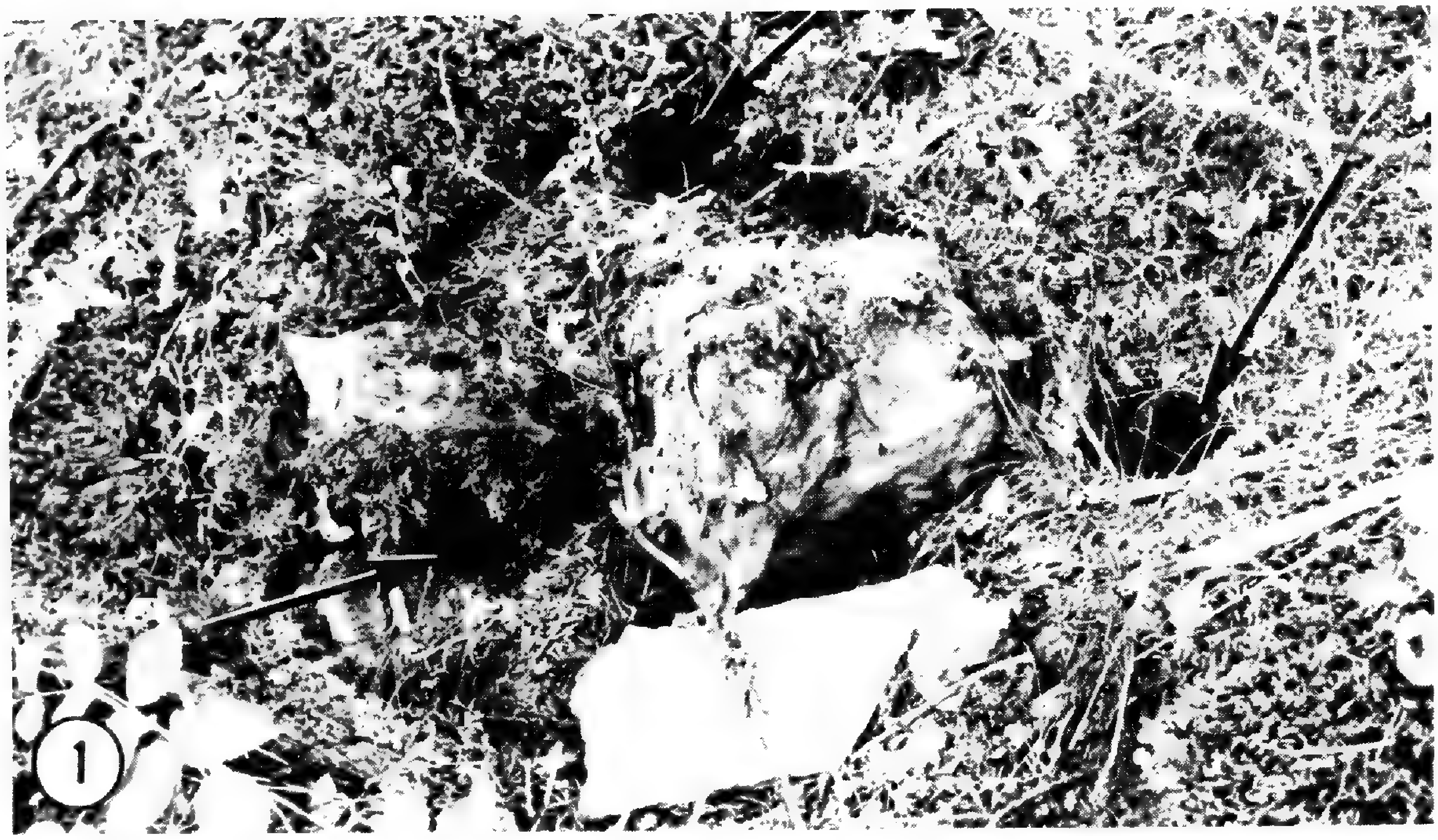
*532 University Ave., Missoula, MT 59801.



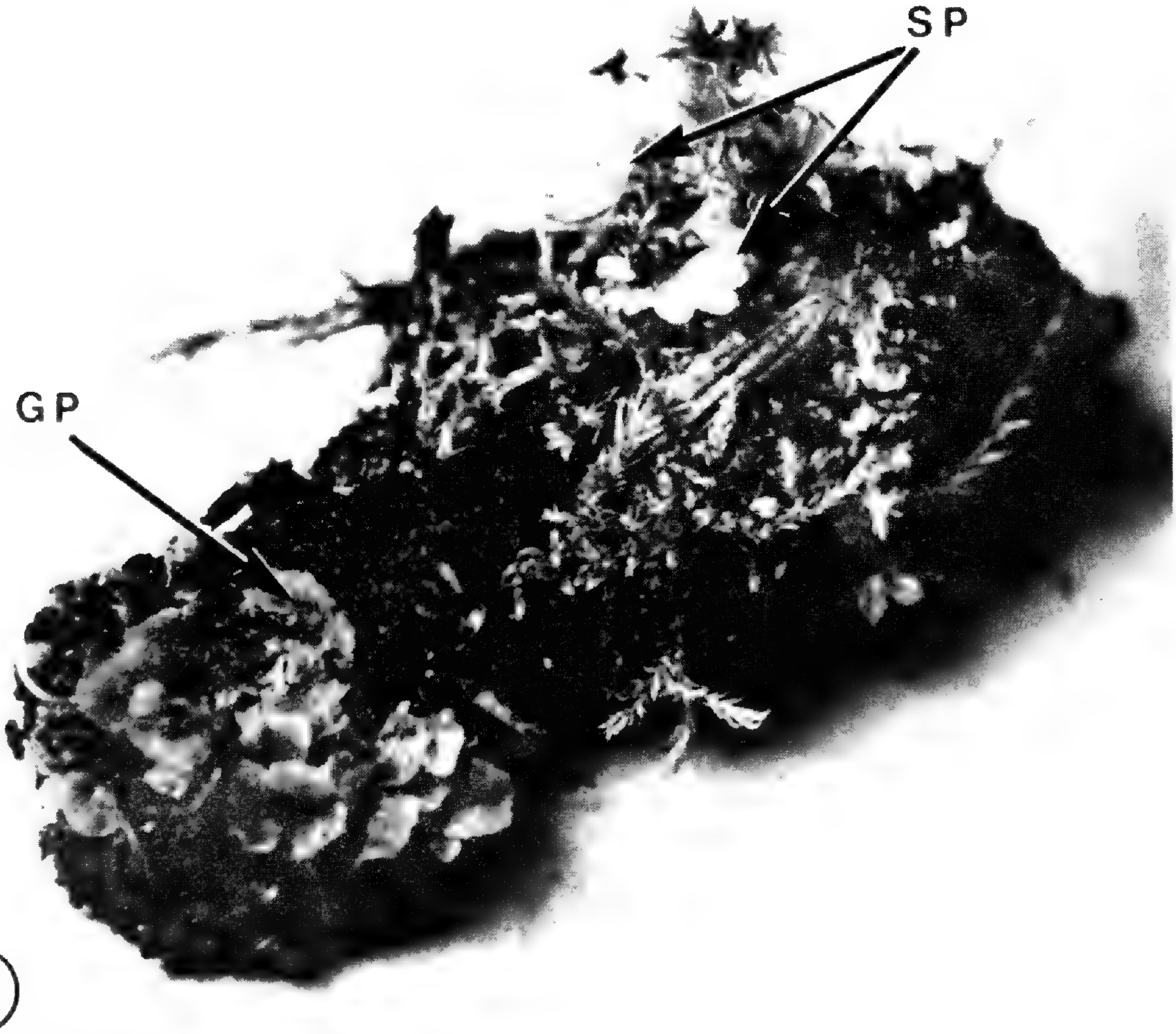


FIG. 1. Talus hollows where *Woodsia scopulina* gametophytes are found. FIG. 2. Two clumps of soil illustrating juvenile sporophytes (SP) in association with mosses and gametophytes (GP) growing on bare soil.

Quantitative data on the substrate preferences of gametophytes were gathered by examining all the cave-like talus hollows on a chosen talus slope. Sixty-one hollows were inspected. For each, the presence or absence of gametophytes and nature of the substrate (bare soil, litter on soil, moss and litter on soil, etc.) were recorded. (We define litter as decomposing but still recognizable plant material upon soil or rock surfaces.)

In order to compare the habitat preferences of *W. scopulina* gametophytes and sporophytes with those of a typical mesophytic forest fern, we familiarized ourselves with the habitats of the life cycle phases of *Athyrium filix-femina* (L.) Roth. The study sites for this fern were located in the moister forested areas of the University of Montana Biological Station, approximately 12 miles south of Bigfork.

RESULTS

The puberulent, slightly sticky gametophytes of *W. scopulina* were found only in cave-like hollows on the talus slopes *(Fig. 1)* and in crevices on rock cliffs and tables. These talus hollows and rock crevices contain various amounts of soil, bare rock, mosses, and litter. Gametophytes existed only on bare soil over rock (*Fig. 2*). Gametophytes usually were found within talus hollows containing obvious patches of bare soil (23 out of 29 hollows), but seldom were found in hollows with soil mostly covered by litter or mosses (5 out of 32 hollows). Gametophytes were never found in hollows lacking soil. A mere dusting of soil about a millimeter thick was enough to support gametophytes. Soil pH readings from gametophyte substrates ranged from 6.4 to 7.2.

Gametophytes in the various populations were sparse to dense, and were not closely associated with other plants, even with the young, leafy moss shoots. Favorable gameotophyte habitats typically were sheltered from direct sunlight. However, gametophytes did not grow so far back in hollows and crevices that illumination was too heavily diminished, even if other environmental conditions were favorable. Gametophytes were oriented with their apical notches farthest from the opening of the crevice or hollow. Most gametophytes did not lie flat on the substrate, but had the apical two-thirds of their thalli slanted steeply upwards (*Fig. 3*).

Populations of gametophytes giving rise to juvenile sporophytes also grew in the crevices and hollows, but the soil substrate often was not bare (*Fig. 2*). This phase of *W. scopulina* was usually associated with the moss *Brachythecium velutinum* (Hedw.) B.S.G. This small, pleurocarpous moss grew sparingly around gametophytes with new juvenile sporophytes but more robustly around those with more advanced juvenile sporophytes having two or three well-developed leaves (in the latter case the gametophytic tissue was still visable but totally chlorotic). Where *B. velutinum* grew densely, a second moss, *Encalypta vulgaris* Hedw., often occurred intermixed with it. Occasionally, a thin layer of litter also covered the soil. Clusters of tiny juvenile sporophytes grew from gametophytes positioned in the more illuminated portions of the microhabitat as, for example, near the front of talus hollows, but still out of direct sunlight. Those gametophytes furthest back in such a hollow often had few or no sporophytes.

Young, sterile sporophytes were seen growing only out of talus hollows, rock crevices, and upon rock tables. When seen growing upon a rock table, examination of the plants' bases showed them to be anchored to at least a small crack or other irregularity in the rock. These sporophytes usually grew in close association with several mosses such as *Dicranum scoparium* (L.) Hedw., *Rhytidiadelphus triquetrus* (Hedw.) Warnst., *Tortula muralis* Hedw., *Homalothecium* sp., and *Brachythecium* sp. Openings that harbored young, sterile sporophytes supported only one per opening.

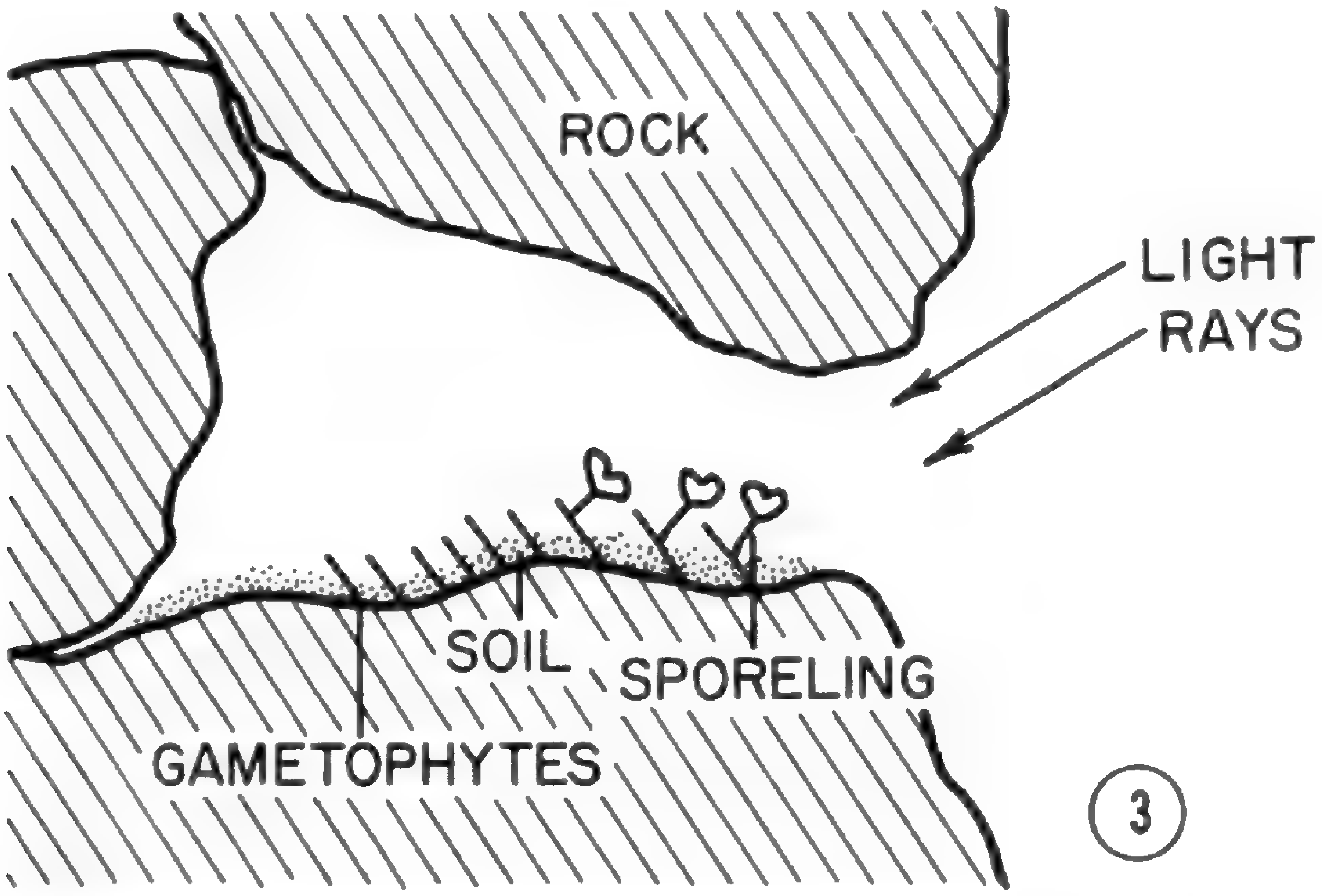


FIG. 3. Position of gametophytes and juvenile sporophytes within a typical talus hollow.

Fully developed, fertile sporophytes of *W. scopulina* were found growing out of talus hollows, rock crevices, and from irregularities on rock tables and cliffs. Their fronds always extended completely out of the rock opening of their origin, but grew in filtered to direct sunlight, depending on the presence of overstory shrubs or trees. Mature sporophytes had huge systems of fine roots. These roots were much greater in extent and density than we expected for a fern so small as *W. scopulina*. The roots never grew on bare rock. Instead, they grew within a layer of soil over rock and spread down into even the thinnest layers of soil between rocks. Thick mats of the same mosses associated with young, sterile sporophytes commonly covered the soil substrate. *Woodsia* sporophytes were not associated with thick growths of grasses and did not occur on sites with a great abundance of deciduous litter. The pH of the soil substrates we tested ranged from 6.2 to 6.8.

The prothalli of *Athyrium filix-femina* were found only on bare soil or moist, heavily rotted wood in shady microhabitats. As was true for *W. scopulina* gametophytes, *A. filix-femina* gametophytes did not grow among mosses or upon forest litter.

Sporophytes of *A. filix-femina* occurred in mesic forest conditions, often beneath gaps in the tree canopy. Mature sporophytes grew in association with many herbs, shrubs, and thick layers of mosses.

DISCUSSION

We conclude that there are at least three salient differences in the ecologies of *Woodsia scopulina* gametophytes and sporophytes: (1) Gametophytes become established only in secluded microhabitats where sunlight is diffuse for most or all of the day. Sporophytes, on the contrary, can tolerate exposure to intense direct sunlight for many hours each day. (2) Competitive abilities of the two generations differ. Gametophytes cannot coexist with other plant growth, including the mere leafy shoots of small bryophytes. On the other hand, even the youngest sporophytes are often surrounded by mosses with no apparent ill effects. Association with mosses may even benefit sporophytes by reducing desiccation of their roots. Sporophytes also grow well in close proximity to widely spaced herbaceous and woody angiosperms. (3) Gametophytes cannot grow upon or under litter, but sporophytes are not disadvantaged by moderate litter accumulations.

The above conclusions conflict with certain general statements in the literature. such as that by Nayar and Kaur (1971) who claim that "sporophytes and gametophytes have nearly the same ecological requirements."

The first difference in ecological requirements mentioned above is a function of place and, of course, results from sporophytes growing towards sunlight. Gametophytes typically orient towards sunlight, but they do not grow towards it to any extent. The latter two ecological differences mentioned above are a function of time rather than place. The microhabitats that provide suitable conditions for gametophytic growth contain patches of fresh, bare soil in talus hollows and rock crevices. Such microhabitats are ephemeral and exist due to very recent accumulation of dust and soil or to soil-churning rock movements. Sporophytes grow in the same places, but after other plant life has invaded and litter has accumulated.

Although the sporophytes of *W. scopulina* and *A. filix-femina* are adapted to different habitats, their gametophytes exist in strikingly similar habitats. Gametophytes of both genera grow on bare substrates in relatively moist and shady microhabitats. Difference in the sporophytes' yet similarity in the gametophytes' habitat requirements of these two ferns suggests that specialization of the haploid generation of *W. scopulina* has lagged behind that of the diploid phase. This observation reinforces the concept that the evolution of ferns is primarily a diploid affair (Wagner, pers. comm.). It also is in harmony with the suggestion of Cousens (1979) that a potential exists for some degree of independent evolution by the two generations. Cousens' suggestion is based upon the observation of Pray (1968) that differences among populations of *Pellaea andromediifolia* gametophytes were not correlated with differences in the sporophyte generation. *Woodsia scopulina* gametophytes are evolutionary conservatives, developing only in the most mesic, forest-like microhabitat available on the otherwise xeric, rocky macrohabitat to which the sporophyte has become adapted.

Nonetheless, it may be that *Woodsia* gametophytes have made modest advances towards becoming xerophytes. Unicellular glandular hairs and a slightly sticky surface coating may be desiccation-inhibiting adaptations. (We note however that Stokey (1951) states that hairs of this type are widely distributed and usually not of generic significance.) Also, the nonoccurrence of *Woodsia* gametophytes on rotting wood in the immediate vicinity of the study sites indicates that spore germination on this substrate has been selected against. Perhaps the ability to grow on wood has been traded for some xerophytic adaptation.

Our studies suggest that the frequency and abundance of *W. scopulina* gametophytes in suitable microsites is greater than that of *A. filix-femina* gametophytes. This has interesting implications. Perhaps ferns that do not reproduce extensively by means of their rhizome system, such as *W. scopulina*, produce gametophytes of greater vigor than ferns capable of such asexual reproduction and dispersal, such as *A. filix-femina*.

In a study of this type, the tremendous individual mortality due to random phenomena and intraspecific competition that may take place as plants of a species struggle to advance from one developmental stage to another becomes highly evident. For example, only those spores of *W. scopulina* that happen to land on properly illuminated bare soil in specially protected areas among rocks will germinate and develop into gametophytes. Spore wastage must be incredibly high. Of the gametophytes that do develop, some are not in the right portion of the microhabitat to give rise to new sporophytes, such as gametophytes found towards the inner recesses of talus hollows. The threshold light intensity allowing gametophyte development may be too low for the growth of new sporophytes. Alternatively, it may be that not enough free water reaches the deeper parts of talus hollows to allow much sperm transfer from antheridia to archegonia. Thus, innumerable gametophytes are also wasted. Further, out of the mats of juvenile sporophytes that arise from part of a gametophyte population, only one ultimately survives to occupy the crevice or hollow as a young, sterile and latter as a fertile plant.

In *W. scopulina*, almost all intraspecific competition takes place between juvenile sporophytes. New sporophytes promptly kill their parent gametophytes, possibly by secreting a toxic chemical or by parasitism, thereby avoiding competition from other sporophytes that otherwise might arise on the same gametophyte. Competition between juvenile sporophytes of different gametophytes probably is mostly for available light. The reason most intraspecific competition takes place between juvenile sporophytes is because of the small size and spotty distribution of microhabitats suitable to nurture the birth, growth, and continued survival of *W. scopulina* sporophytes.

We extend deep graditude to Dr. W. H. Wagner, Jr., whose counsel made this study possible. Special thanks are also due Dr. C. N. Miller for valuable support throughout the study. We would like to extend our appreciation to the other readers of our final report, Dr. D. E. Bilderback, Dr. F. Wagner, and R. Moran. We also thank R. Hoham for aid in moss identification, Dr. C. A. Speer for providing darkroom facilities, D. Watson for help in preparing photographs, and the students and faculty of Yellow Bay Biological Station for their friendly support.

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REVIEW

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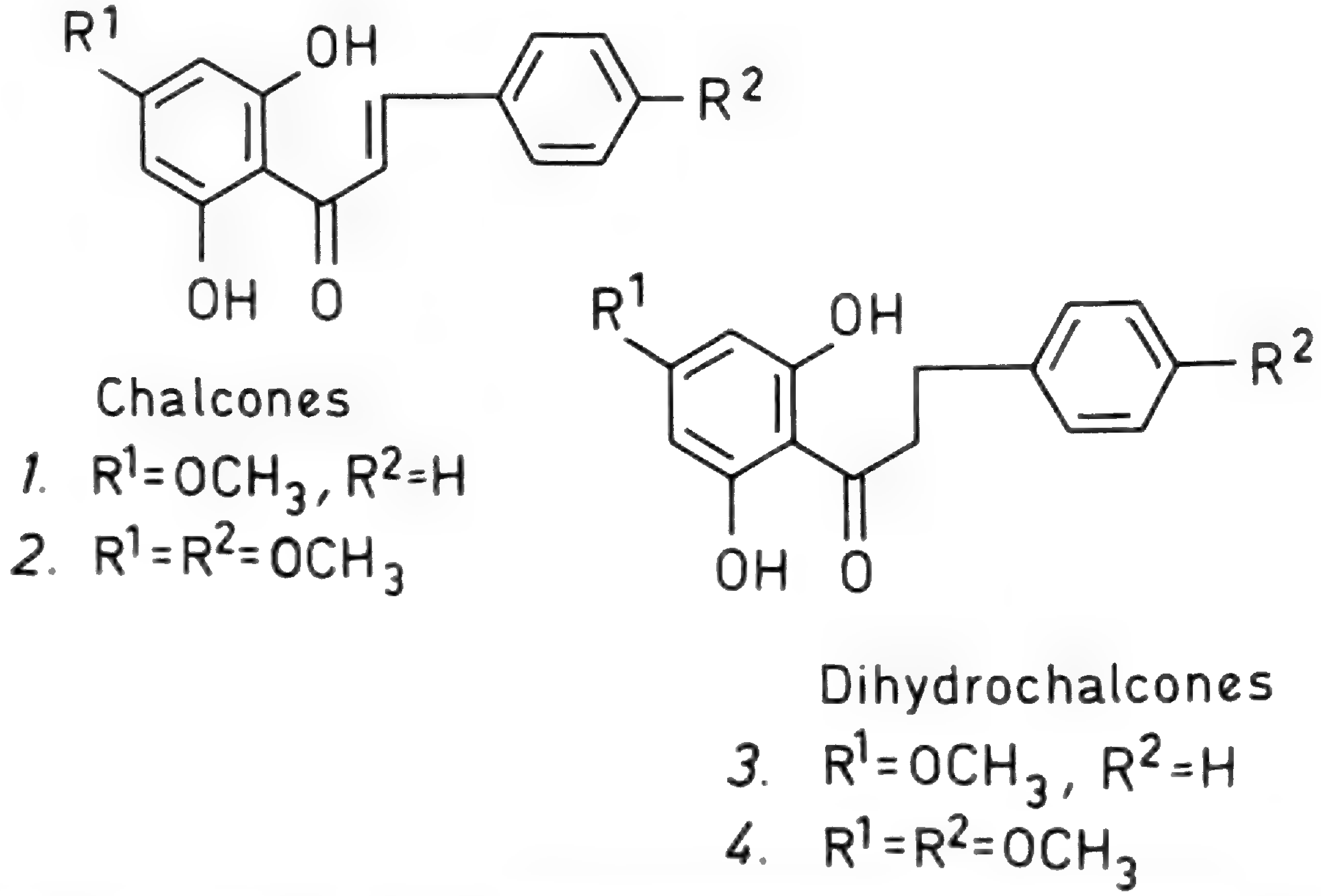
"FERNS, FERN ALLIES AND CONIFERS OF AUSTRALIA," by H. T. Clifford and J. Constantine. xviii + 150 pp. illustr. University of Queensland Press. 1980. ISBN 0-7022-1447-7. $24.25.— Although this book is subtitled "A Laboratory Manual," and does contain illustrations of morphological details, it is a good introduction to the pteridophyta of Australia, and, by extension, to the Old World tropics. Two-thirds of the book concerns pteridophyta. For those interested in identifying Australian ferns and fern allies, there are keys down to species, interesting and useful generic descriptions with notes on habitats, and tables of distribution by species within Australia and Tasmania. Species descriptions are missing, and are not really compensated for in the brief keys to species. Fortunately, the genera of Australian ferns are diverse and mostly with only a few species, and so identification is likely to be easy in most cases. References and literature cited, a table of vegetative characteristics of major vascular plant groups, a list of synonyms of Australian pteridophyta with the names accepted by the authors, a short glossary, and an index conclude this useful work.—*D. B. L.*

Scale Insects Feeding on Farinose Species of Pityrogramma

ECKHARD WOLLENWEBER and VOLKER H. DIETZ*

Several well known species of the fern genus *Pityrogramma* are called Silverback Ferns or Goldback Ferns because of the conspicuous white or yellow farinose deposit on the abaxial surface of their fronds. This material is composed of flavonoid aglycones, mostly of dihydrochalcones and chalcones (Wollenweber, 1978; Wollenweber & Dietz, 1980). The correct structural formulae of these compounds are shown in *Fig. 1*; the formulae in both cited papers are incorrect. These lipophilic phenolic compounds are secreted by glandular trichomes and form quasi-crystalline rods or filaments on the surface of the enlarged terminal cell of the capitate glands (Wollenweber, 1978, pp. 13–15).



Chalcones

1. $R^1=OCH_3, R^2=H$

2. $R^1=R^2=OCH_3$

Dihydrochalcones

3. $R^1=OCH_3, R^2=H$

4. $R^1=R^2=OCH_3$

FIG. 1. Correct structural formulae of chalcones and dihydrochalcones, which form the major constituents of the farina on *Pityrogramma* fronds.

No doubt, glandular trichomes are anatomical features developed for some definite function, and the natural compounds secreted ought not to be regarded merely as waste products (cf. Swain, 1977). The farinose indument of *Pityrogramma* has been the subject of speculation as to its physiological and ecological function for about a century. Among the postulated functions are protection of the lower frond surface and the young spores against wetting on the one hand, and against water loss by transpiration on the other hand. Antibacterial and antifungal effects of such

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*Institut für Botanik, Technische Hochschule Darmstadt, Schnittspahnstrasse 3, D-6100 Darmstadt, Federal Republic of Germany.

phenolic substances have some likelihood. Insect deterrence also has been discussed (Wollenweber, 1978). Field observations indicate that these ferns are rarely attacked by feeding insects (L. D. Gómez, pers. comm.). Höhlke (1902) favored the latter function of the farinose deposits because he had observed that "plants in the greenhouse are free of destructive insects even in the summer." There is as yet no evidence for any of the foregoing functions; allelopathy from frond exudates has been demonstrated (Star, 1980).

FIG. 2. *Saissetia* on the pinna costa and pinnules of *Pityrogramma austroamericana*, showing older and younger glandular trichomes covered with exudate (Leitz Reprovit II). FIG. 3. Close-up of *Saissetia* (Cambridge Stereoscan 600), × 30.

For several years, we have been growing plants of *Pityrogramma austromaericana*, *P. calomelanos*, *P. chrysophylla*, and *P. trifoliata* in a greenhouse at Darmstadt. We were astonished to discover that a certain species of scale insect of the genus *Saissetia* (Coccidae) thrives on our Silverback and Goldback ferns. The insects are found on the abaxial costae surface of old fronds, and also on the pinnule surface. The insects seem to be not harmed or irritated by the rich flavonoid deposits, and they grow and reproduce quite well while sitting in and between the exudate (*Figs. 2* and *3*). We are able to rid the plants of the insects for several months by removing infested fronds.

It is not our intent to refute the possibility that flavonoid exudates may function to deter some insects, even though they do not deter *Saissetia*. Observations of other insects, especially in the field, would be welcome. We wish to thank Mrs. R. Heger

(Darmstadt) for the photograph and Dr. W. Bartholott (Heidelberg) for the SEM picture. We are grateful to Dr. D. R. Miller of the U.S. Dept. of Agriculture (Beltsville) for determining the genus of the scale insect.

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REVIEW

/ **"FERNS AND FERN ALLIES OF KENTUCKY,"** by R. Cranfill, Kentucky, Nat. Pres. Comm. Sci. Techn. Ser. 1. 284 pp. 1980. $4.50.—This new pteridophyte Flora is a model for what state floristic treatments should be. General topics, covered in about 35 pages, include collecting history, phytogeography and ecology, pteridophyte life history, identifying pteridophytes, and a statistical summary of Kentucky's pteridophytes (69 species and 10 hybrids in 29 genera are known). The technical treatment includes a synoptical key to families, a key to genera using fertile and another using sterile material (the latter a very worthwhile novelty for ecologists), and treatments of the genera and species, including keys, synonymies, notes, and illustrations. Although there are no descriptions, the keys are fairly extensive and very thorough notes help to distinguish critical taxa. Distribution maps grouped at the back of the book show the location of each species and the herbarium where vouchers documenting the locations may be found. Seventeen herbaria were consulted, as well as the literature, in compiling the maps. An illustrated glossary, extensive literature cited, and an index conclude the volume. This book is a must for anyone studying ferns in the east-central portion of the United States. It is available from the Kentucky Nature Preserves Commission, 407 Broadway, Frankfort, KY, 40601.—*D.B.L.*

Spore Germination and Young Gametophyte Development of Botrychium and Ophioglossum in Axenic Culture

DEAN P. WHITTIER*

Spores of the Ophioglossaceae have been sown by numerous investigators, but few have succeeded in germinating them (Boullard, 1963). Du Buysson (1889) reported germinating the spores of *Ophioglossum vulgatum* and *Botrychium ternatum*. The spores of *B. virginianum* and three tropical species of *Ophioglossum* (*O. moluccanum, O. pendulum,* and *O. intermedium*) were germinated by Campbell (1895, 1907). Recent studies have shown that spores of *B. dissectum* f. *obliquum* (Whittier, 1972) and *B. multifidum* (Gifford & Brandon, 1978) can germinate in axenic culture.

Spores sown in axenic culture required darkness, took weeks to germinate, and, at least for *B. dissectum*, produced a three-dimensional gametophyte immediately after germination (Whittier, 1973; Gifford & Brandon, 1978). None of the earlier reports by Campbell and du Buysson gave any indication that darkness was required for germination. In soil cultures, *O. moluccanum, O. vulgatum,* and *B. ternatum* germinated in a few days, which is a period comparable to that for spores of the Polypodiaceae (Campbell, 1907; du Buysson, 1889). Young gametophytes of *O. vulgatum* and *B. ternatum* were illustrated by du Buysson (1889) with filamentous and two-dimensional growth habits which are similar to those for polypodiaceous gametophytes. Consequently, the present study of additional species was carried out in axenic culture to determine how the requirements for germination and the type of early gametophyte development for these species compared with the results from previous studies.

MATERIALS AND METHODS

Spores of eight Ophioglossaceae species, *Botrychium biternatum* (Sav.) Underw., *B. dissectum* Spreng. var. *dissectum, B. lunarioides* (Michx.) Swartz, *B. matricariifolium* A. Braun, *B. virginianum* (L.) Swartz, *Ophioglossum engelmannii* Prantl, and *O. vulgatum* var. *pycnostichum* Fern. and var. *pseudopodum* (Blake) Farw., were used in this study. With the exception of the spores of *B. matricariifolium* and *O. vulgatum* var. *pseudopodum*, which were from Ontario, the spores were collected in the southeastern United States. Voucher specimens are on deposit in the Vanderbilt University Herbarium (VDB).

The techniques of Whittier (1973) were employed. The spores were sown on 15 ml of nutrient medium in culture tubes with a diameter of 20 mm. The tubes had screw caps which were tightened to reduce moisture loss. The nutrient medium was composed of Knudson's solution of mineral salts, minor elements, FeEDTA, and 0.6% agar (Whittier, 1973). The medium was supplemented with 0.5% sucrose and had a pH of 6.3. The spores were cultured at 24±1°C in the light at an intensity of 1400 lux from cool white fluorescent lamps or in darkness. For some treatments, the cultures were maintained at 3±1°C in a cold room.

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*Dept. of Biology, Vanderbilt University, Nashville, TN 37235.

For the first eight weeks after sowing, the spores were removed weekly from at least six cultures of each species and examined for germination. After eight weeks, the cultures were sampled at irregular intervals. The percentage of germination was determined after examining 1000 or more spores.

Early gametophyte stages of development were cleared and stained with acetocarmine-chloral hydrate according to Edwards and Miller (1972). The cleared and stained gametophytes were drawn with a camera lucida for study. No effort was made to indicate either the walls of cells lying behind illustrated cells or the spore coat if one was present. However, the nuclei of cells positioned behind other cells are denoted by dotted lines.

OBSERVATIONS

A few of the spores of most species studied germinated in the dark on the nutrient medium at 24°C (*Table 1*). Lengthening the dark periods for those spores which germinated under these conditions increased the amount of their germination. Even after extended periods of time, the spores did not germinate in illuminated cultures.

TABLE 1. GERMINATION OF SPORES OF THE OPHIOGLOSSACAE IN AXENIC CULTURE.

Species	*Weeks in darkness*	*Percent germination*
Botrychium biternatum	4	0.5
B. dissectum var. dissectum	8	0.1
B. lunarioides	3	0.7
B. matricariifolium	8	0.5
B. virginianum	52	0
Ophioglossum engelmannii[1]	52	0
O. vulgatum var. pseudopodum	16	0.7
O. vulgatum var. pycnostichum	52	0

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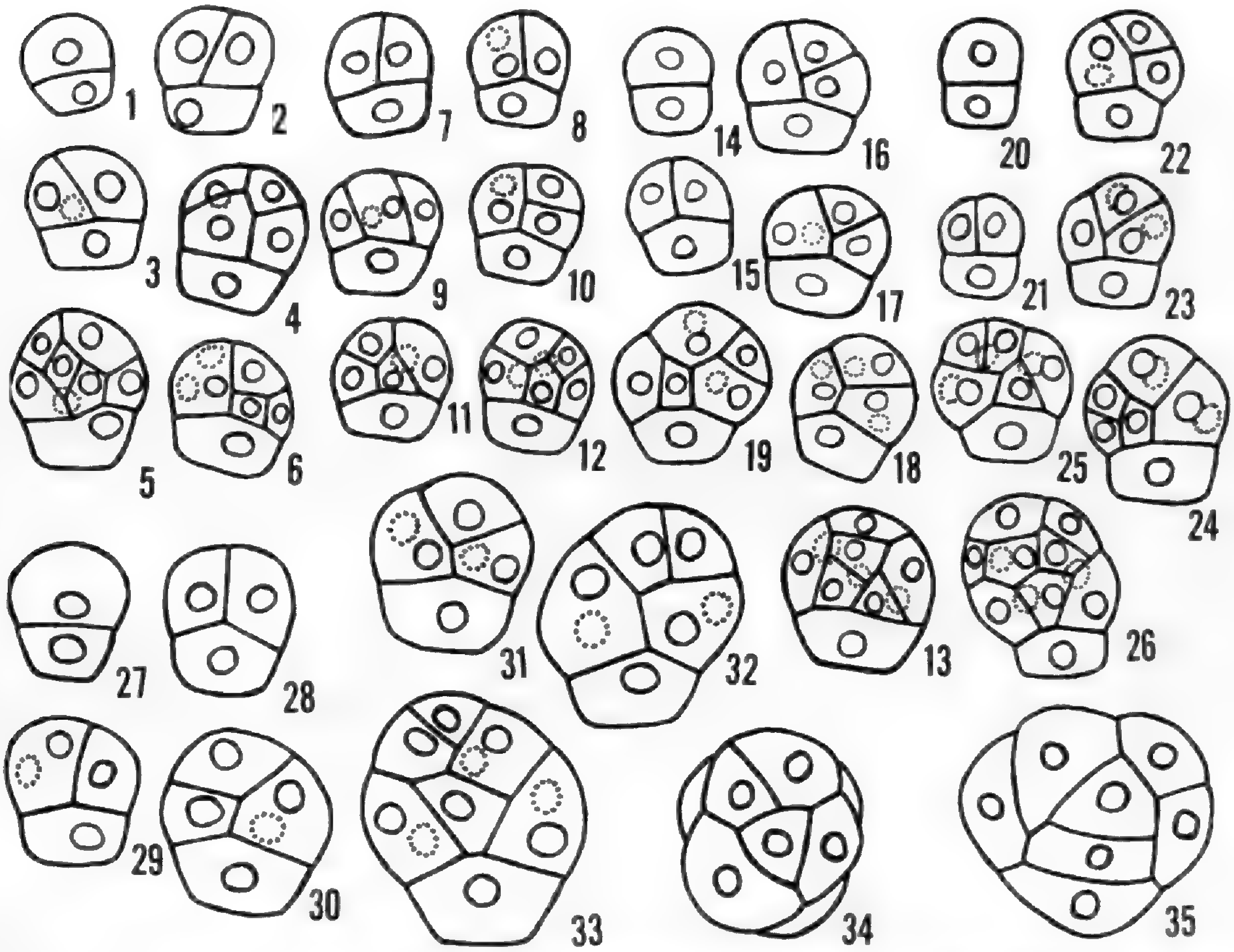
[1] See text for conditions which promote germination

The length of time in darkness before germination varies considerably. The fastest germination was three weeks for *B. lunarioides*. The spores of *O. vulgatum* var. *pseudopodum* took the longest time to germinate at 24°C; although the cultures were not sampled on a weekly basis after eight weeks, initial gametophyte stages were found in the cultures of this species after 16 weeks in the dark, which indicated that the spores had germinated recently. Thus, under these conditions, spores of the Ophioglossaceae do not have identical dark requirements for germination.

Sowing the spores in darkness at 24° did not promote germination in *B. virginianum*, *O. vulgatum* var. *pycnostichum*, or *O. engelmannii*. However, 0.1% of the spores of *O. engelmannii* germinated in the dark when maintained at 24°C for three months, followed by 3°C for three months, and returned to 24°C for six months. Germination did not occur during the cold treatment; consequently the final warm period was necessary for germination. When the first warm period was omitted and the spores were placed directly into the cold (3°C) for three months, no germination occurred. Other modifications of the warm and cold temperature regime are now under investigation in an attempt to increase the amount of germination. Although successful for *O. engelmannii*, the regime of warm and cold temperatures in the dark failed to bring about germination in *B. virginianum* and *O. vulgatum* var. *pycnostichum*.

The early developmental stages of gametophytes were studied in the five species which germinated in the dark at 24°C (*Table 1*). Spores of these species exhibited similar early development. The spore coat cracked open at the triradiate ridge and the spore divided transversely to its polar axis (*Figs. 1, 14, 20* and *27*), producing a distal cell (away from the triradiate ridge) and a somewhat smaller proximal cell (near the triradiate ridge). The proximal cell enlarged, forcing the three lobes of the cracked spore coat apart, and bulged out of the spore coat. The distal cell, which remained inside the spore coat for a longer period of time, continued to divide. The second division was longitudinal and divided the distal cell into two nearly equal cells (*Figs. 2, 7, 15, 21* and *28*). The third division, which was either longitudinal or transverse, occurred in one of the two distal cells (*Figs. 3, 8, 16*, and *29*). The fourth division occurred in the other cell at the distal end. Usually the plane of division was perpendicular to the plane of the third division (*Figs. 10, 17, 22*, and *30*) but occasionally its plane was almost the same as the plane of the third division (*Figs. 4* and *9*). The development to the 5-celled gametophyte usually occured inside the spore coat. Usually the gametophytes lost the spore coat by the 10-celled stage, although it was seen occasionally on gametophytes with more cells.



FIGS. 1–35. Stages in the early development of *Botrychium* and *Ophioglossum* gametophytes. ×275. The bottom cell in Figs. 1–33 is the proximal cell. FIGS. 1–6. *B. matricariifolium*. FIGS. 7–13. *B. dissectum* var. *dissectum*. FIGS. 14–19. *B. lunarioides*. FIGS. 20–26. *B. biternatum*. FIGS. 27–35. *O. vulgatum* var. *pseudopodum*.

The exact pattern of the later divisions was not followed for two reasons: there was more variation in the sequence of the later divisions (*Figs. 5, 6, 11, 12, 18, 23, 24,* and *25*) and the three dimensional form of the young prothalli made it difficult to follow the divisions. However, a small, more or less spherical or globular gametophyte formed as a result of these later divisions (*Figs. 13, 19, 33,* and *36*). The mature gametophytes with morphology typical of the species developed from the globular stage.

The early sequence of divisions in the gametophytes of *O. vulgatum* var. *pseudopodum* was similar to that for the species of *Botrychium*. However, at about the 7-celled stage (*Fig. 32*), the *Ophioglossum* gametophytes appeared to have an apical cell. Side and apical views of 10-celled gametophytes showed definite apical cells (*Figs. 33* and *34*). Older gametophytes had a typical apical cell with three cutting faces (*Fig. 35*). *Botrychium* gametophytes of similar sizes or cell numbers had no recognizable apical cells (*Figs. 13* and *26*).

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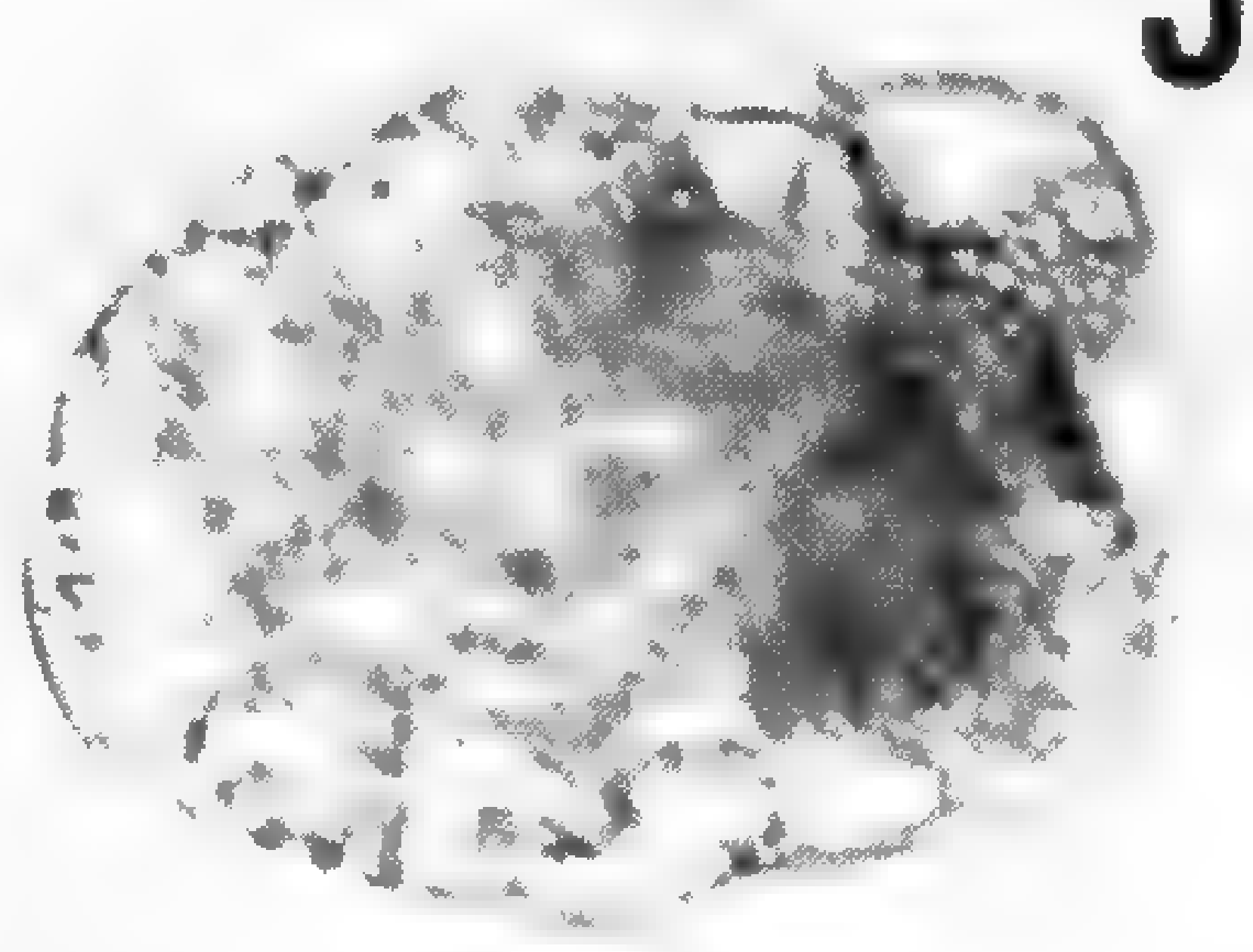

FIG. 36. Young globular gametophyte of *O. engelmannii*, ×275.

The young gametophytes of *O. vulgatum* var. *pseudopodum* were larger than those of *Botrychium* because the individual cells of the *Ophioglossum* gametophytes were larger. More than likely, the larger cell size in *Ophioglossum* gametophytes is controlled by the same factor which caused the spores of *O. vulgatum* var. *pseudopodum* to be larger than those of the *Botrychium* species. The average long dimension for *O. vulgatum* var. *pseudopodum* spores was 43.8 μm; *Botrychium* spore averages ranged from 31.0 to 34.9 μm. The spores of *O. vulgatum* var. *pseudopodum* were not exceptional; those of the other *Ophioglossum* species studied also were larger, with their longest dimensions averaging greater than 40 μm.

DISCUSSION AND CONCLUSIONS

The dormancy of those *Botrychium* and *Ophioglossum* spores which germinated is broken by culturing them in the dark. Thus, the findings of Whittier (1973) and Gifford and Brandon (1978) are corroborated by the results of the present study. However, not all the spores germinate after a dark period at 24°C. In *O. engelmannii*, germination occurs after a sequence of warm and cold periods in the dark. Although the germination in *O. engelmannii* is limited and does not increase with extensions of the final warm/dark period, the sequence of warm/dark, cold/dark, and warm/dark periods is the only treatment which promoted germination. It remains to be determined if increasing the duration of the first warm/dark period and/or the cold/dark period would increase germination in *O. engelmannii*. In *B. virginianum* and *O. vulgatum* var. *pycnostichum* spores, there is no germination after a dark period of 52 weeks at 24°C or following a sequence of warm and cold periods, as for *O. engelmannii*. Although the dormancy of most species' spores is broken by a dark period, spores of *O. engelmannii*, *O. vulgatum* var. *pycnostichum*, and *B. virginianum* demonstrate that either a longer period in the dark at 24°C or a more elaborate treatment is necessary for germination.

Campbell (1895, 1907) germinated spores of four species of Ophioglossaceae, including those of *B. virginianum*, on soil or humus. These spores must have germinated in the light because Campbell noted whether or not there was a trace of chlorophyll in the young gametophytes. In three of the species, germination was slow (taking a month or more), but the spores of *O. moluccanum* (now *O. petiolatum*) from Java germinated in three days. Sussman (1965) suggested that Campbell possibly used old spores which had lost their dormancy. At least for the *Ophioglossum* species, this seems unlikely because Campbell (1907) discussed collecting and sowing the spores in a relatively short time. The germination of these *Ophioglossum* spores in the light is contrary to the findings for axenic culture. In *Lycopodium*, on the other hand, the speed of germination varies considerably (Barrows, 1935). Some of the more tropical species of *Lycopodium* tend to germinate rapidly and on the surface of the soil, compared to the slower underground germination of the more temperate species. Possibly a similar situation exists with *Ophioglossum*, with the spores of the tropical species germinating more rapidly and in the presence of light.

The spores of *B. virginianum* which germinated for Campbell (1895) but which failed to germinate in axenic culture present a different problem. These spores are from a temperate zone species in which dormancy is not broken in axenic culture. Although the age of the spores used by Campbell is unknown, their age may not be that significant because spores of *B. virginianum* up to two years old failed to germinate in axenic culture. More time may be necessary for germination; Campbell (1895), for instance, found early stages of germination after 18 months. Jeffrey (1897), after failing to get germination after 18 months, suggested that the warmer climate in which Campbell worked may have been a factor. Increasing the duration of the experiments and employing higher temperatures along with other variations are now being tested on the spores of *B. virginianum*.

The earliest stages of gametophyte development for the five taxa studied in detail are consistent with the reports of Campbell (1895, 1907). The gametophytes in axenic culture never produced a filament or plate of cells. Within a few divisions and usually before the young gametophyte had completely broken out of the spore coat, a 3-dimensional growth pattern was established. Although Campbell (1907) reported that the proximal cell usually divided in the early stages of the species he observed, the proximal cell remained undivided in the young gametophytes of the present study. However, there are indications that the proximal cell may divide at later stages in the development of the gametophytes in axenic culture. The undivided proximal cell in the young gametophytes and the total lack of chlorophyll (because the gametophytes in axenic culture were grown in total darkness) are essentially the only differences found between the gametophytes from axenic culture and those observed by Campbell (1895, 1907). All the species that have been studied have a similar pattern of early development which produces a small, globular gametophyte.

Campbell (1907) suggested that an apical cell was established very early in *Ophioglossum* gametophytes. In the present study, *O. vulgatum*, which has a prominent apical cell in the mature gametophyte (Bruchmann, 1904), set off an apical cell at possibly the sixth division. In slightly older gametophytes (10 or 11 cells), a characteristic apical cell with three cutting-faces was present. Campbell (1907) observed the earliest stages of apical cell formation in side view, but apparently he did not obtain apical views to confirm the presence of a typical apical cell. No apical cell is found in the young gametophytes of *Botrychium*, which probably is not surprising because the mature gametophytes of *Botrychium* are generally without a prominent apical cell or sometimes even without a recognizable apical cell (Bierhorst, 1958).

The report of du Buysson (1889) on spore germination and early gametophyte growth of *B. ternatum* and *O. vulgatum* must be considered separately because of his unusual observations. He reported germination times comparable to that for spores of the Polypodiaceae, gametophytes with filamentous and two-dimensional growth patterns, and young gametophytes with large amounts of chlorophyll. The characters described by du Buysson (1889) are typical for the Polypodiaceae, but not for the Ophioglossaceae. The possibility that spores of the Ophioglossaceae he sowed never germinated and that stray spores of the Polypodiaceae (he was also studying the development of other fern gametophytes) germinated instead would explain his results. It is probably best to question or ignore the observations of du Buysson until they have been repeated.

Some differences exist between the observations of Campbell and those from axenic culture. Whether these differences are related to the source of the spores (tropical as opposed to temperate) or to environmental variations (soil as opposed to axenic culture) remains to be investigated. Nevertheless, the studies in axenic culture basically substantiate Campbell's descriptions of the early development of gametophytes of the Ophioglossaceae.

I want to thank Mr. Alan Anderson (University of Guelph), Dr. Robert Kral (Vanderbilt University), and Dr. R. Dale Thomas (Northeastern Louisiana University) for supplying spores of *O. vulgatum* var. *pseudopodum*, *B. biternatum*, and *B. lunarioides*, respectively; Dr. W. H. Wagner, Jr. (University of Michigan) for confirming the identification of *B. biternatum;* and the Vanderbilt University Research Council for support of this research.

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New Species of Moonworts, Botrychium subg. Botrychium (Ophioglossaceae), from North America

W. H. WAGNER, JR. and FLORENCE S. WAGNER*

Since the genus *Botrychium* was last revised (Clausen, 1938), much research on it has been done, and many of our taxonomic ideas concerning the use of infraspecific categories (subspecies, variety, form) have changed (Wagner, 1960). Many *Botrychium* species can be distinguished only by subtle differences, and there is often a high level of variability, even in single populations. In the little Moonworts, *Botrychium* subg. *Botrychium*, taxonomic difficulties are exacerbated by the small size of the plants and the tendency for the segments to become folded when pressed. To gain an idea of the distinctness of the species, careful field studies of sizeable populations are needed, and the specimens must be pressed so as to spread out the segments. Finding these usually rare and local plants requires "a labor of love." Together with colleagues and students, we have spent an extaordinary amount of time exploring for Moonworts over the past several decades. Some of the fruits of this quest are described here.

In making our taxonomic judgments, we have adhered to a strict requirement of consistency. Plants from one locality to another must display the same characteristics. Likewise, the differences from other species must be consistent; there should be no connecting forms. We have emphasized the ability of two critical taxa to occur together in the same habitats without intergrading. Mixed populations have thus been of value in making decisions. We also have used the method of mutual associations—the ability of two taxa to maintain their differences in their separate habitats, even though their mutually associated relatives stay alike. Thus if taxon A grows with taxon C in one habitat, and taxon B grows with C in another, and if taxon C remains uniform in both habitats, then the differences between A and B are probably genetically fixed.

The four new Moonworts described here have been studied in wild populations, and in all cases the evidence upholds their validity as discrete species. We treat each only briefly, but we hope that the description and comments will give other workers a preliminary idea of their distinctions and also will lead to finding new populations. More detailed reports on all of these plants will be made in the future.

The measurements are based upon the best-developed and most distinctive specimens from each of several collections. Small specimens may be hard to identify, and all of these species include tiny fertile individuals less than 3 cm tall. Spores were mounted in Hoyer's solution (Beeks, 1955) and measured along the largest diameter. The ranges represent the averages of several different collections.

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*Herbarium and Department of Botany, University of Michigan, Ann Arbor, MI 48109.

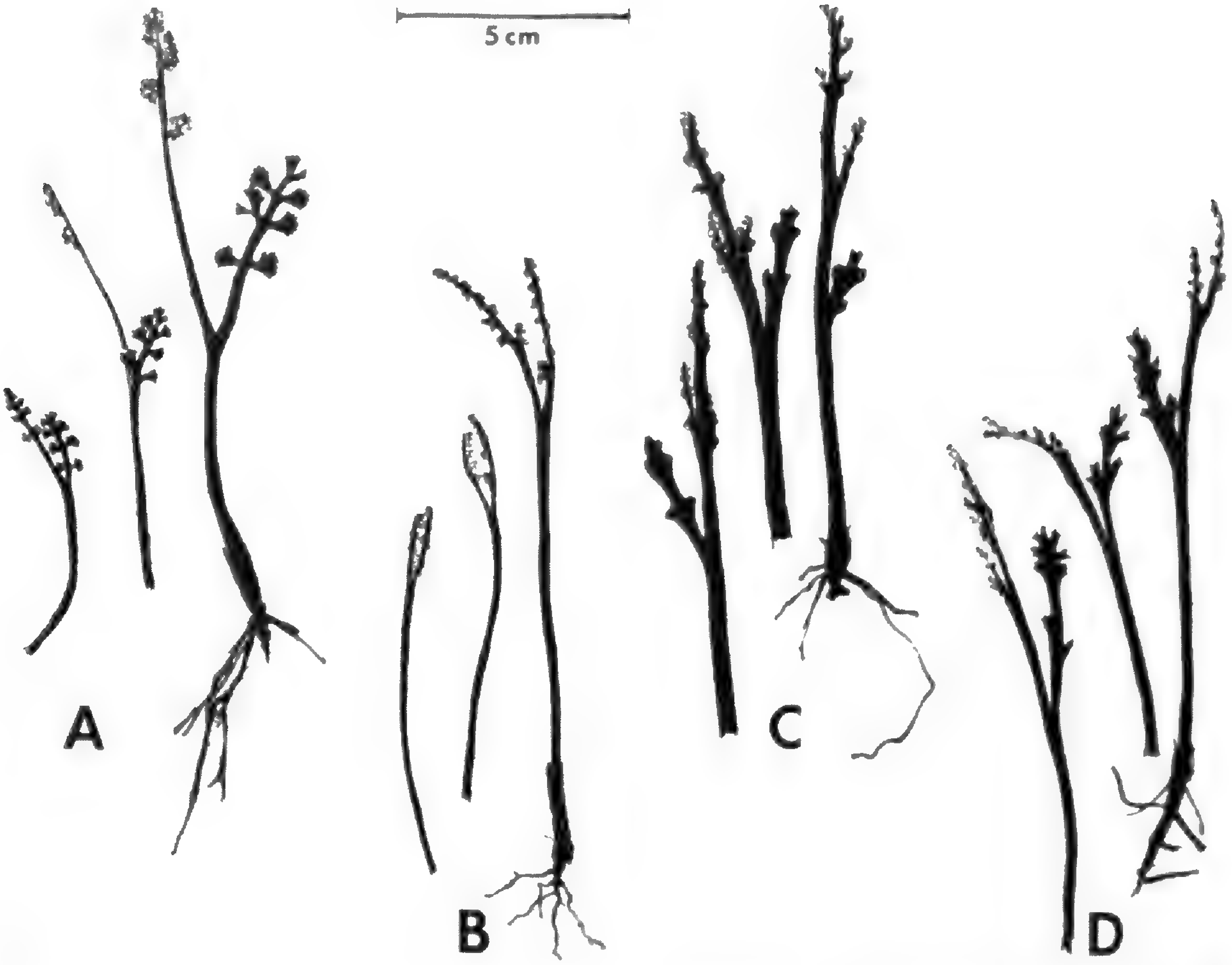

FIG. 1. Silhouette drawings of four new species of moonworts. A. *Botrychium crenulatum*. B. *B. paradoxum*. C. *B. mormo*. D. *B. montanum*.

Botrychium crenulatum W. H. Wagner, sp. nov. Figs. 1A, 2.

Folium 10 (6–16) cm altum, herbaceum, flavo-virens; segmentum sterile dispositum altum in axe, stipite 5 (1–17) mm longo, lamina ovato-oblonga vel lineari-oblonga, 2 (1.5–6.5) cm longa, 1.2 (8–18) cm lata, divisionibus lateralibus 3 (2–5) paribus, cuneatis, remotis, 6 (3–12) mm longis, 5 (3–12) mm latis; margines crenulati, et interdum paucincisi.

Leaf 10 (6–16) cm tall, texture herbaceous, color (living and freshly pressed) yellowish green; common stalk 0.60 (0.50–0.80) of the total leaf length; sterile segment stalk 5 (1–17) mm long, the blade (pressed) ovate-oblong to linear-oblong, 2 (0.5–6.5) cm long, 1.2 (0.8–1.8) cm wide; segments 3 (2–5) pairs, wedge-shaped, the lower and upper margins of the medial pinnae an angle of 70° (20°–110°), their outer edges separated by 80 (30–120)% of the width of the pinnae, often narrowly cuneate toward the base, the largest pinnae 6 (3–12) mm long, 5 (3–12) mm wide, with 15 (10–25) veins reaching the distal margin; margins crenulate (entire to crenate or dentate), and in very large specimens sometimes with 1–5 incisions 1/5 (up to 1/2) of the pinna length; fertile segment 4.5 (2.5–9.5) cm tall, the sporangial branches confined mainly to the upper 1/2 (1/3–2/3), without major proximal sporangial branches; spores 45 (40–48) μm in diam.; chromosomes $2n = 90$.

TYPE: Mt. Baden-Powell Trail, Hamell Springs, San Gabriel Mountains, Los Angeles Co., California, 7745 ft., *L. L. Kiefer 1488* (MICH; isotype UCLA).

OTHER COLLECTIONS:

CALIFORNIA: San Bernardino Co.: San Bernardino Mts.: Santa Ana River: Big Meadows, *Hilend 373* (LA). Bluff Lake Meadow, 1 specimen with *B. simplex*, *Hilend 238* (LA). S Fork of Santa Ana River, with *B. simplex*, *Munz 6164* (DS). San Gabriel Mts.: N of Baldy Notch, headwaters of Coldwater Fork of Lytle Creek, *Kiefer 1489* (LA). San Gorgonio Wild Area: S Fork of Santa Ana River, ca. halfway between Poopout Hill and Slushy Meadows, *Kiefer 815* (LA). South Mountain: Fern Canyon, branch of Mill Creek near Mill Creek Falls, opposite Vivian Creek Falls, *Robertson* in 1907 (DS). **Tulare Co.:** Southern Sierra Nevada, ridge between forks of Monache Creek, SW of Olancha Peak, *Munz 15333* (DS).

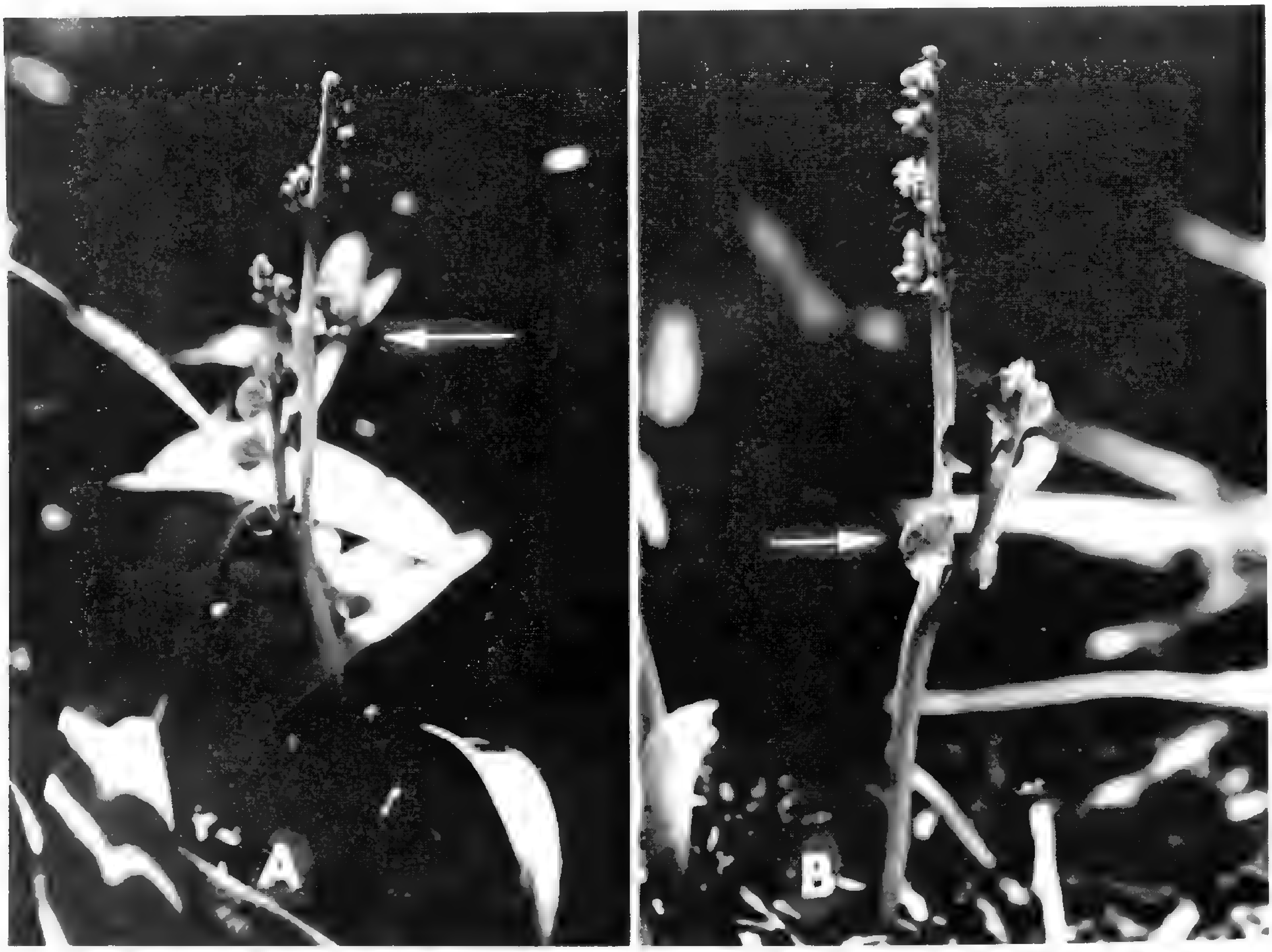

FIG. 2. *Botrychium crenulatum* from the type locality in the San Gabriel Mts., CA. A. View of living plant, showing outline of fertile segment. B. Same, showing spacing and shape of sterile divisions. Leaf 8 cm tall.

One might be tempted to treat this as a geographical subspecies of the worldwide and variable Common Moonwort, *B. lunaria* L. However, there are several reasons why we cannot do this. There are no intermediate populations, nor any evidence of geographical transition. The new species is approximately equally distinct morphologically from *B. lunaria* and the endemic North American tetraploid species *B. minganense* Vict. (cf. Wagner & Lord, 1956). *Botrychium crenulatum* (*Figs. 1A* and *2*) may be distinguished from *B. lunaria* by its herbaceous (not fleshy) texture, yellow (not dark-green) color, higher placement of the sterile segment on the leaf, stalked rather than sessile sterile portion, an average of three pinna pairs (rather than five), much more remote, smaller, and narrower segments, with fewer veinlets terminating along the distal margin[1], and the prevalence of crenulate, as opposed to nearly entire, outer margins (except in *B. lunaria* f. *subincisum* (Roeper) Milde, with the distal margins shallowly toothed, and f. *incisum* (Milde) Holmberg, with pinnae more or less deeply cut; both usually are highly sporadic). The spores of *B. crenulatum* average 6 μm larger in diameter than those of *B. lunaria*.

Superficially, *B. crenulatum* resembles *B. minganense* more than *B. lunaria* because of the over-all proportions of the leaf and its parts. Several of the collections have been identified as *B. lunaria* var. *minganense* (Vict.) Clausen. However, *B. crenulatum* differs from *B. minganense* in its more delicate texture, the more abrupt reduction of the apex, with fewer, coarser, and more angular, rather than more numerous, smaller, and rounder ultimate and penultimate segments, in the mostly crenulate rather than mostly entire distal pinna margins, in the apex of the sterile segment in the leaf primordium for the following year overtopping the fertile and clasping it (in contrast to equally and paralleling it), and in the chromosome number of $2n=90$ rather than $2n=180$.

Whether the plant described here is the same as the one named *B. lunaria* subsp. *occidentalis* by Löve et al. (1971) is questionable. They distinguish it from typical *B. lunaria* in being smaller and having a yellower color. However, the type locality, above Graymont in Clear Creek Co., Colorado, is remote from the known range of *B. crenulatum*. We know of no localities in Colorado or its surrounding states where *B. crenulatum* has been found. The specimens were probably depauperate sun-forms of *B. lunaria*, judging from the characters given. Crenulations are not mentioned.

This Southwestern Moonwort is very rare, judging from the few collections that exist. It may occur locally, however, in large numbers. Most of the specimens come from southern California, especially San Bernardino County, at altitudes averaging around 2500 (2100–3400) m. The fern extends in the mountains of California as far north as Butte County, where we discovered it in 1949 in company with Dr. E. B. Copeland. Possibly *B. crenulatum* has a wider range than given here. Plants we previously identified as the South American *B. dusenii* (Christ) Alston from various western states may prove to be variations of *B. crenulatum*. Also, in Oregon and Montana, moonworts with extremely narrow segment divisions may be conspecific or closely related.

Botrychium crenulatum grows in the drier places of damp meadows, boggy areas, and marshes, either on hillsides or flat lands where there are wet banks or springy spots. The plants are rooted in tussocks or "rises" around isolated trees or shrubs, or in depressions that dry out during the summer, or at the edges of marshes. They may occur either in sun or shade, but evidently prefer partial shade.

The associated genera that have been recorded include woody plants *Pinus* and *Salix*, and herbs *Dodecatheon*, *Hypericum*, *Liparis*, *Mimulus*, *Smilacina*, and *Veratrum*. Various sedges and grasses under which these moonworts grow can make detecting the plants very difficult. Associated species of grapeferns include commonly *B. simplex*, and rarely *B. multifidum*.

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[1] Some collections (e.g., *Wagner 4609*, *Johnston 2080*) have relatively wider segments, with angles approaching those of *B. lunaria*.

Botrychium paradoxum W. H. Wagner, sp. nov. **Figs. 1B, 3.**

Folium 7–15 cm altum, glaucum; segmentum sterile in segmentum fertile omnino transmutatum; dua segmenta fertilia 0.5–4.0 cm alta, inaequilonga vel aequilonga, erecta, approximata, fasciculis lateralibus sporangiorum pro parte maxima sessilibus, ex 2 vel 3 sporangiis constantibus.

Leaf 9 (7–15) cm tall, the stalk 0.5–2.0 mm. in diameter; texture varying from delicately herbaceous to robust and fleshy, color glaucous; sterile segment absent, replaced by a second fertile segment; the two fertile segments 2.5 (0.5–4.0) cm tall, unequal, the shorter one 2/3 the length of the longer one, to equal in length, erect and approximate to one another, nearly sessile to stalked, the stalks up to 1/2 the total fertile segment length; fertile portion mainly linear in outline because the lateral branches are sessile or nearly so and short, usually only 1–3 mm long; sporangia mostly 2 or 3 (1–12) per lateral branch. Spores 40 (36–43) μm in diameter. Chromosome number unknown.

FIG. 3. *Botrychium paradoxum*. A. Small form of deep shade. Marias Pass, MT. Leaf 3 cm tall. B. Large form of open meadows from the type locality at Storm Lake, MT. Leaf 15 cm tall.

TYPE: Storm Lake, ca. 6 mi S of Georgetown Lake, Deerlodge National Forest, Flint Ridge Mountains, Deerlodge Co., Montana, *Wagner 80128* (MICH: 9 plants observed).

OTHER COLLECTIONS:

CANADA: Alberta: Waterton Lakes National Park, 1 mi NW of Red Rock, *Blair & Nagy 1280* (LEA: 6 plants observed). **U.S.A.: Montana:** Glacier Co.: 2 mi W of N end of Swiftcurrent Lake, Many Glaciers Trail to Fishermancap Lake above Wilbur Creek, *Wagner 78547* (MICH: 2 plants). Ca. 1 mi W of Marias Pass, Pondera and Flathead county line, *Wagner 78528, 80117*. (MICH: 45 plants).

This extraordinary Moonwort is surely one of the most peculiar ferns in North America. It shows modifications of the leaf as profound as, for example, those in *Schizaea pusilla* (Schizaeaceae). Two species of *Ophioglossum* lacking sterile segments have been described: *O. kawamurae* Tagawa from Osumi Province, Japan, and *O. lineare* Schlechter & Brause from New Guinea. These plants are morphologically different from *Botrychium paradoxum*, however, in that the sterile segment has been lost rather than transformed. The Sumatran *O. simplex* Ridley has vestiges of the sterile segment (Tagawa, 1939; see also Sahashi, 1980). The fact that bladeless species of the sister genus *Ophioglossum* have been reported points up the fact that these are strongly mycorrhizal plants that may lose much or all of the photosynthetic lamina. In *Botrychium* we can find a progression from forms like *B. lanceolatum* (Gmel.) Ångstr. to such extremes as *B. montanum* and *B. mormo* with the ample blade replaced by a narrow, much reduced blade. In *B. paradoxum*, the sterile lamina is not really lost, but has become converted to a second fertile segment. The two fertile segments are both apparently positively phototropic and negatively geotropic, so that they are held erect and parallel. In other words, what might be an expected loss of the sterile segment, as illustrated partially in *B. montanum*, *B. mormo*, and *Ophioglossum simplex*, and completely in *O. kawamurae* and *O. lineare*, does not take place.

In regard to the western flowering plant, the Leafless Wintergreen, *Pyrola aphylla* Smith, Camp (1940) wrote that ". . .the Pyrolaceae are on the physiological borderline between autophytism and parasitism," and he showed that several species of wintergreens were capable of developing aphyllous forms. Similar physiological conditions no doubt prevail also in the Ophioglossaceae. All of the fronds we have studied are without laminae. It is interesting to note, however, that there is a distinctive Moonwort, the sterile segments of which have remote and narrow divisions, that has been found at two of the four *Botrychium paradoxum* localities. This may represent the atavistic form of *B. paradoxum*, but our evidence for this is tenuous; it may be merely a coincidence.

The four localities for *B. paradoxum* are all near the Continental Divide, extending 200 miles (325 km), and the altitudes range from ca. 1700 m to 2500 m.

Plants of this species are very scarce. In spite of intensive searches by many people, the numbers of specimens observed are low, as noted in the citations of collections above. The plants occur in diverse habitats with two very different extremes—open, sunny meadows and closed, shaded fireweed clones. The Waterton Lakes specimens were taken in a moist drainage area on a grassy slope and those from Storm Lake in meadows only a few feet from the shore. The Marias Pass population grows in black muck and rotting plant materials under a dense cover.

Prominent woody plants growing near *Botrychium paradoxum* include *Pinus contorta*, *Picea englemannii*, *Abies lyallii*, *Potentilla fruticosa*, and shrubby species of *Salix*. The herbaceous vegetation is very different between the open and closed sites. In the open, such as at Storm Lake, we find *Astragalus alpinus*, *Carex atrata*, *Erigeron simplex*, *Ligusticum tenuifolium*, and *Solidago multiradiata* with it, while closed sites are dominated by *Epilobium angustifolium* (Fireweed), *Geum macrophyllum*, *Heracleum lanatum*, *Osmorhiza occidentalis*, and *Senecio foetidus*.

as in the habitat near Marias Pass. Weeds are found in small numbers (*Taraxacum officinale* and *Bromus inermis*). Our largest specimens of *Botrychium paradoxum* were found in open sites, where they reached 15 cm in height with stalks 2.0 mm in diameter (*Fig. 3A*). The heavily shaded plants of *B. paradoxum* are very delicate, reaching only 7 cm in height with stalks 0.5 mm or less in diameter (*Fig. 3B*). Some individuals reached only 3 cm in height and had fertile branches only 1–2 mm tall with only 1 or 2 sporangia each. The latter appeared to be very young juveniles.

In the Fireweed habitats, plants are easily found by parting the large herbs and searching the soil below. But in the open meadows, the plants are challenging to find because of close interlacing with other vegetation and the presence of "look-alikes." The inflorescences of various small grasses, sedges, and plantains may superficially resemble the fertile segments of *B. paradoxum*. The inflorescences of the tiny knotweed, *Polygonum* (*Bistorta*) *viviparum* are especially troublesome.

Botrychium mormo W. H. Wagner. sp. nov. **Figs. 1C, 4, 5.**

Folium 8.6 (7–12.5) cm altum, succulentissimum, flavo-virens, nitidum; segmentum sterile lineare, 2 (1.3–4.1) cm longum, 5 (3–7) mm latum, stipite 1 (0.5–1.6) cm longo, lobis 2 (1–3) paribus, acutis vel truncatis, marginibus distalibus integris vel parum crenatis, nec acute dentatis nec irregulariter laceratis; segmentum fertile 4.5 (2.5–7.5) cm altum, plerumque in parte tertia proximali ramosum.

Gametophyte commonly persisting at the bases of even the largest plants; leaf 8.6 (7–12.5) cm tall, very succulent, yellow-green, shiny; the common stalk making up 50 (20–70)% of the total length; sterile segment linear, 2 (1.3–4.1) cm long, 5 (3–7) mm wide, the stalk 1 (0.5–1.6) cm long; lobes 2 (1–3) pairs, round-pointed to truncate, the distal margins entire or shallowly crenate, not sharply dentate or irregularly lacerate, and with no tendency for exaggerated basal lobes; the tip usually with 2–4 angular triangular or squarish lobes; fertile segment 4.5 (2.4–7.5) cm tall, commonly branched in the lower third, the branches 1/3 to 2/3 as long as the main axis; sporangia large, sunken, not opening until late September and October, the aperture narrow, only 15–30°; spores 49 (45–53) μm in diameter; chromosomes $2n=90$.

TYPE: Rich woods on W side of route 9, 8.15 mi N of Bagley City Park, Clearwater Co., Minnesota, *Wagner 79314* (MICH).

OTHER COLLECTIONS:

MICHIGAN: Alger Co.: Grand Sable Lake, *Hagenah 2550* (BLH). Gorge at Sable Falls, near Grand Marais, *Hall & Hagenah 831* (BLH). **Cheboygan Co.:** Without definite locality, *Hagenah 2511* (BLH). 0.5 mi WSW of Riggsville Corners, *Wagner 8062* (BLH). **Chippewa Co.:** E of Trout Lake, *Hagenah 3480* (BLH). **Dickinson Co.:** 3 mi N of Norway, *Hagenah 2920* (BLH). **Luce Co.:** N of Hendriks Quarry, *Hagenah 3205* (BLH). **Otsego Co.:** Without definite locality, *Hagenah 2717* (BLH). **MINNESOTA: Becker Co.:** N side of Route 143, NE of Twin Island Lake, *Wagner 79327* (MICH). **Beltrami Co.:** S and N of Route 1, ca. 1.5 mi E of Clearwater Co. line, *Wagner 73196* (MICH). **Cass Co.:** N side of Leech Lake, Ottertail Peninsula, *Trana 75615* (MIN). **Clearwater Co.;** U. of Minn. Biol. Station, Lake Itasca, Bearpaw Point, *Wagner 73104* (MICH; 1 specimen mixed with *B. minganense*), *Rosendahl 5929* (MIN). Lake Itasca, Garrison Point, *Wagner 73291* (MICH). Route 200, ca. 1/3 mi W of Wild Rice River, *Wagner 73127* (MICH). **Mahnomen Co.:** E side of county road 4, 1 mi N of Route 200, *Waterway 122* (WIS). **WISCONSIN: Ashland Co.:** Chippewa Twp., Sec. 10, *Peck 79-590* (UWL), *Moran 917* (MIL). **Forest Co.:** N of Route 8, 2 mi W of Crandon, *Wagner* in 1951 (MICH). **Iron Co.:** 3.5 mi NW of Hurley, *R. M. Tryon 4023* (WIS). **Wood Co.:** Arpin, *Goessl 3001* (MIL).

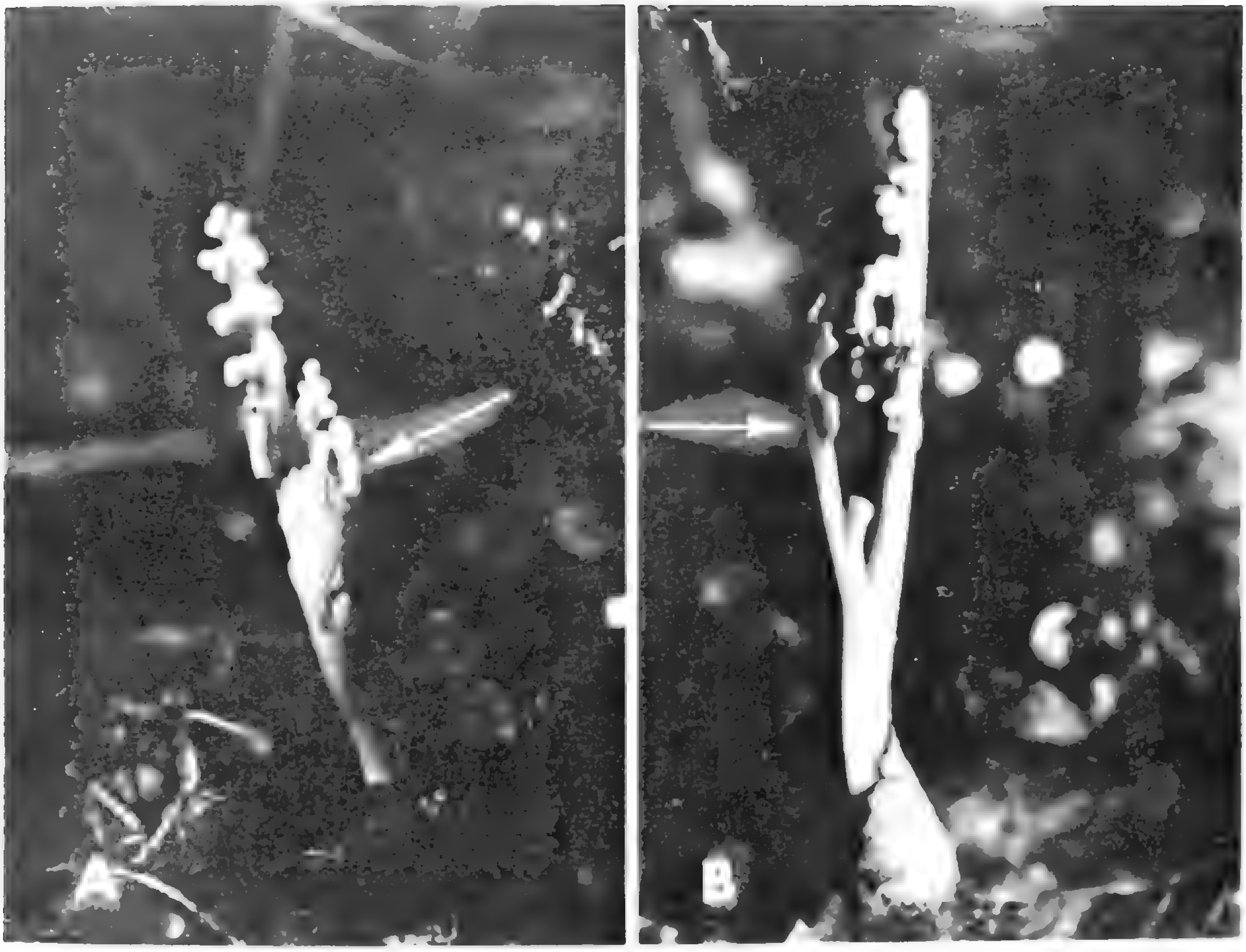

FIG. 4. *Botrychium mormo*. Mature plants. A. Leaf 8 cm tall. Note low branching of fertile segment. B. Leaf 7 cm tall. Note form of segment divisions. Lake Itasca, MN.

FIG. 5. *Botrychium mormo*. Young plants 1-1.5 cm tall. Note highly reduced sterile and fertile segments at tip of petiole, with only 2-4 sporangia. Lake Itasca, MN.

We have studied this Moonwort for three decades and have determined that it is totally consistent. Among the many curious features of *B. mormo*, we include the tendency for persistence of the gametophyte even on full-sized sporophytes, the narrow range, the habitat in mesic forest, and the disappearance of the plants during drought periods. *Figure 4* shows well developed, mature specimens and *Fig. 5* shows the rudimentary, immature specimens. The extremely "chubby" form is nicely illustrated by Peck (1980).

This, together with the following species, may constitute a distinct section of subg. *Botrychium*. Although some small leaves may resemble juvenile or shade specimens of *B. simplex* E. Hitchc., the fully developed leaves show important differences. Mature individuals have the sterile segment higher on the axis, unlike mature *B. simplex* ("Blade inserted almost basally or toward the middle of the plant," Clausen, 1938). The sterile segment has lower divisions approximately equal to those above, but in *B. simplex* these are normally enlarged in mature individuals, in the fullest development producing a ternate blade. The strongly truncate and adnate lateral lobes of the two new species differ from the rounded lobes and spatulate to lunate, more or less stalked pinnae of *B. simplex*. (Indeed, many medium and large specimens of *B. simplex* have middle and upper lateral divisions so flabellate as to resemble *B. lunaria*). The tip of the sterile segment is usually toothed to deeply cleft, unlike the mainly undivided and entire tip of *B. simplex*. The usual habitats of *B. mormo* and *B. montanum* are shaded forest floors under mature trees, rather than those of *B. simplex*, which are open, marshy places, meadows, and edges of wet woodland pond shores.

On the campus of the Lake Itasca Biological Station in Minnesota, sizeable populations of both *B. mormo* and *B. simplex* are found within a quarter of a mile of each other. Class studies have revealed over twenty differences between these species.

Botrychium mormo is very difficult to find and apparently very rare. It if does occur in areas other than Michigan, Wisconsin, and Minnesota, it has been overlooked. Our students have made extensive searches for the plants in many localities. We estimate that only one in fifty seemingly suitable sites have yielded specimens.

The plant grows in rich leaf mold in Basswood *(Tilia americana)*—Sugar Maple (*Acer saccharum*) forests. East of Marquette, Michigan, these dominants are joined by Beech *(Fagus grandifolia)*. The little plants push their way through the leaf litter or simply lie under the litter, failing to appear at all. The goblinish appearance and behavior of this odd plant has inspired the English name of Little Goblin and the scientific epithet *mormo*. Often very small plants less than 1.5 cm tall *(Fig. 5)* will dominate a population. In drought years, even large plants may fail to send up a leaf, or one has to scrape off the litter to find any plants, these whitish and apparently lacking chlorophyll. It is not clear why as many as half the individuals, including specimens of all sizes, retain gametophytes at their bases. These are readily detected as swollen, brown masses 1–6 mm long, protruding among the roots.

The grapeferns that most commonly grow with or near *B. mormo* are *B. virginianum* and *B. minganense*, and more rarely *B. lunaria*, *B. lanceolatum*, *B.*

matricariifolium, *B. dissectum*, and *B. multifidum*. None of these other species shows the peculiarities of *B. mormo* such as the persistent gametophytes, extremely succulent texture, and peculiar shiny yellow color. We conclude, therefore, that the habitat is not responsible for its distinctive characteristics. They are evidently genetically fixed.

Botrychium montanum W.H. Wagner, sp. nov. **Figs. 1D, 6.**

Folium 8.7 (4–12.5) cm altum, herbaceum, glaucum, hebes; segmentum sterile oblongum vel lineare, 2.1 (0.7–4.0) cm longum, 5.5 (2–9) mm latum, stipite 0.7 (0.3–1.5) cm longo, lobis 3 (1–6) paribus, irregularibus, angustis acustisque, oblongis, quadratis, saepe aggregatis vel confluentibus, marginibus distalibus irregulariter dentatis vel laceratis, saepe linearidentatis; segmentum fertile 3.7 (1–6.5) cm altum, non (vel raro) sub parte 2/3 distali ramosum.

FIG. 6. *Botrychium montanum* from the type locality at Swan Valley, MT. Largest plants 8 cm tall. Note shape of divisions of sterile segments.

Leaf 8.7 (4–12.5) cm tall, herbaceous, glaucous, dull; the common stalk making up 60 (40–90) per cent of the total length; sterile segment oblong to linear, 2.1 (0.7–4.0) cm long, 5.5 (2–9) mm wide, the stalk 0.7 (0.3–1.5) cm long; lobes 3 (1–6) pairs, irregular, narrow and pointed, oblong, square, often grouped or confluent, the distal margins irregularly toothed to lacerate, frequently with linear teeth, basal lobes lacking tendency for enlargement; the blade tip usually with 2–4 angular, triangular to oblong teeth or lobes; fertile segment 3.7 (1–6.5) cm tall, not (or only rarely) branched below the upper two-thirds; sporangia not sunken, opening in July and August, the aperture wide, 40–90°; spores 54 (47–57) μm in diameter; chromosome number unknown.

TYPE: Crane Mountain Rd. (Route 498), 3.6 mi S of junction with Ferndale Road, Swan Valley, Lake Co, Montana, cedar swamp forest, *Wagner 80110* (MICH).

OTHER COLLECTIONS:

MONTANA: Flathead Co.: Glacier National Park, Johns Lake, *Wagner 78510* (MICH). S end of Lake McDonald, N of Apgar, *Wagner 78522* (MICH). Avalanche Creek, *Wagner 78532 (MICH)*. **Lake Co.:** Station Creek, near Flathead Lake, *Wagner 78534* (MICH). W side of Cedar Bay Road, *Wagner 80114* (MICH). Soup Creek, 1 mi E of Route 83, *Wagner 80121* (MICH).

Botrychium montanum differs from *B. mormo* in characters that are especially evident in living plants (*Fig. 6*) The leaf is herbaceous (not succulent), glaucous (not yellow-green), and dull (not shiny). The position of the sterile segment along the vertical axis tends to be higher, and the fertile segment only rarely branches near the base. The cutting of the sterile segment is most distinctive: the lobes are more deeply cut and irregular in pattern, with some narrow and some broad (due to grouping or confluence), and most have sinuses of various sizes. Sporangial dehiscence takes place a couple of months earlier than in *B. mormo*, and the sporangial valves open wider. We were unable to find persistent gametophytes in *B. montanum* as we did in *B. mormo*.

Botrychium montanum is relatively easy to find, and we are surprised at the paucity of herbarium collections. A single locality may have hundreds of plants in a small area (*Fig. 6*). It is most abundant in moist, springy Western Red Cedar (*Thuja plicata*) forests. The species may grow in habitats which are quite different, however, as along grassy trail edges (Logan Pass and Many Glaciers, Glacier National Park). Although all of the known localities for *B. mormo* are at less than 1500 ft (450 m) altitude, *B. montanum* grows at altitudes from 3200 ft (970 m) at Swan Lake to 6000 ft (1800 m) at Logan Pass.

The fern may occur in pure stands, but generally it is associated with *B. virginianum* and more rarely with *B. lunaria*, *B. lanceolatum*, *B. boreale*, and *B. minganense*.

We acknowledge the support of NSF Grant DEB 800 55 36, "Evolution and Systematics of the Grapefern genus Botrychium." William R. Anderson kindly translated the Latin diagnoses. A large part of the information we have about the species described here was obtained by our students in Pteridology courses at the Lake Itasca Biological Station, Minnesota, and the Flathead Lake Biological Station, Montana.

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SHORTER NOTE

RANGE EXTENSIONS FOR TWO LYCOPODS ON BARANOF ISLAND, SOUTHEASTERN ALASKA.—Early in 1976, I discovered a colony of Tree Clubmoss (*Lycopodium dendroideum* Michx.) at Thimbleberry Bay, about 5 km southeast of Sitka, Alaska (57°02'N, 135°16'W). Sitka is located on the outer coast of Baranof Island, one of the larger islands of southeastern Alaska. The small, vigorous colony of about five plants grows on a moss-covered rock bench about 1 m above the extreme high tide line. This collection re-extends the range of the species in southeastern Alaska about 200 km to the northwest. It is the first authenticated report of *L. dendroideum* from the large outer islands. The voucher collected in 1979 (*Muller 2854*) is in the herbarium at the University of Alaska Museum, Fairbanks, Alaska (ALA).

During the early 1840's Eduard Blashke, a physician and botanist stationed in Sitka, found *L. dendroideum*. Franz Joseph Ruprecht, curator of the herbarium at St. Petersburg, Russia, published Blashke's sighting. However, in 1941, Eric Hultén expressed doubts about the century-old report of *L. dendroideum* at Sitka (Hultén, E. 1941. Flora of Alaska and Yukon, 1. Lunds Univ. Årsskr. N. F., avd. 2, vol. 37. pp. 69–70).

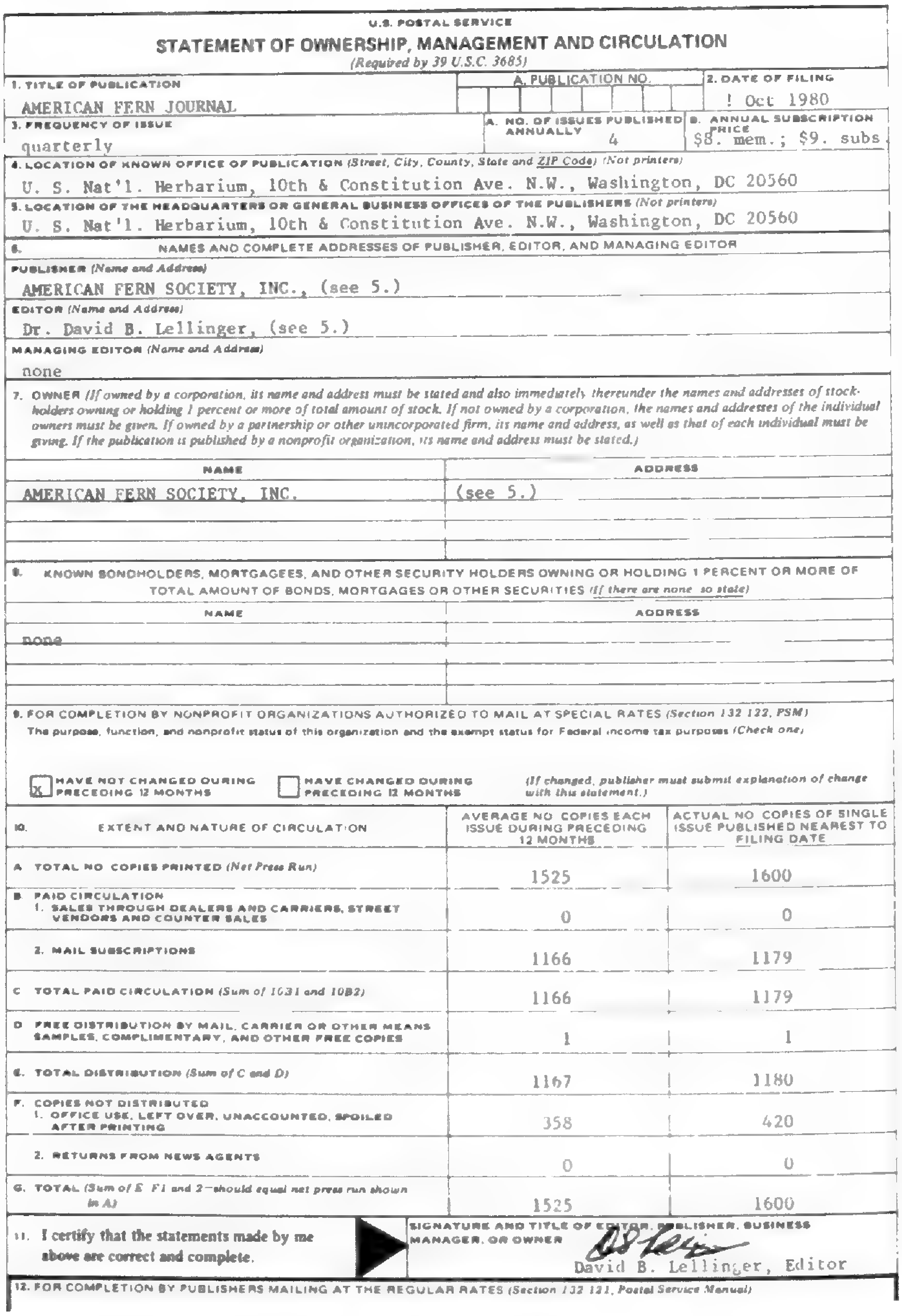
The species occurs at widely scattered localities in the main part of Alaska and is known to grow in the Alaska panhandle (southeastern Alaska) south and east from Wrangell. A previously unreported collection of *L. dendroideum* was made in June of 1973 at Thomas Bay east of Petersburg, a northward range extension of 65 km within the Alaska panhandle. The specimen (*Robuck 1403*) is in the herbarium of the U.S.D.A. Forest Service, Forestry Sciences Laboratory, Juneau, Alaska.

In October 1980, several colonies of the Bog Clubmoss (*Lycopodium inundatum* L.) were found about 25 km south of Sitka, 1/3 km northwest of Big Bay at the southeastern end of an unnamed lake system (56°49'N, 135°21'W). These plants were growing on a thin muskeg mat overlying granitic rock at the edge of a shallow lake. Vouchers (*Muller 4181*) are at ALA and the University of Washington herbarium (WTU). In Alaska, the plant is known to occur along lake shores and in muskeg areas in the vicinity of Ketchikan and Wrangell. The Big Bay collection is a range extension of about 200 km to the northwest. This is the first time *L. inundatum* has been reported from the large outer islands of the Alaska panhandle.

Since southeastern Alaska is sparsely settled and travel is difficult and expensive, a lack of botanical information is not surprising. More range extensions can be expected as botanists investigate southeastern Alaska more thoroughly.—*Mary Clay Muller, Chatham Area, Tongass National Forest, P.O. Box 1980, Sitka, AK 99835.*

PTERIDOPHYTES FOR THE FLORA MESOAMERICANA

The Flora Mesoamericana Project, run by a consortium of museums, aims at producing a comprehensive vascular plant flora covering southern Mexico (Chiapas, Tabasco, Quintana Roo, and Yucatán) south to the Panama/Colombia border. Although pteridophytes initially were to be excluded, a decision was made in November 1980 to include them. The volume on Pteridophyta, scheduled to appear around 1986, will be edited by Ramón Riba and Luis Diego Gómez. Pteridologists interested in contributing generic or family treatments are urged to contact the editors for general information. Please write to Flora Mesoamericana—Pteridophytes, Museo Nacional de Costa Rica, Apartado 749, San José, Costa Rica, C. A.



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Azolla filiculoides New to the Southeastern United States[1]

VERNON M. BATES, JR.* and EDWARD T. BROWNE, JR.**

When studying specimens of *Azolla*, one is often confronted with a large number of sterile collections that cannot be identified with confidence. Although Svenson (1944), in his monograph of the New World species of *Azolla*, based his classification on characteristics of the infrequently occurring sporocarps and paid little attention to vegetative characters, we believe that megaspore ornamentation provides the only suitable means of identification.

Through SEM examination of its megaspores, we have confirmed the identification of a collection of *A. filiculoides* Lam. from Georgia. The collection was made 15 April 1956 from plants floating in a large fresh-water lake at the north end of Sapelo Isaland, McIntosh Co., Georgia (*Wilbur H. Duncan 19969*, with William P. Adams and Clyde Connell, TEX). Apparently this is a new record for the southeastern United States. We found that the megaspore ornamentation agreed very closely with Svenson's (1944) line drawings and description; the "raised, hexagonal markings" reported by Svenson actually are localized masses of fused excrescences which form a flattened to slightly convex reticulum (*Fig. 1*). Although there has been no previous ultrastructural study of *Azolla* megaspores from North America, recent descriptions of European material support our identification (Pieterse, de Lange & van Vliet, 1977: Martin, 1978).

Traditionally, *Azolla* in the southeastern United States has been thought to be *A. caroliniana* Willd. Megaspores apparently never have been described for this species in North America (Svenson, 1944; Correll & Correll, 1975). Di Fulvio (1961) illustrated a cross-section of the perispore of an *A. caroliniana* megaspore, but the source of her material and the voucher documenting it are not stated. Unfortunately, so little is known about the cytology of *Azolla* that it cannot be said whether or not *A. caroliniana* is a sterile hybrid; it has been reported as $2n=48$ in Europe (Löve, Löve & Pichi Sermolli, 1977, p. 373). Finding consistently sterile material over the entire range of a species does, however, raise the possibility that the material is hybrid or otherwise incapable of forming spores, perhaps as a result of aneuploidy.

Svenson reported the distribution of *A. filiculoides* as widely scattered along the Pacific Coast from Alaska southward into Washington, Oregon, California, and Mexico. Although he believed that this species was naturalized in the New England states, he never attempted to explain two New York collections of *A. filiculoides* which may not have been the result of artificial introductions: Riverhead, Long Island, Suffolk Co., 20 Aug 1938, *Muenscher & Curtiss 6647* (US) and Oak Orchard, Orleans Co., Aug 1876, *Herb. N. L. Britton s. n.* (NY).

If, as some have suggested (Smith, 1955), *Azolla* is disseminated by adhering to the feet of migratory waterfowl, it seems strange that *A. caroliniana* and *A.*

---

* Data Communications Corp., 3000 Directors Row, Memphis, TN 38131.

** Dept. of Biology, Memphis State University, Memphis, TN 38152.

[1] Portion of a Master of Science thesis submitted to the Department of Biology, Memphis State University, 1980.

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filiculoides would be limited to the Atlantic and Pacific coasts, respectively. In light of the large number of sterile collections of *Azolla* from the eastern United States which cannot be identified with certainty, it seems quite possible that *A. filiculoides* is more widely distributed in the eastern United States than has been thought. Our discovery of *A. filiculoides* in Georgia, considered with those specimens already known from New York, supports the hypothesis that this species may be widely distributed along the Atlantic coast. Unfortunately, this cannot be confirmed until more fertile collections are observed or until vegetative differences can be found to distinguish the various species of *Azolla*.

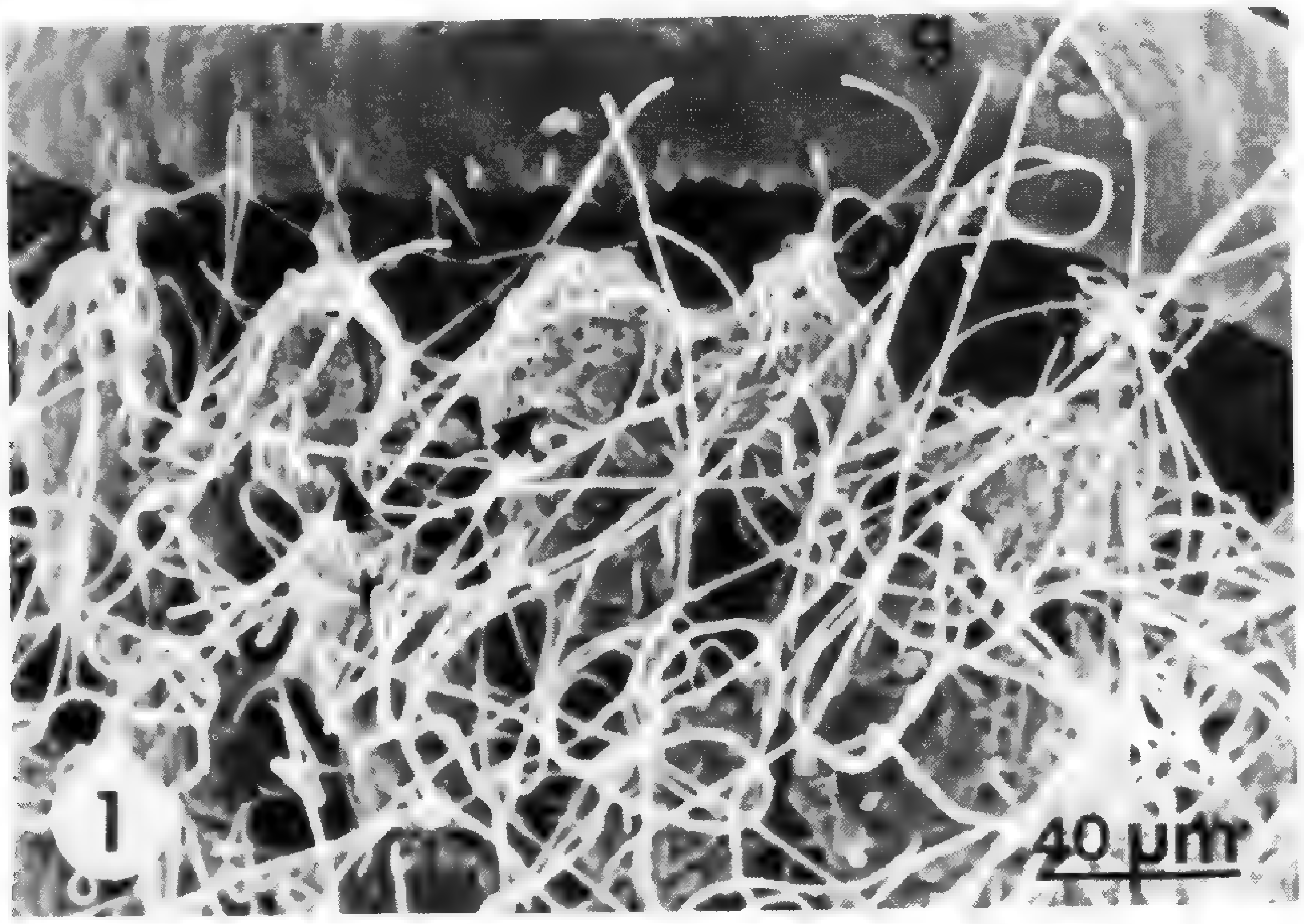

FIG. 1. Scanning electron micrograph showing characteristic features of the megaspore of *Azolla filiculoides*. Proximal to the girdle (g), elevated masses of excrescences form a distinct reticulum (r).

We wish to express our appreciation to Dr. Lewis B. Coons and Mrs. Naomi Roberts for their kind assistance in obtaining the micrograph. We are also especially indebted to Dr. Billie L. Turner, curator of the Herbarium, University of Texas at Austin, who loaned us collections of *Azolla* to examine. In addition, we are very grateful to Dr. W. Carl Taylor, curator of the Vascular Herbarium, Milwaukee Public Museum, for reading the manuscript and making valuable suggestions.

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The Genus Nephrolepis in Florida

CLIFTON E. NAUMAN*

The recent addition of *N. multiflora* (Roxb.) Jarrett ex Morton to the Florida flora (Gillis & Proctor, 1975) and the description of a new hybrid species (Nauman, 1979a) has created a need for a revised treatment of the genus in Florida.

This treatment is based on a study of more than 120 morphological characters involving more than 1000 specimens. A transplant experiment and ecological observations (Nauman, 1979b) also aided in interpreting morphological variability.

This study was based in part on a Masters thesis, and I would like to express my appreciation to D. F. Austin (Florida Atlantic University) for his guidance during the course of study and for advice and assistance in the gathering of data. Appreciation is also given to the curators and staff of the following herbaria for the loan of materials and types: B, BM, BR, F, FAU, FLAS, FSU, FTG, GH, K, MA, NY, P, PENN, PH, S, TENN, UC, US, USF, UWFP.

KEY TO THE FLORIDA SPECIES OF NEPHROLEPIS

1\. Adaxial costa surface of medial pinnae glabrous (sometimes with a few scales); indusium reniform, hippocrepiform, or lunate, ca. 1.2 mm or more wide.

  2\. Pinnae falcate with acute to attenuate tips; plants never bearing tubers; rachis scales appearing concolorous or obscurely bicolorous .... 3. *N. exaltata*

  2\. Pinnae not falcate or slightly so with blunt tips; plants sometimes bearing tubers; rachis scales distinctly bicolorous (pale with a dark point of attachment) .... 2. *N. cordifolia*

1\. Adaxial costa surface of medial pinnae sparsely to densely covered with short erect trichomes (often also with scales); indusium orbicular, ca. 1.0 mm wide.

  3\. Basal portions of mature stipes covered with dark brown, appressed scales with pale margins. 4. *N. multiflora*

  3\. Basal portions of mature stipes not covered with dark brown, appressed scales, but often with a few loose, reddish to light brown scales or the scales absent.

    4\. Adaxial costa surface sparsely pubescent, the trichomes 0.4 mm long; pinnae mostly falcate; blade length/width ratio 6.8–17.9, mean 9.5 .... 5. *N.* × *averyi*

    4\. Adaxial costa surface densely pubescent to tomentose (rarely glabrous), trichomes 0.3 mm long; pinnae not falcate or slightly so; blade length/width ratio 3.8–7.8, mean 5.1. 1. *N. biserrata*

1. Nephrolepis biserrata (Swartz) Schott, Gen. Fil. text to pl. 3. 1834.

Aspidium biserratum Swartz, J. Bot. Schrad. 1800(2):32. 1802. TYPE: Mauritius. *Groendal*, (S-Hb. Swartz !).

Nephrodium biserratum (Swartz) Presl, Rel. Haenk. 1:31. 1825.

Hypopeltis biserrata (Swartz) Bory in Bél. Voy. Indes. Or. Bot. 2:65. 1833.

Lepidoneuron biserratum (Swartz) Fée, Gen. Fil. 301. 1852.

Nephrolepis exaltata var. *biserrata* (Swartz) Baker in Mart. Fl. Brasil. 1(2):493. 1870.

Nephrolepis hirsutula δ *biserrata* (Swartz) Kuntze, Rev. Gen. Pl. 2:816. 1891.

Aspidium acutum Schkuhr, Krypt. Gew. 32, *pl. 31*. 1806. TYPE: Locality and collector not stated (Hb. Breyne presumably destroyed).

Nephrodium acutum (Schkuhr) Presl, Rel. Haenk. 1:31. 1825.

Nephrolepis acuta (Schkuhr) Presl, Tent. Pterid. 79. 1836.

Nephrolepis hirsutula α *acuta* (Schkuhr) Kuntze, Rev. Gen. Pl. 2:816. 1891.

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*Department of Biological Sciences, Florida Atlantic University, Boca Raton, FL 33431.

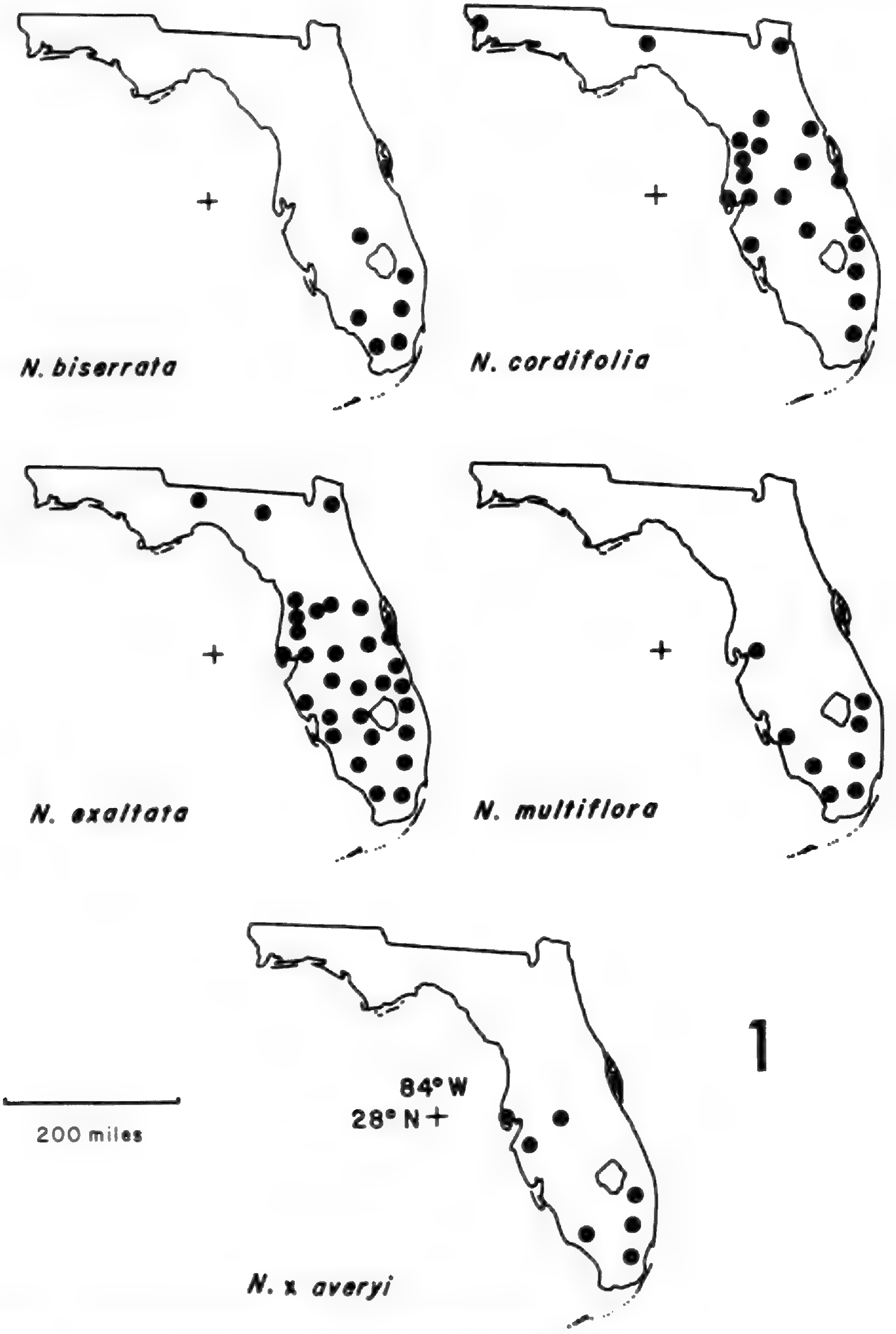

FIG. 1. County distributions of the species of *Nephrolepis* in Florida.

DISTRIBUTION AND HABITAT: This is a species of swamps and wet hammocks in which it is usually terrestrial, but may be epiphytic or epipetric. The general distribution is pantropical; in Florida it is largely restricted to Florida's tropical fringe (*Fig. 1*). Distribution in Florida appears to be limited by the plant's ability to tolerate cold temperatures as revealed by transplant experiments.

Nephrolepis biserrata is best distinguished from the other Florida *Nephrolepis* species by its size, hyaline margined scales on the rhizome and croziers, pubescent pinnae, and orbicular indusia. The species is closest to *N. multiflora* in indumentum and sori, to *N.* × *averyi* in size, and to *N. cordifolia* in spores.

REPRESENTATIVE SPECIMENS:

Broward Co.: *Durand 58, 64, 72* (FAU); *Leeds 342* (NY, PH); *Moldenke 483* (NY, PH, US); *Nauman & Nauman 380* (FAU); *R. P. St. John 1751* (FLAS). **Collier Co**.: *Correll 6081* (FLAS); *Diddle 698* (FLAS); *Evans* (TENN); *Lakela et al. 27996* (USF); *Nauman & Austin 555* (FAU). **Dade Co**.: *Avery & Loope 1918* (FAU); *Britton 428* (F, NY); *Buswell* (FAU); *Carter 204* (PH); *Correll 5897* (GH, US); *Eaton* (F); *Long et al. 1941* (NY, USF); *Munroe* (GH, NY, UC); *Safford & Mosier 105* (US); *Small & Mosier 5890* (NY, US). **Highlands Co**.: *Garrett 60* (FLAS); *McFarlin 10714* (GH). **Monroe Co**.: *Delchamps & Wherry* (PH); *Lakela & Almeda 30526* (USF). **Palm Beach Co**.: *Durand 25, 80* (FAU); *Hill 152* (NY); *McJunkin* (FAU).

2. Nephrolepis cordifolia (L.) Presl, Tent. Pterid. 79. 1836.

Polypodium cordifolium L., Sp. Pl. 2:1089. 1753. TYPE: Petiver, Pterigr. Amer. *t. 1, f. 11*. 1712 (!). The Petiver plate is supposedly a copy of Plumier, Tract. Fil. Amer. *t. 71*. 1705 (!). The Plumier plate is a poor drawing of what might be a species of *Nephrolepis*. Until plants can be examined from the area where Plumier obtained his material, application of the epithet *N. cordifolia* will be problematical.

Aspidium cordifolium (L.) Swartz, J. Bot. Schrad. 1800(2):32. 1802.

Aspidium tuberosum Bory ex Willd., Sp. Pl. ed. 4, 5:234. 1810. TYPE: "Bourbon sur les arbres, No. 111, *Bory de St. Vincent*" (B-Hb. Willd. 19759 photo FAU !, photo GH !; isotypes P photo FAU !, FI, not seen).

Nephrodium tuberosum (Bory ex Willd.) Desv., Mém. Soc. Linn., Paris 6:252. 1827.

Nephrolepis tuberosa (Bory ex Willd.) Presl, Tent. Pterid. 79. 1836.

Nephrolepis cordifolia var. *tuberosa* (Bory ex Willd.) Baker in Mart. Fl. Brasil. (1)2:491. 1870.

Nephrolepis exaltata β *tuberosa* (Bory ex Willd.) Kuntze, Rev. Gen. Pl. 2:816. 1891.

DISTRIBUTION AND HABITAT: Whether or not this species is native to Florida is uncertain. Wherry (1964) considered it possibly native to the southernmost portions of the State. Though widespread, the plants are almost entirely persistent from cultivation in dumps and at abandoned homesites. I know of only one site where the plants may have colonized without the help of man. This is on the Sturrock estate in West Palm Beach. The plants were reported to have been blown in by a hurricane in the late 1940's (Sturrock, pers. comm.). This species' distribution is scattered in Florida and doesn't conform to any apparent trends in temperature extremes *(Fig. 1)*. The general distribution is possibly worldwide in the tropics and subtropics, also in Japan and New Zealand.

Tubers are the most distinctive feature of this species, although tuberless colonies are frequent throughout Florida. Whether tuber production, or the lack of it, is controlled by environmental or genetic factors is at present uncertain. There appears to be a correlation between the substrate in which the plant is growing and tuber production. In the Florida populations, tuber production seems restricted to plants growing in humus and has not been seen in epiphytic plants or plants growing in drier sites. These observations suggest some specific soil and moisture requirements for tuber production.

The distinctly bicolorous rachis scales are as diagnostic as tuber-production and may be used to distinguish this species from any of the other Florida species, even in the absence of other key features..

REPRESENTATIVE SPECIMENS:

Brevard Co.: *Hollister* (US); *Shuey M1084* (USF). **Broward Co.:** *McCart & Snyder 9523* (FAU). **Citrus Co.:** *R. P. St. John 197* (FLAS). **Dade Co.:** *Evans* (TENN); *Hardy 5* (PH). **Duval Co.:** *Darling* (US). **Escambia Co.:** *Burkhalter 5919* (UWFP). **Hernando Co.:** *Cooley et al. 8307* (GH, USF); *Mickel et al. 1782* (UC); *Moldenke & Moldenke 29488* (US). **Highlands Co.:** *McFarlin 8957* (FLAS). **Hillsborough Co.:** *Evans 2303* (TENN); *Mickel et al. 1789* (US); *Scudder 441* (FAU). **Leon Co.:** *Hume* (FLAS). **Marion Co.:** *Mickel et al. 1742* (UC). **Martin Co.:** *Austin et al. 6469* (FAU); **Orange Co.:** *Githens 2579* (PH); *Medgser* (UC). **Palm Beach Co.:** *Austin* (FAU); *Baker* (FAU); *Cassen 89* (USF); *Hill 149* (NY); *Nauman et al. 218, 410* (FAU); *Wilhelm 121* (FAU). **Pasco Co.:** *Carpenter* (GH). **Pinellas Co.:** *Genelle & Fleming 2508* (USF); *Scudder 436* (FAU). **Polk Co.:** *Cooley 11783* (USF); *Buswell* (USF). **Saint Lucie Co.:** *Nauman & Tatje 518* (FAU); *Nauman et al. 255* (FAU). **Sarasota Co.:** *Wherry* (PH). **Sumter Co.:** *E. P. St. John* (FLAS). **Volusia Co.:** *Lakela 31864* (USF).

3. Nephrolepis exaltata (L.) Schott, Gen. Fil. text to pl. 3. 1834.

Polypodium exaltatum L. Syst. Nat. ed. 10(2):1326. 1759. TYPE: Sloane, Jam Voy. *t. 31*. 1707, which is based on a specimen communicated to Sloane by *Dr. Sherard* from Jamaica (BM not seen, photo FAU).

Aspidium exaltatum (L.) Swartz, J. Bot. Schrad. 1800(2):32. 1802.

Nephrodium exaltatum (L.) R. Brown, Prodr. Fl. Nov. Holl. 1:148. 1810.

DISTRIBUTION AND HABITAT: This is the most common of the Florida species. It is found in a wide variety of habitats, such as tropical hammocks, low hammocks, and swamps. Frequently *N. exaltata* is found as an epiphyte on *Sabal palmetto* or species of *Quercus*, but it also may occur epipetrically or terrestrially. In Florida, *N. exaltata* is found from Dade and Monroe to Duval Counties *(Fig. 1)*. Occasionally it occurs farther north, but only in cultivation. The plants are most common south of Lake Okeechobee, becoming occasional to rare northward. The general distribution has been traditionally construed as pantropical, but studies by Proctor (1977) and Stolze (pers. comm.) have implied that *N. exaltata* may have a more restricted range than previously thought. Examination of herbarium specimens shows that a large proportion of plants identified as *N. exaltata* is actually *N. multiflora*, *N. biserrata*, *N. cordifolia*, or *N. rivularis* (Vahl) Mettenius. The misapplication of the epithet *exaltata* is so widespread that a thorough monographic study will be necessary to determine the actual range of this species. Authentic specimens are known from Florida, Jamaica (the type locality), the Antilles, Bermuda, and Mexico.

REPRESENTATIVE SPECIMENS:

Brevard Co.: *Baldwin 83* (PENN, PH); *Burgess 697* (F, NY); *Long et al. 4038* (USF); *Small et al. 10802* (NY). **Broward Co.:** *Durand 15, 73* (FAU); *Hopkins 31* (FAU): *Janda 29* (FAU); *Nauman 826* (FAU). **Charlotte Co.:** *Ward A-69* (FLAS). **Citrus Co.:** *E. P. St. John* (FLAS). **Collier Co.:** *Austin & Austin 6669* (FAU); *Austin el al. 6763* (FAU); *Clewell 286* (FSU); *Cooley 786* (USF); *Evans* (TENN); *Eyles & Eyles 8235* (GH); *Hitchcock* (F); *Lakela & Almeda 29941* (USF); *Long et al. 2393* (USF); *Nauman et al. 328* (FAU); *Sturtevant 44* (FLAS, US). **Dade Co.:** *Garber* (F, NY); *Hill 3079* (FTG); *Moldenke 436* (NY); *Small 7384* (NY, TENN); *Tracy 9135* (F, NY, PENN, US). **Duval Co.:** *Calkine* (F). **Glades Co.:** *Ward 1-10* (FLAS). **Hardee Co.:** *Kirk* (FLAS). **Hendry Co.:** *Jennings* (USF); *Ward* *et al. 2396* (FLAS, FSU). **Hernando Co.:** *E. P. St. John* (FLAS). **Highlands Co.:** *Evans 2292* (TENN); *Lakela 26793* (USF); *Mickel et al. 1815* (FSU, UC); *Nauman 90* (FAU); *Porter & Porter 10618* (NY, UC); *Wilbur & Webster 2610* (GH, NY, US). **Hillsborough Co.:** *Mickel et al. 1789.* (UC). **Indian River Co.:** *Small 8849* (NY). **Lake Co.:** *Nash 1288* (F, GH, NY, PH, UC, US); *Underwood* (F, GH). **Lee Co.:** *Brumbach 5348* (FAU, FLAS); *Correll 5919* (GH); *Hitchcock 542* (F, GH, US); Standley *124* (F, GH, NY). **Leon Co.:** *Jackson* (FSU). **Martin Co.:** *Nauman 527* (FAU); *Nauman & Tatje 520* (FAU); *Popenoe & Popenoe 688* (FTG). **Monroe Co.:** *Long et al. 1703* (USF). **Okeechobee Co.:** *McCart 10287* (FAU). **Osceola Co.:** *Mearns 31* (US). **Palm Beach Co.:** *Austin 6636* (FAU); *Cooley et al. 4877* (GH, USF); *Durand 77, 81* (FAU); *Hitchcock 2402* (F); *Kral 5680* (FSU); *Meagher 895* (FTG); *Nauman et al. 702.* (FAU); *Randolph 140* (GH); *Underwood 2219* (NY). **Pasco Co.:** *Underwood 1931* (NY). **Pinellas Co.:** *Curtiss 3764* (F, NY, UC); *Genelle & Fleming 1640* (USF); *Ralphs 750* (F); *Scudder 104* (FAU); *Thorne 10315* (UC). **Polk Co.:** *Jennings & Jennings* (USF); *Smith* (US); *Wherry* (PH). **Saint Lucie Co.:** *Austin et al. 6454* (FAU); *Leeds 344* (PH); *Small & Matthaus 9640* (NY). **Sarasota Co.:** *Smith* (PH). **Seminole Co.:** *Lambert 18* (PH); *Nauman et al. 293* (FAU). **Sumter Co.:** *E. P. St. John* (FLAS, NY); *Smith* (US). **Suwannee Co.:** *Leonard 6667* (FSU).

4. Nephrolepis multiflora (Roxb.) Jarrett ex Morton, Contrib. U. S. Natl. Herb. 38:309. 1974.

Davallia multiflora Roxb., Calcutta J. Nat. Hist. 4:515, *t. xxxi* left hand. 1844. LECTOTYPE: India, *Roxburgh* (BR not found, *fide* Lawalrée *in litt.*, fragment US!), chosen by Morton.

DISTRIBUTION AND HABITAT: Occasional in disturbed sites, usually near canals and other bodies of water in loose, well drained soil, frequently in full sun. Scattered in southern Florida, but reaching as far north as Pinellas and Hillsborough Counties *(Fig. 1)*. Like *N. biserrata,* the distribution appears limited by tolerance to cold temperatures. A native of the Old World tropics, *N. mulitflora* is widely naturalized in the New World. The species was first reported for Dade County, Florida by Gillis and Proctor (1975). Though the data are inconclusive, this species seems to have arrived in Florida in the late 1940's or 1950's somewhere in Lee County and is actively spreading. This conclusion is based on the dates of collection of this species throughout the State, but may be biased by the uneven collecting of certain areas. *Nephrolepis multiflora* was reported by Proctor (1977) to occur in the Bahamas and the Antilles. I have seen specimens from these areas, as well as Central America, Brazil, and Venezuela.

REPRESENTATIVE SPECIMENS:

Broward Co.: *Avery & McPherson 1327* (USF); *Lakela & Long 1598* (USF). **Collier Co.:** *Austin et al. 6767* (FAU); *Correll & Popenoe 47290* (FTG); *Lakela & Almeda 29988* (GH, USF); *Lassiter et al. 9* (USF). **Dade Co.:** *Avery 1329* (FLAS, USF); *Evans* (TENN); *Gillis 10856* (FTG). **Hillsborough Co.:** *Long et al. 2942* (USF); *Scudder 439* (FAU); *Shuey* (USF). **Lee Co.:** *Austin 6625* (FAU); *Brumbach 8743* (NY, US); *Cooley 2548* (FLAS, GH, NY, US). **Martin Co.:** *McCart 10406* (FAU, FLAS); *Nauman & Tatje 258* (FAU); *Nauman et al. 200* (FAU). **Monroe Co.:** *Avery* (FLAS). **Palm Beach Co.:** *Brawner* (FAU); *Durand 5, 85* (FAU); *Nauman 312* (FAU); *Nauman & Austin 181* (FAU); *Nauman et al. 400* (FAU).

5. Nephrolepis × averyi Nauman, Amer. Fern J. 69:69. 1979.

TYPE: Fakahatchee Strand off West Grade, 50 ft E of Indian Mound Slough Bridge, Collier Co., Florida, 29 Jan 1979, *Nauman et al. 635* (US; isotypes FAU, FLAS, GH, MSC, NY).

DISTRIBUTION AND HABITAT: Terrestrial, epiphytic, or epipetric in hammocks and swamps. Known to occur only with its putative parents, *N. biserrata* and

N. exaltata, in mixed colonies, in Florida south of Lake Okeechobee to as far north as Pinellas County (*Fig. 1*). Distribution outside Florida is uncertain; one specimen seen from Jamaica.

Nephrolepis × *averyi* is best distinguished from *N. biserrata* by its falcate pinnae and narrower fronds, and from *N. exaltata* by its larger size and lightly pubescent adaxial costa surface.

REPRESENTATIVE SPECIMENS:
Broward Co.: *Durand 4, 49, 56, 67, 70* (FAU); *Nauman 318, 434* (FAU); *Nauman et al. 647* (FAU). **Collier Co.:** *Beck 2027* (FSU); *Field & Lazon* (US); *Fischer 8* (US); *Howell 855* (US); *Nauman et al. 631.* (FAU). **Dade Co.:** *Curtiss 5460* (FLAS, UC, US); *Eaton 991* (F); *Garber* (F, FLAS, PH); *Hardy 10* (PH); *Lakela 31449* (USF); *Small 7384* (NY); *Tatnall 805* (PH). **Manatee Co.:** *Cuthbert* (FLAS). Palm Beach Co.: *Stevens* (FAU). **Pinellas Co.:** *Bebb* (F). **Polk Co.:** *White* (FLAS).

SPECIES AND FORMS EXCLUDED

Several cultivated forms of *Nephrolepis* are occasionally found in Florida. These forms are usually in cultivation or are persistent from cultivation. The distribution is scattered from Dade to Duval Counties. Forms represented in the herbaria are: *N. exaltata* cv. 'Bostoniensis,' cv. 'Elegantissima,' cv. 'Florida Ruffles,' and cv. 'M. P. Mills'; *N. falcata* f. *furcans* (Moore in Nicholson) Proctor [=*N. biserrata* cv. 'Furcans']; and *N. hirsutula* cv. 'Superba.'

Nephrolepis pectinata (Willd.) Schott was reported by Wherry (1964) for southern Florida. I have seen no specimens of this species in the herbaria or field. It is doubtful that this species exists in Florida.

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PROCTOR, G. R. 1977. Pteridophyta. *In* R. A. Howard, A Flora of the Lesser Antilles. Vol. II. Arnold Arboretum, Harvard University, Jamaica Plain, MA.

WHERRY, E. T. 1964. The Southern Fern Guide. Doubleday, Garden City, NY.

The Branching Pattern of Hypolepis repens

THERESA M. GRUBER*

Hypolepis, a pantropical genus of the Dennstaedtiaceae, is a terrestrial fern with usually large leaves and rather slender, long-creeping stems bearing trichomes and long, fibrous roots. *Hypolepis repens* (L.) Presl may form large colonies, and a single plant was measured in Puerto Rico with 42 meters of stem (R. and A. Tryon, pers. comm.). The leaves may be up to three meters or more long and often are partially supported by surrounding vegetation. Roots occur along the entire length of the stem, but are especially numerous at the leaf bases.

The morphology of *Hypolepis repens* and other species has been studied by Gwynne-Vaughan (1903), Bower (1923), Troop and Mickel (1968), and Imaichi and Nishida (1973). These treatments are limited, however, to describing the vascular system and analyzing single branch units. This paper considers the branching pattern of the stem and its components of entire plants of *H. repens* and the development and adaptive significance of the pattern.

MATERIALS AND METHODS

Stems of *Hypolepis repens* were studied in a *Liquidambar* cloud forest located about 12 km south of Misantla, Veracruz, Mexico at an altitude of 1400 meters. A large plant *(Fig. 1)* was excavated and exposed *in situ;* it was measured, mapped, and portions were taken for dissection. The plant was growing on a 35–45° slope in loose humus in association with herbaceous angiosperms. The stem length totaled 30 m and occupied an area of 13 m^2. In clear weather, most of the colony received sunlight between 10:00 AM and 1:00 PM, despite the surrounding tree canopy. A smaller plant *(Fig. 2)* was collected intact from a nearby wooded area. It was growing in loose humus on a slope of about 30° around a tree base nearly a meter in diameter.

The vascular system of the stems was studied by dissection and the anatomy of the branch unit by means of a cinematographic record of the surface between serial slices (Tomlinson, 1971).

OBSERVATIONS

The pattern of stem growth, with its branches, buds, and leaves is shown in *Figs. 1* and *2*. An analysis of these diagrams revealed a surprising regularity of pattern, which is illustrated schematically in *Fig. 3*. The following regular components of the whole stem and leaf system were noted.

(1) Each bifurcation of the stem *(Fig. 3,* axis 1) produces a leaf *(Fig. 3,* axis 2) and a continuing stem *(Fig. 3,* axis 1).

The bifurcation may be described as dichotomous since the division of the parent stele into stem and leaf is equal *(Fig. 4)*. However, this designation may be inappropriate because dichotomous branching usually refers to the production of two

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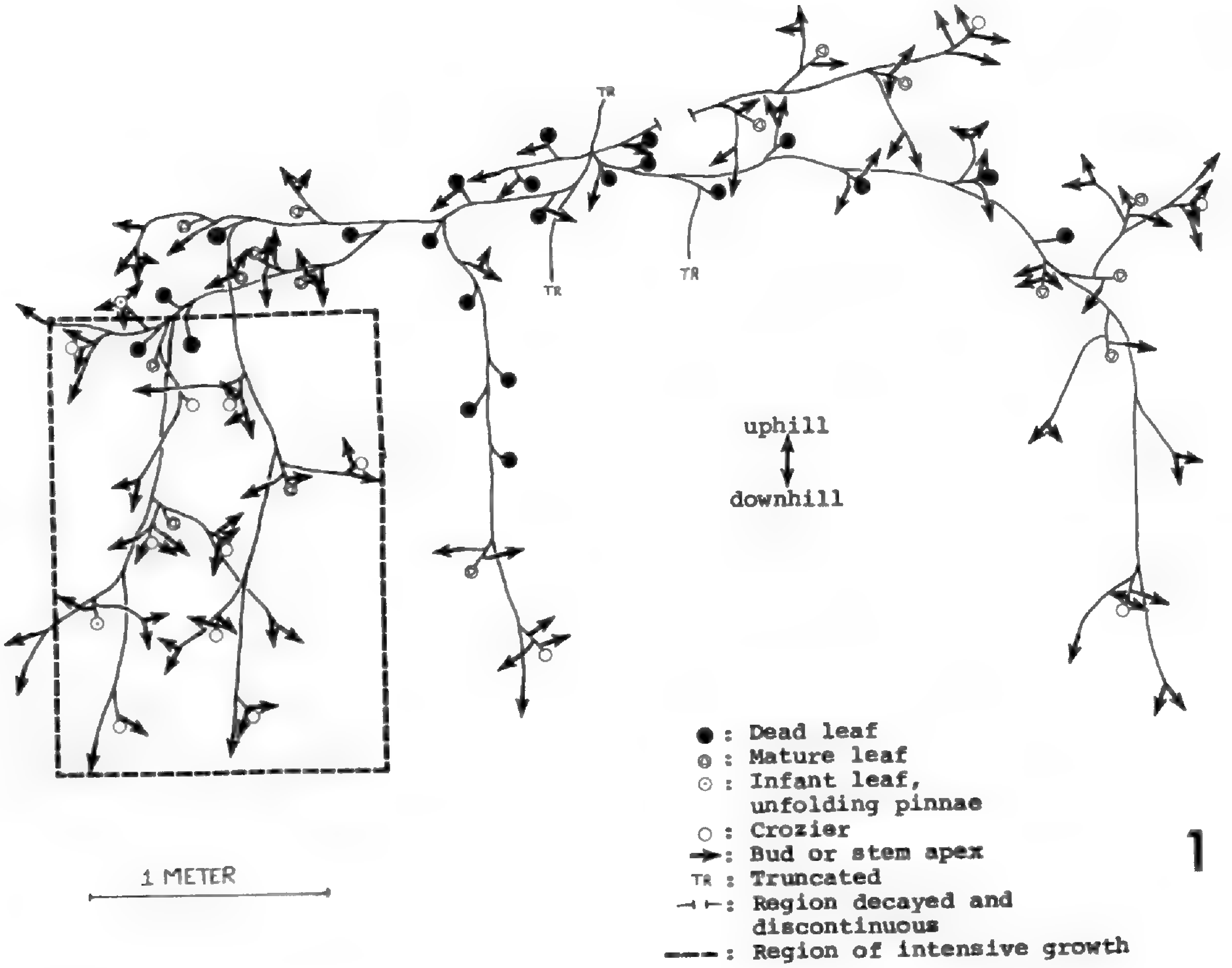
*6206 Braidwood Drive, San Antonio, TX 78249.



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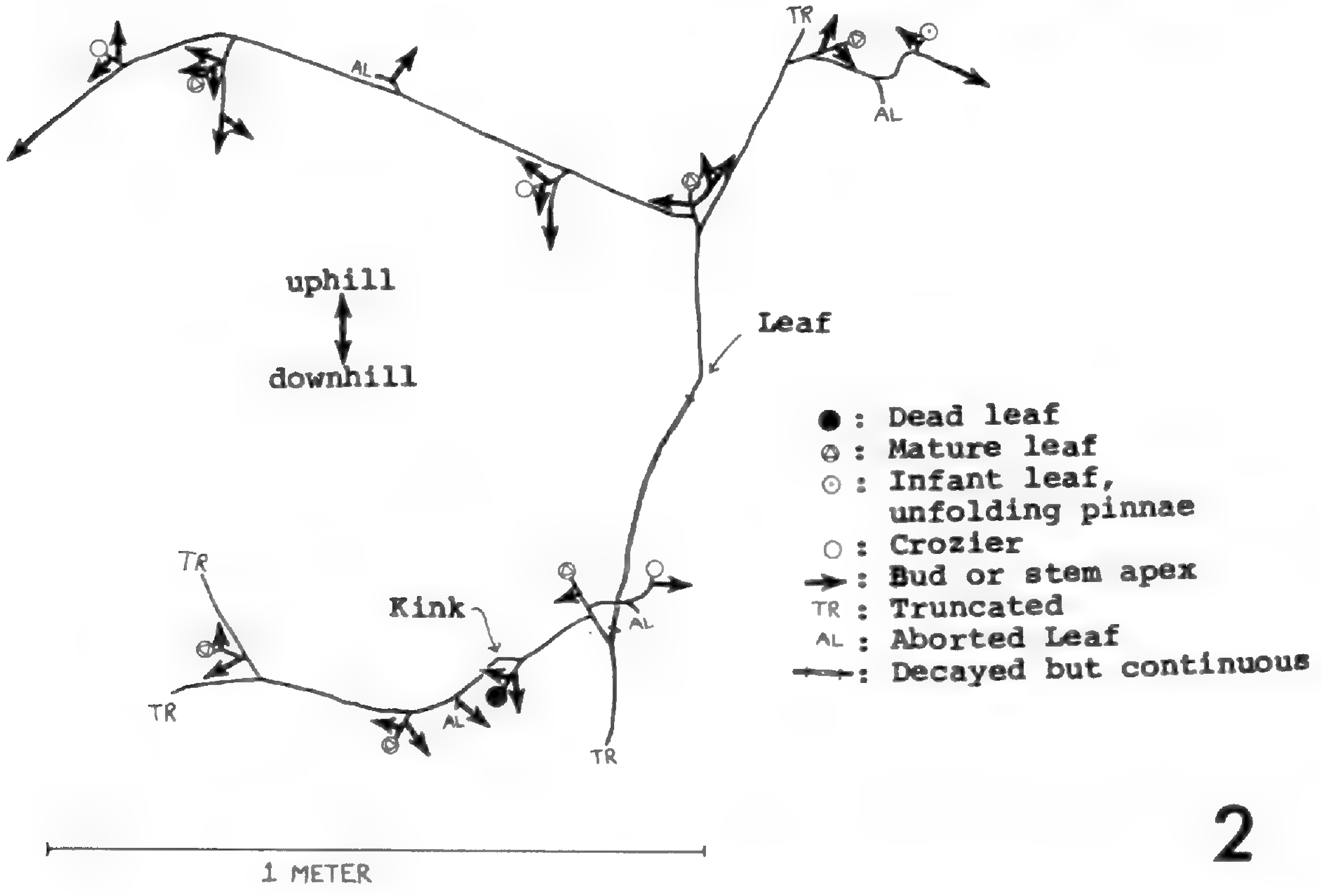

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FIG. 1. Diagrammatic sketch of *Hypolepis repens*, mapped *in situ*. FIG. 2. Diagrammatic sketch of *Hypolepis repens*, collected intact and later mapped.

initially equivalent organs rather than a stem and a leaf and because it is not known whether the bifurcation arises from a division of the apical cell.

Sections of the vasculature illustrated in *Fig. 4* agree with the observations of Gwynne-Vaughan (1903) and Troop and Mickel (1968), except that the leaf petioles arise on the lateral rather than the upper side of the stem.

(2) Leaves are produced successively on alternate sides of the stem. The simplest assumption for descriptive purposes is that the system is monopodial, that is, the leaf is an appendage of the stem axis.

(3) The petiole (*Fig. 3*, axis 2) bears 1–4 buds (*Fig. 3*, axes 3–6) which may develop into stems (*Fig. 3*, axes 3, 4) that function like the stem from which their parent leaf originated.

An analysis of the number of buds on the petioles showed that of a total of 41 petioles on the plants in *Figs. 1* and *2* in condition to study, two had no buds, five had one bud, ten had two, 22 had three, and two had four buds. The third and fourth buds, when present, were borne in the region of the petiole where it became erect and they grew down toward the ground, perhaps providing support for the leaf.

(4) The proximal bud that develops into a branch (*Fig. 3*, axis 3) is always on the side of the petiole (*Fig. 3*, axis 2) opposite to the continuing main axis (*Fig. 3*, axis 1); successive buds that may develop into branches (*Fig. 3*, axes 4–6) are alternate beyond the proximal bud.

It follows that the second bud is always on the side of the petiole nearest to the continuing main axis.

(5) When the proximal bud develops into a stem (*Fig. 3*, axis 3), the symmetry of its resulting next higher-order branch unit (*Fig. 3*, leaf 7 and petiolar buds 8, 9) is identical to that of the unit (*Fig. 3*, leaf 2 and petiolar buds 3–6) from which the branch originated.

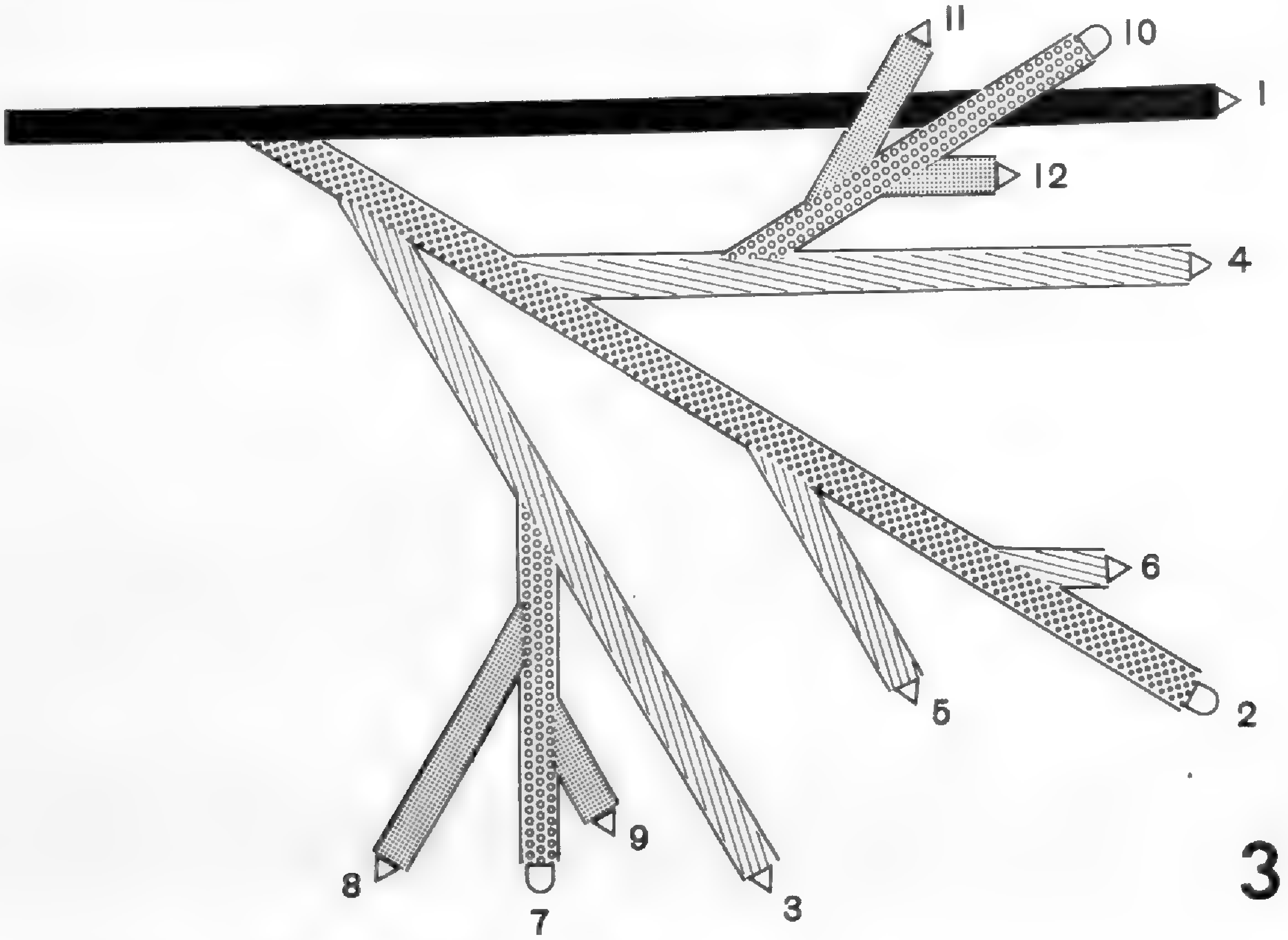
(6) When the second bud develops into a stem (*Fig. 3*, axis 4), the symmetry of its resulting next higher-order branch unit (*Fig. 3*, leaf 10 and petiolar buds 11, 12) is the mirror image of that unit (*Fig. 3*, leaf 2 and petiolar buds 3–6) from which the branch originated.

(7) All stems developing beyond the first branch unit repeat the patterns laid down in (1) through (6).

The distance between leaves and the angle between bifurcations of axes were both rather variable.

The spacing of the leaves varied widely in each of the plants investigated. The small plant *(Fig. 2)*, which was growing in a heavily shaded locality, had the leaves an average of 19.5 cm apart, with two 28 cm apart. The large plant *(Fig. 1)*, which was growing in a somewhat exposed site, had the leaves an average of 33.9 cm apart and two were as much as 68 cm apart. Apparently the distance between leaves is influenced by the immediate environment and is not a fixed characteristic of the branching pattern.

The angle between bifurcations of the stem and leaf approximates 60°. In a total of 17 branch units of the small plant *(Fig. 2)*, the angle was 40° in two units, 50° in four, 55° in one, 60° in eight and 90° in two (an average of 59°). The angle between the petiole and its first bud averaged 63°, for the nine that were measurable.



3

4

FIG. 3. The Branch Complex. Branch order is represented by the different patterned axes: main axis, solid; first-order, solid dots; second-order, stripes; third-order, open circles; fourth-order, stippled. The individual axes are numbered according to their ontogenetic appearance. An axis terminated by a circular tip represents a leaf; a triangle represents a stem apex. FIG. 4. Serial sections of the vasculature of the branching unit of *Hypolepis repens*, from a cinematographic record.

DISCUSSION

Ecological Implications. — Bell and Tomlinson (1980) noted the infrequency of adequately detailed accounts of basic branching patterns in rhizomatous systems, especially among the ferns. Ferns are ideal for this kind of study because they have no secondary cambial growth.

A fern with a creeping, branching stem, as exemplified by *Hypolepis repens,* has important advantages over its relatives which have short-creeping or erect stems. An environment such as the *Liquidambar* cloud forest presents a substantial limitation to gametophytes in the form of competition for open space. An elongate, branching stem provides a means of vegetative propagation which alleviates the necessity for local propagation through sexual reproduction. Interestingly enough, not a single fertile frond was found during several days of mapping and excavating.

In addition, a regular method of branching enables the plant to survive destruction of one or more stem apices. When growth along one axis is unsuccessful, that shoot may abort without the loss of the entire plant. The closely related *H. punctata* Mett. ex Kuhn responds to the destruction of the leaf apical cell by the development of the most proximal bud into a leaf or shoot (traumatic reiteration, Imaichi and Nishida, 1973). *Hypolepis repens* probably responds in a similar manner, as indicated by the development of the proximal bud in two out of four aborted leaves (*Fig. 2*).

A branched network with bifurcation angles of 60° tends to form hexagons, a pattern which covers a maximum amount of surface area with a minimum path length (Stevens, 1974). This patterned branching enables the plant to make a systematic exploration of the local environment with a minimal energy output. This same pattern enables the plant to reenter territory, over a span of time, which previously proved favorable to growth.

A shoot might be expected to be sufficiently plastic to respond to an especially favorable environment. This theory of "adaptive reiteration under supra-optimal conditions" is difficult to prove, as was pointed out by Bell and Tomlinson (1980). The difficulty lies in there being no established basis for quantification. A favorable environment could exist in time, such as especially favorable weather during a growing season, or in space, such as nutrient-rich soil or good light availability. Adaptive reiteration could refer to the production of a maximum amount of photosynthetic material within a limited amount of time or space, exceeding that observed to be average. *Hypolepis repens* appears to support this theory, as indicated by the inordinate number of croziers within the area delineated by broken lines in *Fig. 1*. Furthermore, within this same region, there are three examples of advanced development of the second of the second-order branch (as in *Fig. 3*, axis 4), a relatively rare occurrence in the two plants.

These ecological advantages and the predictability of the morphology of *Hypolepis repens* suggest that this particular pteridophyte has genetically fixed growth and branching patterns.

Development. — It is interesting to speculate on the possible mode of development for a branching system as well defined as that of *H. repens*. A superficial examination of the rhizome raises the question of whether branching in this species is sympodial, monopodial, or dichotomous. If the first were the case, the question of development would be simplified from a descriptive point of view; all the leaves would be terminal and all branches could be produced in the same way. However, the anatomy of *H. repens* and the developmental studies of the closely related *H. punctata* by Imaichi and Nishida (1973) indicate otherwise. Instead, there are two types of branches in a branch complex: (1) the stem (*Fig. 3*, axis 1) bifurcates to produce a leaf (*Fig. 3*, axis 2) and a continuing stem; and (2) and one to four buds (*Fig. 1*, axes 3–6) branch off from the base of the leaf (*Fig. 3*, axis 2).

The first type of branching may be dichotomous in the strictest sense, that is, by a division of the apical cell of the parent stem axis (*Fig. 3*, axis 1). The equal distribution of the vasculature between the daughter stem and leaf favors this explanation (see *Fig. 4*). On the other hand, the two daughter products are not the same. This might result from a lateral mode of branching, that is, one where meristematic tissue proximal to the apical cone of the continuing stem differentiates into and terminates as a leaf.

The methods by which the buds branch from the leaf are somewhat less clearly defined. Bower (1923) theorized that the formation of extra-axillary buds in *H. repens* represented a modification of dichotomous branching of the rhizome system; that, in effect, the basal bud (*Fig. 3*, axis 3) bore the leaf (*Fig. 3*, axis 2). The regular pattern of buds on the leaf base strengthened his argument that these buds were part of a regular branching system and therefore did not develop adventitiously. Imaichi and Nishida's (1973) decapitation experiments and ontogenetical observations of the related *H. punctata* demonstrated that the bud meristem is formed *after* the leaf is established, making Bower's theory untenable.

In his developmental studies of *Onoclea sensibilis*, *Dryopteris aristata*, and *D. filix-mas*, Wardlaw (1943) demonstrated that adventitious buds occur only in specific positions corresponding to those occupied by detached meristems. These superficial bud meristems develop from the region of the shoot apical meristem not involved in the development of leaves. In the case of *D. filix-mas*, every bud initially occupies an axillary position. It may then become separated from the leaf with which it originally was in an axillary relationship by displacement onto the enlarging base of another leaf which was lateral to it in the earlier developmental phase. Since the bud develops more slowly than the leaf, its vasculature tends to become joined with that of the leaf it had been carried up on, rather than with that of the stem from which it originated. In summary, Wardlaw (1943) demonstrated that each bud of *D. filix-mas*, despite its position on the petiole of an adult leaf, occupies an approximately axillary position on the shoot at the time of its formation. Wardlaw concluded that extra-axillary buds in other fern species might originate in a similar fashion.

It is possible that some interaction of hormones produced by the petiolar roots and/or developing frond may trigger the differentiation of meristematic cells produced by the apical cone of the leaf. Only a thorough investigation of the developmental process will provide the insight needed to explain the origin of the interesting branching pattern of *Hypolepis repens*.

Field work in Veracruz, Mexico was supported by the Atkins Garden Fund, Harvard University, and assistance in Mexico was obtained from the Instituto de

Biología, Universidad Nacional Autónoma de México. I am grateful for the help and encouragement of Professor Rolla Tryon and Dr. Alice Tryon and especially for the guidance of Professor P. B. Tomlinson in preparation of the film. Appreciation is also extended to Scott Clempson, Kathleen Buckley, David Karachuk and the staff of the Gray Herbarium and Arnold Arboretum Library.

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Diplazium japonicum and Selaginella uncinata Newly Discovered in Georgia

WAYNE R. FAIRCLOTH*

The Japanese Twin-sorus Fern, *Diplazium japonicum* (Thunb.) Bedd., has been reported as escaped from cultivation in Gadsden County, Florida since 1957 (Wherry, 1964), and recently Short (1980) published an account of its discovery in Lee County, Alabama. This species subsequently has been found in three widely disjunct locations in Georgia (*Fig. 1*).

In late summer of 1980, my wife and I led a fern field trip in central south Georgia for the Georgia Botanical Society. During the field trip, Marge White and Frieda Polsfuss (fern hobbyists from middle Georgia) showed several of us some pressed fronds of a fern which Mrs. White had collected in Houston County, Georgia. Upon superficial examination, most of us identified the plant as a form of *Athyrium*, although the possibility of its being a *Diplazium* was suggested. A frond was given to Lloyd H. Snyder, Jr. (a fern hobbyist from Atlanta), who discovered the same fern beneath a highway bridge in Berrien County, Georgia the following day. Specimens from Houston and Berrien Counties were shown to Dr. Murray Evans of the University of Tennessee, who confirmed the identity of both as *Diplazium japonicum*.

The two sites were rechecked in October to determine the extent and condition of the colonies. The team of White, Polsfuss, and Snyder visited the Houston County site, which is located in dense, deciduous woods between Hatcher Road and Fagin Mill Road southwest of Warner Robins. Two groups of approximately a dozen plants each about 1000 m apart were found along the edge of a small stream in association with *Asplenium platyneuron*, *Athyrium asplenioides*, *Onoclea sensibilis*, *Osmunda cinnamomea*, *O. regalis*, *Polystichum acrostichoides*, and *Thelypteris torresiana*.

My wife and I found the *Diplazium* in Berrien County growing beneath a slough bridge of the Withlacoochee River, west of Nashville on Georgia Highway 125. Thirteen plants bearing fertile fronds were clustered together in an area of three square meters. Eighty-two sporelings were widely scattered beneath the bridge, indicating that the colony was successfully reproducing and expanding. Other ferns found beneath the bridge were: *Asplenium platyneuron*, *Lorinseria areolata*, *Lygodium japonicum*, *Onoclea sensibilis*, *Ophioglossum petiolatum*, *Osmunda regalis*, *Pteridium aquilinum*, *Thelypteris dentata*, *T. kunthii*, *T. torresiana*, and *Woodwardia virginica*.

On 2 January 1981, I discovered an immense colony of the Japanese Twin-sorus Fern on the Farmer's Branch prong of Sofkee Creek in Grady County, Georgia. Hundreds of plants were growing thickly on both banks of this spring-fed stream for a distance of 28 m; in addition, scattered plants were found downstream for a distance of approximately 120 m. Most of the fertile plants were robust, with fronds

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*Department of Biology, Valdosta State College, Valdosta, GA 31601.

commonly as long as 65 cm. The only ferns growing in association with *D. japonicum* at this site were *Dryopteris ludoviciana, Lorinseria areolata*, and *Osmunda cinnamomea*.

Houston County is located in the Upper Coastal Plain Province, almost in the center of the state and very near the Fall Line (the junction with the Piedmont Province). Geographically, it is similar to the Fall Line location in Lee County, Alabama. Grady County also is in the Upper Coastal Plain Province, but is about 140 miles to the southwest and borders Gadsden County, Florida. Berrien County is located in the Lower Coastal Plain Province, a region which differs from the Upper both in elevation and in having predominantly sandy soils. Unlike the rolling, well drained Upper Coastal Plain, the Lower is very flat, with numerous ponds, vast swamps, and broad river systems.

FIG. 1. Distribution of *Diplazium japonicum* (circles) and *Selaginella uncinata* (triangles) in Alabama, Florida, and Georgia.

Not only do these new locations extend the range of *Diplazium japonicum* significantly, the species is a new addition to the vascular flora of Georgia. Recent papers by Bruce, Jones, and Coile (1980) and by Duncan and Kartesz (1981) do not include *D. japonicum* as a component of Georgia's flora.

Specimens from the three locations (Berrien County, *Snyder 697, Faircloth 8518;* Houston County, *Snyder 757;* Grady County, *Faircloth 8521)* are on deposit in the herbaria at the University of Georgia (GA) and Valdosta State College (VSC).

Another addition to the vascular flora of Georgia is *Selaginella uncinata* (Desv.) Spring. The location of an unfamiliar Spike-moss in Decatur County was first mentioned to me by Angus Gholson, U. S. Army Corps of Engineers, Resource Manager for Lake Seminole, Chattahoochee, Florida. My wife and I visited the site in late March, 1980. We found an extensive colony of the Blue Spike-moss growing luxuriantly on the banks of a small stream in a ravine immediately north of Greenshade Cemetery between Faceville and Fowltown (*Fig. 1*).

Shoot development at that season of the year was strictly sterile because a late freeze on 1 March 1980 had killed the aerial shoots back to ground level. There was evidence of abundant strobili development the preceeding year, although I could find no microspores or macrospores that had been retained. My identification, based upon sterile material, was confirmed by Dr. John T. Mickel (pers. comm.). Fertile material was collected later in the summer; specimens (*Faircloth 8531*) are on deposit in the Valdosta State College Herbarium.

Naturalized *Selaginella uncinata,* a native of China, has been known from Florida and some of the Gulf Coast states for more than 20 years (Brown & Correll, 1942; Lakela & Long, 1976). With the return of horticultural interest in hanging baskets, it has lately been cultivated and widely sold as a hanging basket plant under the names of Rainbow-fern and Parlor-moss. Its iridescent, blue-green foliage and arching-trailing growth habit make it a choice plant for this purpose. The origin of the colony in Decatur County is puzzling. There are no homesites nearby, and its location in close proximity to a cemetery appears coincidental because the plant is not likely to be used either as a potted plant or in other types of floral arrangements for cemetery ornamentation. Mr. Gholson's familiarity with the site indicates that the colony is at least four years old but judging from its size, it is perhaps as much as 8 to 10 years old.

I wish to thank the following people for their help in field work and in providing information for this report: Juanita N. Faircloth, Marge White, Frieda Polsfuss, Leslie Garland, Lloyd H. Snyder, Jr., and Angus Gholson.

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Notes on Selaginella, with a New Variety of S. pallescens

ROBERT G. STOLZE*

One of the most variable neotropical species in the genus *Selaginella* is *S. pallescens* (Presl) Spring. It may grow on soil or rocks, in sun or in deep shade, from sea level to over 3000 m elevation, and it occurs in Mexico, Central America, Cuba, Jamaica, and parts of South America. The species belongs to the heterophyllous subg. *Stachygynandrum*, which is characterized by the stems (at least distally) and the vegetative leaves of branches having 2 rows of smaller, usually appressed, median leaves and 2 rows of larger, spreading lateral ones. Contrasting with this is subg. *Selaginella*, with plants homophyllous throughout, *i.e.*, leaves are borne on all sides of the stem and branches and all are appressed for most of their length. Subgenus *Stachygynandrum* is sharply divided into two groups, one having stems articulate, or at least constricted at or near the nodes and here usually discolored, and with rhizophores produced dorsally. The other group, containing *S. pallescens*, has stems neither articulate nor with discolored or constricted nodes, and with rhizophores produced ventrally, *Selaginella pallescens* and its nearest relatives commonly have the stems densely caespitose, often forming rosettes. They tend to curl inward when dry, then uncurl again when moisture is introduced, thus giving rise to the common name "Resurrection Plant."

Taxonomy of the entire *S. pallescens* complex in the neotropics needs careful re-examination. There are several species which I feel are not truly distinct, and yet there are some hitherto unrecognized variants, which perhaps should be formally treated as varieties or forms. Some very closely related species are: *S. cuspidata* (Link) Link and var. *elongata* Spring, *S. harrisii* Underw. & Hieron., *S. microdendron* Bak., *S. millspaughii* Hieron., and *S. pulcherrima* Liebm. During a study of the genus for the "Ferns and Fern Allies of Guatemala," it appeared to me that most of these species might better be included under *S. pallescens*, for whatever differences were noted by previous authors appear to be thoroughly inconsistent. On the other hand, some new features have come to light which seem significant and consistent enough to indicate recognition of some specimens at the varietal level.

In his study of the spores of heterophyllous *Selaginellae*, Hellwig (Ann. Mo. Bot. Gard. 56:444–464. 1969) annotated a number of specimens in various herbaria as *S. pallescens*, "red-stemmed variant." Some other minor features have been discovered to be consistent with stem color on these specimens, and the combination of characters support a decision to name the following new variety.

Selaginella pallescens (Presl) Spring var. acutifolia Stolze, var. nov.

Varietas haec a varietate typica *[S. pallescens* (Presl) Spring var. *pallescens]* differt caulibus rubellis, foliis lateralibus acutis (nec acuminatis nec aristatis), et interdum pallide roseo-tinctis, et foliis medianis acutis (nec acuminatis nec aristatis).

TYPE: Rocky hills near Santa Rosalía, 2 mi south of Zacapa, alt. 200 m; Depto. Zacapa, Guatemala, 1939, *Steyermark 29293* (F).

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*Department of Botany, Field Museum of Natural History, Chicago, IL 60605.

In forests or wooded ravines, commonly on rocks, cliffs, or rock outcrops, from sea level to 1100 m; Guatemala, Honduras, El Salvador, Nicaragua, and Costa Rica.

Plants epipetric or terrestrial; stems reddish, at least at base; lateral leaves acute, rarely subacute, sometimes a few of the older ones becoming streaked or tinged with pale red; median leaves commonly acute at apex.

SELECTED SPECIMENS EXAMINED:

GUATEMALA: Chiquimula: Damp thicket along road between Chiquimula and Zacapa, 400–600 m, *Standley 74517* (F, US). **Escuintla:** Medio Monte, Palén, *Mario Dary Rivera* 755 (F). **Jutiapa:** Quebrada near Mangoy, 550 m, *L. O. Williams 14201* (F). **HONDURAS: Choluteca:** Moist bank above San Antonio de Flores, 30 m, *Williams & Molina 16714* (F). **Morazán:** Sabana Grande, 1100 m, *J. Valerio Rodriguez 3260* (F, UC, US). **El Paraiso:** Drainage of Río Yeguare, 600 m, *Molina 4014* (F, US). **EL SALVADOR: Chalatenango:** Hills outside San José Cancasque, 400 m, *Seiler 365* (F). **San Miguel:** Riverside, Canton San Antonio Chavez, 300 m, *Seiler 541* (F). **La Unión:** Humus, woods N of La Unión, *Morrison & Beetle 8761* (F, US). **NICARAGUA: León:** Canyon of Río Sinecapa, near Santa Rosa, 200 m, *Williams & Molina 42442* (F). **Nueva Segovia:** Ravine W of Ocotal, *Seymour 840* (F). **COSTA RICA: Guanacaste:** Margen rocosa del Río Recreo, 80 m, *Jiménez 1172* (F).

The most conspicuous difference between this and the typical variety is the reddish coloration present in the plants (a phenomenon not uncommon in the subgenus). The stems are always reddish at base, and the color often extends halfway to the apex. Also, as the lateral leaves begin to age, some become tinged with red. Typical *S. pallescens* has stems pale greenish to stramineous throughout; and if lateral leaves turn color with age, it is to a dull whitish or tawny hue. Most median and lateral leaves in var. *acutifolia* are never more than acute, whereas in var. *pallescens* the leaves are acuminate or even aristate. The new variety prefers low altitudes from sea level to 800(1000) m, and is most common in rocky habitats. The typical variety is found occasionally near sea level, but most frequently occurs between 800 and 2500 m. It, too, is found in rocky situations, but seems equally at home on the forest floor.

Lepisorus kashyapii in the Western Himalayas

S. S. BIR and CHANDER K. SATIJA*

Lepisorus kashyapii (Mehra) Mehra is a polymorphic species closely related to *L. excavatus* (Bory) Ching. The two species are known to hybridize in the Himalayas (Bir & Trikha, 1969, p. 271). The latter species was studied in detail by Bir and Trikha (1974).

These two species of *Lepisorus* are more easily separated in the field than in the herbarium. The rhizomes of *L. kashyapii* are loosely attached to trees or rocks by long, straight roots, whereas *L. excavatus* has rather tightly adherent rhizomes. *Lepisorus kashyapii* laminae are thicker and have more obscure veins, and their color is paler yellow-green. According to a note by R. R. Stewart in the U.S. National Herbarium, *L. kashyapii* has quickly deciduous, dark brown, contorted hairs on the abaxial surface. Unfortunately, these characteristics are mostly difficult to observe in herbarium material. The rhizome scales of the two species are very similar. Although there is some variation, the sori of *L. kashyapii* are more round and only slightly immersed in the laminae, whereas those of *L. excavatus* are oval and more deeply immersed. *Lepisorus kashyapii* tends to dry brown, whereas *L. excavatus* usually dries green. These characteristics will aid in separating the two species in the herbarium.

During a study of various collections of *Lepisorus* from the Himalayas, *L. kashyapii* was found to be morphologically very interesting. Some specimens from various localities around Nainital, a popular health resort located in the northwestern Himalayas, exhibit variations from typical *L. kashyapii* that proved to be two new varieties. These, along with var. *kashyapii*, are distinguished in the following key.

KEY TO THE VARIETIES OF LEPISORUS KASHYAPII

1. Fronds linear to linear-lanceolate, 7.5–11.5 cm long, 0.5–1 cm wide; rhizome scales long-acuminate at the apex ....3. *L. kashyapii* var. *minor*
1. Fronds narrowly to sometimes broadly elliptic-lanceolate, (12)15–35(42) cm long, 1.5–3.5(5.5) cm wide; rhizome scales acute to acuminate at the apex.
    2. Laminae bright brown on drying; rhizome scales peltate-lanceolate, dark brown, strongly clathrate in the center, yellowish and not clathrate at the margins, especially around the peltate base, the margins contorted and finely toothed when young, usually worn away and merely erose in age; sporangial paraphyses all peltate, clathrate ....1. *L. kashyapii* var. *kashyapii*
    2. Laminae dull brown on drying; rhizome scales narrowly ovate-lanceolate, yellowish-brown throughout, clathrate in the center, less so at the margins, the margins erose and hyaline; sporangial paraphyses hair-like as well as peltate, clathrate ....2. *L. kashyapii* var. *major*

1. Lepisorus kashyapii (Mehra) Mehra in Bir, Res. Bull. Panjab Univ. n.s., 13:23. 1962, var. kashyapii.

Polypodium kashyapii Mehra, Panjab Univ. Publ. 24, *f*. 5. 1939. TYPE: Not stated; a lectotype should be chosen from Mehra's material at Panjab University, Lahore (LAH).

Pleopeltis kashyapii (Mehra) Alston & Bonner, Candollea 15:208. 1956.

Rhizomes long-creeping, 3–5 mm in diam.; rhizome scales peltate-lanceolate, the central portion clathrate, brown to dark brown in mass, the marginal portions

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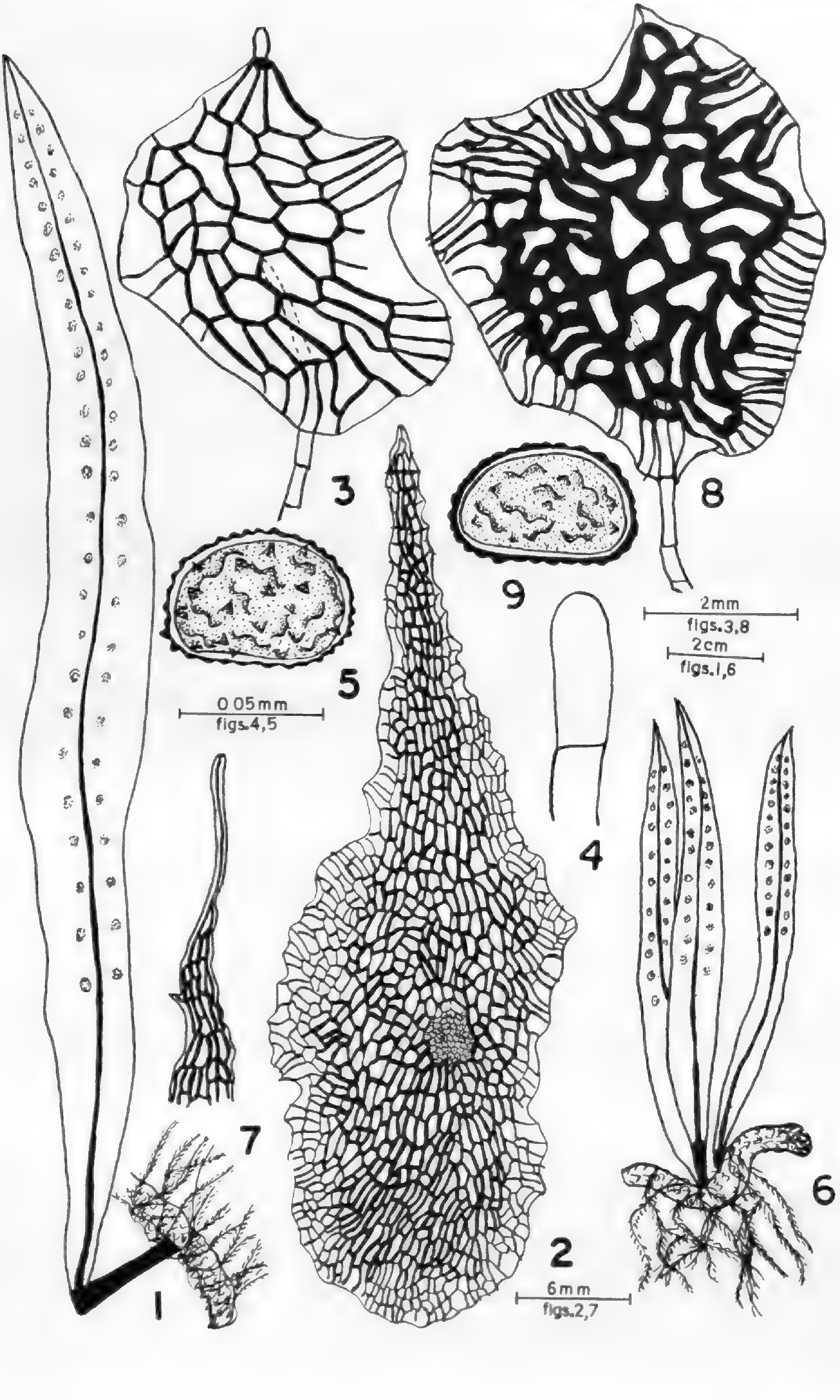
*Department of Botany, Punjabi University, Patiala 147002, India.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9
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figs.3,8
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figs.4,5
4
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1
6mm
figs.2,7

scarcely or not clathrate, yellowish, broader around the peltate base than toward the apex, the margins contorted, finely toothed, usually worn away and merely erose in age. Stipes 2–5 cm long, yellowish, bearing a few, usually somewhat contorted scales. Laminae narrowly to sometimes broadly elliptic-lanceolate, (12)15–35(40) cm long, 1.5–3.5(5.5) cm wide, bright brown on drying, acute above an acuminate base, acuminate at the apex, entire or slightly wavy along the margin; sporangia protected by subpersistent, clathrate, peltate paraphyses; spores reniform or oval, plane to concavo-convex, brown, minutely verrucose, ca. 42–60 μm long, 30–50 μm wide; chromosome number $n=36$.

OTHER CITATIONS: Mehra & Bir, Res. Bull. Panjab Univ. n.s., 15:168. 1964; Bir & Trikha, Bull. Bot. Surv. India 11:271–273. 1969 [1971].

ILLUSTRATIONS: Mehra (1939, pp. 24–25, *fig. 5a–g*); Bir & Trikha (1969, pp. 271–273, *figs. 41–45*).

SPECIMENS EXAMINED:

INDIA: Himachal Pradesh: Simla: Near Shali Peak, 2400 m, Sept 1969, *Bir 1046* (PAN); Sanjouli, 2100 m, Aug 1969, *Bir* (PAN), Sept 1958, *Bir* (PAN); Chharbara, 2400 m, Aug 1960, *Bir* (PAN). Dalhousie: Satdhara, 2000 m, Sept 1968, *Trikha 106 (PUN)*. **Uttar Pradesh:** Mussoorie: 1800 m, Aug 1959, *Bir* (PAN); Nag Tiba, 2400 m, Sept 1947, *Fleming 82* (US); Lal Tiba, 2400 m, Sept 1968, *Bir 44* (PUN), 2250 m, Sept 1968, *Trikha 1070* (PUN). Nainital: Laria Kanta, 2400 m, Sept 1967, *Bir* (PUN); Tiffon Top, 2100 m, July 1971, *Trikha 1901* (PUN); Khurpatal, Sariyatal, 1600 m, July 1971, *Trikha 1904* (PUN). **West Bengal:** Darjeeling: Senchal forest, 1500 m, July 1957 *Malhotra 744* (PAN); Manibhangang–Tonglu Road, 2400 m, July 1957, *Bir 774* (PAN), 2000 m, July 1957, *Bir* (PAN); Near Dingle Kothi, 1800 m, July 1969, *Trikha 1025* (PUN); Senchal Lake, 2400 m, Aug 1969, *Trikha 1030* (PUN); without definite locality, *Thomson* (US).

NEPAL: Shotibas, 3000 m, Oct 1958, *Polunin, Sykes & Williams 5568* (US); Garpung Kholen, 3000 m, Sept 1962, *Polunin, Sykes & Williams 5410* (US).

2. Lepisorus kashyapii var. major, Bir & Trikha, var. nov. Figs. 1–5.

Squamae rhizomatis ovatae, acuminatae, flavescenti-brunneae, margine eroso, hyalino; lamina lanceolata, 29–42 cm longa, 2.7–3.5 cm lata, statu sicco obscure brunnea; sporangia paraphysibus biformibus, unis, umbelliformibus, parietibus cellularum comparate tenuibus, alteris bicellulatis, uniseriatis, piliformibus; sporae verrucosae vel tuberculatae 55–67 μm longae, 33–55 μm latae; chromosomatum numerus $n=36$.

TYPE: Cheena Peak, Nainital, Uttar Pradesh, India, epiphyte, 2400 m, July 1971, *Trikha 1906* (PUN 1240; isotypes PUN 1241, 1242).

PARATYPE: Tiffon Top, Nainital, Uttar Pradesh, India, lithophyte, 2100 m, July 1971, *Trikha 1907* (PUN 1357).

3. Lepisorus kashyapii var. minor Bir & Trikha, var. nov. Figs. 6–8.

Squamae rhizomatis ovatae, longe acuminatae, brunnescenti-atrae, margine eroso; lamina linearis vel lanceolato-linearis, 7.5–11.5 cm longa 0.5–1 cm lata, statu sicco laete fusca; sporangia paraphysibus solum umbelliformibus, clathratis, parietibus cellularum fortibus, crassis; sporae verrucosae, 50–67 μm longae, 38–50 μm latae; chromosomatum numerus $n=35$.

FIGS. 1–5. Holotype of *Lepisorus kashyapii* var. *major (Trikha 1906*, PUN). FIG. 1. Habit. FIG. 2. Rhizome scale. FIG. 3. Peltate sporangial paraphysis. FIG. 4. Hair-like paraphysis. FIG. 5. Spore. FIGS. 6–9. Holotype of *Lepisorus kashyapii* var. *minor (Trikha 1096*, PUN). FIG. 6. Habit. FIG. 7. Scale from rhizome apex. FIG. 8. Peltate sporangial paraphysis. FIG. 9. Spore.

TYPE: Tiffon Top, Nainital, Uttar Pradesh, India, epiphyte, 2100 m, July 1971, *Trikha 1096* (PUN 1175; isotype PUN 1243).

Our grateful thanks are due to Prof. K. U. Kramer (Zurich) for the Latin diagnoses, to Dr. D. B. Lellinger for advice on taxonomic matters, and to the keepers of the cited herbaria for the loan of material.

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Taxonomic Notes on Jamaican Ferns—III

GEORGE R. PROCTOR*

This paper continues my series concerning the taxonomy of the ferns of Jamaica (see Proctor, 1965, 1968).

The genus *Thelypteris* is the largest and one of the most complex genera of ferns in Jamaica, when construed in the broad sense, with a total of 59 known species. In recent years, this world-wide taxonomic group has received intensive scrutiny, especially by R. E. Holttum (Old World) and A. R. Smith (New World). The former has presided over the disintegration of the genus into numerous small "splinter" genera, a process already initiated by Ching and others; Smith has developed an integrated classification exercising the concept of subgenera and sections. The present writer prefers the latter approach.

The first of Smith's subgenera is *Amauropelta*. This is the largest and most difficult group of *Thelypteris* species occurring in Jamaica, with a total of 24 species, nine of them believed to be endemic. *Amauropelta* was classified by Smith (1974) in nine sections, all but one of which are represented in Jamaica. The position of the Jamaican species in these sections may be summarized as follows:

1. **Adenophyllum**: *decrescens*.
2. **Phacelothrix**: *thomsonii*.
3. **Uncinella**: *negligens*, *oligocarpa*, *germaniana*, *linkiana*, *gracilis*, *heteroclita*.
4. **Amauropelta**: *firma*, *basiattenuata*, *balbisii*, *trelawniensis*, *randallii*, *sancta*, *nockiana*, *underwoodiana*, *harrisii*, *gracilenta*, *resinifera* vars. *resinifera* and *caribaea*.
5. **Blennocaulon**: *cheilanthoides*.
6. **Pachyrhachis**: *pachyrhachis*, *malangae* var. *sitiorum*.
7. **Lepidoneuron**: *rudis*.
8. **Blepharitheca**: *concinna*.
9. **Apelta**: (not represented in Jamaica).

Three of the above species are new to science and are described herein, along with a new minor form of *T. rudis*; four other names represent new combinations requiring validation. The localities of these taxa are shown in *Fig. 1*. The writer is grateful to Dr. John Mickel for helping to locate, at the New York Botanical Garden, types of species described by Jenman.

Thelypteris decrescens Proctor, sp. nov.

Subg. *Amauropelta*, sect. *Adenophyllum*. Ex affinitate *T. pilosulae* a qua stipitibus multo brevioribus, densissime minutissimeque stipitato-glandulosis, glabratis vel parce pilosulis; laminis minoribus, utrinque, sed plerumque subtus abundanter glandulosis, glandulis stipitatis, flavis resinaceis differt.

Rhizome stout, erect, its scales yellow-brown, lance-attenuate, the margins subentire with a few minute colorless stipitate glands. Stipe very short, 3–4 cm long, scaly at base, puberulous, and, together with the rhachis, densely and minutely stipitate-glandular, the glands colorless; also bearing few to many long, soft, pluricellular hairs. Blades narrowly elliptic to oblanceolate, 35–50 cm long,

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*Harvard University Herbaria, 22 Divinity Ave., Cambridge, MA 02138.

10–15 cm broad at or above the middle, markedly decrescent downward with 7 pairs or more of reduced pinnae; longest pinnae oblong-linear, sessile, acuminate, up to 7 cm long, 1–1.7 cm wide at the base, with up to 20 pairs of oblong or narrowly deltate-oblong segments, these blunt at the apex and 1.5–2.5 mm wide, the margins flat or very narrowly reflexed; veins 5–8 pairs, simple, scarcely prominulous but with slightly enlarged tips (seen from the upper side). Sori supramedial, round; indusium delicately reniform, densely glandular (the glands minute, globular, and sessile to stipitate), soon withering. Rhachis and other vascular parts densely pubescent on the upper (adaxial) side with whitish pluricellular hairs; similar hairs less dense beneath; all parts on both sides, but more abundantly beneath, beset with stipitate yellow-resinous glands.

TYPE: Upper west slope of Blue Mt. Peak, Parish of St. Thomas, Jamaica, 6500–7325 ft (1981–2233 m), *L. M. Underwood 1513*, 11–12 Feb 1903 (NY). Paratype from lower western ridge of Blue Mt. Peak, 5500–6318 ft (1700–1950 m), 4–9 July 1926, *W. R. Maxon 10025*, (NY, US).

This is the first species of sect. *Adenophyllum* to be reported from the West Indies. Most of the other species of this section are South American, but the closely related *Thelypteris pilosula* (Mett.) Tryon has an extensive range from southern Mexico to Peru, and has been reported from Jamaica and Hispaniola.

Thelypteris negligens (Jenm.) Proctor, comb. nov.

Nephrodium negligens Jenm. Bull. Bot. Dept. Jamaica, n.s. 3:21. 1896. TYPE: Jamaica, without exact locality, *Jenman s.n.*, (NY).

Thelypteris trelawniensis Proctor, sp. nov.

Subg. *Amauropelta*, sect. *Amauropelta*. Ex affintate *T. balbisii* a quo laminis subtus pubescentibus; rhachidi et costis laminarum supra sulcatis earum marginibus pilis incurvatis multicellularibus ca. 0.2 mm longis; venis 9–11 paribus differt.

Rhizome decumbent-ascending or suberect, clothed at the apex with dark brown, lustrous, glabrous, lance-attenuate scales 3–4 mm long. Fronds few, erect-arching, up to 65 cm long; stipes 4–8 cm long, deciduously scaly toward the base, minutely stipitate-glandular throughout and lightly clothed with small, curved, pluricellular hairs. Blades lanceolate, 45–60 cm long and up to 18 cm broad below the middle, rather abruptly narrowed at the base, acuminate at the apex. Rhachis yellowish-brown, together with the costae densely clothed just inside the adaxial groove with short (ca. 0.2 mm long), stiffly incurved, pluricellular hairs; underside of the rhachis minutely stipitate-glandular and sparingly clothed with a few long, transparent, septate hairs up to 1.5 mm long. Pinnae mostly at right-angles to the rhachis, but the lower reduced ones somewhat reflexed, the largest linear- to narrowly deltate-oblong, 1.5–2 cm wide at the base, sessile, acuminate, deeply pinnatifid, with up to 23 pairs of segments; very small, brown aerophores present at abaxial base of costae. Segments oblong-subfalcate, 2.5–3.5 mm wide and not over 6 mm long, subacute at the apex, the margins strigillose-ciliate, and with 9–11 pairs of simple veins. Veins lightly strigillose on upper (adaxial) side; veins and tissue beneath with small, erect, unicellular, straight hairs and numerous sessile, reddish-resinous glands. Sori medial to supramedial; indusium erect, glabrous, densely resinous-glandular; sporangia glabrous.

TYPE: 1 mile N of Spring Garden, Parish of Trelawny, Jamaica, 1500–1700 ft (457–518 m), 2 Mar 1978, *G. R. Proctor 37704* (IJ).

This species is known only from the type specimen. It appears to be related to *Thelypteris balbisii* (Spreng.) Ching, but differs in the nature of its indument, in the deflexed lower pinnae, and in the more oblique segments with fewer veins. From the related *T. randallii* Maxon & Morton ex Morton it differs in the much thicker rhachis clothed on the sides of the adaxial groove with stiff, incurved hairs, and in having sessile, reddish-resinous glands only beneath. These three species and the next (*T. harrisii*) differ from the rest of sect. *Amauropelta* in having pluricellular hairs; in *T. balbisii* such hairs, however, may be present or absent.

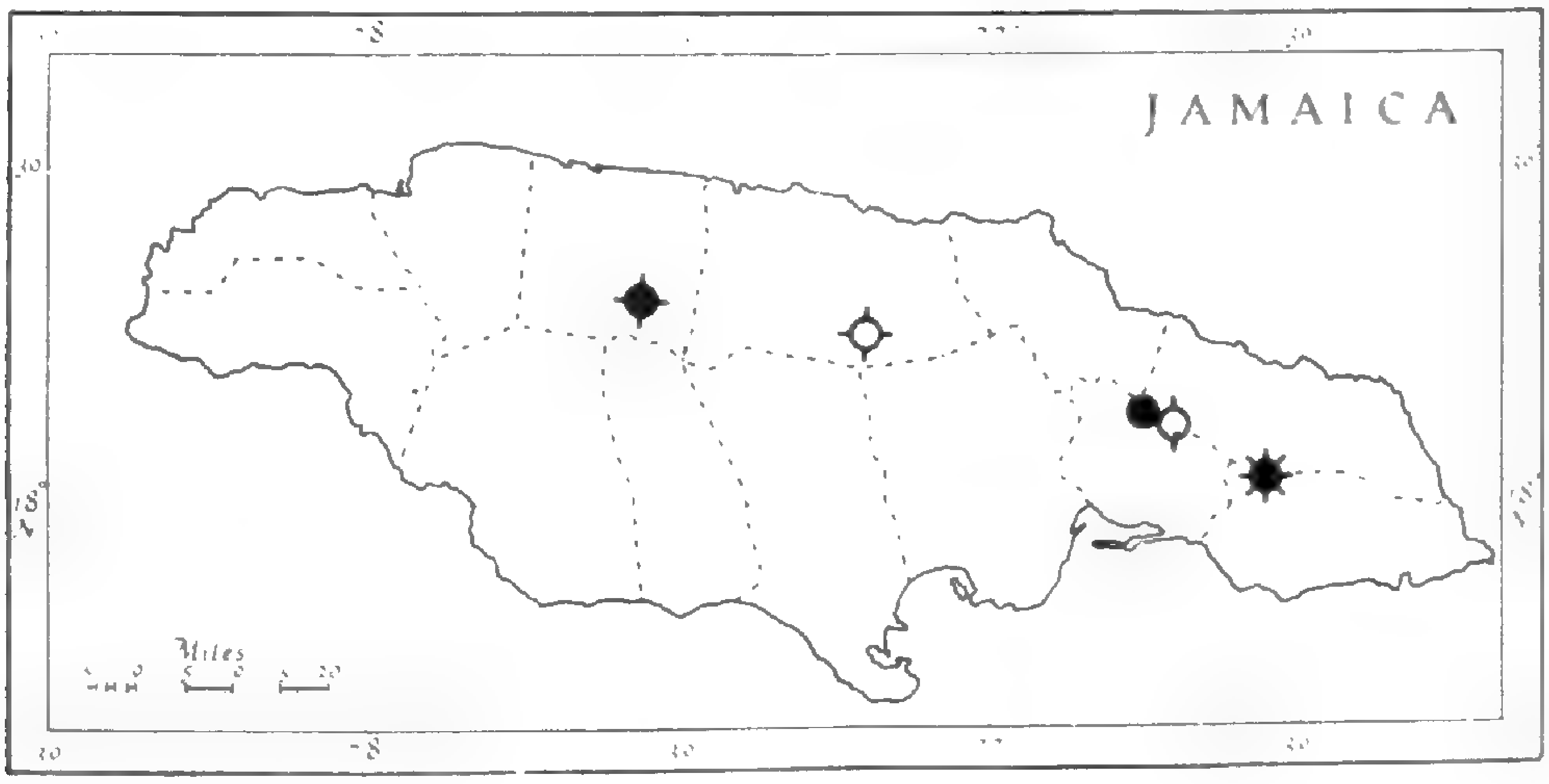

FIG 1. Known localities of cited species and varieties of *Thelypteris*. In order from west to east (left to right): *T. trelawniensis*, *T. resinifera* var. *caribaea*, *T. harrisii* and *T. malangae* var. *sitiorum*, *T. negligens*, and *T. decrescens*.

Thelypteris harrisii Proctor, sp. nov.

Nephrodium kaulfussii sensu Jenm. Ferns Brit. W. Ind. & Guiana 210. 1908, *non* Hook., 1862. Jenman believed that this plant had been treated by Grisebach (Fl. Brit. West Ind. 691. 1864) as a variety of what is now called *Thelypteris oligocarpa*, and rightly rejected this assignment. However, in taking up the name *kaulfussii*, he resurrected an epithet whose antecedents had been hopelessly confused by Hooker (Sp. Fil. 4:97. 1862), and which cannot be applied to the present taxon.

Subg. *Amauropelta*, sect. *Amauropelta*. Ex affinitate *T. underwoodianae* a qua rachide dense pilosa, pilis ca. 1 mm longis vel longioribus; indusiis pilis sed nonglandularibus differt.

Rhizome erect, clothed at the apex with small brown scales. Fronds erect; stipes (6)15–25 cm long, glabrate and sparingly clothed with scales toward the base, pilose distally with pluricellular hairs. Blades lance-oblong or broadly lanceolate, 40–55 cm long, 15–19 cm broad, abruptly narrowed at base with 2 or 3 pairs of reduced pinnae, the lowest often being mere auricles; rhachis finely puberulous throughout and also soft-pilose with long, spreading, whitish pluricellular hairs 1 mm long or longer. Pinnae mostly linear-oblong, long-acuminate, up to 10 cm long, 1.5–1.8 cm broad above the sessile base; costae and other vascular parts pilose throughout with soft hairs; tissue freely resinous-glandular beneath and nearly glabrous. Segments close, strongly oblique, oblong, acute, up to 3 mm broad, the margins narrowly reflexed; veins 7–9 pairs, the lower ones often forked, all strongly prominulous on the upper (adaxial) side. Sori supramedial; indusium relatively large, round-reniform, densely long-pilose and ciliate, but without glands, deciduous; sporangia glabrous.

TYPE: Moody's Gap, border of Parishes of St. Andrew and Portland, Jamaica, ca. 3000 ft (914 m), 22 Oct 1898, *W. Harris 7430*, (IJ; isotypes BM. K, NY). Paratype from same locality, 13 Feb 1900, *W. N. Clute 173* (NY).

Thelypteris harrisii seems to be related to *T. underwoodiana* (Maxon) Ching, but clearly differs in its much longer stipes, denser, longer, and softer pilosity, and in having the indusium pilose but without glands, instead of ciliate and resinous-glandular.

Thelypteris gracilenta (Jenm.) Proctor, comb. nov.

Polypodium gracilentum Jenm. Bull. Bot. Dept. Jamaica, n.s. 4:129. 1897. TYPE: Jamaica, without exact locality, *Jenman s. n.* (N.Y.)

This species somewhat resembles a large. *T. gracilis* in general appearance, but markedly differs from that species in details of the indument, sorus, and indusium. It is not clear why Jenman placed it in *Polypodium*, in view of its evident indusium, unless through faulty observation. Also, he stated that it is "common from 3,500 to 5,000 ft. altitude, in grass by the sides of open shallow streams and in similar wet exposed places." The total lack of any subsequent collections indicates, however, that it must in fact be very rare, and its continued existence needs confirmation.

Thelypteris resinifera var. caribaea (Jenm.) Proctor, comb. & stat. nov.

Nephrodium caribaeum Jenm., J. Bot. Brit. For. 24:270. 1886. TYPE: North slopes of Mt. Diablo, Parish of St. Ann, Jamaica, *Sherring s. n.*, (K photo US; isotypes IJ, US).

Dryopteris caribaea (Jenm.) C. Chr., Ind. Fil. 257. 1905.

Thelypteris caribaea (Jenm.) Morton, Amer. Fern J. 53:65. 1963.

In recognizing this plant as a distinct species, Morton stressed characters which do not provide clear and sharp differentiation from *T. resinifera*, but which in each case are more a question of degree (*e.g.*, relative cell width vs. cell length in the clathrate rhizome scales, relative hairiness of the indusium). Although the ensemble of differences suggests a recognizable local variant of *T. resinifera*, more can hardly be said until living plants are rediscovered.

Thelypteris malangae var. sitorium (Jenm.). Proctor, comb. nov.

Nephrodium jenmanii var. *sitiorum* Jenm. J. Bot. Brit. For. 17:261. 1879. TYPE: Jamaica, without exact locality, *Jenman 38*, in 1878 (K; isotype US).

Nephrodium conterminum sensu Jenm. Bull. Bot. Dept. Jamaica n.s. 3:45. 1896, *non Aspidium conterminum* Willd. in L., 1810.

Dryopteris consanguinea var. *aequalis* C. Chr. Smiths. Misc. Coll. 52:380. 1909. TYPE: Second Breakfast Spring, Parish of St. Andrew, Jamaica, *W. R. Maxon 997* (US) (= *Underwood 2131*, NY).

Differs from typical *T. malangae* of Hispaniola in having narrower, more tapering pinnae (mostly 1.5–1.8 cm wide vs. usually over 2 cm wide), the segments usually distinctly crenulate and relatively shorter and broader, and in the presence on

Jamaican plants of widely scattered, very minute, colorless, stipitate glands, especially in the adaxial grooves of the rhachis and costae. In addition, the sori of var. *malangae* are approximately medial, whereas those of var. *sitiorium* are submarginal.

Thelypteris rudis f. cristata Proctor, f. nov.

A forma typica marginibus pinnarum apicem versus integerrimis, apice ipso cristato-laciniato differt.

Differs from the typical form in having the distal part of the pinnae entire, at the end expanding into a cristate-laciniate apex.

TYPE: Jamaica, without definite locality or collector, *J. P. 1232–a* (K; isotype IJ). This plant was gathered in 1885, probably by J. H. Hart or one of his colleagues in the then Botanical Department of Jamaica.

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SHORTER NOTES

NOTES ON NORTH AMERICAN LOWER VASCULAR PLANTS–II.—Field work in Arizona and examination of herbarium specimens at ASU, LL, and NY have revealed several new state records for Arizona and various states in northern Mexico. Also presented here are range extensions for two species within states where previously reported, one for Arkansas and one for Arizona. I am especially grateful to have been able to examine the numerous fine collections of Marshall C. Johnston and his former students, Thomas L. Wendt and Fernando Chiang C.

A second locality in Arkansas is now known for *Cheilanthes eatonii* Baker in Hook. & Baker. The collection data are: Benton Co., Arkansas, *E. N. Plank s. n.* in 1899 (NY). The species was first reported in Arkansas in Baxter Co., by W. C. Taylor & D. Demaree (Rhodora 81:514. 1979). They reported it as *C. castanea* Maxon, which I do not recognize as distinct from *C. eatonii* [A monograph of the fern genus *Cheilanthes* section *Physapteris* (Adiantaceae), Ph.D. Dissertation Arizona State University, 1979].

Cheilanthes × *parishii* Davenp. (pro sp.) has been found new to Arizona. The collection data are: Dushey Canyon, Harquahala Mts., Maricopa Co., Arizona, growing near *C. covillei* Maxon and *C. parryi* (D. C. Eaton) Domin, desert scrub vegetation with Saguaro, Ocotillo and Jojoba, igneous substrate, 3000 ft elevation, *Reeves 7127* (ASU). Reported previously from three localities in southern California by A. R. Smith (Madroño 22:377. 1974). I agree with Smith that this is a sterile hybrid between the species listed above. A single plant was found at this site where the presumed parents are abundant.

The first collection from Chihuahua, Mexico for *Notholaena bryopoda* Maxon has been made. The collection data are: Sierra del Roque, N of Julimes and N and NW of Rancho el Sauz, 28°39′–28°41′N, 105°20′18″–105°20′30″W, 1450–2150 m elevation, matorral desertico con espinos laterales, steep slopes of limestone mountains, limestone gravel, with *Acacia neovernicosa, Dasylirion, Agave lecheguilla, Fouqueria splendens,* and *Parthenium incanum, M. D. Johnston et al. 12314* (LL). Previously known from Coahuila and Nuevo León, where it occurs on gypsum, according to R. M. Tryon (Contr. Gray Herb. 179:77. 1956).

Notholaena greggii (Kuhn) Maxon is now known from Nuevo León. The collection data are: Sierra Madre Oriental, Nuevo León, Mexico, calcite and limestone hills beyond Pablillo toward Santa Clara, 15 mi SW of Galeana, scattered on bank of calcite, *C. H. & M. T. Muller 1080* (LL). Previously known from Texas, Chihuahua, Coahuila, and Durango (Tryon, 1956, p. 76).

The first collection of *Notholaena neglecta* Maxon in Nuevo León has been made. The collection data are: Minas "Manto Blanco" y "Sabana Blanca" just N of the Cañon de Potrerillos, Nuevo León, Mexico, 26°04′N, 100°45′W, 950–1000 m elevation, crasi-rosulifolios espinos, limestone ridge, gypsiferous clay loam, with *Agave lecheguilla, Hechtia, Fouqueria, Larrea,* and *Opuntia rufida, M. C. Johnston et al. 10248C* (LL). Previously known in Texas, Arizona, Chihuahua, and Coahuila (Tryon, 1956, p. 76).

Notholaena parvifolia Tryon has been collected in San Luis Potosí. The collection data are: Estación Microondas "Pastoriza" about 22 km S of Matehuala, San Luis Potosí, Mexico, 23°25′05″–23°25′25″N, 100°38′50″–100°39′00″W, 1550–1650 m elevation, crasi-rosulifolio espinoso, a few patches of matorral, limestone hills, calcareous gravelly soil, with *Orthosphenia mexicana, Cnidoscolus* sp., *Eysenhardtia* sp., and *Agave lecheguilla, M.C. Johnston et al. 11111B* (LL). Previously known from New Mexico, Texas, Chihuahua, Coahuila, Nuevo León, Tamaulipas and Zacatecas (Tryon, 1956, p. 99).

The first record for *Pellaea intermedia* Mett. ex Kuhn in San Luis Potosí has the following collection data: 1 km by winding road below and W of Real de Catorce, on road to Estación Catorce, above Socavon La Purisima, San Luis Potosí, Mexico, 23°41′40″N, 100°53′50″W, 2400–2450 m elevation, crasi-rosulifolio espinoso, badly disturbed agriculturally, very steep canyon slopes of metamorphic rock, with *Agave* spp. and *Opuntia* spp., *M. C. Johnston et al. 11070A* (LL). Known previously from Arizona, New Mexico, Texas, Chihuahua, Sonora, Coahuila, Nuevo León and Zacatecas, according to A. F. Tryon. (Ann. Missouri Bot. Gard. 44:179. 1957).

Pityrogramma triangularis (Kaulf.) Maxon var. *triangularis* is now known to occur in Arizona. The collection data are: Frehner Canyon, Virgin Mountains, Mohave Co., Arizona, very scarce, steep rocky N slope, granite, with Piñon, *Quercus turbinella, Ephedra, Galium, Stipa, Sitanion,* and *Thamnosma,* 5000 ft elevation, *R. Gierisch 4598* (ASU). This variety was previously known from southern British Columbia, Washington, Oregon, California, Baja California, southern Nevada, and southwestern Utah, according to K. S. Alt and V. Grant (Brittonia 12:155. 1960). Variety *maxonii* Weath. occurs in central and southern Arizona. The locality reported here for variety *triangularis* is in the extreme northwestern corner of Arizona.

The first collection of *Polypodium glycyrrhiza* D. C. Eaton in Arizona has been made. The collection data are: Devil's Chasm, Sierra Ancha, Gila Co., Arizona, narrow, deep gorge, one large patch ca. 6 × 6 ft on cliff, ca. 5000 ft elevation, *B. Warner s. n.*, 10 Jan 1979 (ASU). Known previously from Kamtchatka, the Aleutian Islands, Alaska and coastal British Columbia, Washington, Oregon, and California (south to central part of state), according to R. M. Lloyd and F. A. Lang (Brit. Fern Gaz. 9:171. 1964). The specimen examined has the "sweet" rhizome and free venation of *P. glycyrrhiza*, in contrast to the acrid rhizome and usually anastomosed venation of *P. californicum* Kaulf. The material does not resemble *P. hesperium* Maxon, which is rather widely distributed in Arizona. The presence of *P. glycyrrhiza* in Arizona brings to three the number of predominantly Pacific Coast ferns found disjunctly in central Arizona. The other two are *Dryopteris arguta* (Kaulf.) Watt. and *Woodwardia fimbriata* J. E. Smith in Rees.

Selaginella eremophila Maxon is now known from several additional localities in southwestern Arizona. The collection data are: Sierra Estrella Regional Park, Maricopa Co., Arizona, W-facing wash on west face of Squaw Tit, moist desert under rocks with *Penstemon antirrhinoides, Salvia mohavensis, Notholaena standleyi,* and *Castilleja lanata,* 2400 ft elevation, *E. & M. Sundell 177* (ASU); West side of White Tank Mountains, Maricopa Co., Arizona, slope leading up to light 1, lower sonoran desert slope, at base of cliff, *D. Keil 4088* (ASU); 7 mi S of Buckeye on U.S. 80, 2.4 mi along Buckeye Recreation Area Park road, on S-facing slope, under rocky ledge, 1189 ft elevation, *A. Pierce 211 p. p.* (a small fragment is apparently *S. arizonica* Maxon); Cabeza Prieta Game Range, Yuma Co., Arizona, S4, T14S, R15W, ca. 6 mi NW of Tule Well, E-facing slope of low mountain, *E. Lehto et al. 23548* (ASU, NY, US). This species previously was known in Arizona from a single collection near Tinajas Altas, Yuma Co., collected by Jaeger in 1934, according to R. Tryon (Ann. Missouri Bot. Gard. 42:80. 1955). All of the cited collections previously had been identified as *S. arizonica,* which is more common in Arizona than is *S. eremophila.* So far as I know at present, the two species occur together only at the Buckeye locality. I have seen material of *S. arizonica* from the White Tank Mountains, but from a different locality than the one cited above for *S. eremophila. Selaginella eremophila* is otherwise known from southern California and Baja California (Tryon, 1955).

Field work in Arizona was supported by National Science Foundation Dissertation Improvement Grant 77-00182 to Dr. D. J. Pinkava and the author. I thank the curators of the cited herbaria for permission to examine their collections.—*Timothy Reeves, Biological Science Center, Boston University, Boston, MA 02215.*

EQUISETUM ARVENSE IN ALABAMA.—The Common Horsetail, *Equisetum arvense* L., has been reported from Alabama by various authors from Small (Ferns of the Southeastern States, 1938) to Evans in Radford, Ahles, and Bell (Manual of the Vascular Flora of the Carolinas, 1968), none of whom gave any indication of locality. According to Dean (Ferns of Alabama, 1969, p. 153), "A large colony was discovered in Marengo County by Dr. R. M. Harper." This was puzzling because Marengo County is in the coastal plain of southwestern Alabama, but *E. arvense* is a northern plant reaching its southern limit in Alabama. One would expect the plant to be present only in the northern part of the state; indeed, Wheatstone and Atkinson (Castanea 44:1–8. 1979) found it in Morgan County in central northern Alabama in 1974. It also has been found recently in Calhoun County (*R. R. Haynes,* UNA). While boating on the Black Warrior River in Greene County in October 1978, I was quite surprised to find a thriving colony of *E. arvense* on the west bank of the river. This locality is in the coastal plain about 20 miles upstream from Demopolis, which is in Marengo County. Therefore, this find lent credence to the report from that county. The Greene County colony was much larger and denser than the Morgan County population. It was growing in damp, partially shaded sand at the base of a wet chalk bluff, just above the normal level of the river (*Short 1183,* AUA, and duplicates to be distributed). On a visit to the U.S. National Herbarium in April, 1980, I examined a specimen of *E. arvense* (*R. M. Harper 121,* US) collected on October 11, 1908 in Marengo County on the bank of the Tombigbee River about 10 miles downstream from Demopolis. The plants were growing in sand at the base of a wet chalk bluff. This evidently is the collection referred to by earlier authors.—*John W. Short, 905 McKinley Ave., Auburn, AL 36830.*

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AMERICAN FERN JOURNAL: VOLUME 71 NUMBER 3 (1981)

Arachniodes simplicior New to South Carolina and the United States

JUDITH E. GORDON*

During the past year, a population of about 100 plants of *Arachniodes simplicior* (Mak.) Ohwi was found along nearly 100 m of the bank of a small, unnamed tributary of the Savannah River in North Augusta, South Carolina. The species was identified using Ching's (1934) treatment of Asiatic species of *Rumohra* Raddi, a genus now correctly designated *Arachniodes* Blume, as explained by Tindale (1961). The identification was confirmed by the United States National Herbarium. Specimens from the American population are described as follows (see also *Figs. 1, 2*):

Rhizome moderately creeping, commonly 5–8 mm in diameter, densely covered with tan to cinnamon-brown, papery scales, these long triangular with auricular-clasping bases, 0.5–2.5 mm wide, 3–8 mm long, the tips one cell wide and 2–4 cells long, the margins entire except for 1–3 trichomes, 3–5 cells long, near scale bases and a few basal teeth formed from outward distensions of two cell end junctures. Stipes commonly 0.5–4 cm apart, 15–46 cm long, 4–6 mm diameter at the base, often equal to or longer than the laminae, sub-terete, flattened on the upper surface and grooved toward the apex, tan at the base, pale green above, aging to a straw-yellow color, somewhat scabrous from small protuberances on which scattered scales are borne, the scales more densely distributed toward the stipe base, 2–12 mm long, and similar to those of the rhizome except more elongate and chocolate-brown, the venation consisting of 2 large and 3 small bundles at the base, reduced to 3 at the apex. Rachis unwinged, pale green, the upper surface grooved, the scales like those of the stipe except smaller. Costae yellow-green, with grooves continuous with those of the rachis, the scales smaller and more abruptly narrowing. Laminae 24–39 cm long, 26–34 cm wide, deltoid-pentagonal, 2–3-pinnate, coriaceous, perennial, the adaxial surfaces glossy dark green with yellow-green streaks along the costae and adjacent bases of pinnules, the abaxial surfaces uniformly pale green and not glossy, the apex gradually acuminate. Pinnae generally 1-pinnate, 3–4 alternate pairs below the terminal pinna, 1–6 cm distant, at 30–45° to the rachis, 8–16 cm long, 2–4 cm wide at the base except the basal pair, 2-pinnate with the base 8–10 cm wide, the petiolules 1–6 mm long, the apices gradually acuminate, the pinnules and venation anadromically arranged on all pinnae. Pinnules, except the lower pairs on the basal pinna pair, 16–22 alternate pairs, asymmetrically ovate-auriculate with an acroscopic basal lobe, 13–22 mm long, 5–10 mm wide, the petiolules narrowly winged, sessile or up to 1 mm long, the apices aristate, the margins with spines up to 1 mm long, with a few trichomes along the larger veins; basal pinnule pair on the basal pinna pair basiscopically produced with the upper about ⅓-½ the length of the lower, the latter 6–10 cm long, the ultimate segments resembling the pinnules of the 2-pinnate pinnae. Pinnule venation free, semi-dichotomous, not extending to the margins, the first branch arising anadromically. Sori dorsal, globular, arranged in a single row on each side of the pinnule main vein, terminal on smaller lateral veins, somewhat closer to the main vein than the margin. Indusia 0.5–1.0 mm in diameter, orbicular-reniform, attached at a deep sinus with often overlapping lobes, tan to slightly darker brown in the center, glabrous, the margins entire, persisting for about two months before being shed. Sporangia with stalks composed of three rows of

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*Department of Biology, Augusta College, Augusta, GA 30910.

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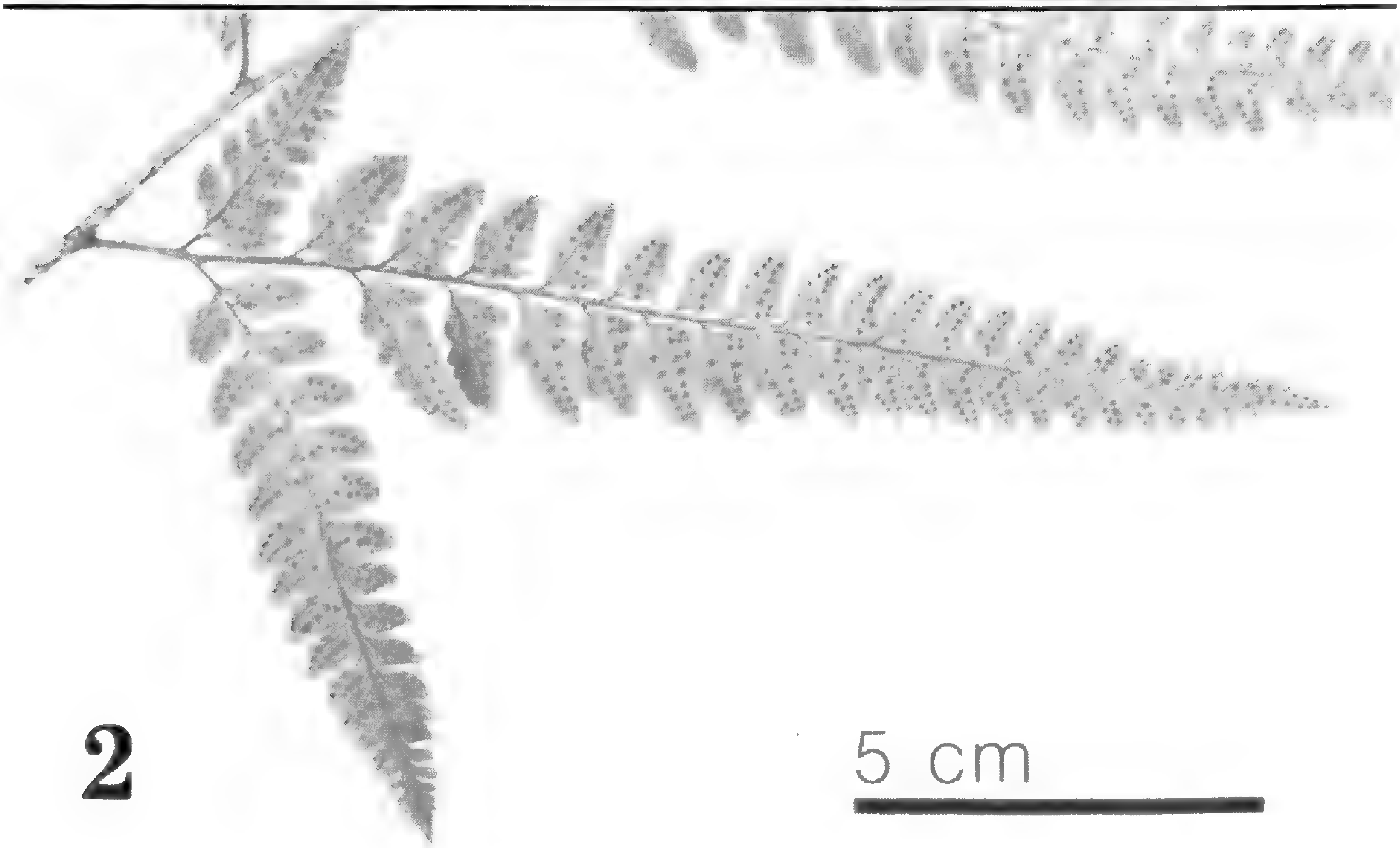

FIGS. 1 and 2. Photographs of *Arachniodes simplicior*. FIG. 1. Frond as seen in natural habitat. FIG. 2. Lowermost basal pinna, dorsal view.

cells, 0.3–0.4 mm long, englandular, the annulus of 13–16 thickened cells. Spores bilateral, dark brown, rugose-reticulate, 41–44μm × 28–32μm. Chromosome number $2n = 164$ (Löve et al., 1977), undetermined for this population.

The unusual nature of the habitat deserves further mention. The area, although within the city limits, is accessible only by foot and is characterized by steep, southwest-facing cliffs and heavy undergrowth within southern hardwood forest that probably has not been logged. The area surrounding the creek is dominated by *Fagus grandifolia* with a scattering of *Celtis occidentalis* and various species of *Quercus*. The understory is dominated by a species of *Aesculus*, apparently a hybrid between *A. pavia* and *A. sylvatica*. *Polystichum acrostichoides* (Michx.) Schott plants grow intermixed with the population of *A. simplicior*, but are less numerous. A small population (ca. eight plants) of *Pteris multifida* Poir., a naturalized species, is also present along the creek bank. The site has the following coordinates: 33°30′11″ N Lat., 81°58′54″ W Long., 42–53 m elev. This places the site along the western edge of the Hammond Hills subdivision.

The area is seldom visited by hikers, but there have been two major disturbances within the last 50–55 years according to city officials. About 1927–29, the Georgia and Florida Railroad extended a line northward through the area. The rail bed was built with fill (source unknown) rising about seven meters above the creek bed, the creek water being piped through at the base. Plants of *A. simplicior* grow within a meter of the pipe. Use of the rail line was discontinued about 1954, at which time the city laid a sanitary trunk sewer line through the area. The sewer pipe, which is elevated about seven meters, parallels the old rail bed and is downstream about 60 m. If the population were present in 1954, it would have been disturbed by the construction of the sewer line.

Observations of greenhouse and field plants show a growth pattern based on two new fronds produced yearly, usually in April in the North Augusta area. The persistence of the old frond bases permits a rough estimate of individual rhizome age, obtained by counting old bases and dividing by two. Ten rhizomes were examined; ages ranged from 2–15 years, using this method of calculation. Considering the likely decay of older rhizome portions, the population size, and possible establishment from a spore source, it appears that the population is at least 20–25 years old.

There are several possible spore or rhizome sources in the vicinity, including several nurseries, although none is within a mile radius of the site. One of the nurseries reported selling *A. simplicior* about three years ago, but not prior to that time nor within the last year. Another source of spores or rhizomes would include plants purchased by residents of the Hammond Hills subdivision, which was established about 1955. The probability of someone having actually planted the fern at the site is highly unlikely since access to the area is difficult. Based on the available information, I believe the population was probably established from a spore source shortly after the construction of the sewer line in 1954. Further studies centering on chromosome counts and gametophyte developmental stages are anticipated.

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REVIEW

VASCULAR PLANTS OF CONTINENTAL NORTHWEST TERRITORIES, CANADA, by A. Erling Porsild and William J. Cody. 1980. 667 pp. National Museums of Canada Publ. Div., Ottawa, Canada K1A OM8. ISBN 0-660-00119-5. Can$80.00.—This admirable volume provides descriptions, keys, habitat data, and maps for 1113 species of vascular plants which occur in the region immediately north of British Columbia, Alberta, and Saskatchewan. Information also is included on a number of species expected by the authors to occur in the region. There is an excellent survey of the history of collection in the region and a worthwhile bibliography.

The pteridophytes are treated as 40 species, one subspecies, and one variety present, with four more species expected. Nearly half are fern allies. There are no great surprises in this subarctic flora; no hybrids or taxonomic novelties were noted. The limestone plants are of interest.

I found the distribution maps to be curious and unexpected. They include Alaska and the Aleutians to the west, Greenland and Iceland to the east, and Chicago to the south. Thus, they are too small for detailed distributions within the region covered by the book. They do nothing to support the six phytogeographic zones designated by the authors, and certainly do not give a clear picture of the tree line, areas well collected, or other extrapolations one usually extracts from dot maps.

Although we are warned (p. 3) that the maps are "in no way complete" for the Canadian distributions and are meant to show a "broad picture," they have serious shortcomings. A person interested in Newfoundland might conclude that *Woodsia alpina* or *Phegopteris connectilis* does not occur there. Also, no fiddleheads in New Brunswick where they are canned in quantity? More serious are the maps which record more than the taxon being treated, *e.g.*, *Botrychium lanceolatum* versus subsp. *lanceolatum*, *Gymnocarpium dryopteris* versus subsp. *disjunctum*, and *Woodsia oregana* versus *W. cathcartiana*.

I think it is a great pity that the authors fall back on names such as *Dryopteris disjuncta* for *Gymnocarpium dryopteris* and *D. phegopteris* for *Phegopteris connectilis*. I do not like *Polypodium vulgare* subsp. *virginianum* for *P. virginianum* or *Dryopteris dilatata* (the common tetraploid of Europe) for *D. expansa*, but these are newer and more problematical changes.

All in all, this book is a most useful compendium of the pteridophytes of a broad area of boreal, sub-arctic and arctic Canada and will be a constant source of reference for anyone interested in this part of the world.—*D. M. Britton, Dept. of Botany and Genetics, University of Guelph, Guelph, Ont. N1G 2W1, Canada.*

A New Isoëtes from Jamaica

R. JAMES HICKEY*

The genus *Isoëtes* L. is poorly represented in the Caribbean, with only two species reported to date. *Isoëtes cubana* Baker collections made by Wright in the western, lowlands of Cuba. To my knowledge, there have been no subsequent collections of this species from Cuba, although certain collections from Belize strongly resemble the Cuban material and probably are conspecific with it. *Isoëtes tuerckheimii* Brause is known from several collections made in the Cordillera Central in the Dominican Republic at altitudes of 2200–2900 meters. Thanks to the generosity of Dr. George Proctor, who kindly supplied spirit and herbarium material, I am able to report the discovery of a third Caribbean species which is endemic to Jamaica.

Isoëtes jamaicensis Hickey, sp. nov. **Figs. 1-4, 6, and 8**

Radices dichotome ramosae. Cormus trilobatus, 1–2 cm diametro. Folia 20–55 ($\bar{x} = 38$), 8–20 cm longa, 0.5–0.8 mm lata in medio, attenuatissima, recurvata. Stomata et fasciculi fibrosi peripherales praesentes. Velum parvum. Margines ligulae hyalini, ephemeri; area centralis triangularis, attenuata versus apicem. Megasporae albidae, 320–440 ($\bar{x} = 398$) μm, tuberculatae. Microsporae cinereae, ellipticae, 30–40 ($\bar{x} = 36$) μm longae, 22.5–32.5 ($\bar{x} = 27.3$) μm latae, cum papillis cavis.

TYPE: In mud of drying seasonal rain pools, ca. 350 ft, Harris Savanna, Clarendon Parish, Jamaica, 26 Nov 1974, *G. R. Proctor 34357* (IJ).

PARATYPE: Harris Savanna, Clarendon Parish, Jamaica, 26 Nov 1974, *G. R. Proctor 34358* (IJ).

In habit and spore morphology, *I. jamaicensis* most closely resembles *I. montezumae* Eaton of Mexico (see *Table 1* for comparison with other Mexican and Caribbean species). Although the distinctness of the latter species from *I. mexicana* Underw. has been questioned (e.g., Reed, 1953; Pfeiffer, 1922), preliminary examination of numerous Mexican collections, including type specimens, suggests that hybridization, possibly involving the formation of partially fertile hybrids, has caused the confusion between these species. In light of this possibility, *I. montezumae* certainly merits provisional specific status until my more detailed study of these species and *I. pringlei* Underw. is completed.

Isoëtes jamaicensis and *I. montezumae* differ in several respects, of which the more salient are discussed here. The corm of *I. jamaicensis* is distinctly three-lobed, whereas in the latter it is deeply bilobed. The membranaceous margin at the base of the leaves is less pronounced in *I. jamaicensis* than in *I. montezumae*. In the former, it is 1–2 mm wide and merges into the leaf proper 5–10 mm above the sporangium; in the latter, the margin is 1.5–2 mm wide and extends 10–20 mm above the sporangium. Both species have similar velum coverage of the sporangium. Eaton (1897) reported a very narrow velum in megasporophylls and virtually none in microsporophylls of *I. montezumae*. In *I. jamaicensis*, there is little dimorphism in

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*Biological Sciences Group, U-43, University of Connecticut, Storrs, CT 06268.

TABLE 1. COMPARISON OF MEXICAN AND CARIBBEAN ISOËTES SPECIES.[1]

Character	*I. jamaicensis*	*I. mexicana*	*I. montezumae*	*I. pringlei*	*I. cubana*	*I. tuerckheimii*
Habitat	amphibious	amphibious	amphib-terr	amphibious	amphibious	amphib-aquat
Altitude (meters)	ca. 100	1830–2150	—	—	>50	2200–2900
Corm lobing	3	2	2	2	3	2
Leaf number	20–55	8–30	8–20	10–20	10–50	10–35
Leaf length (cm)	8–20	9–23	8–14	16–25	15–40	5–15
Leaf diameter (mm)	0.5–0.8	0.3–1.2	0.6–1.2	0.5–1	1–2	0.75–1.75
Stomates	+	+	+	+	+	+
Fibrous strands	+	+	+	+	+	–
Velum coverage	>¼	rudimentary	>¼	>⅓	rudimentary	⅓–½
Megaspore color	white	grey-white	white	white	grey-white	white
Megaspore ornamentation	tuberculate	± smooth	tuberculate	cristate-echinate	tuberculate	smooth
Perispore strands	± united	separate	± united	separate	all united	separate
Megaspore size (μm)	320–440	250–375	350–510	475–610	290–400	380–530
Microspore color	ash-grey	fawn	ash-grey	fawn	fawn	brown
Microspore ornamentation	papillate	smooth-echinate	papillate	smooth	echinate-papillate	smooth
Microspore length μm	30–40	25–38	30–38	32–43	25–33	26–35
Microspore width μm	22–33	25–33	23–28	27–33	20–25	22–28

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[1] Data obtained from original descriptions, Pfeiffer's monograph (1922), and personal observations.

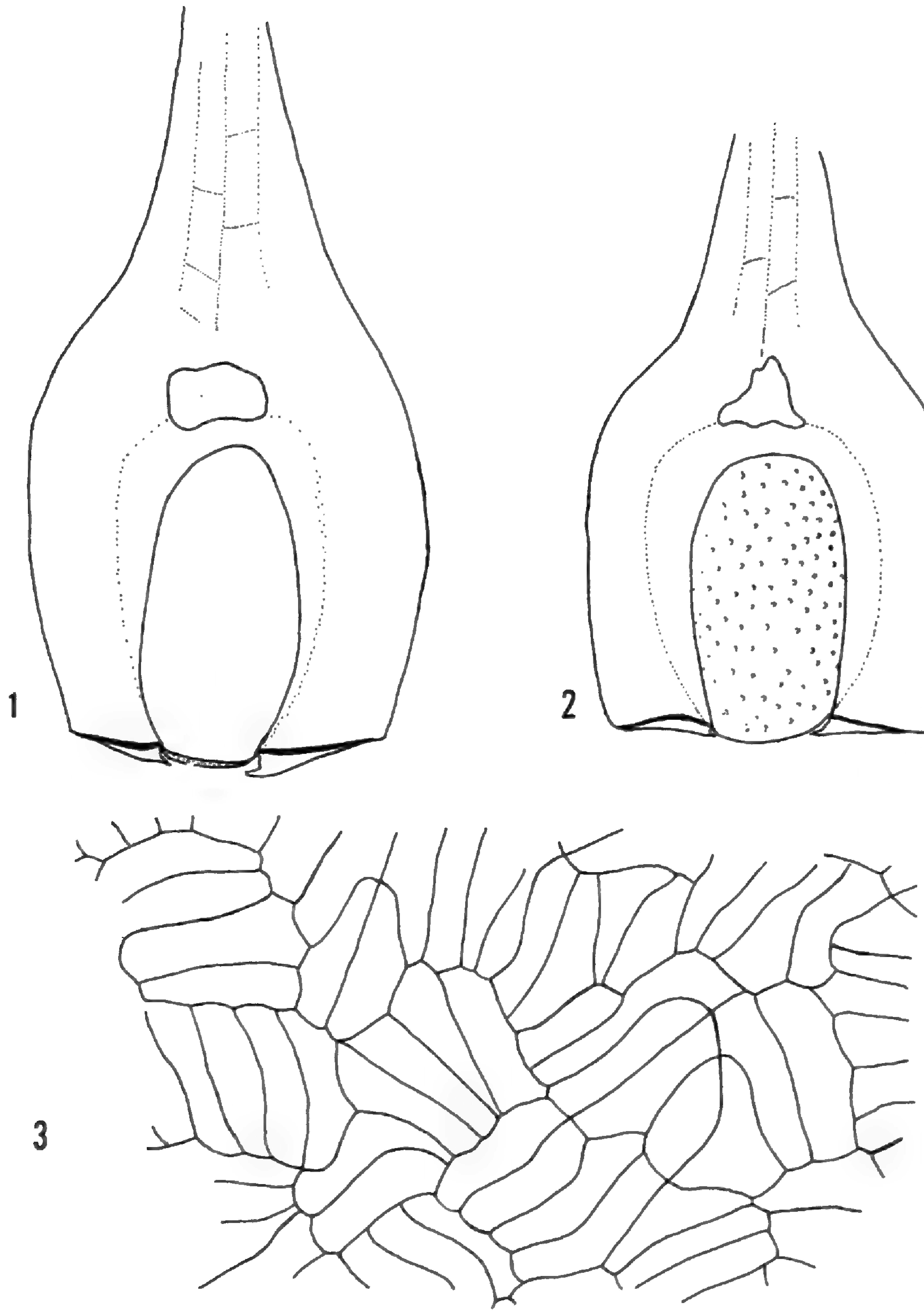
velum coverage between the megasporohylls and the microsporophylls; most of the leaves show some velum coverage (*Fig. 1* and *2*), although in a single microsporophyll of the type collection there was no appreciable velum development. Ligule characteristics show considerable variability due to the ephemeral nature of the hyaline margin and due to the delicate nature of the central region, which deteriorates rapidly with age (*Figs. 1* and *2*). The sporangium wall is unspotted and consists of thin-walled cells in *I. jamaicensis (Fig. 3)*, just as it does in many specimens of *I. montezumae*.

The tuberculate megaspores of both species are quite similar (*Figs. 4* and *5*). However, *I. montezumae* has consistently larger equatorial ridges and is more variable in the extent of ornamentation; the spores range from distinctly to indistinctly tuberculate. *Isoëtes jamaicensis* is more consistent in possessing well developed tubercles. Specimens of *I. montezumae* also show variation in tubercle distribution. On the distal surface, the tubercles diminish in size and increase in frequency close to the equatorial ridge. The tubercles of the proximal surface are always less well developed. In *I. jamaicensis*, on the other hand, the tubercles are uniformly developed and distributed.

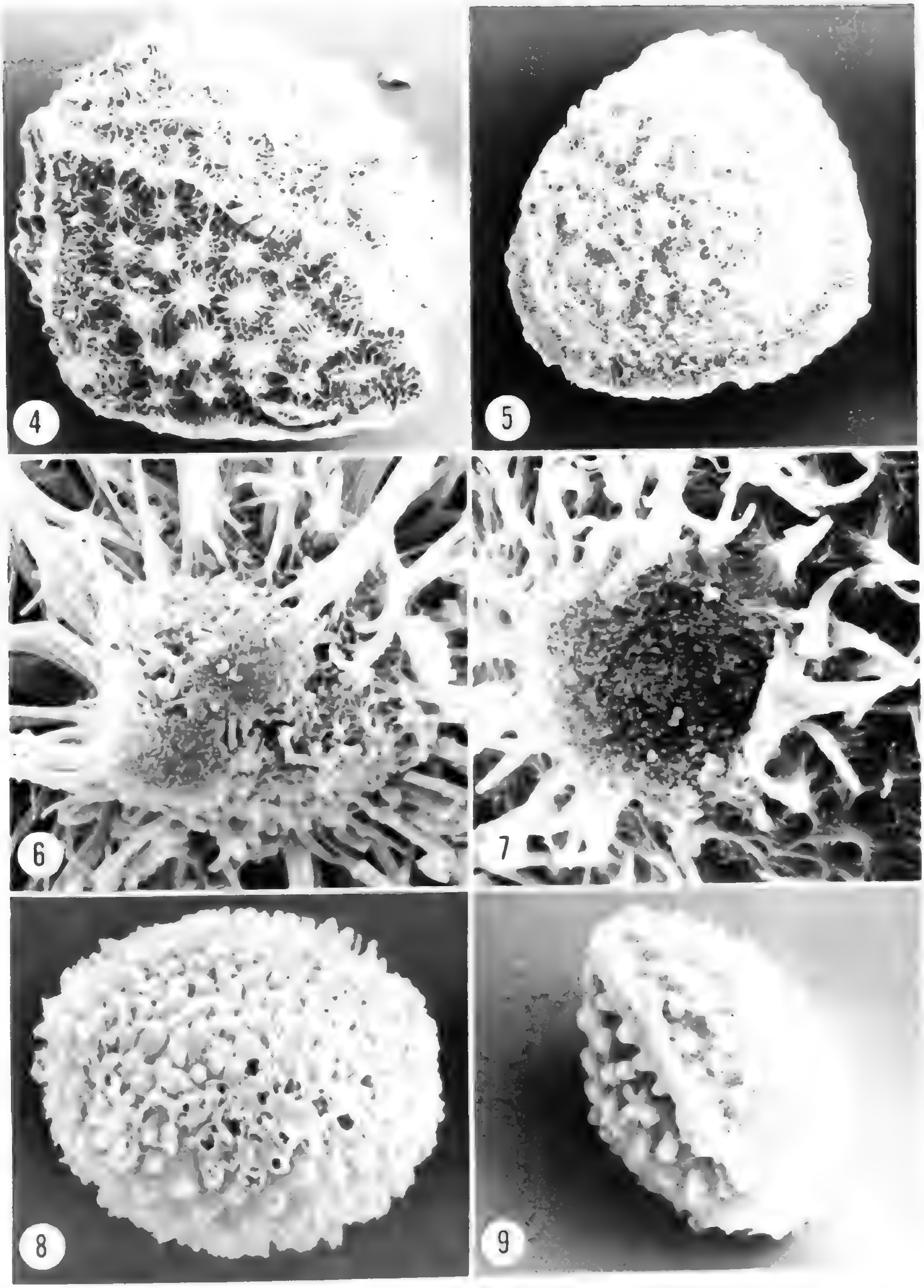
The tubercles of both species consist of solid masses of perispore material extending outward from the spore surface (*Figs. 6* and *7*). In both species, cords of perispore material radiate out from the tubercles, giving the spores a cobwebby appearance. While superficially similar, a closer examination of the spores and tubercles shows some distinct morphological differences. In *I. montezumae*, the perispore layer between the tubercles consists of very slender, interwoven strands which form a mat-like surface (*Fig. 7*, lower right). These small strands merge and two groups of them twist together to form the cords which can be seen radiating out from the tubercles. The cords in *I. jamaicensis* are also composed of smaller strands, but they are larger than those in *I. montezumae*, parallel, and are never interwoven. Between the tubercles, these small strands are isolated from one another and do not form any sort of solid structure.

The microspores of *I. jamaicensis* are ornamented with numerous, conical, hollow papillae (*Fig. 8*). In some spores of the type collection, the papillae are quite pointed, approaching echinate projections in form, and are occasionally branched apically. The bases of the papillae are confluent. In *I. montezumae (Fig. 9)*, the papillae are sparse, rounded, and give no indication of being hollow (as evidenced by their invariably unbroken appearance). The papillae are quite distant, and between them the microspores are covered with a finely granular perispore. Unlike *I. jamaicensis*, the equatorial ridges are visible in *I. montezumae* when the microspores are viewed from the side. Both species have a prominent proximal suture. The holotype of *I. montezumae (Pringle 3459*, MO) shows no indication of spore abortion, nor do either of the collections of *I. jamaicensis*. Spore abortion is not uncommon in many of the Mexican collections of *Isoëtes*.

Isoëtes jamaicensis inhabits seasonal rain pools in open xerophytic scrub of the Harris Savanna. This region receives 35–40 inches of rain annually during seasonal rainfalls. However, according to Dr. Proctor, the pools containing *I. jamaicensis* form only once every four or five years, when the rains are particularly heavy.



FIGS. 1–3. Leaf morphology of the type of *Isoëtes jamaicensis (Proctor 34357,* IJ). FIG. 1. Megasporophyll showing incomplete velum and degraded ligule, × 9.6. FIG. 2. Microsporophyll from a more central region of the corm showing velum and ligule which still retains a portion of the apex of the central region, × 9.6. FIG. 3. Cellular detail from outer sporangial wall of a megasporangium, × 396. All drawings made with a camera lucida drawing tube.



FIGS. 4–9. Spores of the types of *Isoëtes jamaicensis* (*Proctor 34357*, IJ) and *I. montezumae* (*Pringle 3459*, MO). FIG. 4. Megaspore of *I. jamaicensis*, equatorial view, × 125. FIG. 5. Megaspore of *I. montezumae*, distal view, × 125 FIG. 6. Megaspore of *I. jamaicensis*, close up of a partially developed tubercle, distal surface, × 2500. FIG. 7. Megaspore of *I. montezumae*, close up of a partially developed tubercle, distal surface, × 2500. FIG. 8. Microspore of *I. jamaicensis*, equatorial view, × 1665. FIG. 9. Microspore of *I. montezumae*, near proximal view, × 1665

Whether the corms break their dormancy in drier years is not known, but observations on other species of similar habitats suggest that they may not (Hall, 1971). Considering the unusual habitat and apparent sporadic growth of this plant, it is not surprising that it has eluded detection this long. It will not be surprising if this species is collected in other areas of Jamaica or perhaps on some of the other islands of the Greater Antilles.

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Leaf Turnover Rates and Natural History of the Central American Tree Fern Alsophila salvinii

RALPH L. SEILER*

There are few studies of growth rates of tropical trees. Moreover, the growth of tree ferns in their native habitats has seldom, if ever, been studied because of their slow growth and the need to make observations over a long period of time. As a Peace Corps volunteer in El Salvador I had the chance to study the growth of the cloud forest tree fern *Alsophila salvinii* Hooker (Cyatheaceae).

Bosque Montecristo is a cloud forest that covers about 15 km^2 and is located at the common borders of El Salvador, Guatemala, and Honduras. Approximately 60 percent of the forest is in El Salvador and has been set aside as a national park and wildlife preserve. The highest point in the forest, the summit of Cerro Montecristo, has an altitude of 2414 meters. Bosque Montecristo receives an average of 2250 mm of rain annually. Fog drip during the night deposits about the same amount of water on the forest (Reyna, 1979). March and April are the driest months. The rainy season begins in mid-May or early June and continues until December.

Bosque Montecristo is a subtropical, lower montane, very humid forest according to the Holdridge life zone classification (Holdridge, 1975). The cloud forest proper begins at ca. 2100 m and extends to ca. 2350 m, where it is replaced by an ericaceous shrub association on the mountain summits. The ecotone between the cloud forest and the pine-cypress association below occurs between 1900 and 2100 meters. Secondary forest is found in the whole zone wherever there has been logging (Reyna, 1979).

The majority of the trees in the cloud forest are evergreen. The emergent trees in the forest canopy are principally oaks, which are thickly covered with epiphytes (Reyna, 1979). Tree trunks near the forest floor support lush growths of mosses, filmy ferns, and many other ferns such as *Asplenium*, *Grammitis*, and *Elaphoglossum*. Reyna (1979) reports 175 species of trees in the Montecristo area and 71 species from the cloud forest proper. In the area where the present study was undertaken three tree ferns are common: *Dicksonia gigantea* Karst., *Trichopteris schiedeana* (Presl) Tryon, and *Alsophila salvinii* Hooker.

Alsophila salvinii is a cloud forest tree fern known from southern Mexico, Guatemala, Honduras, and El Salvador (Stolze, 1976). It is one of the most conspicuous ferns in Bosque Montecristo and is the most common tree fern. In very wet parts of the forest, *A. salvinii* forms large, dense thickets, often in areas where a large tree or branch has fallen. The thicket shown in *Fig. 1* is brightly lit during the morning from holes in the forest canopy. The thicket appears to be perpetuating itself, as there are hundreds of very young tree ferns present with trunks as yet undeveloped. Fronds of these are only about 30 cm long, whereas fronds of adults are about 2.5 m long.

Alsophila salvinii is also found in relatively dry, open secondary forest at ca. 2050 meters in Bosque Montecristo. The ferns in the secondary forest don't form dense

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*3977 S. 775 W., Bountiful, UT 84010.

FIG. 1. The thicket of tree ferns in which the study was undertaken. FIG. 2. *Alsophila salvinii* showing persistent stipes and rachises of dead fronds.

thickets, are less common, and in general appear less robust than the ferns of the cloud forest proper. Young tree ferns are not seen in the secondary forest. The absence of young tree ferns in the secondary forest might be partially due to grazing by cattle; cattle from a nearby pasture have been observed in the forest eating fiddleheads from the crowns of adult tree ferns.

The fronds of *A. salvinii* are tripinnate, and when the fronds die only the secondary pinnules fall; the stipe and main rachis remain attached to the trunk for several years (*Fig. 2*). The base of the stipe is closely appressed to the trunk for about 15 cm and then arches out to support the frond. Eventually the dead rachis and most of the stipe will break off, but the appressed stipe bases remain attached to the trunk. The bases decay slowly and for many years will hold water either from the roots or captured from rainfall and condensation. The outer trunk of *A. salvinii* is not thickly covered with adventitious roots as it is in some tree ferns such as *Dicksonia gigantea*.

The goals of this study were to investigate frond production rates, death rates, and lifespan; frond phenology; the relation between trunk length and tree age; the effects of water stored in the appressed stipe bases on frond production and death rates; and the factors affecting tree mortality.

METHODS

In late June 1978, twenty-eight mature, healthy trees of *Alsophila salvinii* were chosen from a dense thicket (*Fig. 1*) in very wet forest at 2300 m altitude on Cerro Montecristo and were tagged with forester's flagging tape. All fiddleheads on these trees were separately tagged and their subsequent development followed. All dead fronds were cut from the tree ferns, but the appressed stipe bases were left intact. The mean trunk length of the 28 selected ferns was 1.18 m (s = 0.47). The ferns were randomly divided into equal control and experimental groups. Holes were cut in the bottoms of the dead stipe bases of the trees in the experimental group with a pocket knife so that they could no longer hold water.

At irregular intervals over the next two years, eleven visits were made to Bosque Montecristo to observe the tree ferns. All mature, immature, and dead fronds present on each fern were counted. Fiddleheads and young fronds in which the pinnules had not fully expanded were considered immature. All living fronds with fully expanded pinnules were considered mature. Because dead fronds were removed at the beginning of the study, the ferns had no dead fronds at the first observation. Obtaining an accurate count of the number of fronds that died over the period of the study would have been difficult if dead fronds fell without leaving a trace; this was not a problem, however, because dead fronds remained attached to the trunk.

RESULTS AND DISCUSSION

Means of mature, immature, and dead fronds per tree in the control group during the two year period from late June 1978 to May 1980 are shown in *Fig. 3*. There is a rapid flush of fronds produced starting at the end of the dry season in early May. The immature fronds of *A. salvinii* do not develop synchronously. The first fiddlehead of the season may be nearing maturity as the last fiddlehead just barely

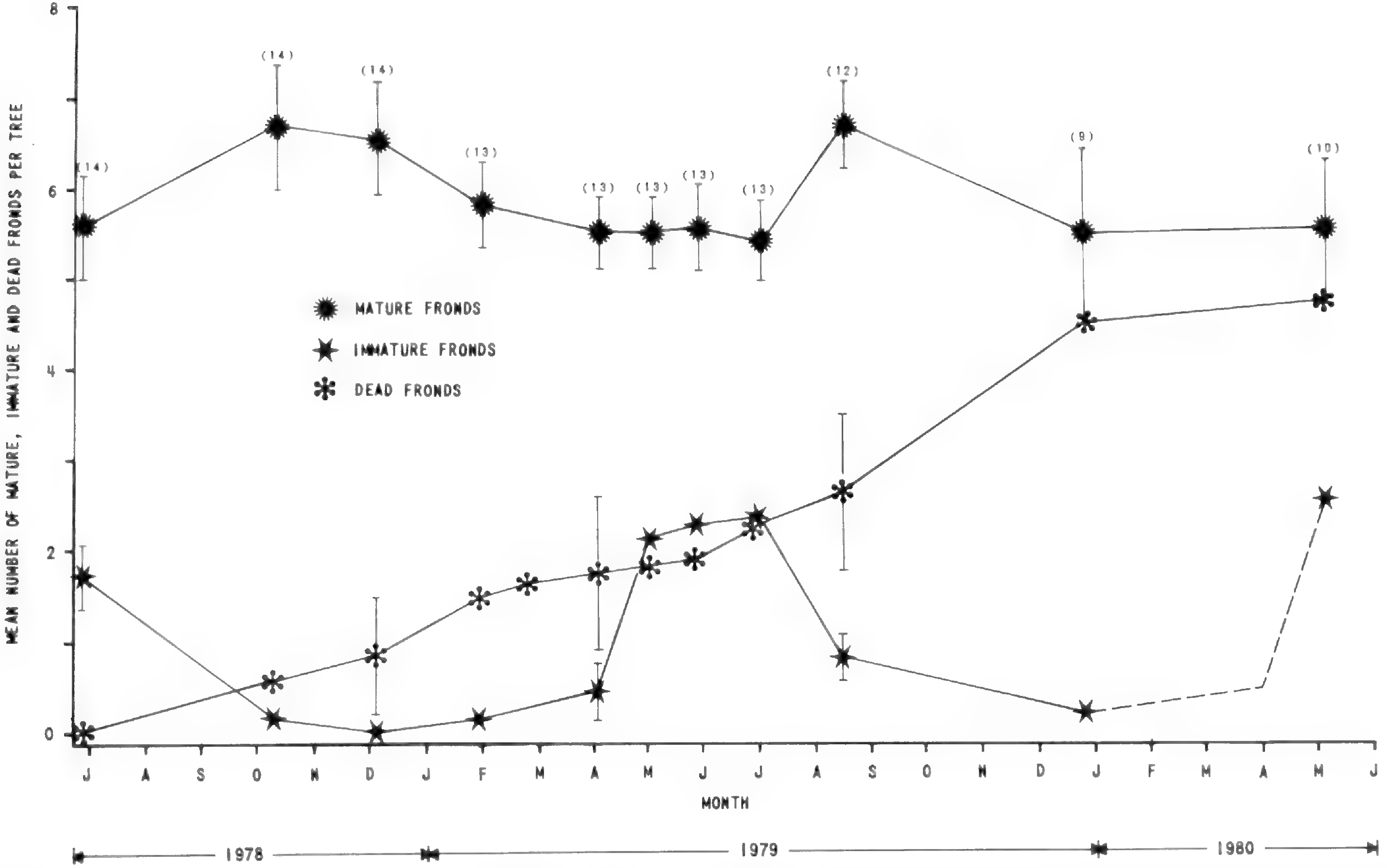

FIG. 3. The mean number of mature, immature, and dead fronds per tree of *Alsophilia salvinii* in the control group during the period June 1978 to May 1980. Vertical bars indicate 95% confidence limits for the means; number of individuals is shown in parentheses.

protrudes from the crown. The asynchronous production of fronds by *A. salvinii* is not typical of all tree ferns; in some tree ferns such as *Dicksonia gigantea*, all the fiddleheads produced during one growing season develop and are mature nearly synchronously (personal observation).

Throughout the year, even during the dry season, fiddleheads are present on a few ferns, but these normally just barely protrude above the trunk apex. In February and April 1979, several very young fiddleheads were tagged and the time required for their maturation was observed. Fiddleheads initiated in February, just before the driest part of the year, required 3–4 months to mature, and one of the tagged fiddleheads died during this period. Many of the pinnae of the surviving fronds were undeveloped, dead, and dried out when observed in April. Fiddleheads tagged in April 1979, at the end of the dry season, required 2–3 months to mature and all survived.

Frond death rate fluctuates seasonally (*Fig. 3*). Few fronds died during the dry part of the year (January to June). Nearly dead fronds with only a few pinnules remaining survived this entire period. In June, at about the time the pinnules of the fronds initiated in April began to expand, the frond death rate sharply accelerated and was quite constant from June to January. However, the end of the period of rapid frond death does not coincide with the time the fiddleheads were finally mature.

On 1 April 1979, the ferns averaged 1.7 dead fronds per tree; one year later they averaged 4.7 dead fronds per tree (data interpolated from *Fig. 3*). This indicates an average frond death rate of three fronds per year per tree. During this same period, there was no net gain or loss of mature fronds, which together with the calculated death rate, indicates an average frond production of three fronds per tree per year. Since the number of mature fronds per fern averages about six, the death rate of three fronds annually implies a frond lifespan of about two years. The period from April to April was used to measure net changes in the number of mature and dead fronds because April is in the middle of a 3–4 month period when there are no rapid changes in the number of mature and dead fronds.

The lives of the 27 fiddleheads tagged in late June 1978 were followed for two years. By October 1978 all the tagged fiddleheads were mature. In February 1979, about half the fronds had begun to drop some pinnules. In July 1979, one year after the fronds were initiated, all those not killed by catastrophe were alive, although nearly all were dropping pinnules. By December 1979, one of the fronds was dead, but at the last observation in May 1980 (22 months after the fronds were initiated) no more had died. It is probable that the fiddleheads tagged in June 1978 died during the 1980 wet season.

If the number of fronds produced by a given length of trunk is constant, the age of a tree fern can be estimated. To determine the number of fronds produced in 50 cm of trunk, ten ferns not previously included in the study were selected from the same thicket. The number of stipe bases between 20 and 70 cm below the crown was counted on the ten tree ferns; the mean was 18.1 fronds/ 50 cm ($s = 1.59$). Since about three fronds are produced annually, about 12 years are needed to grow a meter of trunk under the wet conditions of the primary forest. The growth rate may be different in the drier secondary forest. The exact age of a tree fern cannot be calculated from its trunk length because neither the time needed for establishment nor the rate of frond production in very young individuals is known.

The lifespan of some of the tree ferns may be in excess of 50 years. In the primary forest, one vigorous fern with a trunk 4.6 meters long was observed; assuming a growth of 1 meter/12 years, the plant was about 55 years old. Such longevity apparently is not common. Of 92 healthy adult tree ferns measured in both the primary and secondary forests, only one other trunk over 4 meters long was noted and the third largest was only 3.3 m long. The median length of the 92 tree trunks was 1.3 meters.

One of the most common natural catastrophes in the forest is the falling of large epiphyte-covered trees or their branches. Winds in the forest can reach 80 kph (Reyna, 1979). In February 1979 a large oak branch fell at the edge of the thicket and completely crushed and broke one of the tagged tree ferns; although it did no harm to the trunk of another fern, all the fronds except one immature frond were broken off.

The ferns seem to be able to withstand extraordinary damage without being killed. Few of the tree ferns in the thicket have erect trunks, most are inclined away from the vertical, and some nearly lie on the ground. Probably this is caused by falling branches or trees knocking the ferns over. The ferns recover from being knocked over by turning the crown and growing upright (*Fig. 1*). One fern was seen which had had its direction of growth radically changed at least twice, and possibly three times, with no apparent ill effects.

Water is retained in the persistent petiole bases of the ferns during the entire wet season and part of the dry season. It was originally thought that this might be advantageous to the ferns during the dry season, perhaps providing additional water trapped from rain or condensation. Observations indicate otherwise; the tree ferns which could not store water in their punctured petiole bases did not differ significantly from the control in number of fronds produced annually or in the frond death rate. The results might have been different in the drier secondary forest, where the ferns are less vigorous.

Possible reasons for tree fern mortality were investigated. Falling branches kill some trees; nevertheless, being knocked over or the loss of fronds may not kill the fern. The tree that lost all except one immature frond subsequently developed normal fronds. No sign of insect damage to fronds was ever observed. Two fronds on one tree fern were stricken by a blight; normal fiddleheads developed into twisted, stunted fronds with only a few functional pinnules. This did not kill the fern during the period of the study, and no other fronds seen were affected by a similar blight.

Relatively few dead tree ferns were seen, as the soft wood of the trunk probably decays rapidly in the wet conditions of the forest. Nevertheless, several dead individuals were observed in which the trunk diameter was sharply constricted at the crown. Living trees with this syndrome were easily recognized by their extremely small fronds, which usually were only 40–50 cm long. The crowns of several of these living trees were examined by splitting them open; there was no evidence of rot or decay in the crown or of damage to the base or roots of the trees. It may be that the constricted trunk and the very small fronds are symptoms of senescence in the trees. Further research on these ferns could provide evidence supporting the hypothesis that death from old age is fairly common in the population. Data supporting the hypothesis would include a relatively high frequency of ferns with this syndrome occuring in the population and evidence that these trees are old compared with the population median.

ACKNOWLEDGMENTS

Agradezco sinceramente a la Unidad de Parques Nacionales y Vida Silvestre del Ministerio de Agricultura y Ganaderia y a la Fundación Freund por el apoyo recibido para la realización de este estudio. Expreso mi aprecio a la Lic. Maria Luisa Reyna V. por su valiosa ayuda con la descripción del bosque y ademas a la Lic. Kathy DeRiemer, Lic. Dennis Witsberger y Señor Gabriel Calderon Hernández quienes hicieron las observaciones en la parte final del estudio por encontrarme afuera de El Salvador. Asimismo a los Señores Amadeo, Julio y Ricardo Martinez, encargados de los jardines de Los Planes de Montecristo; al Señor Juan Escobar, motorista de Parques Nacionales; y al Señor Pedro Hernandez y los demás vigilantes por su plena cooperación en el trabajo del campo.

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Nomenclatural Notes on Micronesian Ferns

F. R. FOSBERG and M.-H. SACHET*

Three problems concerning the names of ferns found in Micronesia have arisen during the preparation of a geographical checklist of Micronesian pteridophytes. Our solutions to these problems are as follows. In addition, a new synonymy is given for the western Pacific species *Thelypteris immersa*.

Thelypteris guamensis (Holtt.) Fosb. & Sachet, comb. nov.

Christella guamensis Holtt. Allertonia 1:222. 1977. TYPE: 3 mi S of Agat, on Agat–Umatac Road, Guam, Mariana Islands, by small stream, *Grether 4384* (BISH not seen; isotype US). PARATYPE: *Grether 4385* (US).

Since we accept the genus *Thelypteris* Schmidel in a broad sense, including such segregates as *Christella* Léveillé, it is necessary to provide the appropriate combination for *C. guamensis* in *Thelypteris*. Wagner and Grether (Occ. Pap. Bishop Mus. 19:56. 1948) list as *Cyclosorus dentatus* (Forsk.) Ching the two collections cited by Holttum (*Grether 4384, 4385*). We could not match these exactly in the considerable series of specimens from Guam labelled *T. dentata* or *T. parasitica*. The thickened, reddish, glandular hairs scattered over the underside of the lamina, the pubescence of two ranges of length, the broad fronds with the lowest pinnae only slightly or not reduced, and the short-creeping rhizome would seem to place *T. guamensis* between *T. dentata* and *T. parasitica*. We follow Holttum in recognizing *T. guamensis* as a separate species, but with some misgivings. The Guam plants of this affinity do not sort well into three, and even less well into two, populations.

Thelypteris immersa (Blume) Ching, Bull. Fan Mem. Inst. Biol. 6:306. 1936.

Aspidium immersum Blume, Enum. Pl. Javae 156. 1828. TYPE: Gaenaeng Parang, Java, *Blume* (L not seen, Morton photo 1164).

Dryopteris immersa (Blume) Kuntze, Rev. Gen. Pl. 2:313. 1891; Hosokawa, Trans. Nat. Hist. Soc. Formosa 28:147. 1938.

Glaphyropteris palauensis Hosokawa, Trans. Nat. Hist. Soc. Formosa 32:285. 1942. TYPE: Peliliu Island, Palau, *Hosokawa 9221* (TAI not seen).

Amphineuron immersum (Blume) Holtt. in Nayar & Kaur, Comp. Bedd. Handb. 203. 1974.

Thelypteris peliliuensis Fosb. Smiths. Contr. Bot. 45:4. 1980, *nom. nov.* for *G. palauensis* Hosokawa, *non T. palauensis* (Hosokawa) Reed.

Professor R. E. Holttum (*in litt.* 1 Mar 1981) informed us that he studied the type of *G. palauensis* and found it to be his *Amphineuron immersum*, a widely distributed East Asian and Western Pacific species. Hosokawa himself had reported this earlier as *Dryopteris immersa*. Since we regard *Amphineuron* as a part of *Thelypteris*, *T. peliliuensis* must go into synonymy under *T. immersa*.

Trichomanes falsinervulosum (Nishida) Fosb., Smiths. Contr. Bot. 45:4. 1980.

Microgonium falsinervulosum Nishida, J. Jap. Bot. 32:156. 1957. TYPE: Aimiriik, Babeldaob, Palau, 8 Sept 1939, *Tsuyama* (TI not seen).

This combination was made after checking recent indices and publications on

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*Department of Botany, National Museum of Natural History, Smithsonian Institution, Washington, DC 20560.

Malesian and Micronesian ferns. After its publication, Dr. Lellinger called our attention to C. V. Morton's combination *T. "falsivenulosum"* (Nishida) Morton (Contr. U. S. Natl. Herb. 38:192. 1974), based on *Microgonium "falsivenulosum"* Nishida (J. Jap. Bot. 32:156. 1957). We find no such name published by Nishida; because the references are identical, it seems likely that Morton misread the epithet or unintentionally changed the epithet to one that meant exactly the same thing.

If this were an obvious typographical error or a simple orthographic error that involved only a connecting vowel or similar change, it could be regarded under ICBN Art. 73 as a correctible error. However, when the change produces a different Latin root which could properly be used in this position in an epithet, it seems most advisable to treat the two as different epithets and to index the resulting combinations as different names. This will save future workers from rechecking to account for the difference. The present wording of Art. 73 does not make it clear where the line should be drawn between correctible and non-correctible errors. Therefore, one's best judgment must be followed. In this case we choose to use the 1980 combination.

Trichomanes motleyi (v. d. Bosch) v. d. Bosch, Nederl. Kruid. Arch. 5(2):145. 1861.

Microgonium motleyi v. d. Bosch, Hym. Jav. 5, *t. 1, f. 1, 2.* 1861. SYNTYPE: "Hab. Insula Borneo (pr. Laboan), Motley No. 203 (comm. ill. W. J. Hooker)" (L not seen).

SYNTYPE CITED WITH T. MOTLEYI: "Hab. Ins. Borneo (pr. Laboan) Motley (H. Hook.)" (L not seen).

In verifying the original publication of this species, a curious circumstance was noticed. Van den Bosch published *M. motleyi* and *T. motleyi* independently in different publications in the same year, each with a slightly different description and statement of type material, and each with no reference to the other.

No firm evidence is available to us as to which publication is earlier, other than that the "Hymenophyllaceae Javanicae" has an introduction dated "Mart. 1860" and a prefatory note in the other publication is dated "Aug. 1860."

Presumably Motley's two sheets are different sendings of the same material, although they could be different collections from the same place. Since van den Bosch published the two species only a few months apart, it is likely that he had both sheets at hand while both publications were being prepared. Therefore, both collections should be considered as syntypes. In response to an inquiry directed to the Leiden Herbarium concerning the Motley specimens, G. J. de Joncheere informed us (*in litt.* 17 Oct 1980) that one sheet is labelled in van den Bosch's hand "Trichomanes motleyi v. d. B. from Laboan (Borneo) no. 203 Mr. Motley ad truncos arborum." This sheet bears two small specimens which are, according to de Joncheere, apparently the plants from which the excellent illustrations in the "Hymenophyllaceae Javanicae" were made. Attached to the other sheet is a description written by van den Bosch which is similar to but not identical with the two published descriptions, which are themselves similar but not identical. Interestingly, none of the annotations on either of these sheets mentions *Microgonium*; all refer to *Trichomanes motleyi*. We here designate the sheet with the description as the lectotype of *M. motleyi*.

As to the exact status of the two names, we can do no better than to quote from de Joncheere's letter:

> From the above you will see that indeed the names Microgonium motleyi and Trichomanes motleyi are independently published, strictly speaking. However, as the dual names originated at about the same time from the same man from the same type and were apparently just the result of a wavering mind, one cannot regard these names as truthfully unconnected: on the contrary these publications are very much connected and should in my opinion be treated as the publication of a new species and a new combination, depending on what exact date of publication of the V. D. B. articles in question can eventually be ascertained.

We are prepared to accept this well considered opinion. Since the scanty evidence from the introductory statements indicates that *M. motleyi* may have appeared earlier, we treat the *Trichomanes* as a transfer. Copeland (Phil. J. Sci. 51:201–202. 1933; 67:62. 1938), in his major works on Hymenophyllaceae, used both names without raising any question of the propriety of their publication.

This species was reported as *Microgonium motleyi* by Ito (Bot. Mag. Tokyo 67:219. 1954) from Aimiriik, Babeldaob, Palau, Caroline Islands, *Okabe 16* (TI not seen).

REVIEW

"SINOPSIS DE LAS ESPECIES DE LYCOPODIUM L. (LYCOPODIACEAE PTERIDOPHYTA) DE LA SECCION CRASSISTACHYS HERTER," by Cristina H. Rolleri. Revista del Museo de La Plata, n.s. 13:61–114. 1981.—In the first half of this century, Herter and Nessel published several papers and one book ("Die Bärlappgewächse") which thoroughly confounded the taxonomy and nomenclature of *Lycopodium*. So complete was the chaos introduced by these authors, especially in the tropical members of the genus, that subsequent botanists often have avoided studying them. The synopsis now published by Dr. Rolleri goes a long way toward resolving the problems that were introduced in sect. *Crassistachys*, a largely terrestrial group of mostly Andean species. Dr. Rolleri has studied the anatomy and morphology of the plants in great detail, which is evident from her key to the 56 species of the section. A synonymy, statement of habitat and range, and brief description are given for each species. A rather long list of excluded names, many of which are of uncertain application because the author was not able to obtain type material, indicates that there is yet more work which must be done before the taxonomy and nomenclature of this section of *Lycopodium* can be completely understood, but the progress in the present synopsis is very great and will be most helpful to all who must deal with these confusing plants.—*D. B. L.*

× Asplenosorus shawneensis, a New Natural Fern Hybrid Between Asplenium trichomanes and Camptosorus rhizophyllus

ROBBIN C. MORAN*

The Appalachian spleenworts constitute one of the most interesting and diverse groups of ferns in North America. They are popular with amateur fern growers due to their beauty and ease of culture. To professional botanists, the study of these small ferns has contributed to advances in cytology, chemical systematics, reticulate evolution, hybridization, and ecology. Knowledge of the Appalachian Spleenwort complex is still far from complete; indeed, new hybrid ferns and cytogenetic races have only recently been described. The purpose of this paper is to describe a new, naturally occurring spleenwort hybrid.

In October, 1979, while botanizing in the Shawnee Hills of southern Illinois, I discovered one plant of a hybrid between *Asplenium trichomanes* and *Camptosorus rhizophyllus*. The hybrid was found on a north-facing crevice in a sandstone canyon where a large number of the parent species were present. The elongate-triangular shape of the blade at once suggested *C. rhizophyllus*; however, the base of the blade was cut into opposite, pinnate lobes that looked very much like enlarged basal pinnae of *A. trichomanes*. The stipe resembled that of *A. trichomanes* due to its narrow diameter and dark brown color that extended a short distance up the rachis (*Figs. 1* and *3*). Furthermore, the frond venation was both dichotomously free branched, as in *A. trichomanes*, and anastomosing, as in *C. rhizophyllus* (*Fig. 3*). The suspected hybrid was removed and brought to Southern Illinois University, where it was grown for further study.

To gain further evidence of the plant's hybrid nature, alpha and beta esterase isoenzymes were studied using starch gel electrophoresis in the suspected hybrid and the putative parents. It was hypothesized that the suspected hybrid would show isoenzyme banding patterns present in both parents and perhaps intermediate bands as well.

The electrophoretic system followed was that of Steiner and Johnson (1973). Their instructions for specific esterase stains and gel and electrode buffer were used exclusively. Only mature blade tissue was ground. This eliminated variation in the results which could be caused by using fronds of different ages. Plants of *A. trichomanes* and *C. rhizophyllus* used for the analysis were collected at the same site where the hybrid was found. Electrophoresis was run until a standard marker dye had migrated about 3.5 cm. After staining the starch gel, it was possible to differentiate the beta esterase enzymes that stained pink–purple from the alpha esterases that stained black (Brewer, 1970, p. 88). The resulting zymograms were wrapped with clear plastic wrap, stored in a refrigerator at 1° C, and later photographed with Ektachrome film. Several replicates were made to confirm the validity of the results.

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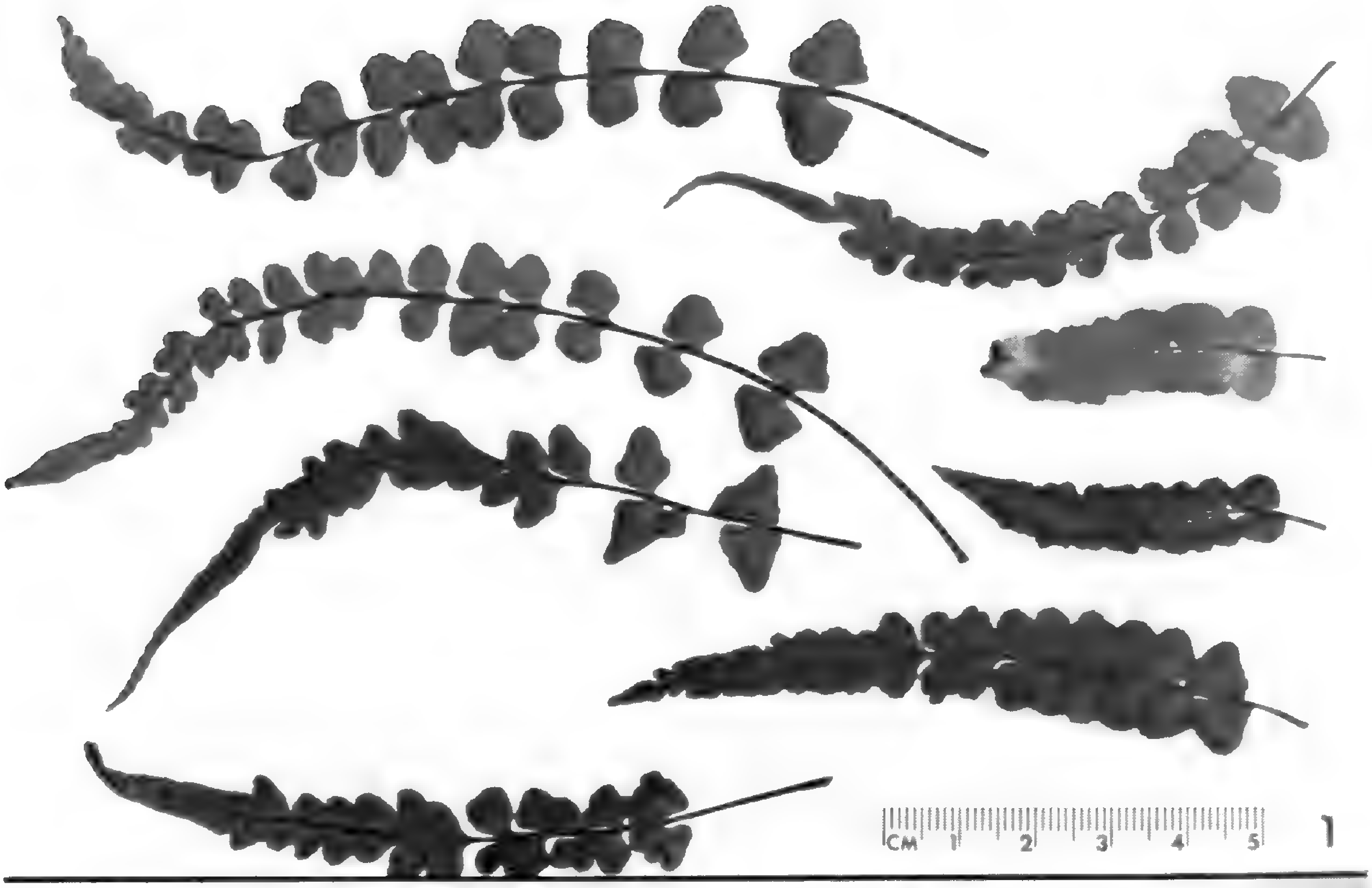
*Department of Botany, Southern Illinois University, Carbondale, IL 62901. Present address: Illinois Natural History Survey, Natural Resources Bldg., 607 E. Peabody Dr., Champaign, IL 61820.



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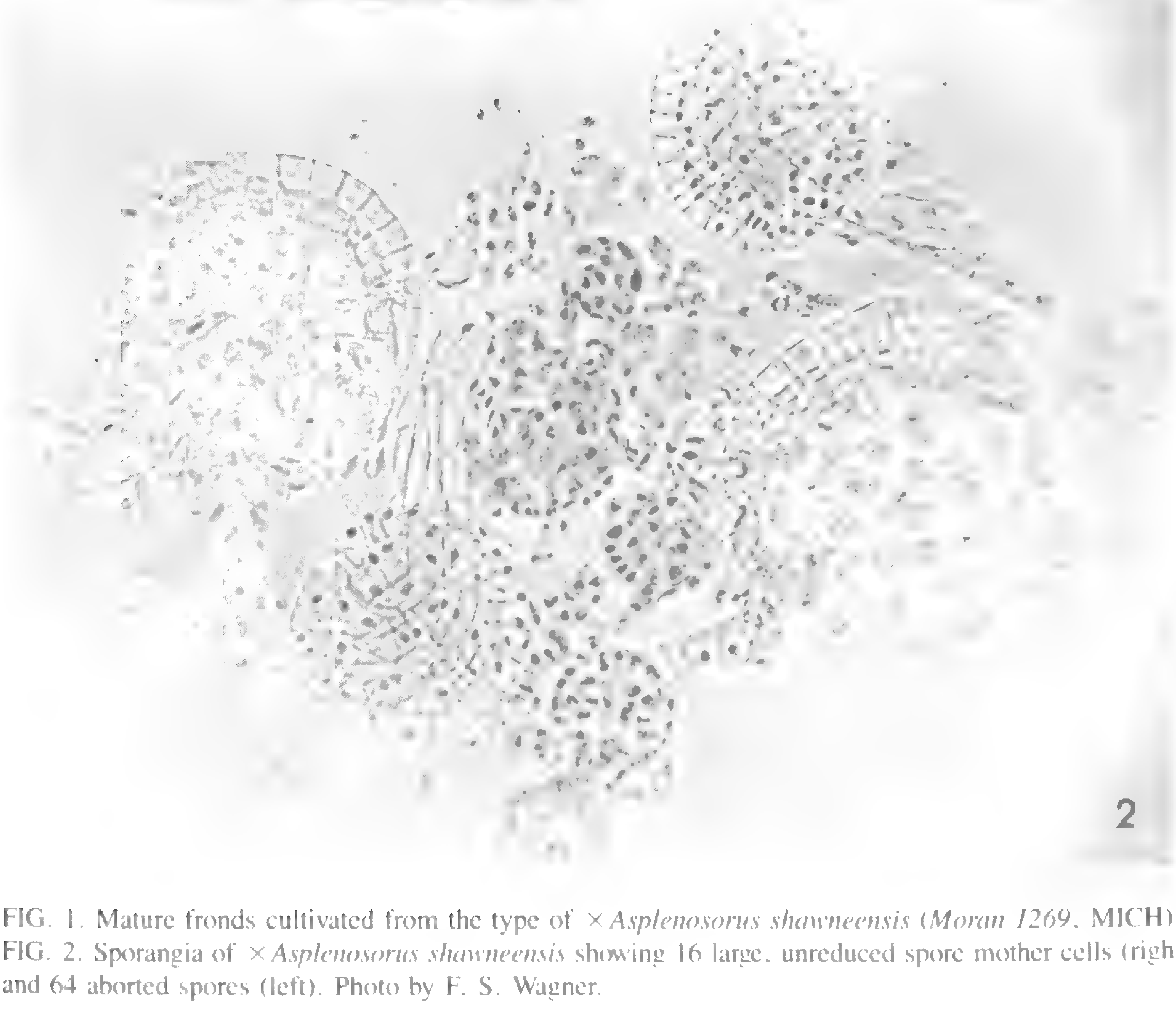

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FIG. 1. Mature fronds cultivated from the type of ×*Asplenosorus shawneensis* (*Moran 1269*, MICH).
FIG. 2. Sporangia of ×*Asplenosorus shawneensis* showing 16 large, unreduced spore mother cells (right) and 64 aborted spores (left). Photo by F. S. Wagner.

The hybrid combines the esterase isoenzyme banding patterns of *A. trichomanes* and *C. rhizophyllus* (*Fig. 4*). Isoenzyme band numbers seven and nine, present in *C. rhizophyllus*, were the only parental bands undetected in the hybrid; they may have been present in the hybrid but simply not seen due to their extreme faintness. Isoenzyme band number eight, present in *A. trichomanes* and the hybrid, is distinct from all other bands because it is a purple-staining beta esterase band. All other bands are black-staining alpha esterases. No intermediate bands were observed. The hybrid esterase isoenzyme banding patterns provide strong evidence that *A. trichomanes* and *C. rhizophyllus* are indeed the parents.

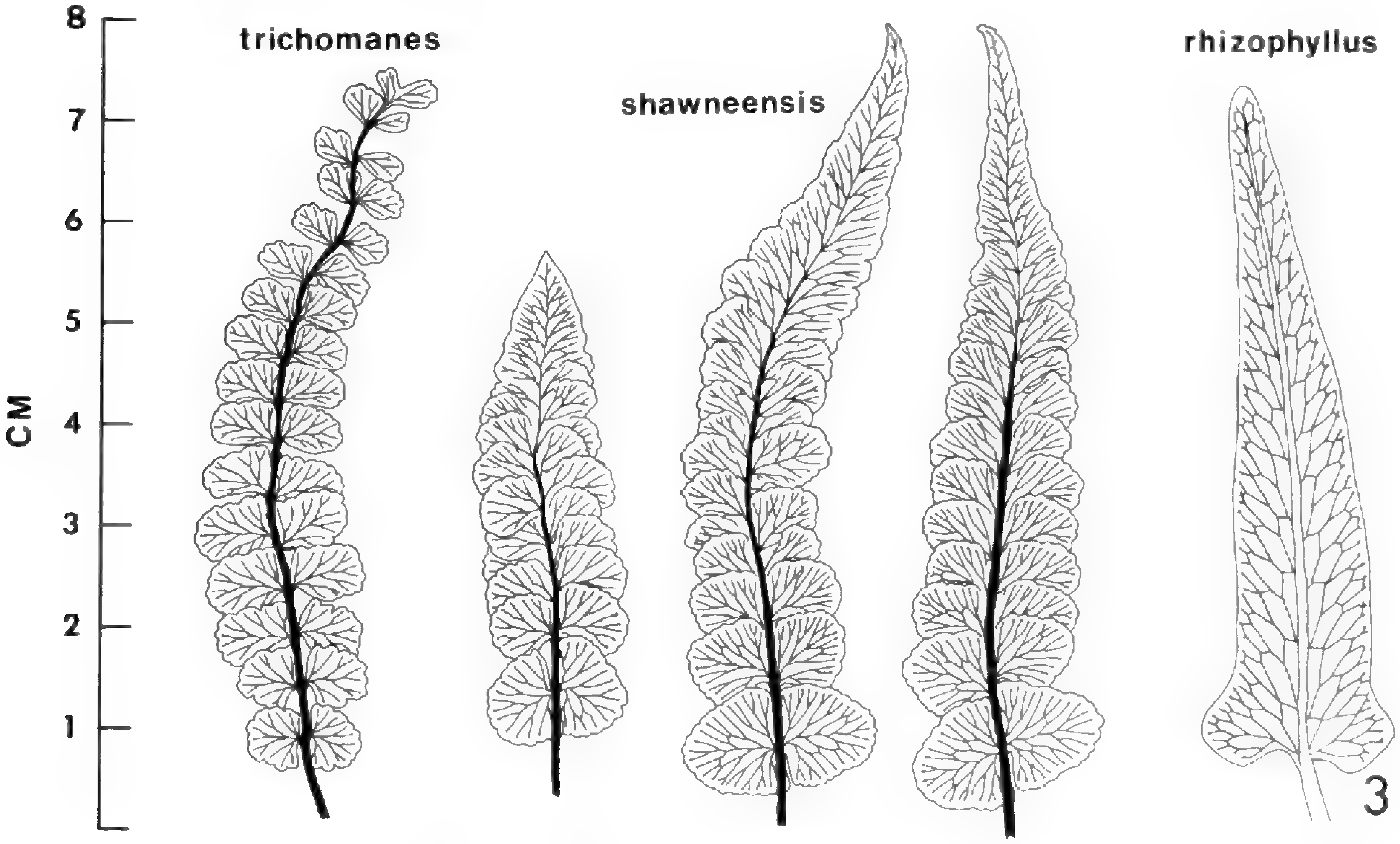

FIG. 3. Frond outlines and venation patterns drawn from cleared fronds of ×*Asplenosorus shawneensis* and its parents.

Esterase zymograms of two other common spleenworts in southern Illinois, ×*Asplenosorus pinnatifidus* and *Asplenium platyneuron*, were made in order to ascertain if they were involved in the hybrid's formation (*Fig. 4*). Both species produced banding patterns suggesting that they were not involved.

× Asplenosorus shawneensis R. C. Moran, hybr. nov. Figs. 1 and 3

Taxon hybridae originis ex *Asplenio trichomane* L. et *Camptosoro rhizophyllo* (L.) Link. Rhizoma breve, reptans; squamae nigricantes, clathratae. Frondes humilo-patentes, caespitosae, sempervirentes, usque ad 15 cm longae. Stipites filiformes, atrobrunnei, nitidi, usque ad 4 cm longi. Lamina leviter coriacea, long-attenuata vel linearis, pinnata ad basim, pinnatifido-crenata ad medium, integra ad apicem, marginibus undulatis, nervis anastomosantibus vel discretis, apice radicanti non observato. Pinnae basales 2 vel 4, subglobosae vel perlate ovatae, usque ad 1 cm latae, marginibus non profunde crenatis. Rachis atrobrunnea usque ad 7 cm ad basim, viridis ad apicem. Sori usque ad 4 mm longi.

TYPE: East of Devil's Kitchen Lake, Williamson County, Illinois, T10S, R1E, sec. 15, in crevice of a shaded, north-facing sandstone canyon, with *Asplenium trichomanes* and *Camptosorus rhizophyllus* growing abundantly nearby, 21 Oct 1979, *Robbin C. Moran 1269* (MICH).

Observations of the hybrid's chromosomes showed 72 univalents at early meiotic metaphase. Thus, ×*Asplenosorus shawneensis* is an allodiploid with the genomic constitution R^1T^2, with no pairing between members of the two different genomes (R and T are the respective genomes and superscripts the pairing controls). The spores of ×*A. shawneensis* vary between 64 aborted spores and 16 unreduced spores per sporangium (*Fig. 2*).

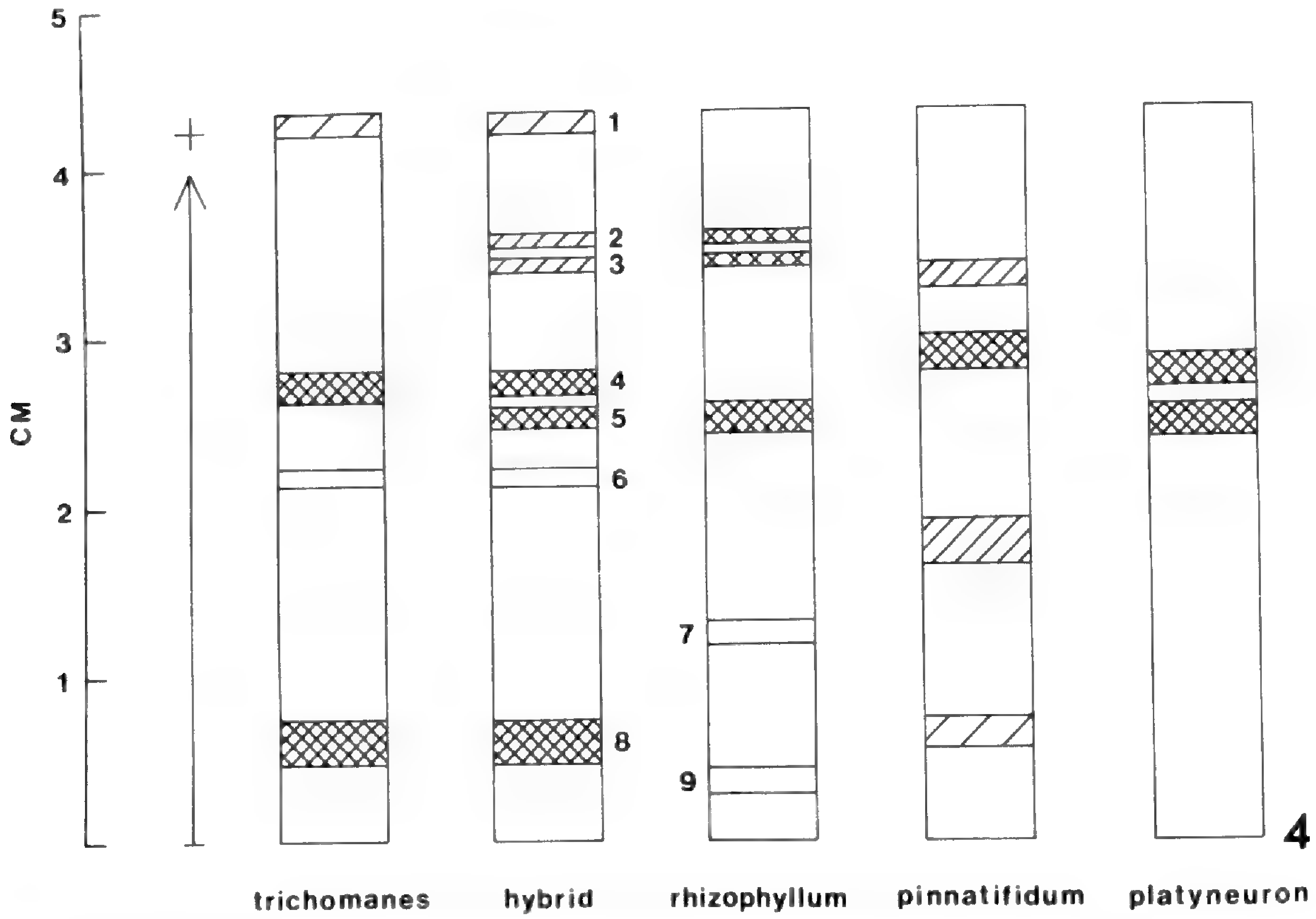

FIG. 4. Esterase isoenzyme banding patterns obtained with starch gel electrophoresis in five spleenworts. Relative darkness of the bands is indicated by cross-hatching. Band 8 is a beta esterase; all other bands are alpha esterases.

The following key has been provided to distinguish ×*A. shawneensis* from the similar ×*A. ebenoides*:

Costae poorly developed; veins in the laminae commonly anastomosing; pinnae crenate-dentate at the margin, not auriculate at the upper base; fronds rather regular in outline .... ×*A. shawneensis*

Costae well developed; veins in the laminae rarely anastomosing, strongly pinnate; pinnae mostly entire or shallowly dentate at the margin, auriculate at the upper base, with the auricle tending to overlap the rachis; fronds often very irregular in outline .... ×*A. ebenoides*

It is extraordinary that ×*A. shawneensis* has not been found previously since both parents occur commonly in similar habitats throughout the eastern United States. Furthermore, *C. rhizophyllus* is involved in all the primary Appalachian Spleenwort hybrids except one, *Asplenium ×bradleyi*, and is a common hybridizer with *A. platyneuron* to form ×*A. ebenoides*. It is significant that two other localities for Spleenwort hybrids involving diploid *A. trichomanes* have recently been discovered in the lower Ohio River Valley of southern Illinois and Indiana. At both localities, diploid *A. trichomanes* hybridizes with ×*A. pinnatifidus* to form the triploid hybrid known as *A. herb-wagneri* (Gastony, 1971; Wagner & Wagner, 1969). Perhaps the absence of hybrids involving diploid *A. trichomanes* from the rest of the well-botanized eastern United States indicates there is a diploid strain of *A. trichomanes* in the lower Ohio River Valley that does not have the barriers to hybridization present in outside populations.

In conclusion, I would encourage pteridologists to look for sites where *A. trichomanes* and *C. rhizophyllus* occur together in order to find additional specimens of this interesting fern hybrid. I would like to thank Dr. Robert H. Mohlenbrock, Dr. W. Carl Taylor, Drs. W. H. and F. S. Wagner, and Dr. Charlie Werth for their help with various aspects of this study.

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Notes on North American Ferns

DAVID B. LELLINGER*

Recent research I have conducted on the pteridophyta of the United States and Canada necessitates publication of a few brief notes on some of the species.

Asplenium platyneuron (L.) B.S.P. Prel. Cat. Anth. Pterid. 3. 1888.

The combining authority for this species usually is cited as "Oakes ex D. C. Eaton." Dr. Stephen Smith (pers. comm.) has pointed out to me that Eaton (1878, p. 21) accepted *A. ebeneum* Ait. as the correct name for the Brown-stem Spleenwort. He wrote, "Although the Linnaean name for the present fern is unquestionably the oldest, it is scarcely probable that those authors who are disposed to insist upon an inflexible law of priority will attempt to replace the name which has been accepted by nearly all botanists for nearly a century by one so utterly inappropriate as *platyneuron*. Yet, lest they should do so, it may be worth while to note that this fern was named *Asplenium platyneuron* by the late Mr. Oakes of Ipswich, in a marginal note in a copy of the old 'Flora Virginica,' now in my possession." Therefore, the combination attributed to Eaton clearly is a *nomen provisorium*.

Despite Eaton's "publication" of the combination, the earlier epithet *platyneuron* did not displace the more familiar *ebeneum* with any regularity for about twenty years. The impetus for change was provided by Underwood in Britton and Brown (1896, p. 23), who made the transfer properly and cited the basionym and Aiton's name in synonymy. However, Underwood is antedated by Britton, Sterns, and Poggenburg, who cited the species as *Asplenium* "platyneuron, (L.) (*A. ebeneum, Ait.*)." Although they did not cite a literature reference, "platyneuron, (L.)" must be considered a valid indirect reference. Therefore, the correct combining authors apparently are B.S.P., unless the combination was made validly in some obscure local Flora published between January 1878 and 25 April 1888.

One would have thought that Underwood, being a fern specialist, would have made the combination prior to Britton, but such is not the case. At the time Britton, Sterns, and Poggenburg made the combination, Underwood (1888, p. 104) maintained the epithet *ebeneum;* he did not adopt *platyneuron* in his writings until five years later (Underwood, 1893, p. 104).

Asplenium trichomanes-dentatum L. Sp. Pl. 2:1080. 1753.

According to Morton and Lellinger (1966, p. 24), this name has been "rejected universally as being confusing, not in binomial form, and probably due to an oversight on the part of Linnaeus." However, the name is not a *nomen confusum* in the usual sense. Although it is not in binomial form (which in itself is not necessarily a barrier to validity), neither are the well known *A. ruta-muraria*, *A.*

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*U.S. Nat'l. Herbarium NHB-166, Smithsonian Institution, Washington, DC 20560.

adiantum-nigrum, or *Adiantum capillus-veneris*. These three species, of course, were well known to European botanists, whereas *A. trichomanes-dentatum*, from tropical America, and *A. trichomanes-ramosum*, from temperate North America, were not. Linnaeus (Syst. Nat. ed. 10, 2:1323. 1759) renamed *A. trichomanes-dentatum* with the single epithet *dentatum*, but continued to use the compound epithet in post-1759 editions of the "Species Plantarum." It is doubtful that his coining two compound epithets beginning with *trichomanes* was an oversight, although continuing to use two different epithets in separate publications presumably was. Proctor (1977, p. 314) adopted the earlier epithet, and I agree.

Asplenium trichomanes-ramosum L. Sp. Pl. 2:1082. 1753.

This name is analogous to the foregoing one, except that Linnaeus did not rename the species; Hudson did, as *A. viride*.

Asplenium verecundum Chapm. ex Underw. Bull. Torrey Bot. Club 33:193. 1906.

Mickel (1979, p. 56)) considered this species to be a synonym of the tropical American *A. myriophyllum* (Swartz) Presl. It is true that some specimens of the latter species from the Greater Antilles look very much like those of *A. verecundum*, but most specimens do not. In addition, the spores of *A. verecundum* are 56–58 µm long, whereas those of *A. myriophyllum* from the Antilles are (40)44–56(60) µm long and those from South America are only 36–48 µm long. *Asplenium verecundum* is known to be a tetraploid (Wagner, 1963, p. 12), and I believe that it should be maintained as a species distinct from *A. myriophyllum*, which is likely to be a diploid and not present in the United States. The convergence in morphology may well be due to the fact that *A. verecundum* is somewhat stunted and maintains a juvenile habit in its subtropical habitat; a similar phenomenon is known in *Cheilanthes microphylla* (Swartz) Swartz in Florida (Evans, 1975). Similar juveniles of *A. myriophyllum* would be expected in unfavorable habitats in the tropics.

Athyrium alpestre subsp. americanum (Butters) Lellinger, comb. nov.

Athyrium alpestre var. *americanum* Butters, Rhodora 19:204. 1917. LECTOTYPE: Rogers Pass, British Columbia, *Heacock 554* (GH; isolectotype US), chosen by Maxon (Amer. Fern J. 8:120. 1919).

Fuchs (1974) adopted the specific epithet *distentifolium* Tausch ex Opiz, rather than *alpestre* (Hoppe) de Claireville, for the Mountain Lady Fern. He claimed that de Claireville (1813, p. 301) published a new species, rather than a transfer of Hoppe's name, which was not cited. Fuchs also thought that *Aspidium alpestre* Hoppe could be considered a superfluous name because Hoppe thought it might be the same as *Athyrium rhaeticum* Roth. However, this is incorrect, for a superfluous name requires that the author include the type of the name being replaced, and this Hoppe did not do. According to R. M. Tryon, Jr. (pers. comm.), de Claireville's work is an excursion flora in which the introduction states that it is not a technical work. De Claireville's intent was not to name a new species, but to transfer Hoppe's name. Therefore, it seems clear that the epithet *alpestre* (Hoppe) de Claireville should be reinstated.

Botrychium × hesperium (Maxon & Clausen) Wagner & Lellinger, comb. nov.

Botrychium matricariifolium subsp. *hesperium* Maxon & Clausen, Mem. Torrey Bot. Club. 19(2):88, *f. 15*. 1938. TYPE: Glacier Lake, Boulder Co., Colorado, Jul 1914, *Bethel* (US).

?*Botrychium lunaria* subsp. *occidentalis* Löve, Löve & Kapoor, Arct. Alp. Res. 3:141. 1971. TYPE: Above Graymont, Clear Creek Co., Colorado, *Defler & Snyder L 11293* (COLO not seen).

The parents of this hybrid apparently are *B. lanceolatum* (Gmel). Rupr. subsp. *lanceolatum* and *B. simplex* E. Hitch. All three species are known from the mountains of northeastern Colorado; *B.* × *hesperium* and *B. lanceolatum* even were collected by Bethel at the same locality. The parental species are diploids ($2n = 90$). The hybrid has not yet been counted. Its spores are 32–44.5 μm in diam., about the same as those of *B. lanceolatum* (32–42(49.5) μm in diam.), but smaller than those of *B. simplex* ((47)49.5–57 μm in diam.). *Botrychium lanceolatum* belongs to a group of species which have elongate pinnae (or segments in pinnate-pinnatifid forms), whereas *B. simplex* belongs to a group of species with flabellate pinnae (or segments in 2-pinnate forms). Sterile portions of the hybrid's fronds vary in morphology from near the elongate-segment *B. lanceolatum* type to near the flabellate-segment *B. simplex* type. The hybrids always exhibit the exaggerated basal pinnae characteristic of *B. simplex*.

Cystopteris fragilis (L.) Bernh. Schrad. Neu. J. Bot. 1(2):27. 1805.

There are five entities in the *C. fragilis* complex in the United States and Canada. Although depauperate and immature specimens may be difficult to place with certainty, all are distinct species cytologically and usually morphologically. *Cystopteris fragilis* and *C. dickieana* Sim have compact, narrow laminae, a compact rhizome, and a basically northern and western range. They differ from each other in having echinate versus rugose-verrucose spores. The other species have more lax, broader laminae. *Cystopteris protrusa* (Weath.) Blasd. has a long-creeping, villous rhizome and grows in the eastern United States. The more common *C. tenuis* (Michx). Desv. (syn. *C. fragilis* var. *mackayii* Laws.; see Morton, 1967, p. 174) also grows in the eastern United States. According to T. Reeves (pers. comm.), it is a hybrid between *C. protrusa* and what I call *C. reevesiana*. Its rhizomes are less creeping and only slightly villous.

Cystopteris reevesiana Lellinger, nom. nov.

Cystopteris fragilis subsp. *tenuifolia* Clute, Fern Bull. 16:76. 1908. TYPE: Carr Canyon, Huachuca Mountains, Cochise Co., Arizona, in rich soil, Nov 1907, *Ferriss* (Hb. Clute apparently destroyed), *non C. tenuifolia* v.A.v.R. (Bull. Bot. Jard. Buitenz. II, 28:16. 1918).

The epithet honors Dr. Timothy Reeves, whose careful studies in United States and Mexican ferns are of great value to pteridology. *Cystopteris reevesiana* is a rather rare diploid (T. Reeves, pers. comm.) confined to Utah and Arizona. It has large, lax laminae, and its rhizomes lack any sign of villousness that characterizes *C. protrusa* and to some extent *C. tenuis*.

Marsilea fournieri C. Chr. Ind. Fil. 418. 1906.

This species, which has fronds only 1.5–4 cm long, is very distinct in having bilaterally symmetrical, narrowly obovate lamina segments. It was ascribed to the

United States flora by Correll and Correll (1975, p. 57) on the basis of a specimen collected ca. 10 miles west of Hobbs, in Lea County, New Mexico (*Correll & Correll 36062*, LL). This specimen, however, has fronds 2–6 cm long with somewhat asymmetrical lamina segments and clearly is *M. vestita* Hook. & Grev. *Marsilea fournieri* apparently does not occur in the United States.

Polypodium subg. Pectinatum Lellinger, subg. nov.

Rhizoma erectum ascendens vel repens, non carnosum, tenuiter paleaceum, paleis comosis, lineari-triangularis, ad basin late basifixis, ad apicem acuminatis vel filiformis vel paleis non comosis cordatis vel ovatis, ad basin anguste basifixis, ad apicem acutis vel acuminatis. Stipites approximati nitidi atrobrunnei rufobrunnei vel nigri alati, alis angustis viridibus. Laminae pectinatae plus quam 40 segmentis, segmentis linearibus angustis plerumque integris et late adnatis, ad basin laminae plerumque deflexis; costis infra atrobrunneis rufobrunneis vel nigris.

TYPE SPECIES: *Polypodium pectinatum* L.

An examination of the species of *Polypodium* L. subg. *Polypodium sensu lato*, which traditionally includes the free-veined, non-scaly species of the genus, shows that the subgenus is very heterogeneous. Christensen (1928) pointed out that *P. vulgare* L. (the type species of *Polypodium*) is more closely related through its anastomosing-veined allies to species of subg. *Goniophlebium* (Blume) C. Chr. than it is, for instance, to the *P. pectinatum–plumula* group of subg. *Polypodium sensu lato*. It is clear that the distinction between the two subgenera should not have been made on venation type, but on the more general characters of rhizome and lamina architecture. Some species of subg. *Goniophlebium*, like *P. scouleri* Hook. & Grev., belong with *P. vulgare* in subg. *Polypodium sensu stricto*. But the *P. pectinatum–plumula* group, which was monographed by Evans (1969), is sharply distinct and deserves to be placed in a subgenus of its own.

The classification of New World *Polypodium sensu stricto* is summarized in the following key.

1. Laminae sparsely to densely scaly, at least on the lower surface .... subg. *Marginaria*
1. Laminae glabrous or rarely hairy, sometimes scaly on the rachis.
    2. Laminae pectinate, the segments narrow, linear, usually more than 20 pairs per lamina; stipes approximate; rhizomes erect to short-creeping, rarely long-creeping, thin and hard; rhizome scales not clathrate .... subg. *Pectinatum*
    2. Laminae not pectinate, the segments wide, often not linear, usually fewer than 20 pairs per lamina; stipes distant; rhizomes long-creeping, thick and somewhat fleshy; rhizome scales clathrate or subclathrate.
        3. Venation goniophlebioid, the veins from the costae parallel, producing pairs of branch veins that join to form usually several rows of areolae each with a single included veinlet. subg. *Goniophlebium*
        3. Venation free, repeatedly forking, the veins sometimes united toward the segment margin to form usually no more than a single row of areolae, the fertile ones each with a single included veinlet. subg. *Polypodium*

Thelypteris hispidula var. versicolor (R. St. John in Small) Lellinger, comb. nov.

Thelypteris versicolor R. St. John in Small, Ferns Southeast. States 250. *tab.* 1938. TYPE: Brooksville, Hernando Co., Florida, *R. St. John 109* (NY not seen).

This variety formerly was known as *T. quadrangularis* var. *versicolor* (R. St. John in Small) A. Reid Smith.

I wish to thank Ms. Andrea Sessions for measuring spores and Drs. H. E. Robinson, A. M. Evans, T. Reeves, R. M. Tryon, Jr., and W. H. Wagner, Jr. for reading or discussing portions of the manuscript.

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SHORTER NOTES

SALVINIA MINIMA NEW TO LOUISIANA.—An interesting event occurred during the summer of 1980 which ultimately led to the discovery of *Salvinia minima* Baker in Louisiana. Kerney Simoneaux of Franklin, Louisiana, had been collecting aquatic plants from nearby canals in order to feed young Purple Gallinules. After several weeks elapsed, it was noticed that one particular plant was not often eaten by the birds. When this was brought to my attention, I identified the plant as *Salvinia minima*.

The following day, I was taken to the locality where the plants had been collected. *Salvinia* was abundant and covered the small drainage canal. Further searches in adjacent canals revealed extensive populations of the fern. Three different canals were visited, and all were covered with *Salvinia*. The ferns occur in canals along the Chatswort Levee, two miles west of Franklin, St. Mary Parish. *Salvinia* had not been previously reported from Louisiana, although its occurrence in the state was predicted by John W. Thieret in his "Louisiana Ferns and Fern Allies" (1980). The abundance of the plants suggest that they probably were not a recent introduction. Fertile plants were observed and a number of specimens were collected as vouchers *(Landry 7791*, LAF, LSU, and other duplicates to be distributed).—*Garrie P. Landry, Dept. of Biology, University of Southwestern Louisiana, Lafayette, LA 70504.*

AN UNUSUAL RECORD OF ASPLENIUM TRICHOMANES FROM NORTHEASTERN FLORIDA.—Recently, while examining specimens for a study of the *Asplenium trichomanes* L. complex in the United States and Canada, I came across a collection of *A. trichomanes* from Amelia Island, Nassau County, Florida. According to Lakela and Long (Ferns of Florida, 1976) this species is not known from Florida. This specimen represents a new record for that state and is approximately 270 miles disjunct from the nearest recorded location in central Georgia (McVaugh & Pyron, Ferns of Georgia, 1951). The sheet, which is deposited at the University of Illinois Herbarium, Urbana (ILL), consists of two complete plants plus three separate fronds. The specimens are two different collections, one made in April 1857, the other in July of the same year. The specimen was in the herbarium of Dr. R. H. Ward, but he did not collect the specimen. "Amelia Island, Florida, April, 57." and "Wms. t. July, '57" are written on the sheet. Presumably Williams gave the specimens and data to Ward, who annotated the sheet. The identity of Williams is unknown. Examination of the spores showed them to be within the size range typical for the diploid cytotype (subsp. *trichomanes*). Extensive urbanization in the area makes it unlikely that *A. trichomanes* still occurs on Amelia Island. However, if suitable habitat can be found, a search for the plant could be profitable.—*Robbin C. Moran, Herbarium, Illinois Natural History Survey, Natural Resources Building, 607 E. Peabody Dr., Champaign, IL 61820.*

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Bog Clubmosses (Lycopodiella) in Kentucky

R. CRANFILL*

Distributed largely on the Atlantic and Gulf Coastal Plains, the southern members of *Lycopodiella* Holub (= *Lycopodium* subg. *Lepidotis* (Pal. Beauv.) Baker) are rare and local in the interior of the continent. Inland occurrences are scattered as far north as the middle Mississippi Valley, and often are markedly disjunct from populations on the coastal plain. The purposes of this paper are to record recent observations on this genus in Kentucky, to give some explanation of its recent appearance and spread, to describe a new hybrid, and to make a series of new combinations.

It is now apparent that the genus *Lycopodium* in the broad sense may be divided into several smaller, more natural genera (Beitel & Bruce, 1980). To facilitate the use of the segregate genus *Lycopodiella*, the following new hybrid and combinations are necessary.

Lycopodiella × brucei Cranfill, hybr. nov.

Planta hybrida inter *L. appressam* et *L. prostratam* intermedia, a *L. appresso* microphyllis ciliatis et sporophyllis patentibus, a *L. prostrato* rhizomatibus crassiore et strobilis angustiore, minus quam 10 mm latis differt; sporae non abortivae.

TYPE: Borrow pit ca. 200 m ENE of road KY-280, 0.6 mi from its junction with road KY-121, Calloway County, Kentucky, 15 May 1975, *J.G. Bruce 76006* (MICH).

Named in honor of James G. Bruce, III.

Lycopodiella alopecuroides (L.) Cranfill, comb. nov.

Lycopodium alopecuroides L. Sp. Pl. 2:1102. 1753.

Lycopodiella appressa (Chapman) Cranfill, comb. & stat. nov.

Lycopodium inundatum var. *appressum* Chapman, Bot. Gaz. 3:21. 1878.

Lycopodiella × copelandii (Eiger) Cranfill, comb. nov.

Lycopodium × *copelandii* Eiger, Biol. Rev. City Coll. New York 18:21. 1956.
Lycopodium inundatum var. *elongatum* Chapman, Fl. So. States, ed. 2:671. 1883.

Lycopodiella prostrata (Harper) Cranfill, comb. nov.

Lycopodium prostratum Harper, Bull. Torrey Bot. Club 33:229. 1906.

Although much has been written about the *Lycopodiella* population in Kentucky (Johnson & McCoy, 1975; Bruce 1975; Cranfill, 1980), confusion still exists over the number and kind of taxa present. Johnson and McCoy reported *L. appressa* and *L. prostrata* from a large gravel pit in eastern Calloway County. Bruce's (1975) extensive survey of the North American members of the genus includes comments on the Kentucky material, which he concluded is comprised of *L. appressa*, *L.* × *copelandii (L. alopecuroides* × *appressa*), and *L.* × *brucei* (as *L. appressa* ×

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*Division of Biological Sciences, University of Michigan, Ann Arbor, MI 48109. Present address: Department of Botany, University of California, Berkeley, CA 94720.

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prostrata). For want of authentic *L.* × *brucei*, I admitted only the first two species to the flora (Cranfill, 1980). In an attempt to resolve these differences, I undertook fieldwork in Calloway County during the summers of 1979 and 1980. I recorded the topographic and ecological features of each site where *Lycopodiella* was found and made representative collections of each population for further analysis. Results of these studies are reported below.

Reconnaissance on 10 Aug 1979 in the vicinity of the gravel pit where Johnson and McCoy had collected (Site 1) revealed three additional populations (see *Fig. 1*) of *L. appressa* (Site 2, *Cranfill 4730*; Site 3, *Cranfill 4731*; Site 4, *Cranfill 4738a*). All sites are scattered along the bases of Cretaceous ridges composed of sand and partially consolidated gravel and are characterized by low-lying flats of sands with virtually no contamination from silt or organic matter. These plants seem especially sensitive to siltation, for no Bog Clubmoss sites have been found where siltation had occurred. Ground water in the area is soft and acidic and lies at or just below the surface of the flats for much of the growing season. The original pit is the largest and best developed of the four sites, has been abandoned for some time, and contains the most extensive populations of the clubmosses. *Lycopodiella appressa* is abundant, occupying nearly all the moist, open areas, whereas *L.* × *copelandii* is confined to the wettest spots, often around pools. The moss *Aulacomnium palustre* is an associate of both species, and *Cladonia* and *Leucobryum albidum* are scattered about on dryer hummocks. Vascular plant associates include species with decidedly southern affinities, *e.g.*, *Boltonia asteroides*, *Gymnopogon ambiguus*, *Scirpus koilolepis*, *Spiranthes odorata*, *Vaccinium atrococcum*, *Woodwardia areolata*, and

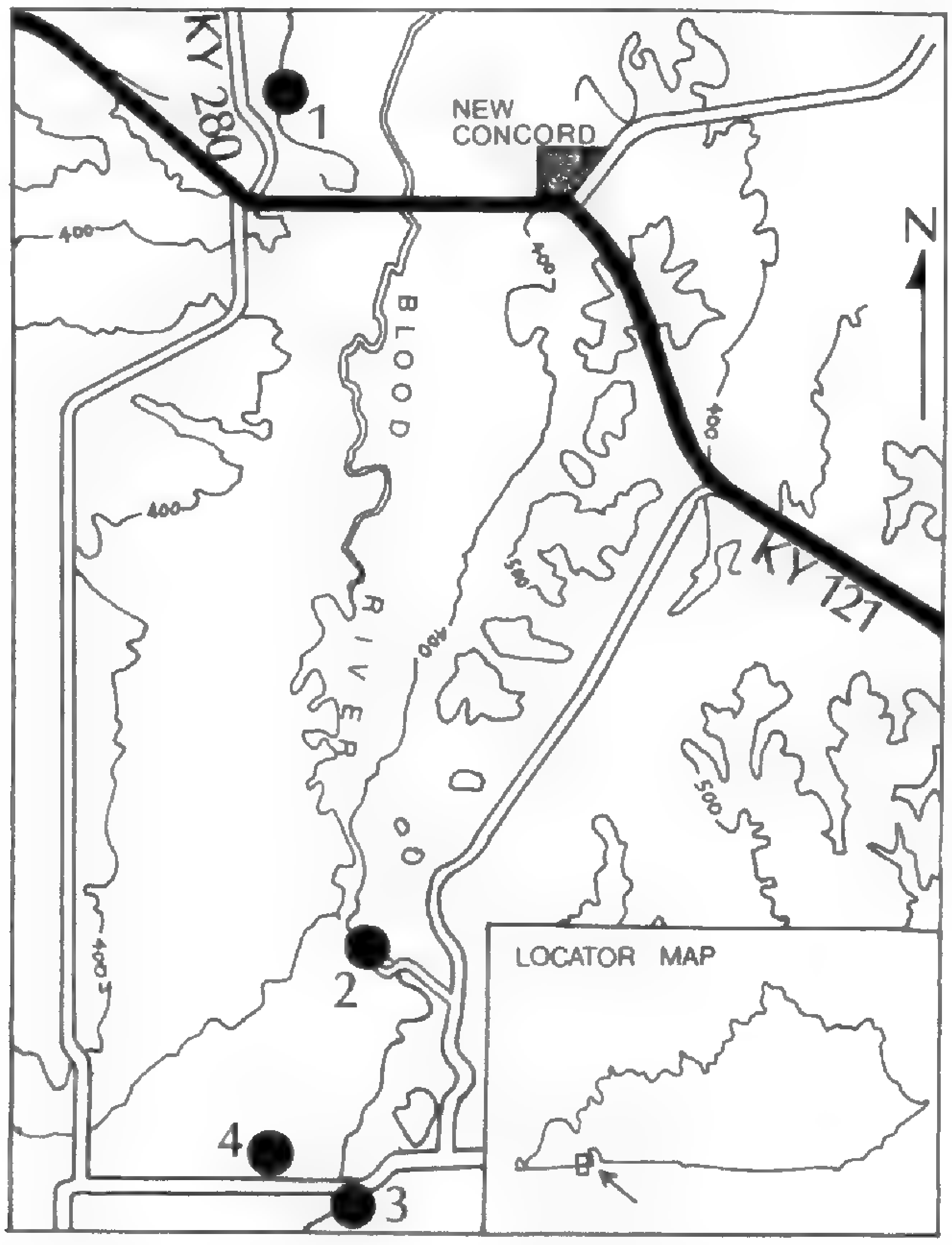

FIG. 1. Portion of south-central Calloway County, Kentucky, showing extant sites of *Lycopodiella*.

Xyris torta. *Pinus taeda* is naturalized along the banks above the pit. Sites 2–4 have been disturbed recently and contain only small populations of *L. appressa*. Few species other than the clubmosses have become established along the roadside ditches and sandy flats, although *Boltonia* was seen at Site 2.

Winter and early spring visits reveal almost complete dieback of the clubmosses during the winter. Bruce (1975) reports the formation of "tubers" in *L. alopecuroides* and *L. prostrata* which serve as food storage organs for the following spring. I observed a similar situation in *L. appressa* at Site 1. Growth is initiated from the tips of these organs in early April.

From these observations, it is evident that any management programs designed to protect these stations must (1) maintain the open nature of the site by controlling the invasion of woody vegetation, (2) attempt to maintain a high water table, which is important not only for reproduction but also perhaps in moderating the harsh winters, and (3) minimize siltation, which appears to have adverse effects on these plants.

Although I have been unable to confirm the presence of *L.* × *brucei* at any of the sites out of ca. 100 individuals that I collected from all populations, recently I received herbarium material of this species (*Bruce 76006*) from Dr. J. G. Bruce. Since *L. prostrata* is the most southern of the species in the complex, it is plausible that it and its hybrids are less winter hardy than other taxa in the pits. Therefore, a combination of harsh winters in the late 1970's and competition with other clubmosses may be responsible for the hybrid's disappearance.

On the other hand, hybrids which occur without one or both parents often have been explained by "long distance hybridization," which may apply in this case. In *Lycopodiella*, hybrids between parents with the same chromosome number exhibit normal pairing of chromosomes at meiosis, and produce what appear to be functional spores (Bruce, 1975). If the spores be viable, the occurrence of isolated hybrids may represent the introduction of single spores from hybrid plants. Such a mechanism for hybrid reproduction and dispersal would be novel among the pteridophytes, which generally produce infertile hybrids that reproduce largely vegetatively.

Although the bog clubmosses may have been present in the area for some time, the evidence points to a relatively recent introduction. In Calloway County, these plants occur in situations which have been created by man's activities in the recent past. This also appears to be the situation with populations in west Tennessee. Natural habitat suitable to *Lycopodiella* is very limited in the northern portion of the Mississippi Embayment and is occupied quickly by the adjacent floodplain forests. It seems likely that these clubmosses have migrated from their metropolis to the south by hopping from one gravel pit to another along the Cretaceous hills in western Kentucky and west Tennessee. If migration is occurring still, close inspection of suitable sites to the north may reveal the presence of these taxa on Cretaceous outcrops in southern Illinois.

I am indebted to M. E. Medley, Laurina Lyle, and D. M. Johnson for assistance in the field, to D. M. Johnson and J. M. Beitel for reading and commenting on the manuscript, and especially to J. G. Bruce, III who helped me in various ways.

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REVIEW

FERNS AND FERN ALLIES in the "FLORA OF BAJA CALIFORNIA" by Ira L. Wiggins, viii + 1025 pp. Stanford University Press, 1980. ISBN 0-8047-1016-3. $65.00—This is the first publication to treat all the known ferns and fern allies of Baja California, Mexico. Sixty-five species and an additional five varieties are included in the treatment, which appears on pp. 51–71 of the book. Descriptions are provided for families and genera. The species and varieties are delimited through rather detailed keys which include comments on the species' habitat, distribution in Baja California, and overall distribution. Line drawings illustrate one member of each genus treated. These are the work of the author in many instances; others are taken from L. R. Abrams' "Illustrated Flora of the Pacific Coast States" (1923). The illustrations are mostly of very high quality and are detailed enough to give an accurate representation of the species illustrated. Two exceptions are the illustrations of *Woodsia plummerae* and *Equisetum laevigatum*, which are not very useful below the genus level.

The taxonomy used is conservative and traditional in treatment of families (e.g., *Polypodiaceae s. lat.* is used) and species and varieties. Three examples of outdated nomenclature to be corrected are: *Pteridium* entry corrected to *Pteridium aquilinum* (L.) Kuhn var. *pubescens* Underw.; *Anemia anthriscifolia* corrected to *A. tomentosa* (Savigny) Swartz var. *mexicana* (Presl) Mickel; and *Pellaea longimucronata* corrected to *P. truncata* Goodd. I have noted several cases of misspelling or incorrect citation of authors. The overall distributions given for the species vary considerably in completeness and accuracy. Several species should be added to the list of ferns known in Baja California (based upon recent literature reports): *Bommeria pedata* (Swartz) Fourn., *Pellaea skinneri* Hook. and *Pellaea seemannii* Hook. (both are *Cheilanthes*, pers. obs. and R. M. Tryon, pers. comm., but there are not available names in *Cheilanthes*), *Cheilanthes fendleri* Hook., and *C. wootonii* Maxon. In addition, I have seen specimens of *C. eatonii* Baker in Hook. & Baker from Baja California.

This treatment of the ferns and fern allies of the exciting botanical region of Baja California is most welcome, as is the treatment of the entire vascular flora. Dr. Wiggins is to be commended for producing such a monumental work.—*Timothy Reeves, Biological Science Center, Boston University, Boston, MA 02215.*

Chain Ferns of Florida

TERRY W. LUCANSKY*

Woodwardia is a genus of rather large, terrestrial ferns with mostly ascending to erect rhizomes. The species native in the United States, however, typically have creeping rhizomes. The genus includes 11 or 12 species, is worldwide in its distribution, and is one of a comparatively few genera characterized by boreal distribution (Copeland, 1947). Three species of *Woodwardia*, commonly known as chain ferns, occur in Florida. *Woodwardia virginica* and *W. areolata* are native species which occur primarily on the Atlantic Coastal Plain and extend from Florida to Texas and northward to Nova Scotia. Scattered inland localities also exist for both species. *Woodwardia radicans* is native to the Old World, but is cultivated and has reportedly escaped in peninsular Florida (Small, 1938). All three species possess distinctive leaf venation, with elongate areoles arranged in chain-like fashion along the costae and/or costules. In *W. areolata*, an extensive network of areoles extends to the margins of the leaf, whereas in *W. virginica* and *W. radicans* the veins are simple and forked beyond the areoles and are free at the margins. Elongate sori also are arranged in chain-like fashion along the costae and/or costules in each species.

Woodwardia virginica, the Virginia or Giant Chain Fern, and *Woodwardia radicans*, the European Chain Fern, were originally placed in the genus *Blechnum* (Linnaeus, 1771), although Smith (1793) later transferred them to his genus *Woodwardia*, with *W. radicans* the type species. Subsequently, Presl (1851) founded the genus *Anchistea* for *W. virginica*, although only the glandular indusia and the presence of a single row of areoles distinguish this species from the other species of *Woodwardia* (Morton & Neidorf, 1956). Today both species are typically included in the genus *Woodwardia* (Copeland, 1947; Wherry, 1964; Fernald, 1970; Lakela & Long, 1976). Some workers, however, still recognize the genus *Anchistea* (Radford et al., 1964; Small, 1938; McVaugh & Pyron, 1951).

Woodwardia areolata, the Net-vein or Dwarf Chain Fern, was first named *Acrostichum areolatum* (Linnaeus, 1753). Smith (1793) included the species in *Woodwardia* (as *W. angustifolia*), although it was not until much later that Moore (1857) called the species *W. areolata*. Today some botanists (Fernald, 1970; Lakela and Long, 1976) use this name. Presl (1851), however, established the genus *Lorinseria*, and many taxonomists (Copeland, 1947; Small, 1938; McVaugh and Pyron, 1951) consider *L. areolata* to be the correct name for the species. Wherry (1964) felt that the completely areolate venation and marked dimorphism of this species justified its segregation into a separate genus.

Much morphological data are available for these species (Shaver, 1954; Wherry, 1964; Small, 1938; Fernald, 1970), but comparative anatomical data are almost totally lacking. In this study, the anatomy of *W. virginica* and *W. radicans* is compared with that of *W. areolata*, and these data are correlated with the two taxonomic systems currently in use for these species.

Plant materials of *W. virginica* and *W. areolata* were collected in Alachua County, Florida. Plants of *W. radicans* were obtained from the Strybling Arboretum in San

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*Department of Botany, University of Florida, Gainesville, FL 32611.

Francisco, California. The plant parts were killed and fixed in formalin-acetic acid-alcohol (FAA), dehydrated in a tertiary-butyl alcohol series and infiltrated with Tissuemat (Johansen, 1940). Sections (8 μm) were stained with a safranin-fast green series and photographed with a 35 mm Zeiss C35 camera. Habit photographs were taken with a 35 mm single-lens reflex camera.

1

2

FIG. 1. Prostrate underground rhizomes of *W. areolata* (above), ×0.4 and *W. virginica* (below), ×0.5. Note adventitious roots. FIG. 2. Erect stem of *W. radicans*, ×0.9. Note large mass of adventitious roots.

RESULTS AND DISCUSSION

Both *Woodwardia virginica* and *W. areolata* occur in wet pinelands, bogs, marshes, and alongside streams and roadside ditches, whereas *W. radicans* is cultivated in fern gardens and has reportedly escaped to swamps and hammocks in the state. *Woodwardia areolata* and *W. radicans* thrive in partial shade around the bases of trees, but *W. virginica* does best in sunny locations and can tolerate a lower degree of acidity in the soil (Cody, 1963; Wherry, 1964).

Both *W. virginica* and *W. areolata* have a branched, creeping rhizome (*Fig. 1*), whereas *W. radicans* has an ascending to erect stem (*Fig. 2*). The stems of *W. virginica* ($\bar{x}$ = 10 mm) and *W. radicans* ($\bar{x}$ = 18 mm) are stouter than the rhizome of *W. areolata* ($\bar{x}$ = 5 mm) and more deeply buried in the soil. Golden brown, elongate scales with either blunt, rounded, or acuminate apices occur on the rhizome and petiole bases of *W. virginica* and *W. radicans*. Pale brown, cordate scales with acuminate apices are found on the rhizome and petiole bases of *W. areolata*. Shaver (1954) reported brown-black, oblong scales with acute apices in *W. virginica* and brown, ovate scales on the rhizome of *W. areolata*. I found small, light-brown, subcordate to cordate scales with acuminate apices abaxially on or proximal to the rachis and midveins of all three species. *Woodwardia virginica* has rather large, subcoriaceous, pinnate leaves, whereas *W. radicans* possesses large, coriaceous, pinnate-pinnatifid leaves with scaly buds produced on the rachis at the bases of the upper pinnae. *Woodwardia areolata*, however, has marked dimorphism, with the taller fertile leaves typically found in the summer and fall, distinct from the pinnatifid sterile leaves.

Stem transections of the three species reveal similar anatomical features, although differences are noted (*Fig. 3–5*). A single-layered epidermis composed of elongate, bulbous, or irregularly shaped, thick-walled cells is partially sloughed off in mature sporophytes of both *W. virginica* and *W. areolata*, whereas the epidermal layer is typically intact and composed of small, thick-walled cells filled with tanniferous substances in *W. radicans*. A hypodermis composed of two zones occurs in the three species, although the outer zone may be sloughed off in *W. virginica* and *W. radicans*. In *W. areolata*, the outer zone consists of irregularly shaped, thick-walled parenchyma cells (*Fig. 6*), whereas in *W. virginica* and *W. radicans* the parenchyma cells of this zone are thicker-walled and more heavily lignified. The inner zone in all species is composed of sclerified, thick-walled parenchyma cells that are filled with tannins or contain starch grains (*Fig. 6*), although the zone is less extensive in *W. areolata* than in the other two species.

In all three species, the bulk of the stem is composed of ground tissue (*Figs. 3–5*). The cortical region is distinguishable from the pith region primarily by the position of the meristeles. The cortex is composed primarily of irregularly shaped, thin-walled parenchyma cells filled with tanniferous substances, starch grains, or both. The pith region is composed of large, thin-walled parenchyma cells filled primarily with tannins, although starch grains are occasionally found in these cells. In *W. virginica*, thick-walled parenchyma cells occasionally comprise this region. In both *W. virginica* and *W. radicans*, certain cells in the cortical and pith regions enlarge singly or in groups, and tanniferous substances partially or totally fill the lumens of these cells (*Fig. 7*). These cell contents are abundant in *W. radicans*, especially around the meristeles, but are lacking in *W. areolata*. Large intercellular spaces occur in the cortical and pith regions of *W. virginica* and *W. areolata* and possibly serve as an adaptation to a marsh habitat. In *W. radicans*, very small intercellular spaces are occasionally noted in the ground tissues.

The stelar pattern in all three species is a dictyostele with overlapping leaf gaps and variously-sized meristeles (*Figs. 3–5*). Each meristele is an amphicribral bundle delimited by an endodermis with distinct Casparian strips (*Fig. 8*). A pericycle of thin-walled parenchyma cells (1– 4 layers) filled with tannins completely encircles the primary phloem. The latter tissue is composed of sieve cells and phloem parenchyma, although protophloem and metaphloem are typically indistinguishable in mature stems. The primary xylem of all species is composed primarily of scalariform-pitted tracheids, although spiral and annular-thickened protoxylem elements do occur. Interspersed among the xylary elements are thin-walled parenchyma cells filled with tannins. Xylem maturation is mesarch.

In all three species, the sterile leaves exhibit similar anatomical features (*Figs. 9–11*), whereas the fertile leaf of *W. areolata* usually is reduced, although it may be

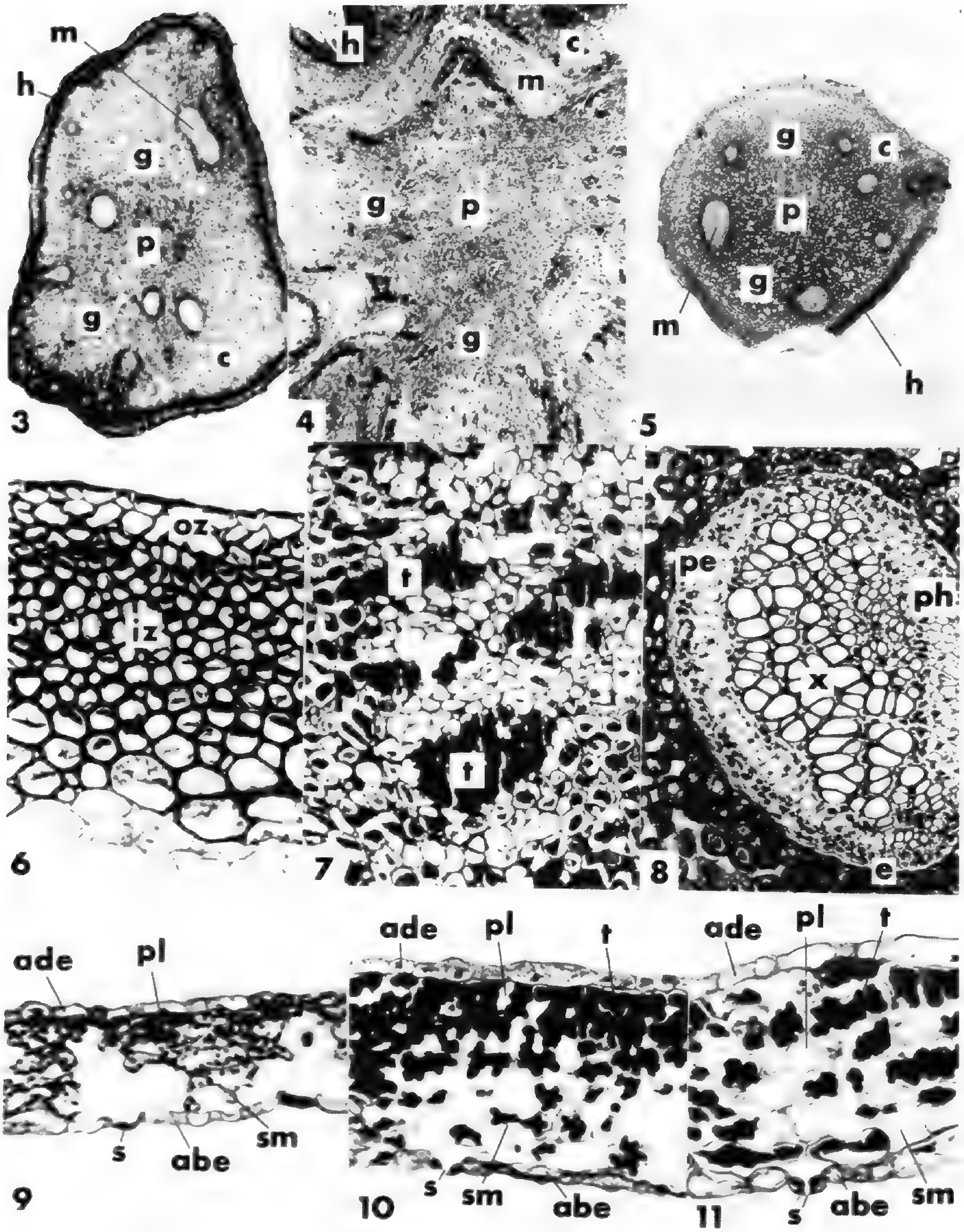

FIG. 3. Stem transection of *W. virginica*, × 10. Note meristeles. FIG. 4. Stem transection of *W. radicans*, × 10. Note dictyostele. FIG. 5. Stem transection of *W. areolata*, × 10. Note meristeles and dictyostelic pattern. FIG. 6. Two-zoned hypodermis of *W. areolata*, ×216. FIG. 7. Tanniferous substances in pith region of *W. radicans*, ×91. FIG. 8. Individual meristele of *W. areolata*, × 117. Note amphicribral arrangement of vascular tissues. FIG. 9. Transection of leaf of *W. areolata*, ×245. Note reduced palisade layer and extensive spongy mesophyll layer. FIG. 10. Transection of leaf of *W. virginica*, × 279. Note tannin-filled palisade layer.. FIG. 11. Transection of leaf of *W. radicans*, ×295. Note extensive tannin-filled palisade layer. The abbreviations are: abe = abaxial epidermis, ade = adaxial epidermis, c = cortex, e = endodermis, g = gap, h = hypodermis, iz = inner zone, m = meristele, oz = outer zone, p = pith, pe = pericycle, ph = phloem, pl = palisade layer, s = stomate, sm = spongy mesophyll, t = tannins, and x = xylem.

partially sterile (Halsted, 1899) or even may resemble a fertile leaf (Waters, 1903). In each of the three species, the single-layered adaxial epidermis is composed of variously sized cells, is covered with a thin cuticle, and lacks stomates. The mesophyll is differentiated into palisade and spongy mesophyll layers, although the palisade layer is much reduced and less extensive in *W. areolata* than in the other two species (*Figs. 9–11*). The palisade layer is composed of loosely arranged, irregularly shaped chlorenchyma cells in *W. areolata*; a more compact and tannin-filled palisade layer characterizes *W. virginica* and *W. radicans*. Although Payne and Peterson (1973) noted an abaxial hypodermis in the leaves of *W. virginica*, none was found in the present study (*Fig. 10*). The spongy mesophyll in all three species consists of loosely-arranged chlorenchyma cells with numerous, large intercellular spaces. This layer is much more extensive and constitutes a greater proportion of the leaf in *W. areolata* than in the other two species (*Figs. 9–11*). In *W. radicans*, the spongy mesophyll layer is greatly reduced and contains small intercellular spaces. Depending upon the species, the spongy mesophyll cells are either larger (*W. areolata*) or smaller (*W. virginica* and *W. radicans*) than the cells of the palisade layer. The chlorenchyma cells of the mesophyll in the latter two species are typically filled with tannins, whereas this ergastic substance is less evident or lacking in the mesophyll cells of *W. areolata* (*Figs. 9–11*). In all species, the abaxial epidermis is composed of variously shaped cells and possesses anomocytic stomates (*Fig. 12*). Typically two or three epidermal cells abut the guard cells, with one cell nearly surrounding the stomatal apparatus. Chloroplasts are infrequently noted in the adaxial epidermis of *W. areolata*, but do not occur in the epidermal layers of the other two species. The presence of chloroplasts in the epidermal cells of land plants is correlated with a deep-shade habitat (Sculthorpe, 1967), and their occurrence in *W. areolata* may be an adaptation to the shaded habitat of this species. The mid-vein (costa) in all three species is surrounded by a bundle sheath of thick-walled parenchyma cells and is delimited by a single-layered endodermis with distinct Casparian strips (*Figs. 13 and 14*). The innermost layer of the sheath may have tanniferous substances in *W. virginica* and *W. radicans*, whereas these cell contents are lacking in *W. areolata*. A pericycle composed of thin-walled parenchyma cells encircles the vascular tissues. The primary phloem is composed of sieve cells and phloem parenchyma. The primary xylem is U- or V-shaped and consists primarily of scalariform-pitted metaxylem elements. Protoxylem is generally restricted to a median position in the concavity of the xylary elements.

The fertile leaves of *W. areolata* show a much reduced structure; no differentiation of the mesophyll occurs, and only a few small intercellular spaces are noted. Stomates are lacking in both epidermal layers of a fertile leaf.

Ground tissue comprises the bulk of the petiole base in the three species (*Figs. 15–17*). This tissue is aerenchymatous and consists of either thick-walled (*W. virginica*) or thin-walled (*W. areolata*) parenchyma cells with numerous intercellular spaces. In *W. radicans*, this tissue consists of thin-walled parenchyma cells or is composed of two zones in the larger petioles (*Fig. 17*). The outer zone consists of thick-walled parenchyma cells, and the inner zone is composed of thin-walled parenchyma cells. Numerous, small intercellular spaces occur in these zones, and the cells are filled with tannins. Occasionally the parenchyma cells of the ground tissues in *W. radicans* enlarge and possess tanniferous substances that partially or totally fill the cell lumen. A single-layered epidermis characterizes the petiole and a hypodermis is found in all three species (*Figs. 15–17*). The latter tissue is much more extensive in *W. radicans* than in the other two species.

The number of vascular strands at the base of the petiole differs in each species. In *W. virginica*, typically five small spherical strands and two large U- or V-shaped strands occur (*Fig. 16*), although a total of five or six strands has been noted.

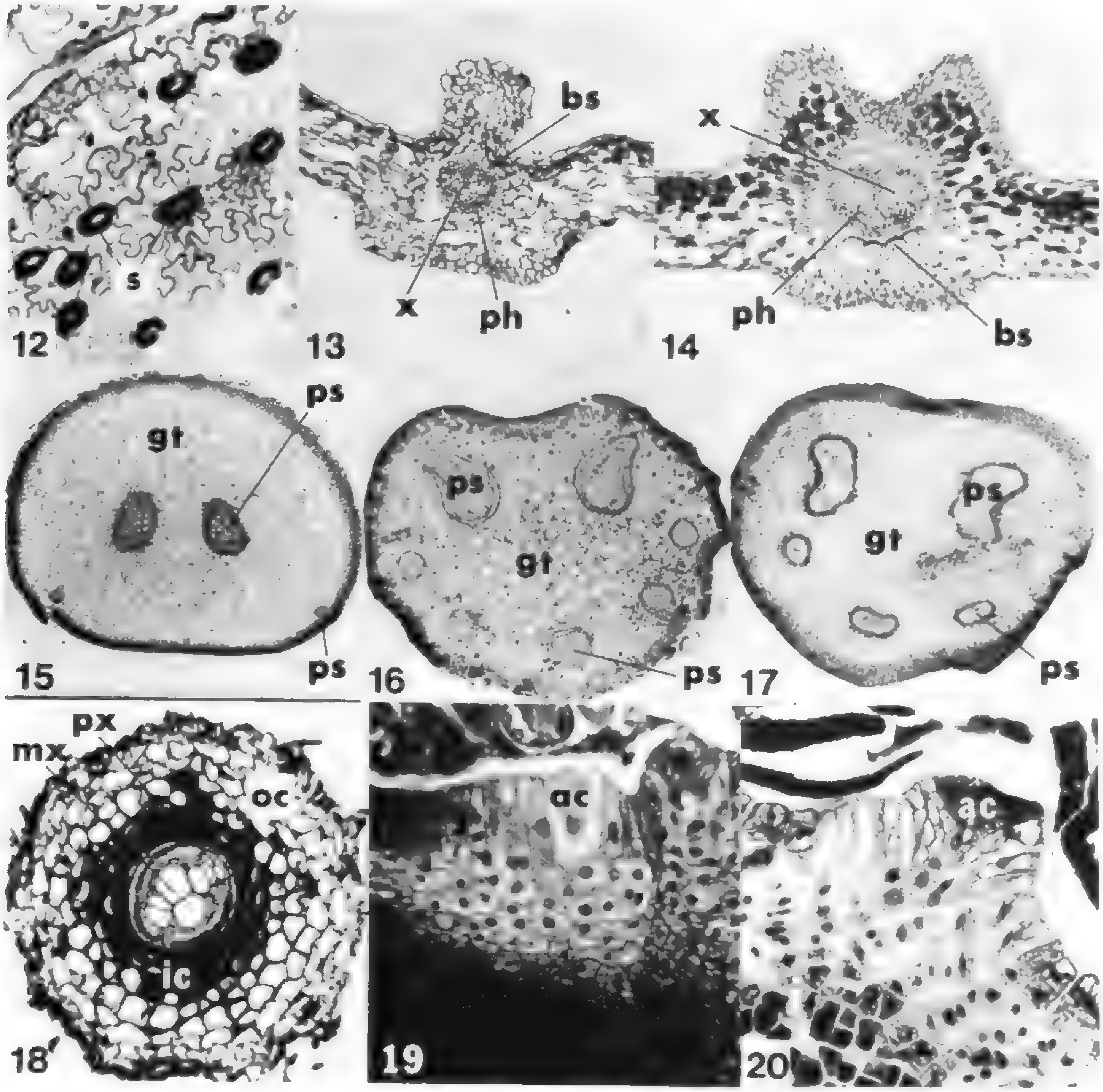

FIG. 12. Anomocytic stomates of *W. virginica*, ×225. FIG. 13. Transection of midvein (costa) of *W. areolata*, ×102. FIG. 14. Transection of midvein (costa) of *W. virginica*, ×100. Note tanniferous substances in bundle sheath cells. FIG. 15. Transection of petiole base of *W. areolata*, ×21. Note two small, spherical abaxial bundles. FIG. 16. Transection of petiole base of *W. virginica*, ×22. FIG. 17. Transection of petiole base of *W. radicans*, ×11. FIG. 18. Transection of adventitious root of *W. virginica*, ×97. Note diarch pattern. FIG. 19. Shoot meristem of *W. areolata*, ×264. FIG. 20. Shoot meristem of *W. virginica*, ×295. Note pyramidal apical cell. The abbreviations are: ac = apical cell, bs = bundle sheath, gt = ground tissue, ic = inner cortex, mx = metaxylem, oc = outer cortex, ph = phloem, ps = petiole strand, px = protoxylem, s = stomate, x = xylem.

Waters (1903) reported seven oval bundles in the petioles of *W. virginica*. In *W. radicans*, four or five petiole strands are noted in the petiole base (*Fig. 17*). Two or three small, spherical to oval bundles occur abaxially and two large crescent-shaped strands are found adaxially in the petiole (*Fig. 17*). In *W. areolata*, typically two large petiole strands are found in a median position in the petiole base, although occasionally four strands occur at a comparable level in the petiole (*Fig. 15*). Waters (1903), however, reported only two oval petiole bundles in *W. angustifolia* (*W. areolata*). When four strands are present, they include two large, median, crescent-shaped strands and two very small, spherical strands located proximal to the hypodermis on the abaxial surface of the petiole. The small abaxial strands originate from the division of the larger strands in the petiole base. In both *W. virginica* and *W. radicans*, small abaxial strands also arise from the division of the two large strands in the base of the petiole. In all species, a bundle sheath composed of large parenchyma cells with tanniferous substances surrounds each petiole strand. Cellular composition and arrangement of the stelar tissues is similar to the midrib (rachis) of a leaf.

Transections of the adventitious roots of all three species show similar anatomical features (*Fig. 18*). The epidermis is typically sloughed off in mature roots, and the outer cortex, which is composed of irregularly shaped, thick-walled parenchyma cells, forms the outer boundary of the organ. The inner cortex consists of isodiametric, sclerified, thicker-walled parenchyma cells that may be filled with tanniferous substances. A single-layered endodermis with Casparian strips delimits the stele. A pericycle composed of 1–3 layers of thin-walled parenchyma cells surrounds the vascular tissue. The primary phloem consists of sieve cells and phloem parenchyma, and the primary xylem is composed primarily of scalariform-pitted metaxylem and some spiral and transitional (reticulate-scalariform) protoxylem. In all three species, the primary xylem is diarch with exarch maturation (*Fig. 18*), although a triarch pattern is infrequently noted in *W. radicans*.

In the species studied, the shoot apical meristem consists of a highly-vacuolated pyramidal apical cell averaging 50 × 80 μm (*Figs. 19–20*). Recent derivatives of the apical cell constitute the promeristem and comprise two groups of cells, the surface and subsurface zones. The promeristem in *W. areolata* is slightly dome-shaped (*Fig. 19*), whereas this tissue has a pronounced dome shape in *W. virginica* and *W. radicans* (*Fig. 20*). The surface zone in these three species consists of large, vacuolated, rectilinear cells and a few isodiametric cells on the periphery. McAlpin and White (1974) found a similar arrangement of the superficial cells in the genera *Dryopteris* and *Quercifilix*. The subsurface zone in *W. areolata* is distinct and consists of small, isodiametric cells (*Fig. 19*), whereas this zone is indistinct in the other two species.

Comparative data indicate a close relationship between *W. virginica*, *W. radicans*, and *W. areolata*. Although the marked dimorphism and venation of the leaves justify the segregation of *Lorinseria areolata* from the genus *Woodwardia*, chromosome numbers (Wherry, 1964) and spore morphology (McVaugh, 1935; Hires, 1965) favor the retention of these species in the same genus. Comparative anatomical data also support the placement of all three species in the genus *Woodwardia*.

Grateful acknowledgment is made to Messrs. Alan Jones and James Neumann for their technical assistance in this study.

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Spore Germination Patterns in Anogramma, Bommeria, Gymnopteris, Hemionitis and Pityrogramma

CLARK S. HUCKABY*, R. NAGMANI** and V. RAGHAVAN**

Based on the morphological characters of the sporophyte and gametophyte, palynological evidence, and spore germination patterns seen in whole mount preparations, the genera *Anogramma, Bommeria, Gymnopteris, Hemionitis,* and *Pityrogramma* have been assigned to different families by fern taxonomists. Bower (1928) included these genera in the group designated as gymnogrammoid ferns, whereas Christensen (1938) placed all except *Gymnopteris* in the polypodiaceous group. Copeland (1947), however, regarded these genera as part of the complex group of pteroid ferns. Holttum (1949) followed Bower in his conception of gymnogrammoid ferns and combined the gymnogrammoid and vittarioid ferns of Bower into the family Adiantaceae. Nayar (1970) placed *Anogramma* in the Adiantaceae, *Bommeria, Hemionitis,* and *Gymnopteris* in the Cheilanthaceae and *Pityrogramma* in the Pteridaceae, whereas Crabbe et al. (1975) treated all five genera as members of the Adiantaceae. According to Haufler and Gastony (1978), gametophytes of *Bommeria* and *Hemionitis* responded differently from those of *Anogramma* and *Pityrogramma* to antheridiogen A, the male sex hormone isolated from the gametophytes of *Pteridium aquilinum,* to merit their further subgrouping.

Previous light microscopic studies (Endress, 1974; Raghavan & Huckaby, 1980; Huckaby & Raghavan, 1981a; Rutter & Raghavan, 1978) on the orientation of the initial cell divisions during germination of spores of certain ferns using techniques generally employed in electron microscopy (fixation in an aldehyde fixative and embedding in glycol methacrylate plastic) have contradicted earlier work on spores of the same ferns based on whole mount preparations. Comparative studies of spore germination in *Anemia, Lygodium,* and *Mohria* (Schizaeaceae) (Raghavan & Huckaby, 1980) and in *Cyathea* and *Dicksonia* (Huckaby & Raghavan, 1981a) have also demonstrated the value of the early division sequence during spore germination as a stable taxonomic criterion in defining affinities of problematic genera. In view of the disagreement among pteridologists on the relationships of *Anogramma, Bommeria, Gymnopteris, Hemionitis,* and *Pityrogramma,* the present work is aimed at evaluating the importance of spore germination patterns in these genera as studied by modern histological techniques and in the scanning electron microscope (SEM) as a new source of taxonomic evidence.

Relatively little information is available in the literature on the initial cell division patterns during germination of spores of *Anogramma, Bommeria, Gymnopteris,*

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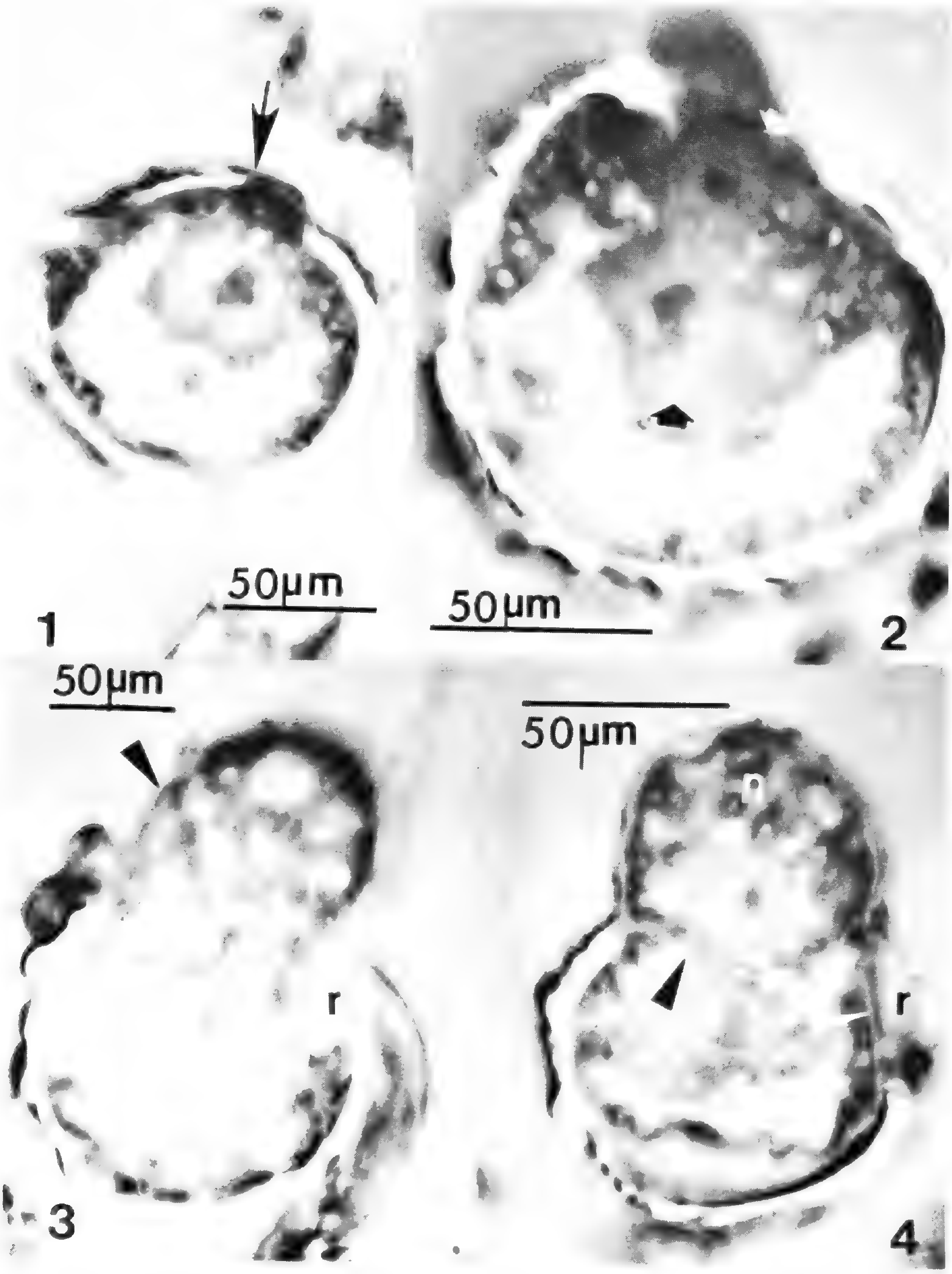
*Department of Biology, Syracuse University, Syracuse, NY 13210.
**Department of Botany, The Ohio State University, Columbus, OH 43210.



FIGS. 1–4. Germination of *Anogramma chaerophylla* spores. FIG. 1. Section showing the rupture of the exine (arrow). FIG. 2. Section showing the formation of the rhizoid. White arrow points to the nucleus of the rhizoid; black arrow points to the nucleus of the distal cell. FIG. 3. Section of a germinated spore showing the lateral displacement of the rhizoid (r) and protrusion of the distal cell (arrow). FIG. 4. Section showing the formation of the protonemal cell (p); (r) is the rhizoid. White arrow points to the wall delimiting the rhizoid; black arrow points to the wall delimiting the protonemal cell.

Hemionitis and *Pityrogramma*. Rao (1949) and Nayar (1956, 1962), who followed the early development of *H. arifolia* gametophytes, make no reference to the spore germination. Nayar's (1964) study of *P. calomelanos* and *P. chrysophylla* gametophytes also lacks details of spore germination. In a study of *G. vestita* gametophytes, Kaur (1972) states, without giving any details, that spore germination is of the *Vittaria* type described earlier by Nayar and Kaur (1968). In this type of germination, a rhizoid is cut off at the proximal pole of the spore by a wall perpendicular to the polar axis. The protonemal cell is formed by a subsequent division of the large distal cell perpendicular to the first division wall. Elongation of the rhizoid parallel to the polar axis of the spore and that of the protonemal cell along the equatorial plane are also characteristic of this type of germination. In their review of the gametophytes of homosporous ferns, Nayar and Kaur (1971) make statements which imply that the germination pattern of *Anogramma, Bommeria, Gymnopteris, Hemionitis,* and *Pityrogramma* spores follows the *Vittaria* type.

Based on whole mount observations, Haufler (1979) recently showed that spores of *Bommeria hispida* germinated by a division wall perpendicular to the polar axis, the small proximal cell differentiating into the rhizoid; origin of the protonemal cell was not traced in this work. However, in a proportion of spores of *B. subpaleacea*, the small (proximal?) cell formed from the first division is believed to yield the protonemal cell, the rhizoid being derived by a division of the same cell as the protonemal. According to Baroutsis (unpublished work cited by Haufler, 1979 and pers. comm.), who followed in whole mounts the pattern of cell division during germination of spores of several species of *Anogramma*, the first division of the spore to form the rhizoid is oblique or nearly parallel to the polar axis. According to this investigator, in *A. osteniana*, the protonemal cell sometimes appeared to form before the rhizoid.

MATERIAL AND METHODS

Spores of *Anogramma chaerophylla, Bommeria pedata, B. ehrenbergiana, B. hispida, B. subpaleacea, Gymnopteris rufa, Hemionitis arifolia, H. palmata, H. pedata, Pityrogramma calomelanos,* and *P. chrysophylla* used in this work were obtained from various sources[1] and stored at 5°C until used. To follow cell division pattern during germination, spores were sown on the surface of 10 ml modified Knop's liquid medium (Raghavan, 1965) contained in 5 cm diameter Petri dishes and allowed to imbibe in the dark for 48 hr. They were then irradiated continuously with red light or exposed to weak fluorescent light during a photoperiod of ca. 12 hr as described earlier (Huckaby & Raghavan, 1981a, b). Samples were collected at intervals of 12–24 hr during an experimental period of 6 days, fixed in 10% acrolein,

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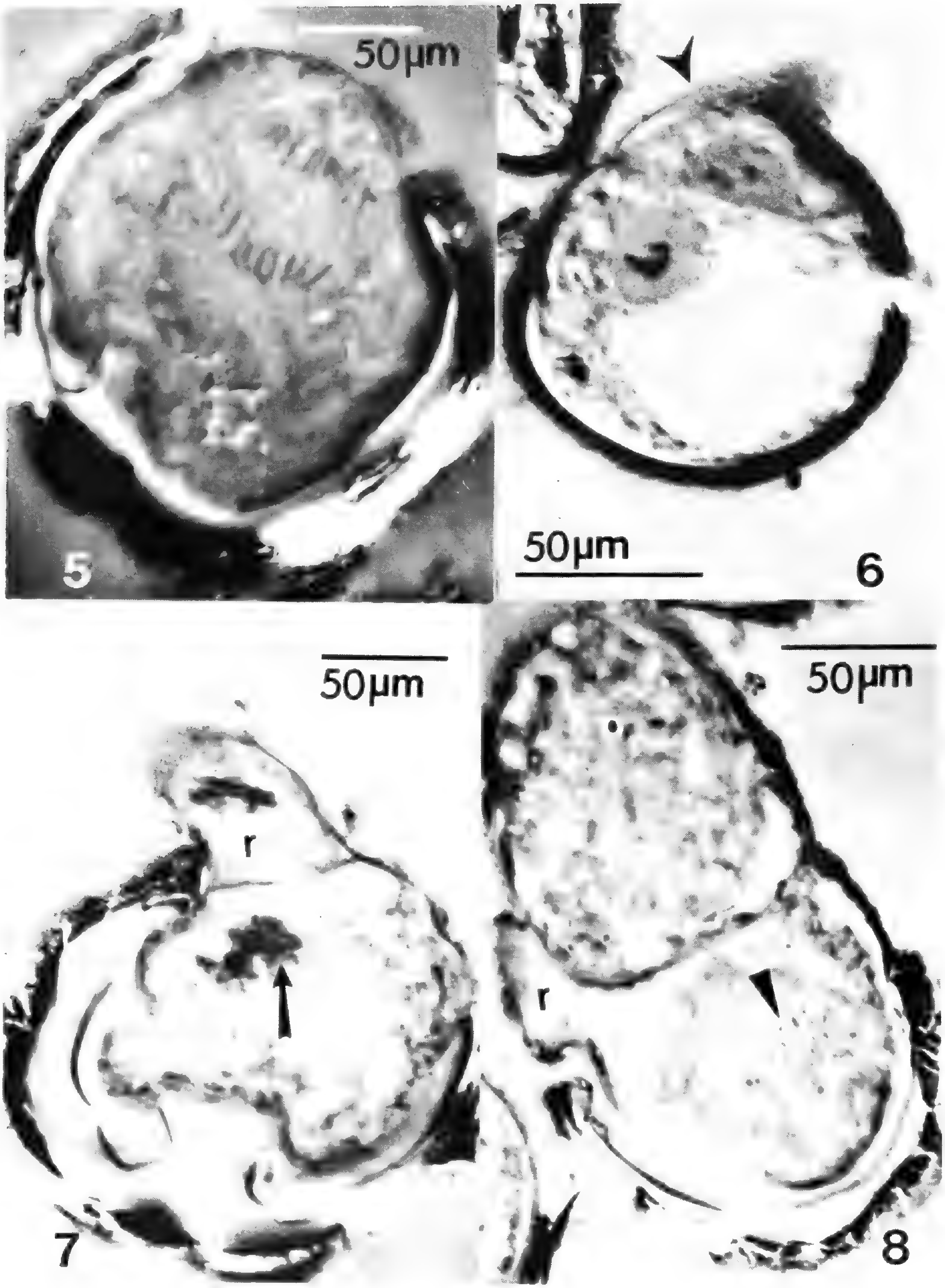
[1] Spores were obtained from the following sources: *A. chaerophylla, B. pedata* and *H. pedata* from Dr. J. T. Mickel, New York Botanical Garden, Bronx, New York; *B. ehrenbergiana, B. hispida, B. subpaleacea,* and *H. palmata* from Dr. C. H. Haufler, University of Kansas, Lawrence, Kansas; *H. arifolia* and *P. calomelanos* from Dr. C. N. Page, Royal Botanic Gardens, Edinburgh, Scotland; *G. rufa* and *P. chrysophylla* from Dr. T. Walker, Royal Botanic Gardens, Kew, England.



FIGS. 5–8. Germination of *Bommeria* spores. FIG. 5. *B. pedata* section showing the rupture of the exine; the spore nucleus is in mitosis. FIG. 6. *B. ehrenbergiana* section showing the formation of rhizoid initial (arrow). FIG. 7. *B. pedata* section showing the rhizoid initial (r). Arrow points to the nucleus of the distal cell. FIG. 8. *B. pedata* section showing the protonemal cell (p); (r) is part of the rhizoid. The nucleus of the distal cell (arrow) is in division.

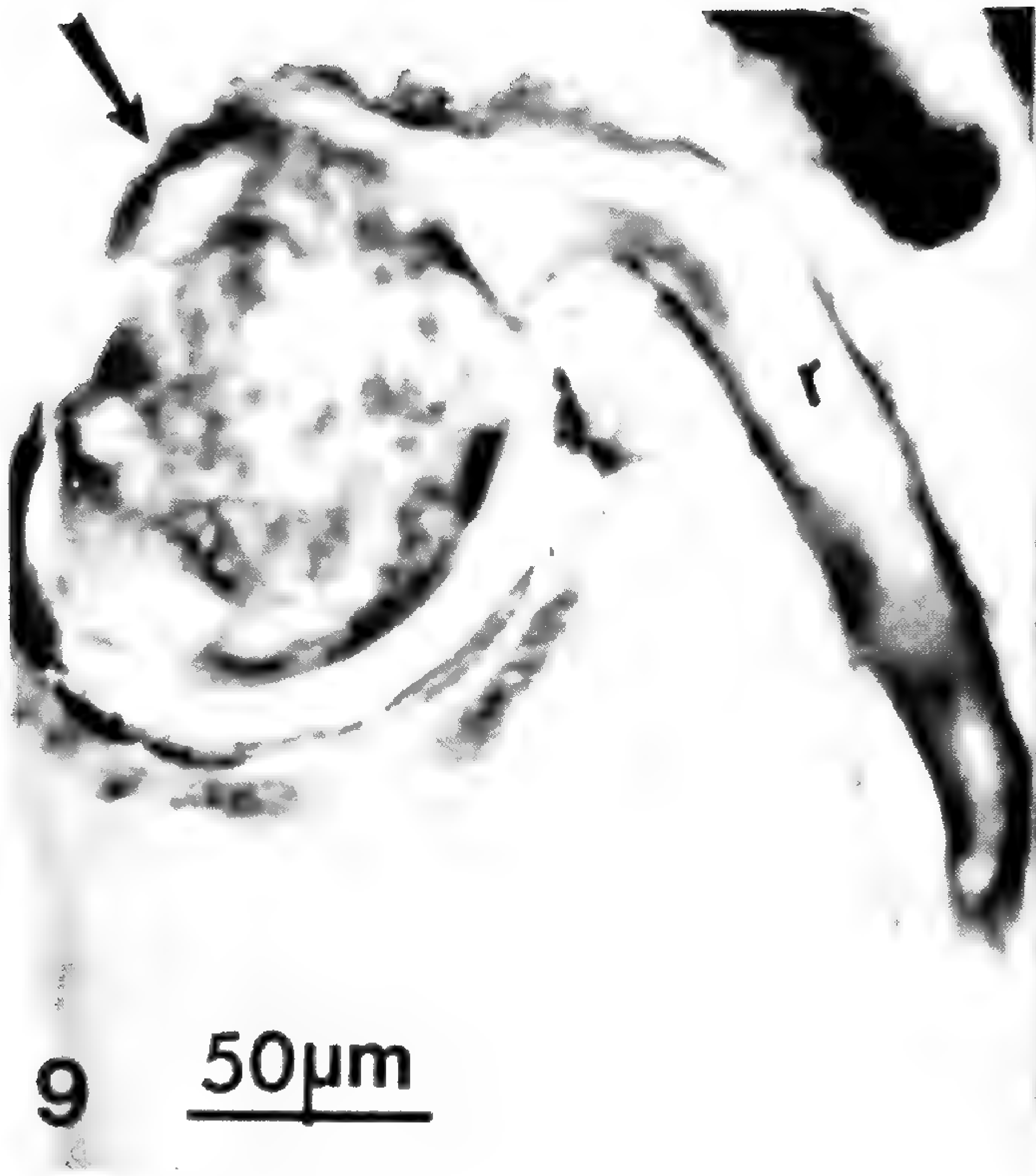
and embedded in glycol methacrylate according to routine procedures previously used (Raghavan, 1976, 1977; Raghavan & Huckaby, 1980; Huckaby & Raghavan, 1981a, b; Rutter & Raghavan, 1978). Sections cut at 7 μm thickness on a rotary microtome equipped with a steel knife were stained in 0.05% toluidine blue, mounted in Euparal, and examined in the light microscope.

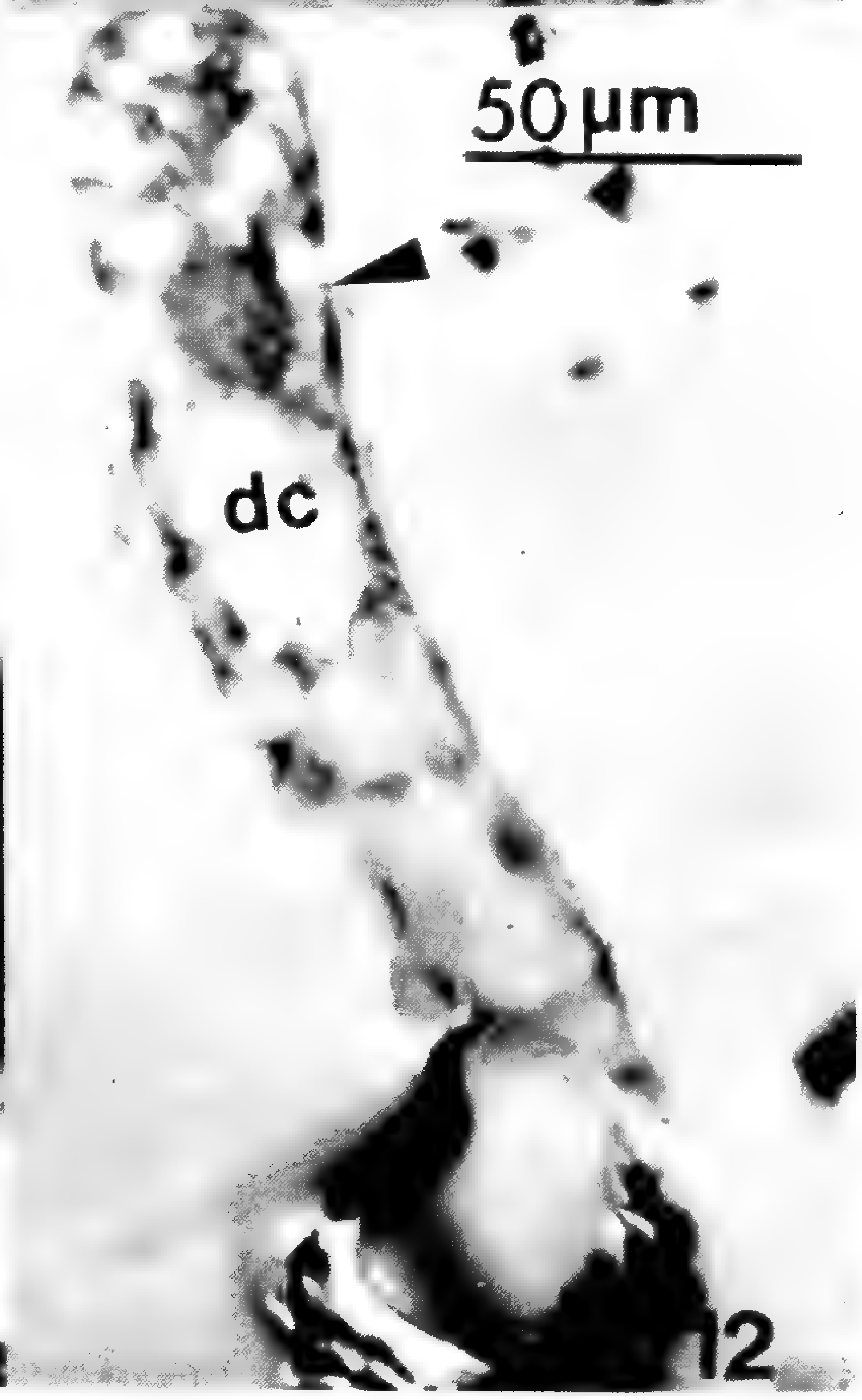
For examination in SEM, spores were fixed in 70% ethanol-acetic acid (3:1) at 4°C, dehydrated in ascending series of ethanol and subjected to critical point drying. They were subsequently mounted on SEM specimen mounts using double-stick cellophane tape, vaccuum-coated with gold, and examined in a Hitachi S-500 instrument.

SPORE GERMINATION RESULTS

Anogramma chaerophylla.—Spore germination was initiated by the splitting of the exine at the proximal pole along the lines of the trilete scar after about 36–48 hr in red light (*Fig. 1*). Following this, the spore protoplast divided by a wall perpendicular to the polar axis, resulting in a small proximal cell and a large distal cell (*Fig. 2*). The former elongated into the rhizoid, with a corresponding enlargement of the latter. The distal cell also acquired chloroplasts and appeared outside through the opening in the exine as a green protrusion, displacing the rhizoid laterally, so that the wall delimiting the rhizoid from the distal cell appeared parallel to the polar axis (*Fig. 3*). The protonemal cell was formed about 72 hr after exposure of spores to red light by the division of the distal cell by a wall perpendicular to the first wall (*Fig. 4*), although due to the elongation of the distal cell, the second division wall barely intercepted the first. The division sequences observed in spores exposed to white light were similar to those seen in red light. In spores germinated in either light regimen, the protonemal cell grew parallel to the polar axis of the spore and the rhizoid grew at a right angle to the protonemal cell. Initial division of the spore protoplast oblique or nearly parallel to the polar axis as described in this genus by Baroutsis (cited by Haufler, 1979 and pers. comm.) was not observed in sections made from our sample.

Bommeria ehrenbergiana, B. hispida and B. pedata.—Spores of *B. ehrenbergiana*, *B. hispida*, and *B. pedata* germinated by cracking of the spore coats at the proximal pole after exposure to red light for about 48 hr. As in the case of *A. chaerophylla*, the first division of the spore protoplast perpendicular to the polar axis yielded a small proximal rhizoid and a large distal cell (*Figs. 5–7*). When spores initially exposed to red light were transferred to white light for 24 hr, protonemal initiation occurred by the division of the distal cell by a wall perpendicular to the first. Occasionally after cutting off the protonemal cell, the nucleus of the distal cell was found to divide again, probably giving rise to a secondary rhizoid (*Fig. 8*). Exposure of spores of *B. ehrenbergiana* and *B. pedata* to white light or red light alone resulted in the elongation of the distal cell through the opening in the exine accompanied by chloroplast accumulation, but its division to form the protonemal cell was not observed during the experimental period. Spores of *B. hispida* exposed to white light gave rise to the rhizoid and protonemal cell according





FIGS. 9 and 10. Germination of *Bommeria hispida* spores. FIG. 9. Section showing the rhizoid (r). Arrow points to the distal cell enlarging preparatory to division to form the protonemal cell. FIG. 10. Section showing the distal cell (arrow), partially loose from the wall, after cutting off the protonemal cell (p); (r) is the rhizoid. FIGS. 11 and 12. Germination of *Gymnopteris rufa* spores. FIG. 11. Section showing the first division giving rise to a small proximal rhizoid initial (r) and a large distal cell (dc). Arrow points to the division wall. FIG. 12. Section showing the elongation of the distal cell (dc) and the migration of its nucleus (arrow) to the tip.

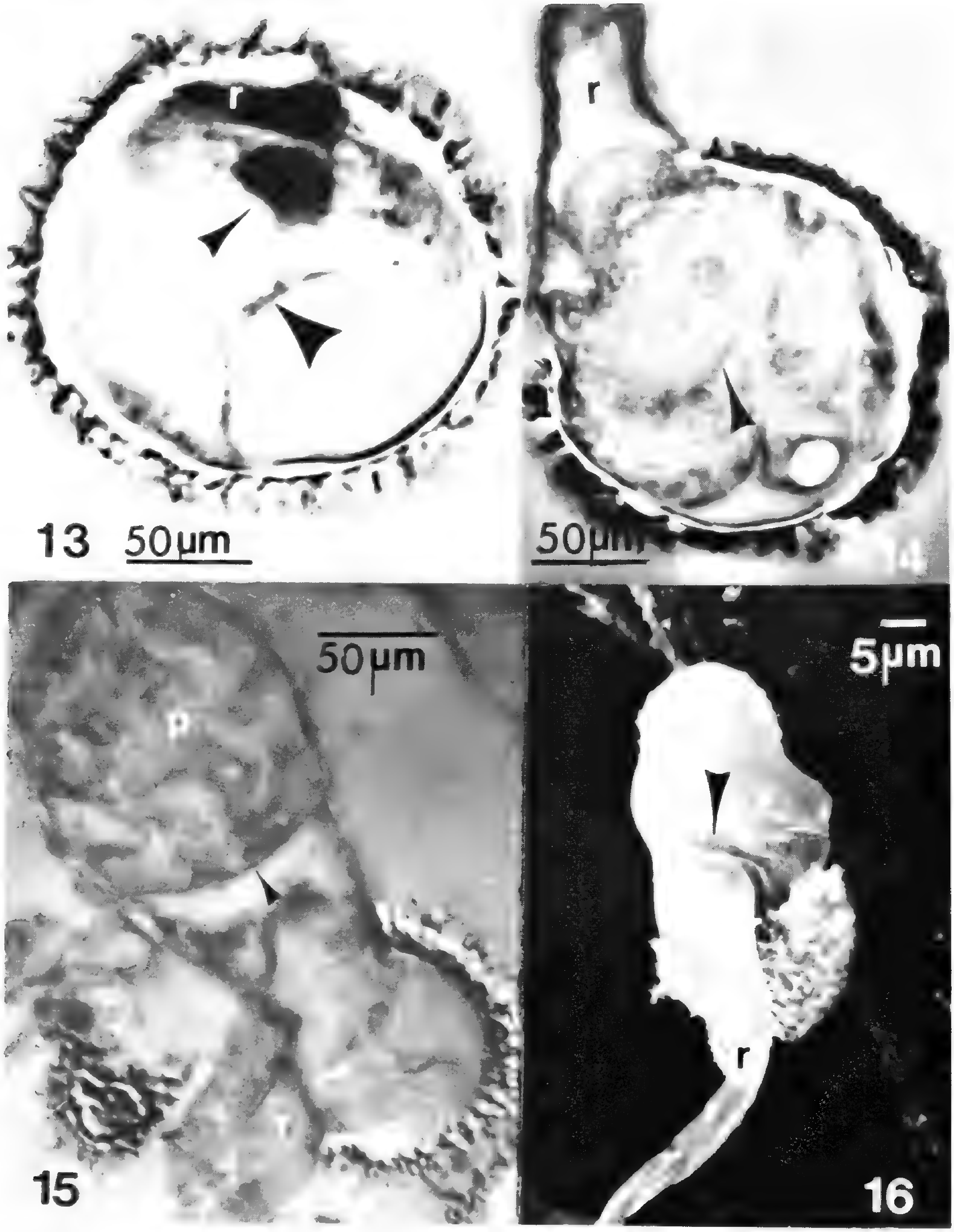
to the same division sequence observed in the other two species. In spores of all three species examined, due to lateral expansion of the distal cell, the orientation of the wall delimiting the rhizoid was changed so that the wall appeared parallel to the polar axis of the spore (*Figs. 9 and 10*).

In spores of *Bommeria* examined by us, the orientation of the initial division wall yielding the rhizoid is similar to that described by Haufler (1979) in *B. hispida*. However, a sufficient quantity of spores of *B. subpaleacea* was not available to us to confirm or refute Haufler's (1979) observation that in some spores of this species, the proximal cell arising out of the first division gave rise to the protonemal cell.

Gymnopteris rufa.—The first division, which occurred in spores exposed to red or white light regimens for 72–96 hr, was perpendicular to the polar axis and yielded a small proximal cell and a large distal cell (*Fig. 11*). This was the only division observed in the germinating spore during the experimental period. As the proximal cell differentiated into a rhizoid, the distal cell elongated, became chlorophyllous and appeared outside as a green cell. Later the nucleus moved from the basal part of the cell enclosed within the exine to its exposed tip (*Fig. 12*). A transverse division occurred at the tip of the distal cell during its further growth in red or white light. A similar pattern of cell disposition has been described in germinating spores of *Pteris vittata* (Raghavan, 1977).

Hemionitis arifolia, H. palmata and H. pedata.—Spores of all three species followed a uniform pattern of germination in which the first division of the spore protoplast by a wall perpendicular to the polar axis gave rise to a small proximal cell and a large distal cell. As seen in other genera, the small cell differentiated into the rhizoid (Figs. 13 and 14). Rhizoid initiation occurred after exposure of fully imbibed spores to a red or a white light regime for 48 hr and was preceded by the opening of the exine at the trilete mark. Formation of the rhizoid was followed by enlargement of the distal cell through the opening in the exine and its division by a wall perpendicular to the first to give rise to the protonemal cell (*Fig. 15*). As seen in SEM preparations (*Fig. 16*), expansion of the distal cell resulted in the displacement of the wall separating the rhizoid from the distal cell to a plane parallel to the polar axis of the spore. In spores of *H. palmata* grown in red or white light regimes, the division of the distal cell to form the protonemal cell was not observed during the experimental period.

Pityrogramma calomelanos and P. chrysophylla.—Spores of both species are characterized by the presence of equatorial flanges of sporoderm material which can be used as a marker for the equatorial plane. Spores responded to white or red light regimes in about 24 hr by the cracking of the spore walls at the trilete mark and by the emergence of the rhizoid (*Figs. 17* and *18*). The latter was traced to the proximal cell formed by the division of the spore protoplast by a wall perpendicular to the polar axis (*Fig. 19*). Following rhizoid formation, the distal cell expanded laterally and elongated through the opening in the exine parallel to the polar axis, displacing the rhizoid in a plane parallel to the equatorial axis (*Fig. 20*). The division of the distal cell to form the protonemal cell was delayed until the nucleus migrated from the base of the cell to its tip, and occurred by a wall perpendicular to the first division wall.



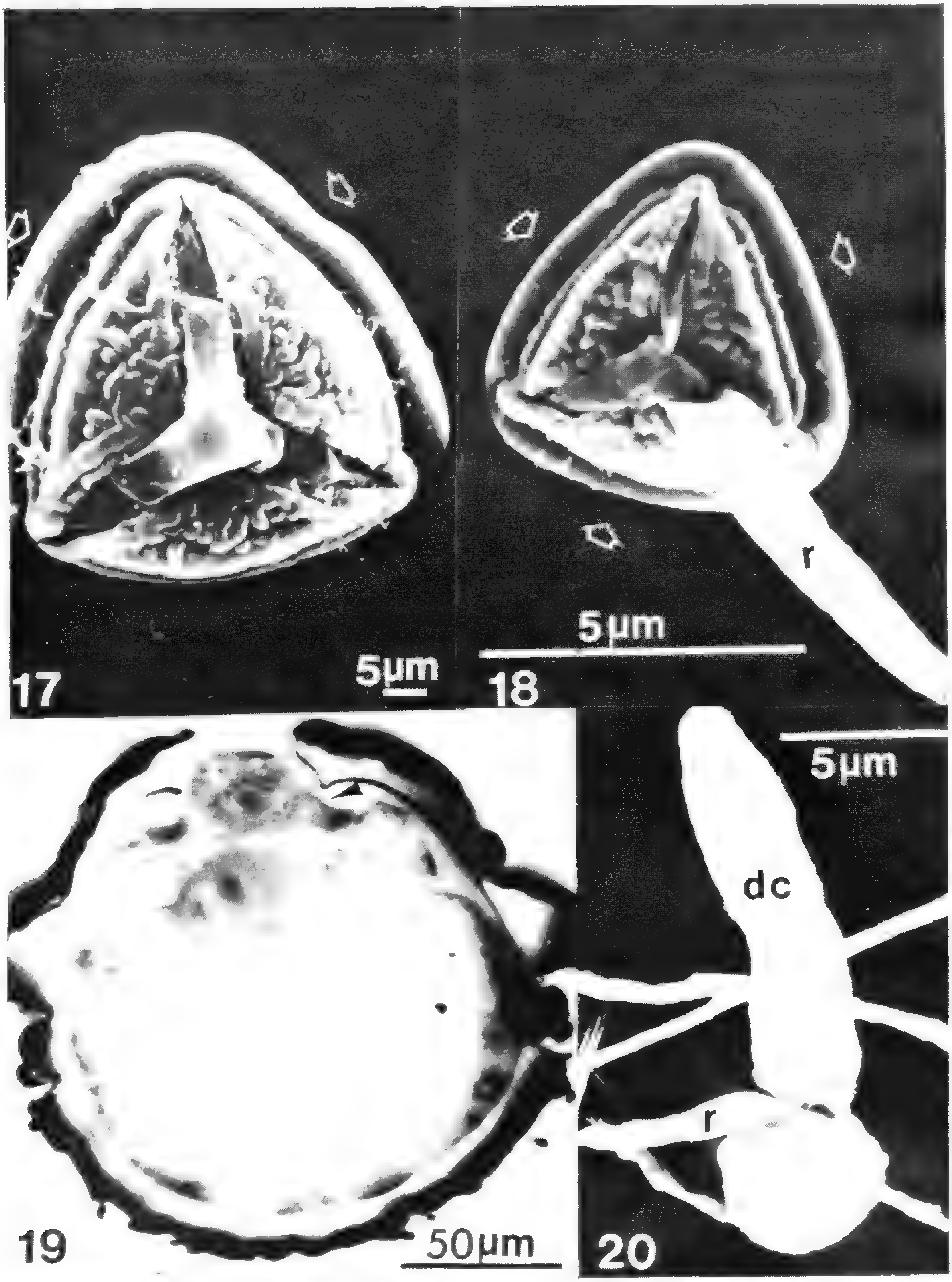
FIGS. 13–16. Germination of *Hemionitis* spores. FIG. 13. Section of *H. pedata* showing the first division to form the rhizoid initial (r) and a distal cell. Small arrow points to the nucleus of the distal cell; part of the distal cell has become loose from the spore wall (large arrow). FIG. 14. Section of *H. arifolia* showing the rhizoid (r) and the undivided distal cell; arrow points to the nucleus of the distal cell. FIG. 15. Section of *H. pedata* showing the protonemal cell (p) and rhizoid (r). White arrow points to the wall delimiting the rhizoid; black arrow points to the wall delimiting the protonemal cell. FIG. 16. Scanning electron micrograph of *H. pedata* showing the displacement of the rhizoid wall (arrow); (r) is the rhizoid.

DISCUSSION

Planes of cell division during germination of *Anogramma, Bommeria, Gymnopteris, Hemionitis,* and *Pityrogramma* spores described here follow the general pattern of the *Vittaria* type of Nayar and Kaur (1968). The spore is divided by two walls, the first one perpendicular to its polar axis yielding a rhizoid and the second, perpendicular to the first, giving rise to the protonemal cell. However, due to the displacement of the rhizoid initial by the expansion of the distal cell, the rhizoid and protonemal cell have been found to elongate in planes opposite to those described by Nayar and Kaur (1968). The only difference noted between the initial division patterns of spores of different genera is in the timing of the second division under the experimental conditions employed. As seen in spores of *Gymnopteris rufa,* the distal cell apparently functions as the protonemal cell due to a delay in the second division, giving the impression that a single division of the spore protoplast is sufficient to give rise to a functional gametophyte. However, the fact that under extended periods in both red and white light regimes, division of the spore protoplast follows the *Vittaria* type, reinforces the stability of this character in the early gametophyte development of ferns. On the basis of our observations, we believe that the report of Baroutsis (cited by Haufler, 1979 and pers. comm.) on the formation of the rhizoid in spores of several species of *Anogramma* by a wall oriented obliquely or nearly parallel to the polar axis is due to failure to identify the first division wall as soon as it is formed. As seen in *Figs. 5, 6, 11, 13,* and *19,* this wall appears before or immediately after the exine is ruptured and by the time the wall is visible in whole mounts, the distal cell would have expanded, displacing the original wall and giving the false impression of its occurrence parallel to the polar axis (*Figs. 3, 9,* and *15*).

If the cell division pattern during spore germination can be considered a stable character for taxonomic purposes, along with other features of the gametophyte and of the sporophyte, the uniformity in the pattern observed in the five genera investigated here tends to support their assignment to a single family, Adiantaceae, as done by Crabbe et al. (1975). Since no distinctive variants of the germination pattern were seen between groups of genera, a further subgrouping separating *Bommeria* and *Hemionitis* from *Anogramma* and *Pityrogramma* as suggested by Haufler and Gastony (1978) is not supported by our data.

A comparison between the cell division patterns observed in sectioned spores of certain genera of Schizaeaceae investigated earlier (Raghavan, 1976; Raghavan & Huckaby, 1980) and of the gymnogrammoid ferns studied here may be of some interest from the point of view of phylogenetic relationships of the two groups. According to Nayar (1970), *Vittaria* type germination is evolutionarily more advanced than the pattern observed in the Schizaeaceae, designated as the *Anemia* type by Nayar and Kaur (1968). However, our earlier studies on the spores of *Anemia, Lygodium,* and *Mohria* (Raghavan & Huckaby, 1980) have questioned the existence of *Anemia* type germination as envisaged by Nayar and Kaur in the Schizaeaceae, suggesting that conclusions concerning the evolutionary significance of the different patterns of cell division during spore germination based on whole mount preparations may be overstated. However, there is an increasing body of opinion (Holttum,



FIGS. 17–20. Germination of *Pityrogramma calomelanos* spores. FIGS. 17 and 18. Scanning electron micrographs showing the trilete mark and emergence of rhizoid (r). Arrows point to the equatorial flange. FIG. 19. Section showing the first division. Arrow points to the rhizoid initial. FIG. 20. Scanning electron micrograph showing elongation of the distal cell (dc) and displacement of the rhizoid (r).

1949; Crabbe et al., 1975) on the possible origin of adiantoid ferns as a distinct group from the schizaeaceous stock. Raghavan and Huckaby (1980) have shown that spores of *M. caffrorum* follow the same route as the five genera studied here to form the rhizoid and protonemal cell, exhibiting typical *Vittaria* type germination. The existence of similar patterns of division during spore germination in the Adiantaceae and in a member of the Schizaeaceae might suggest a close relationship between the two families, but examination of the germination patterns of spores of other species of *Mohria* and of *Schizaea* and *Actinostachys* is necessary before this evidence can be used to support the possible origin of adiantoid ferns from a schizaeaceous ancestry.

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SHORTER NOTES

THE CHEMOIDENTITY OF THE HOLOTYPE OF PITYROGRAMMA TRIANGULARIS.—In recent years, the *Pityrogramma triangularis* complex has been the subject of extensive phytochemical studies, for example, by Smith (Bull. Torrey Bot. Club 107:134–145. 1980 and references therein). The nominal variety tacitly recognized by Weatherby (Rhodora 22:113–120. 1920), var. *triangularis*, has proved to be rather complex in itself with respect to the composition of frond-surface flavonoids and chromosome numbers. The plants subsumed under var. *triangularis* are morphologically very similar, but their extreme chemical differences and distinct regional distribution suggest that further taxonomic revision within this group may prove warranted. It is critical, therefore, to establish the chemical identity of the holotype of var. *triangularis*, since ultimately the one biological entity identifiable with the holotype must bear the name var. *triangularis*.

The holotype, which is in the herbarium of the Berlin Botanical Garden, was collected by the German poet, botanist, and globetrotter Adelbert von Chamisso. It bears a note in his handwriting "*Gymnogramma triangularis* Kaulf. Enum. p. 73, legit deditque A. v. Chamisso, California." According to Eaton, quoted by Alt and Grant (Brittonia 12:153–170. 1960), the specimen was collected in 1816 near San Francisco. It is filed at Berlin under "Polypodiaceae, Gattung No. 62a. *Ceropteris*, Art No. 21 *triangularis*."

A minute fragment of the holotype was made available for analysis of its farina; 22 mg of material was rinsed with acetone to dissolve the exuded flavonoids. These were identified by direct comparison with authentic markers on polyamide-TLC; for experimental details see Wollenweber, Dietz, Schillo and Schilling (Z. Naturforsch. 35c:685–690. 1980). The major constituent is ceroptin; minor components are triangularin and another compound which is not yet fully elucidated, "tvt-11," according to Dietz (unpubl. dissertation, Darmstadt). This flavonoid pattern is characteristic of those plants representing the ceroptin chemotype of var. *triangularis*. The holotype specimen itself chemically resembles those plants of the diploid ceroptin type collected by D. M. Smith from Refugio Pass, Santa Barbara County, California according to Star, Seigler, Mabry and Smith (Biochem. Syst. Ecol. 2:109–112. 1975).

We think it is a most remarkable result that the holotype of *P. triangularis* can be equated unambiguously with the typical and well defined ceroptin chemotype of var. *triangularis*. This illustrates the powerful role that chemotaxonomy can play in determining the application of names by the type method. Thanks are due to Dr. D. Meyer, Berlin, for kindly supplying the fern fragment used in this study.—*Eckhard Wollenweber, Institut für Botanik, Technische Hochschule Darmstadt, Schnittspahnstrasse 3, D-6100 Darmstadt, Federal Republic of Germany* and *Dale M. Smith, Department of Biological Sciences, University of California, Santa Barbara, CA 93106.*

A MAJOR RANGE EXTENSION FOR THELYPTERIS SIMULATA IN THE SOUTHERN APPALACHIANS.—Recently, while examining fern specimens in the Illinois Natural History Survey Herbarium (ILLS), I found a collection of *Thelypteris simulata* (Davenp.) Nieuwl. collected in August 1931 at New Found Gap, Sevier Co., in eastern Tennessee at the North Carolina border (*Pepoon 935*). Herman S. Pepoon was a botanist from Chicago, Illinois and the author of "Flora of the Chicago Region." Pepoon himself had identified the specimen as *Aspidium simulatum* Davenp., and wrote on the label that the plant occurred at "summit elevations, damp woods near New Found Gap." Pepoon deposited several hundred specimens from eastern Tennessee in ILLS, and it is unlikely that a person of his competence would have correctly identified this unusual fern and then would have made a gross error in describing its location. Furthermore, Pepoon's collecting notebooks, which are preserved at ILLS, show that he did not collect in west-central Wisconsin or in the New England states from which this fern presently is known. Thus, it seems unlikely that the specimen represents a false record due to a label mix-up.

The specimen is significant because it represents a disjunction of about 400 miles from the nearest station recorded for this species, which is in northern West Virginia (Tryon & Tryon, Amer. Fern J. 63:66. 1973). In addition, this find may bear upon the species distribution during the late Pleistocene; it seems likely that *T. simulata* was present and probably more widespread in the southern Appalachians during Wisconsinan glacial times, and then gradually became restricted to higher elevations and latitudes as the climate changed and the glaciers receded during the Holocene. Although long-distance spore dispersal can never be completely ruled out, it seems unlikely. Many other pteridophytes show a similar widespread distribution in the north and become gradually restricted or disjunct at high elevations southward in the Appalachians, including *Botrychium matricariifolium B. multifidum, Dryopteris campyloptera, Gymnocarpium dryopteris, Lycopodium annotinum, L. selago*, and *Phegopteris connectilis*. I encourage pteridologists to look for populations of this interesting species in acid, boggy areas at high elevations in the Great Smoky Mountains region.—*Robbin C. Moran, Herbarium, Illinois Natural History Survey, Natural Resources Bldg., 607 E. Peabody Dr., Champaign, IL 68201.*

A NEW INDIANA STATION FOR EPIPHYTIC RESURRECTION FERN.—In 1975, the author discovered a large, healthy population of *Polypodium polypodioides* (L.) Watt growing approximately 30 feet up on a branch of a dead tree at Carnes Mill, Crawford County, Indiana. Hemlock (*Tsuga canadensis*), Yellow Buckeye (*Aesculus octandra*), and Goatsbeard (*Aruncus dioicus*) flourish on the sandstone cliffs and the tight valley slopes encasing the Little Blue River at this point. Although commonly found at similar heights in the south, literature research indicates that this is a relatively rare habitat in the interior northern reaches of this fern's range. It is reported by Deam (Flora of Indiana, 1940) from nine counties in southern Indiana. He stated that he once found it growing in the crotch of a Bur Oak tree in Wabash County, but that "this is the only specimen I have ever seen growing on a tree in Indiana, although it is common in this habitat in the south." Welch in Lindsey (The Natural Features of Indiana, 1966) stated that she had not seen the Resurrection Fern growing on a tree in Indiana.—*Ronald R. Van Stockum, Jr., 810 Kentucky Ave., Frankfort, KY 40601.*

AMERICAN FERN JOURNAL

Manuscripts submitted to the JOURNAL are reviewed for scientific content by one or more of the editors, and, often, by one or more outside reviewers as well. During the past year we have received the kind assistance of J. D. Caponetti, A. M. Evans, R. L. Petersen, H. E. Robinson, R. G. Stolze, W. C. Taylor, R. A. White, D. P. Whittier, and J. J. Wurdack, to whom we are deeply indebted. We welcome suggestions of other reviewers.—*D.B.L.*

INDEX TO VOLUME 71

ERRATUM FOR 1980

Page 67, line 39: For "39: in press." read "n.s. 6:210–238."
