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**A MONOGRAPHIC STUDY OF THE FERN GENUS
CYSTOPTERIS**

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INTRODUCTION

The apparent differences in the form of sori have been in many cases the basis for referring species of *Cystopteris* to other genera. For example, before it was recognized as a distinct genus in 1806, Linnaeus in his *Species Plantarum* (1753) had included two species in the genus *Polypodium* because of the round sorus. Smith (1793) included *Cystopteris fragilis* in *Cyathea* because its bladder indusia resembled the globose indusium of his new genus. Others, including Bernhardt (1802) who referred *Cystopteris bulbifera* to *Cyathea*, continued this practice. Swartz (1801) included three *Cystopteris* species in his genus *Aspidium* which was later construed in various ways making it a mixture of diverse elements.

Bernhardt (1806) was the first to recognize the characteristic indusium and its position of attachment to the receptacle. As a result he created the genus *Cystopteris* and transferred *Aspidium fragile*, *montanum* and *bulbiferum* to it.

In the comprehensive work *Tentamen Pteridographiae* by Presl (1836) *Cystopteris* was maintained as a distinct genus and was placed in section *Cystopterideae* of the tribe *Aspleniaceae*. This designation reflected the globose, laterally attached indusium.

Hooker, in his *Genera Filicum* (1842) followed Presl's treatment, placing *Cystopteris* near genera such as *Acrophorus* and *Leucostegia* based on the indusial position. This relationship was again indicated in Hooker's *Species Filicum* (1846).

The next major change in the expression of generic relationships of *Cystopteris* was that of Christ (1897) who placed this genus with *Hypoderris*, *Woodsia* and others in the family *Aspidiaceae*. Diels (1902) essentially followed this same treatment.

The concept of Bower (1928) in regard to *Cystopteris* relationships was that this genus is near the Cyatheoid derivatives, namely the Woodsioid and Dryopteroid ferns. Christensen (1938) placed *Cystopteris* with *Athyrium* in the subfamily *Asplenoideae*. Ching (1940) followed this same concept by placing *Cystopteris* in his family *Aspleniaceae*, tribe *Athyrieae*.

The most modern comprehensive treatise on fern genera is that of Copeland (1947). He places *Cystopteris* within the largest of his families, the *Aspidiaceae*, which includes such genera as *Athyrium*, *Dryopteris* and *Woodsia*.

A more recent classification by Holttum (1949) places *Cystopteris* in the subfamily *Athyrioideae* of his diverse family *Dennstaedtiaceae*. He believed that there is evidence that these elements arose from a primitive type resembling *Dennstaedtia* but have now become widely divergent.

The postulation of generic relationships is probably beyond the scope of this study, which deals exclusively with the infrageneric categories of *Cystopteris*. However, in studying the apparently primitive members of the genus, it becomes apparent that there are similarities with other genera, primarily *Athyrium*, *Dryopteris* and to a lesser extent *Woodsia*.

The initial plan of this investigation was merely to study the widely variable *Cystopteris fragilis* in an attempt to evaluate whether it is one species or, in fact, a group of superficially similar species. Early in the study, however, it became evident that there are apparently several distinct species; and that the variability of *C. fragilis* is due in part to intergradation and presumed hybridization between rather similar, although recognizable, species. Consequently, it seemed necessary to expand this investigation to cover the entire genus *Cystopteris* in all parts of the world. Some 5,000 specimens were examined altogether; and extensive anatomical studies, primarily with stained clearings of the pinnae, were undertaken to compare technical features of the indusium, laminar hairs, and epidermis of the different taxa. In addition, gametophyte cultures were made; and cytological observations were obtained from living plants procured in diverse areas of the globe. New studies of spore size and spore architecture revealed interesting and pertinent additional facts. A considerable mass of new data was thus brought to bear on the solution of problems in this genus. As a result of these new data, some rather major revisions of the taxonomy of *Cystopteris* had to be made.

In this treatment of the genus *Cystopteris* two subgenera are recognized for the first time, namely subgenus *Cystopteris* and subgenus *Acystopteris*. This subdivision has been made necessary because of the inclusion of two species from eastern Asia which are distinct in most of the diagnostic characters but which have in common with other species of *Cystopteris* two basic features. The subgenus *Cystopteris* has been subdivided into two sections, *Cystopteris* and *Emarginatae* in order to separate two postulated evolutionary lines within the genus. Two binomials have been omitted from this treatment because of the lack of authentic specimens, namely *Cystopteris tasmanica* Hooker and *C. mairei* Brause. *Cystopteris tasmanica* may very well be identical with *C. fragilis* var. *apiiformis* of this treatment. The original description of *C. mairei* indicates a close similarity with *C. sudetica* var. *moupinensis*.

Both herbarium specimens and living plants were studied during this investigation. Herbarium specimens were obtained from nine herbaria. In addition about one hundred and twenty-five living specimens were obtained in the United States and from various parts of the world.

As an important part of this investigation dealt with the anatomy of the pinna, the clearing technique of Foster (1949) was used to great advantage.

After the clearing process was completed, the pinnae were placed temporarily in a Clorox solution to remove any remaining coloration. Following rinsing in water they were ready for staining. The stain which was used exclusively with the pinnae was the ferric chloride-tannic acid stain of Foster (1934). This procedure was modified to the extent of substituting 50% alcohol solutions for aqueous solutions. This change appeared to give a more even stain to the tissues. While most of the pinna anatomy could be observed on the intact pinna, there were occasions when the indusia could not be induced to lie flat. In such cases it was necessary to dissect individual sori from the pinna and to mount them on a slide.

The gametophyte cultures were grown on sterilized soil in pots. They were kept at room temperature in a moist chamber and were placed near a north-facing window. Spores for studying the early stages of germination were grown on the surface of Modified Knop's Solution (Bold 1936).

The cytological material for the determination of chromosome number at meiosis was obtained from plants which were grown at the University of Michigan Botanical Gardens under relatively uniform conditions. Very young fertile fronds were placed directly into Newcomer's Fixative (Newcomer and Brant 1954). The contents of several sori were placed in a drop of acetocarmine and after covering with a coverslip, the squash technique was applied (Manton 1950).

All drawings, with the exception of spore and chromosome figures, were made with the aid of a microprojector. The spore and chromosome figures were traced by camera lucida. The silhouettes of leaves were obtained by following the technique outlined by Manton (1950).

MORPHOLOGY AND ANATOMY

The application of technical details of morphology, anatomy and cytology to the taxonomy and systematics of ferns has been a relatively new innovation. As recently as the 1920's the great bulk of taxonomic treatments dealing with this group were strictly on the basis of gross morphology. To be sure, there had been papers before this time which dealt with isolated morphological and anatomical problems. One example of this type of work is the series of papers on bulblets which appeared at the end of the nineteenth century. Matouschek (1894), Rostowzew (1894), Stevens (1898), Heinricher (1896, 1899, 1900) and Palisa (1900) all studied the morphologically interesting bulblets which are a means of vegetative reproduction in *Cystopteris bulbifera*. These papers, however, deal primarily with developmental and experimental morphology, and do not attempt to discuss taxonomic implications.

The first comprehensive work in which other disciplines were utilized in a taxonomic treatment of ferns was that of Bower (1923-28) in which detailed anatomy and morphology was applied. This type of approach has been continued recently with amplifications in various generic treatments, for example Wagner (1952) on *Diellia*, Brown (1958) on *Woodsia*, Tryon (1957) on *Pellaea* and Kramer (1957) on *Lindsaea*.

Spores

The spores of *Cystopteris* have been studied by several workers in attempts to determine whether the spines which are characteristic of most of the species are associated with the exospore or with a perisporial covering. Luerssen (1889) merely referred to the spines as being associated with the exospore. Hannig (1911), McVaugh (1935) and Christensen (1938) have indicated that the spores lack a perispore, thus supporting the view that the spines are part of the exospore. The opposite view is taken by Selling (1946) who, in working with the Hawaiian species *Cystopteris douglasii*, found that "the spiny sculpture seems to be part of a perisporial covering." Indeed his figure of the spore, which was prepared by the acetolysis method, which commonly removes the perispore, shows the spines to be lacking.

In an attempt to resolve this apparent difference of opinion, spore samples of four species were prepared by the acetolysis method. A sample of *Cystopteris* \times *alpina* spores, which have the architecture characteristic of the majority of *Cystopteris* species, retained the spines after treatment, as did also *C. douglasii*. *Cystopteris japonica* spores also retained their characteristic architecture. On the other hand, a sample of the rugose spore type from *C. fragilis* shows a smooth exospore on which is superimposed a layer which gives the rugose architecture typical of this variety. However, as this outer layer was not removed by the acetolysis technique, one must assume that it may not be a perisporial layer but in fact an integral part of the exospore.

There are three distinct types of exospore architecture within the genus *Cystopteris*. The condition common to the majority of species is that of the echinate spore. The extreme examples of this type are found in the *C. fragilis* complex and *C. diaphana* where the spines are long-attenuate with acute apices (Plate 15, fig. J). Other species such as *C. bulbifera*, *C. montana* and *C. sudetica* possess spores which have a tendency toward shorter spines with the apices of these spines being more rounded (Plate 15, fig. E).

The second type of spore architecture is that which differentiates the plant formerly treated as *Cystopteris dickieana* (but here treated as a

form not worthy of taxonomic designation) from *C. fragilis*. This is the rugose spore (Pl. 15, fig. Q) which resembles closely the spores found in such genera as *Athyrium*, *Dryopteris* and *Woodsia*. It might be appropriate here to suggest the possibility that this spore type may have been possessed by the stock which gave rise to the above genera and *Cystopteris* and is now only of limited occurrence in *Cystopteris*. It is interesting to note that in occasional specimens of *C. montana* the spores approach the rugose condition though they do not duplicate it exactly.

Also, Hagenah (1961), in his extensive studies on the "dickieana" spore type in North America, finds that there is a rather complete transition series between the rugose and the echinate spore within the *C. fragilis* populations. I likewise have found intermediates both in the United States and Europe. Thus, while most specimens may be identified with the respective spore form, there are some populations which become problematical.

The third spore type is found in the subgenus *Acystopteris*. This group of two species is different from the rest of the genus in several respects, of which the architecture of its spores is very distinctive. The projections of the spore are not approximately cylindrical as in subgenus *Cystopteris* but are highly irregular as seen in cross-sectional outline (Pl. 15, fig. F-H).

All three spore types are bilateral and monolete. The shape of the spores is somewhat variable, ranging, depending on the view, from oval to the more general "bean-shaped" outline.

An "average" spore size is not obtainable for the majority of *Cystopteris* species. The reason for the variation is primarily the presence of polyploid series with variations in chromosome number which results in changes in spore size. This phenomenon is treated in the portion of this paper dealing with chromosomes and spore-size.

Gametophyte

The fresh spores of *Cystopteris* require approximately three weeks to germinate. This period, however, may be as much as two weeks longer when older spores are utilized. Viability decreases as the spore age increases and spores over one year old have a very low germination percentage.

The germination of *Cystopteris* gametophytes is very similar to that described for other leptosporangiate ferns, e.g. *Diellia* (Wagner, 1952) and *Woodsia* (Brown, 1958). The exospore cracks open near the central region of the spore in an irregular manner exposing the protoplast which is crowded with chloroplasts. Soon after the exposure of the protoplast, a rhizoid is produced as an extension of the cell wall (Pl. 16, fig. A, B). In fact, two rhizoids have been observed on the initial cell before any further

development of the gametophyte occurs. These rhizoids are unicellular and lack chloroplasts. Under what are assumed to be normal growing conditions (northern exposure and lack of crowding) the cells of the filamentous stage number from two to four with the cells remaining a roughly oval shape. This stage may, however, produce a much extended series of elongate cells under crowded conditions.

Subsequently the lateral expansion of the prothallus is attained by the formation of a longitudinal wall in the terminal cell by lateral divisions of an apical cell and by the creation of an apical meristem (Pl. 16, fig. H-M) similar to that described by Stokey (1951).

The mature gametophytes resemble closely those typical of the higher leptosporangiate ferns (Pl. 17, fig. A). The outline is roughly cordate with broad wings extending to either side of the apical notch. The prothallus is only one cell thick with the exception of the archegonial cushion which is two or three cells thick. The superficial cells and (more commonly) the marginal cells may possess unicellular hairs of the papillate type as described previously by Stokey (op. cit.).

Gametophyte cultures of five species (*Cystopteris fragilis*, *C. douglasii*, *C. protrusa*, *C. diaphana* and *C. bulbifera*) and two putative hybrids (*C. × alpina* and *C. × tennesseensis*) have been grown in an attempt to find specific differences within the gametophyte generation and to determine whether apogamy occurs. All of the taxa examined are similar in the bulk of their gametophytic features and none were apogamous.

There is one aspect of *Cystopteris* gametophyte morphology however which has yielded differences, but as only a few species and populations have been cultured, no definite conclusions can be made as yet. The differences which have been observed concern the abundance and position of papillate hairs on the prothallus. Within the *Cystopteris fragilis* complex (*C. fragilis* and *C. douglasii*) these hairs arise relatively late in the development of the prothallus and they are very sparse (Pl. 17, fig. E). They have not been observed on superficial cells, and appear to be limited to the marginal cells. The marginal cells on which the hairs occur give a smooth outline to the prothallus.

On the other hand, the culture of *Cystopteris diaphana* shows that the hairs appear soon after the cell plate stage is initiated and they are more numerous, being primarily on the marginal cells but occurring also on some superficial cells. The marginal cells do not give a smooth outline to the prothallus and the marginal hairs are most commonly superimposed on cells which extend outward from the main mass of the prothallus (Pl. 17, fig. D) thus forming a rather irregular outline. The hairs are also somewhat longer and narrower than those in the *C. fragilis* complex. A similar distribution of hairs has been observed in the gametophyte of *C. ×*

alpina (which is intermediate between *C. fragilis* and *C. montana* and is presumed to be their hybrid) although the features of the margin are not as striking as that in *C. diaphana*. It might be justified to postulate then that *C. montana* has a gametophyte trichome orientation similar to that of *C. diaphana* though this fact is yet to be determined experimentally.

The sex organs of *Cystopteris* have not been examined critically as they appear to have developmental patterns similar to those of the majority of higher homosporous leptosporangiate ferns. The antheridia originate on the ventral surface among the rhizoids before the archegonial cushion is completely developed. They mature about four to five weeks after spore germination under normal growing conditions and are fully developed well before the archegonia are receptive to sperm. Gametophytes may thus be entirely antheridial when young. This condition may also result from crowded culture conditions or from the reduction in the amount of light available to the prothallus as stated by Stokey (1951). Schlumberger (1911) reported that *C. fragilis* and *C. montana* possess antheridia with undivided cap cells only, unlike the related *Woodsia* and other genera in which the cap consists of two cells.

Under the conditions of culture used in my work the archegonia appear approximately six weeks after spore germination on the ventral surface of the archegonial cushion just below the apical notch. Within six weeks after the appearance of archegonia, sporophytic development is evident providing there has been an adequate water film available so that sperms could swim to the archegonia. This film was created by flooding the culture dishes with water after both sex organs were mature.

The Young Sporophyte

The initial stages of sporophyte development in *Cystopteris* are essentially the same in those species which were observed, namely *C. bulbifera*, *C. fragilis* and *C. × tennesseensis*. The following discussion of the developmental sequence in *C. × tennesseensis* may therefore be applied in a general manner to that of the other species in the subgenus *Cystopteris*. The sporophytic development in the subgenus *Acystopteris* has not been examined to my knowledge.

The first evidence of embryonic activity is the appearance of a protuberance on the ventral surface of the prothallus in the cushion region. The first frond emerges and grows toward the notch between the prothallial lobes. At the same time the first root appears and grows toward the base of the prothallus though its growth is soon directed toward the substrate.

The first frond has a twin-lobed blade with dichotomous venation (Pl. 18, fig. A). (The difference in vein position relative to the margin, which

distinguishes section *Cystopteris* from section *Emarginatae*, appears on the earliest leaf stages in my cultures of *C. fragilis* and *C. × tennesseensis*.) The stipe is heavily clothed with hairs of two types, the multicellular glandular hair and the unicellular glandular hair (Pl. 9, fig. E 2, 3). The multicellular glandular hair type is more abundant toward the base of the stipe and becomes sparse to lacking toward the blade. Occasionally these hairs have superimposed on them the unicellular hair type and may result in a rather complex branched hair (Pl. 9, fig. E 6). The unicellular glandular hair is prevalent throughout the length of the stipe and is widely distributed on both the superficial and marginal cells of the blade. For the most part this hair type is unicellular although occasionally there are two-celled transitional hairs. True scales are entirely lacking on the stipe of the initial frond and, in fact, do not appear until the development of the fourth or fifth frond.

The succeeding steps of the heteroblastic series of leaves (Pl. 18) show the usual transitions to a pinnately organized blade. The apparent overtopping of a vein and expansion of the lamina within one of the two blade lobes results in a three-lobed blade. Subsequent overtopping in sequence gives rise to the pinnate condition common to the genus *Cystopteris*.

The Mature Sporophyte

Root. The roots of the genus *Cystopteris* are fibrous and originate singly at a position on the rhizome which is below the attachment region of each stipe. Numerous very narrow lateral branch roots are borne along the main root axis. The roots of four species (*C. sudetica*, *protrusa*, *bulbifera*, *japonica*) have been examined superficially in order to detect differences, if present, in their anatomy but were found to be very similar in their cross-sectional plan. The outline of the cross section is circular, although the stele is somewhat elliptical. The outer three or four layers of cortical cells are rather heavily sclerified though not totally occluded. The stele is diarch with a group of protoxylem elements at each end of the elliptical stele. The bulk of the xylem is composed of two large metaxylem elements in the species examined with the exception of *C. japonica* in which there were four conspicuous metaxylem elements. This discrepancy may, however, be due to the fact that the roots of this species are more robust and thus have a greater diameter.

Rhizome. The rhizomes of species of the genus *Cystopteris* are primarily wide-creeping, with the exception of *C. fragilis* and *C. bulbifera* where the internodes are very short and the rhizome is essentially sub-erect. The rhizome internodal length of the wide-creeping species varies greatly. In the case of *C. montana*, *C. sudetica* and its Asiatic derivatives the internodal

length is considerable, being from one to three and one-half centimeters. The rhizome of these species ranges up to two millimeters in diameter and has a cord-like aspect. On the other hand, the rhizome of *C. bulbifera* is so thickly beset with stipe-bases that it is only by removing them that the true extent of the rhizome proper may be observed. *Cystopteris protrusa*, *C. douglasii* and *C. japonica* are intermediate in internodal length and have a more robust rhizome, that of *C. japonica* having a diameter of six to eight millimeters or greater.

The internal anatomy of the *Cystopteris* rhizome has been summarized by Ogura (1938). He places the genus with a group of others, including *Woodsia*, *Dryopteris*, *Athyrium* and *Asplenium*, which have in common the possession of a radially arranged true dictyostele. This organization is found in plants with erect as well as creeping stems.

The rhizomes of *C. japonica*, *C. sudetica*, *C. protrusa*, *C. bulbifera* and the apparent introgressant *C. diaphana* \times *fragilis* (traditionally referred to as *C. fragilis* var. *mackayi*) have been examined during the course of this study. In the first three species the radial dictyostele is clearly discernible because the internode distance is relatively great. However, in *C. bulbifera* and to a lesser extent in *C. diaphana* \times *fragilis* a radially organized dictyostele is rarely observed in its entirety because of the short internodes with resultant increase in the number of leaves arising in any given section.

A series of rhizome cross sections have been examined for the species *Cystopteris protrusa* in order to examine the mature anatomy. The cross section of the rhizome proper is roughly a triangle with rounded points, its greatest dimension being between two and three millimeters, depending on its age. The outermost two or three layers of cells are rather heavily sclerified. Within this sclerified layer lies a rather uniform parenchyma ground tissue in which the stelar bundles are arranged radially. The stele is approximately 1.0 mm. in diameter and shows three stelar bundles. The meristemes are oval in outline, being 0.25-0.35 mm. broad and 0.14-0.20 mm. wide.

The dictyostele of *C. protrusa* was dissected out of such a rhizome (by treatment in sodium hydroxide and subsequent boiling) and the gaps were observed to be 1.3-1.8 cm. in length. Near the median position of each gap a double trace arises, one from each side of the gap, and extends into the frond. At the base of the gap arises the trace of the root which accompanies each frond.

Scales of Rhizome and Stipe. The scales which invest the rhizome and basal stipe region in *Cystopteris* differ rather markedly in the various species groups. Primarily they are ovate-lanceolate on the rhizome and become progressively more linear-lanceolate as they extend up the stipe.

The stipe scales show various degrees of cell-wall thickening. Rather thick-walled and sometimes completely occluded cells occur in such species as *C. fragilis*, *C. douglasii*, and *C. bulbifera*. In *C. sudetica* and its Asian relative *C. pellucida* the lateral walls have become uniformly thickened and thus these scales have attained the clathrate condition (Pl. 7, fig. G) which is a distinctive characteristic of several fern families including *Aspleniaceae* and *Vittariaceae*. On the other hand, scales of *C. protrusa* and *C. montana* show relatively little lateral-wall thickening.

The presence of glands on the scales is a rather widespread phenomenon within the genus *Cystopteris* and is considered by the present author to be the primitive condition. The unicellular glands are primarily marginal although superficial glands have occasionally been observed. Glands are present on scales of both species within the subgenus *Acystopteris*. They are also universally present in *C. montana* and *C. sudetica* var. *sudetica*. The Asian relatives of *C. sudetica*, namely *C. sudetica* var. *moupinensis* and *C. pellucida*, have scales without glands. In *C. diaphana* the European and African specimens are generally glandular and this condition is carried over to the scales. However, the Central and South American plants more frequently are eglandular although some glandular specimens have been observed from this region. No members of the complex strictly centering around *C. fragilis* (*C. protrusa*, *C. fragilis*, *C. douglasii*) have been observed to possess glandular scales.

In certain collections, structures intermediate between scales and hairs have been observed in the lower rachis region (Pl. 7, fig. E 4). However they are sporadic and do not seem to be constant for any given species.

The Leaf and its Parts. *Leaf Axis.* The stipe itself does not possess any distinctive features in the various species of *Cystopteris* other than pigmentation, average diameter, and length relative to the blade. These features have been utilized in the segregation of species. A dark almost ebony pigment has apparently evolved separately in two distinctly different *Cystopteris* groups and this condition is considered to be the advanced or derived condition. *Cystopteris japonica* in the subgenus *Acystopteris* possesses this feature which immediately separates it from the other Asiatic species, *C. tenuisecta*, with its stramineous stipes. This pigmentation does not appear until the frond is almost completely expanded. It then advances upward from the base of the stipe and in about fifteen days is characteristic not only of the stipe but also of the rachis and the major axes of the pinnae.

The only other species in which this dark pigmentation occurs is *Cystopteris fragilis*. The distribution of this condition geographically is somewhat sporadic, however, and may be due in part to environmental conditions. It has been observed in plants from northwestern India, eastern Africa,

Europe, along the Andean mountain chain in South America and in Central America. The stipe color in the majority of *C. fragilis* specimens examined by me has been the stramineous or light tan coloration which is characteristic of the remaining species within the genus.

All members of the genus *Cystopteris* possess stipes which are adaxially sulcate. The stipe length ranges from 2.5 centimeters in Alaskan specimens of *C. fragilis* to about 45 centimeters in *C. tenuisecta*. The basal stipe diameter ranges from 0.5 millimeters in some *C. fragilis* specimens to 5.0 millimeters and greater in the Asiatic *C. tenuisecta*.

The relative length of the stipe as compared with that of the blade is rather distinctive in certain of the species. *Cystopteris montana* and *C. sudetica* have stipes which may be as much as two or three times as long as the blade. At the other extreme are *C. fragilis* and *C. diaphana* in which the stipe are almost universally shorter than the blade.

In his treatment of the vegetative anatomy of the pteridophytes, Ogura (1938) describes the internal anatomy of the *Cystopteris* stipe. He stated that the stele consists of two meristeles whose abaxial ends unite with each other in the stipe or in the rachis, so that the stele here forms a V-shape in cross section. Both xylem ends of each meristele are curved into hooks.

The region of the stipe at which the two bundles unit has been used by Shaver (1949) as a character to segregate species. He finds that the bundles are free throughout the stipe in *C. fragilis* and *C. bulbifera* while they are united into a flattened V in *C. protrusa*. So far as I have been able to determine, however, comparable fronds from different species are essentially alike. This character is rather hazardous to use in separating species because the stelar condition fluctuates greatly according to the size of the leaf. Thus a juvenile type of frond of *C. bulbifera* has been observed to have the two bundles united a full one and one-quarter inches below the basal pinna. Cross sections of the stipe of a sterile adult-type frond of *C. sudetica* show the bundles to be free throughout, finally joining in the rachis one-quarter inch above the basal pinna.

In addition to scales which are primarily limited to the rhizome and basal stipe region, three other structures may be present on the frond axis of *Cystopteris*, namely multicellular non-glandular hairs, uni- and multicellular glandular hairs, and vegetative propagules or bulblets.

The multicellular non-glandular hairs are confined, in this genus, to the subgenus *Acystopteris*. Being relatively large, these hairs are visible without magnification. They occur primarily on the frond axes (the rachis, pinna axis and along veins) although they do arise also superficially on both laminar surfaces. The number of cells making up the hair range from seven to twelve (Pl. 10, fig. E).

The unicellular glandular hair is very prevalent on the rachis and minor axes of glandular species of *Cystopteris* and thus is rather widespread in the genus (Pl. 11, fig. E 2-4). Occasionally unicellular hairs are superimposed on the multicellular glandular hairs. Their abundance on individual plants, however, varies considerably and there may commonly be only one or two multicellular glands on a given pinna. The other extreme is that in which the rachis is rather heavily beset with these glands and this led Milde (1867) to place plants possessing this condition in a distinct variety, *C. fragilis* var. *huteri*.

Vegetative propagules occur within the genus *Cystopteris* only in *C. bulbifera*. The stage in origin and development of these propagules has been described in detail by Rostowzew (1894). These "bulblets" occur abaxially primarily near the attachment region of the upper pinnae with the rachis. They sometimes arise, however, on axes of the pinnae. The bulblets are composed of two green fleshy "cotyledons" between which, after the bulblets fall in an appropriate spot, a new sporophyte plant arises. These young plants assume mature features very rapidly and one has been observed in which the first frond (measuring 8.0 mm.) already possesses four sori. The bulblets of *C. bulbifera* are typically glabrous (well illustrated by Geske, 1925) but may also possess a few scales and they abscise readily from the parent frond. However, the apparent hybrids of *C. bulbifera* with *C. protrusa* and *C. fragilis* produce bulblets which remain firmly attached to the frond at maturity. Furthermore they may be covered with dark scales. They are also more or less irregular in form and Wagner and Hagenah (1956) report that there is a tendency for sporangia to occur around the sides and base of the hybrid bulblets.

Much experimental work has been undertaken with vegetative regeneration in the genus *Cystopteris*. This research has probably been stimulated in part by the presence of bulblets in *C. bulbifera*. Heinricher (1896) studied the effects of drying on the bulblets and (1900) reported having obtained the development of adventitious buds on isolated basal parts of the fronds of *C. montana*, *C. fragilis* and *C. alpina*. He also demonstrated that the isolated so-called "cotyledons" of bulblets of *C. bulbifera* will give rise to adventitious buds. Palisa (1900) demonstrated that these buds, whose position is not predetermined, arise from the proliferations of epidermal cells. Lawton (1936) has studied regeneration phenomena in *C. fragilis*.

General Blade Pattern. There are two blade patterns represented within the genus *Cystopteris*. The deltoid outline results from the fact that the basal pinnae are longer than the subsequent pinnae. This frond plan is characteristic of the whole subgenus *Acystopteris* (Pl. 10, fig. A) and the subgenus *Cystopteris* section *Emarginatae* with the exception of *C. dia-*

phana. In addition, it is found in *C. protrusa* and *C. douglasii*. *Cystopteris bulbifera* possesses a modification of this plan in which the apex of the frond is greatly attenuated. The lanceolate plan results when the basal pinnae are shorter than the pinnae directly above them. This plan is represented by *C. diaphana* and *C. fragilis* (Pl. 2, fig. A).

The blade of *Cystopteris* ranges in length from 2.5 cm. in *C. fragilis* to 50 cm. in *C. tenuisecta* and these two species also represent the extremes in blade width.

Pinnation and Venation. The extent of blade dissection varies somewhat even among individual species of *Cystopteris*. Thus *C. fragilis* forms occurring in Alaska, are once-pinnate whereas specimens from Greece may be delicately cut and tripinnate. Specimens of *C. tenuisecta* may be as much as quadripinnatifid (Pl. 11, fig. A).

The range in number of pinna pairs per frond is even more striking within the genus. Mature fronds of *C. fragilis* may have as few as seven pinna pairs whereas *C. bulbifera*, with its attenuate frond, may have as many as 30 or more pairs (Pl. 8, fig. A). The pinnae may be subopposite or alternate on the same frond. The pinnules are arranged anadromically on the pinnae throughout the genus without exception.

The veins within the pinnules are free and branch in an approximately dichotomous manner. In all members of the genus *Cystopteris* with one exception, the elongate epidermal cells which are superimposed on the veins extend to the cells that make up the pinna margin (Pl. 9, fig. C). The exception is found in the southern hemisphere populations of *Cystopteris fragilis* which inhabit New Zealand, the extreme southern tip of South America, the Falkland Islands and South Georgia. In these regions the elongate epidermal cells stop two or three cells short of the margin and normally lobed cells are intercalated between them and the marginal cells. This latter condition resembles very closely that which Brown (1958) reported as being characteristic of the entire genus *Woodsia*.

The position of the vein endings at the margin of the pinna has been found to be extremely important in species descriptions and in the expression of species relationships within the genus *Cystopteris*. In the majority of the species the veins are directed into conspicuous emarginations (Pl. 8, fig. C). This phenomenon is very precise and does not deviate within a species! However, one section of the genus, including *C. protrusa* and *C. fragilis*, has veins which (with rare exceptions) run into the tips of marginal teeth (Pl. 2, fig. C 1-2). The vein endings in subgenus *Acystopteris* are more difficult to interpret in this manner since the lobes of the pinnae are rounded instead of having definite teeth (Pl. 10, fig. C) but they are apparently intermediate in this character.

Laminar Anatomy. Features of the laminar anatomy of *Cystopteris*, namely the epidermis and occurrence of hairs, have been investigated critically in an attempt to find characters of specific distinction. Of these the characteristic patterns of the adaxial epidermal cells were found to be most rewarding. The subject of hair types has been considered in the section dealing with the leaf axis.

Within the subgenus *Cystopteris* there are two distinct upper epidermal cell outlines which may be used to distinguish two very much confused species. *Cystopteris diaphana* has epidermal cells which possess smooth or merely undulating outlines (Pl. 9, fig. B 2). This is in marked contrast to the condition in *C. fragilis* where the upper epidermal cells have outlines reminiscent of pieces in a jigsaw puzzle (Pl. 2, fig. B 2 and 4). Introgressant populations involving these two species show varying degrees of intermediacy in their cell outline. The other members of section *Cystopteris* also possess these lobed epidermal cells. The remaining members of the subgenus show intermediacy in the degree of epidermal cell lobing (Pl. 8, fig. B 2).

The subgenus *Acystopteris* is characterized by the fact that the epidermal cells are on a much more diminutive scale (Pl. 10, fig. 2 and 4) than in plants with corresponding polyploid levels in the subgenus *Cystopteris*. Correlated with this reduction in epidermal cell size is the reduction in guard cell size.

The stomata occur exclusively on the abaxial laminar surface. They vary greatly in size depending on their position, those near the veins and along the margins tending to be smaller than those in the intervenal areas. There is some correlation between polyploidy and stomatal size. The plants with high polyploid levels (Pl. 2, fig. B 1) tend to have larger stomata than the diploid plants (Pl. 8, fig. B 1).

The marginal cells of the lamina are rather uniform throughout the genus *Cystopteris*. They present a rather jagged circumference (Pl. 9, fig. C), when viewed under magnification, similar to that found in some species of *Woodsia* (as illustrated by Brown, 1958). This is a totally different aspect from the species of *Athyrium* (a genus believed to be closely related) which have been examined where the marginal cells are so uniform that one cannot determine, by observing merely the edge of the pinna, where one cell ends and the next one begins.

The Sorus. The development of the sorus in *Cystopteris* has been studied by Goebel (1915) and Bower (1928) among other workers. Goebel, in studying an early stage of the sorus in *C. montana*, found as follows:

Angelegt wird die Placenta—deren Entwicklung nicht lückenlos verfolgt wurde—entweder aus dem Blattrand oder in dessen nächster Nähe auf der Blattunterseite, auf der auch bald das Indusium hervorsprosst.

Die Entwicklung (oder Weiterentwicklung) des Blattrandes wird aber zunächst gehemmt, während die Placenta ziemlich stark anschwillt, tritt der letztere kaum hervor, erst später nimmt er sein Wachstum auf und schiebt dann den Sorus ausgesprochen auf die Unterseite.

Thus Goebel finds the sorus to be essentially a marginal sorus which is later forced to the lower surface by marginal growth. Bower, who studied the young leaf margin of *C. fragilis*, also found the young sorus in close proximity to the margin. He further states: "The facts of development of the sorus in *Cystopteris* thus show a near similarity to those seen in *Lindsaya*, which is held to be a Davallioid derivative: in fact a marginal type." No further studies of soral ontogeny in *Cystopteris* have been made since the studies of Bower.

The fully developed sorus of *Cystopteris* is clearly superficial, however, and is a mixed sorus. It is inserted abaxially and is dorsal on a vein which then continues to the margin of the pinnule. The indusium is attached at the basal portion of the receptacle nearest the pinnule axis and forms a hood which covers the young sporangia. It is free toward the pinnule margin (Pl. 11, fig. D).

The extent of indusial attachment to the base of the receptacle varies within the genus. In *C. fragilis* the attachment region may cover only one-third of the receptacular circumference (Pl. 2, fig. D) while *C. bulbifera* and *C. pellucida*, with their very broad indusia, may extend about two-thirds the distance (Pl. 6, fig. D).

Indusial size, though relatively constant for a given species, differs within the genus. *Cystopteris japonica* possesses such a minute indusium that its protective function, if any, can be available only during the initial developmental stages of the sorus. Indeed, the mature sporangia must be removed in order to observe the indusium (Pl. 10, fig. D). *Cystopteris protrusa* possesses a very delicate and frequently fugacious indusium. In the remaining species, on the other hand, the indusium is more readily evident at all stages of maturity.

The shape of indusial cells aids materially in clarifying the taxonomic elements which have been relegated, in the past, to *Cystopteris fragilis*. An examination of indusial cells of *C. fragilis* shows very narrow linear cells with a rather orderly arrangement. As the sorus matures, mechanical breakage occurs along the longitudinal walls of the cells, especially at the indusium apex. This breakage results in the lacerate indusium which has frequently been described as typical of the species (Pl. 2, fig. D). The *C. diaphana* indusium, on the other hand, is composed of shorter and broader cells, and there appears to be very little tendency for splitting of the indusial apex, so that a relatively entire indusium results (Pl. 9, fig. D).

Cystopteris fragilis and *C. douglasii* have frequently been observed to

possess accessory hairs attached toward the base of the indusium's outer surface. There may be one or more hairs present (Pl. 2 and 4, fig. D). Once a well organized structure resembling a miniature indusium was observed in place of these hairs. This may well have phylogentic significance since both species are in the section *Cystopteris*. Such hairs have not been observed in *C. protrusa* or in any other members of the genus.

Glandularity of the indusium is widespread within the genus *Cystopteris* and is considered to be the primitive condition. However, the glandular condition has evidently been lost secondarily in all evolutionary lines. Species within section *Cystopteris* have not been observed to possess glandular indusia with the exception of a local form of *C. fragilis* on Kerguelen Island in the southern part of the Indian Ocean. However, hybrids and introgressant specimens involving *C. fragilis* may possess glandular indusia. In section *Emarginatae*, *Cystopteris pellucida* and *C. sudetica* var. *moupinensis* lack glandular indusia as does *C. japonica* in subgenus *Acystopteris*.

The sporangium of *Cystopteris* consists of a stalk and capsule and is representative of Aspidioid ferns in general. The stalk is composed of three tiers of cells. The tier below the capsule is three cells wide but the subsequent tiers are reduced to two cells. The stalk is well-developed throughout the genus with one exception. *Cystopteris diaphana* has been observed to possess very short stalks so that the mature capsules may appear to be almost sessile. By dissecting out the sporangia, however, it may be seen that the three tiers of cells are present but that they are very much compressed. The annulus is interrupted and an average of 13-16 thickened cells has been determined for the genus. However, in individual specimens, averages of from 10 to 21 cells have been observed.

CHROMOSOMES AND SPORE SIZE

The study of fern cytology was given great impetus by the pioneering work of Manton (1950). She treated the major cytological phenomena arising in the Pteridophyta with numerous examples to supplement her discussion. It was the difficulty which confronted her while studying the genus *Cystopteris* cytologically that led her to the application of the squash technique to the higher ferns. She states:

The introduction of the squash method resolved the technical impasse at once, but thereby revealed a cytogenetic problem of quite unusual complexity, a circumstance which was nevertheless to be expected in view of the well-known taxonomic confusion prevailing in the genus.

Manton treated three European members of *Cystopteris* in her initial work, and found two different chromosome numbers represented, namely $n = 84$ and $n = 126$. The European *C. fragilis* was found to have both these numbers while *C. montana* possessed the lower number. *Cystopteris alpina* (which is discussed in more detail below in the section on "Hybridization") was found to have the number $n = 126$. This evidence led Manton to postulate the presence of a polyploid series within the genus *Cystopteris* and to predict the probable occurrence of a lower level in the series:

The relationship between numbers as different as 126 and 84 may not at first leap to the eye, yet we can hardly doubt that we are dealing with the upper members of a polyploid series, the lower ones of which are still to seek. If a form with a gametic number of 42 could be found we should have a simple series of 42, 84 and 126 in which the plant bearing them would be diploid, tetraploid and hexaploid respectively.

The next cytological work in the genus *Cystopteris* was the report of Britton (1953) of a diploid species ($n = 42$), namely *C. bulbifera*. This established 42 as the basic chromosome number for the genus. Other chromosome counts for the genus are also given in this publication. This was followed shortly by the discovery (Wagner and Hagenah 1956a) that the taxon known to American botanists as *C. fragilis* var. *protrusa* is also a diploid. To add to the broad cytological picture of the genus, I have found that *C. douglasii*, the Hawaiian segregate of *C. fragilis*, has a chromosome number of $n = \text{ca. } 168$ thus making it an octaploid.

Table 1 lists chromosome numbers which have been obtained from the *Cystopteris* collections which were grown by the author in the University of Michigan Botanical Gardens, including those for three new taxa. Voucher specimens are deposited in the University of Michigan Herbarium. Representative photographs and explanatory diagrams of these chromosome counts are found on Plates 20-22. The earlier reports (Wagner 1955) of chromosomes of "*C. fragilis* var. *tennesseensis*" from Michigan refer to *C. \times laurentiana*; and those of "*C. fragilis* var. *simulans*" from Pennsylvania and Maryland refer to *C. \times tennesseensis*.

Other evidence points to the fact that there are polyploid series within other species of *Cystopteris*, although perhaps not as complete as that within the *C. fragilis* complex. Mr. Dale J. Hagenah (Cranbrook Institute of Science, Bloomfield Hills, Michigan) has studied the North American species of *Cystopteris* rather extensively in order to find if there is any distinct correlation between spore size and the polyploid level of a plant. He has found (Hagenah 1961) that the average spore size of a plant within this genus indicates with great accuracy its polyploid level. His technique is to make measurements at random of ten normal spores on a spore slide.

TABLE 1. *Chromosome observations.*

Species	Chromosome Number
	n
<i>Cystopteris japonica</i> Luerssen	
Oku-musashi, Saitama Pref., Central Honshu, Japan. (<i>S. Kurata</i> , coll.)..	42
<i>C. diaphana</i> (Bory) Blasdell	
a. Agua del Palo, 1000 meters elev., Santiago, Prov. Chile. (<i>P. Valenzuela and F. Vergara</i>).....	42
b. Chicua, 2750 m. altitude, Irazu Volcano, Costa Rica. (<i>J. Leon</i>).....	126
<i>C. protrusa</i> (Weatherby) Blasdell	
a. Gold Hill, Taos Co., New Mexico. (<i>E. F. Castetter 9596</i>).....	42
b. Dream Haven Cottage, near Wonderland Hotel, Elkmont, Tennessee. (<i>H. H. Vannorsdall</i>).....	42
<i>C. fragilis</i> (L.) Bernh.	
a. Slopes near the coast of Nahuel-Huapi-Lake, 780m. elev., Peninsula Que-trihue, Parque Nacional de Nahuel-Huapi, Provincia Neuguen, Argentina. (<i>J. Diem</i>).....	84
b. Germany. (<i>H. Merxmüller</i>).....	84
c. Yates Center, Woodson Co., Kansas. (<i>R. L. McGregor</i>).....	84
d. Italy. (<i>E. Ehrendorfer</i>).....	ca. 126
e. Eastern Alps, Austria. (<i>E. Ehrendorfer</i>).....	126
f. France.....	ca. 126
g. Canterai San Blas, Cuzco, Peru. (<i>C. Vargas</i>).....	ca. 126
h. Simmons Woods near Duel Lake, Mackinac Co., Mich. (<i>R. Blasdell 198</i>)..	84
<i>C. douglasii</i> Hook.	
Puulaau, on west slopes of Mauna Kea, alt. 7600 ft., Hawaii. (<i>E. Horner</i>)..	ca. 168
<i>C. X tennesseensis</i> Shaver	
a. 0.9 mi. W of R 26 and 69 intersection on R 69, at base of rock outcrops along road, Fairfield Co., Ohio. (<i>R. Blasdell 230</i>).....	84
b. ½ mi. SW of Fort Washington, Montgomery Co., Pa. (<i>E. T. Wherry</i>)...	84
c. Catoctin Furnace, Frederick Co., Md. (<i>E. T. Wherry</i>).....	84
<i>C. X laurentiana</i> (Weatherby) Blasdell	
2 mi. W of Deer Lake, near Ishpeming, Marquette Co., Mich. (<i>R. Blas-dell 194</i>).....	126

He then averages these measurements and arrives at a size which corresponds closely with the spore size which is characteristic of one of the polyploid levels. One random sampling is sufficient to determine the chromosome number in a great majority of cases. Occasionally, however, I have found that an average spore size will lie on the border line between two polyploid levels. In such a case, an additional random sampling will place the plant in the correct category. Table 2 gives the size ranges (in microns) of each polyploid level in the genus *Cystopteris* and also the approximate averages, as determined by the present author.

It should be noted that the spore size ranges of certain levels overlap. However, the average spore size is characteristic of a given polyploid level. It was, in fact, the observance by Hagenah of two spore sizes in the Michigan terrestrial populations of *C. fragilis* complex that ultimately led to the discovery by Wagner of the diploid member.

Thus we have a tool for determining from herbarium specimens the

TABLE 2. *Polyloid level correlation with spore size.*

Polyloid Level	Spore Size Range (in microns)	Average Spore Size (in microns)
2x.....	27 - 32	ca. 29
4x.....	32 - 42	ca. 36
6x.....	38 - 48	ca. 43
8x.....	43 - 53	ca. 48

approximate geographical ranges of polyploid levels within individual species. These data are valuable, among other things, for more accurate assignment of putative parents to hybrids as will be shown in the section on hybridization.

I have used the character of spore size rather extensively in an attempt to ascertain the extent of polyploid development within each species of *Cystopteris*. Table 3, though probably incomplete, does show several

TABLE 3. *Polyloid levels within the genus Cystopteris as indicated by spore size.*

Species	2n	4n	6n	8n
<i>C. tenuisecta</i>	X	—	*	—
<i>C. japonica</i>	X*	X	—	—
<i>C. protrusa</i>	X*	—	—	—
<i>C. fragilis</i>	—	X*	X*	X
<i>C. douglasii</i>	—	—	—	X*
<i>C. diaphana</i>	X*	X	X*	—
<i>C. montana</i>	X	X*	—	—
<i>C. sudetica</i>	X	—	—	—
<i>C. pellucida</i>	X	—	—	—
<i>C. bulbifera</i>	X*	—	—	—

* Indicates polyploid levels in which the chromosome number has actually been determined.

interesting features within the genus. First, the diploid condition is apparently extant in all the species groups, in the *C. fragilis* complex being represented by *C. protrusa*. Second, the most completely developed polyploid series are found in the species with more primitive characteristics (described below in the section on species relationships) and/or the wider ranges. This development is very likely correlated with a greater age of these elements, thus providing more time for the evolution of such a series.

A cursory examination of spore size distribution within the genus indicates that the diploid populations are, in the main, restricted in their distribution while the polyploids have much more extensive ranges. Of the diploids, *C. protrusa* (in the *C. fragilis* complex) has the most limited range, occurring in its typical form almost entirely in the Appalachian and Smoky Mountains of the eastern United States. Its apparent range

is greatly extended by introgressant populations into which the genetic material of the southern hemisphere *C. diaphana* has apparently been introduced. Another diploid, *C. bulbifera*, is confined to southeastern Canada and the eastern two-thirds of the United States. Small-spored collections of *C. montana* have been observed from both Canada and Europe but the great majority of collections represent the tetraploid level. *Cystopteris sudetica* and its Asian variety *moupinensis* have uniformly small diploid-sized spores. Thus it is probably the widest ranging diploid species in the genus, extending from Bavaria to Shensi and Szechuan provinces in China. (I have available only ten collections of this species from Russia and Asia so that the distribution data is very scattered.) *Cystopteris pellucida*, a relative of *C. sudetica* and endemic to China, also has small spores.

The polyploid populations of *C. fragilis* increase in abundance the further north they occur. As has already been mentioned, the diploid *C. protrusa*, along with introgressant populations, is prevalent in the eastern United States. The tetraploid *C. fragilis* with its variety *mackayi* (the latter here interpreted as a result of *C. diaphana* introgression) form the bulk of the populations in northern United States and in Canada. Hexaploids, though less frequent, are also present in this region. A similar pattern occurs in Europe, and there tetraploids and hexaploids are apparently present in approximately equal numbers. The lack of diploid populations of the *C. fragilis* complex in Europe may well be attributed to the extensive glaciation which has occurred in that region. It is in the far north, particularly Alaska and northern Canada, that populations yielding extremely large spores become more prevalent. These spores are equivalent in size to those of *C. douglasii*, the Hawaiian endemic in which the octaploid level has been determined. Thus it may be assumed that these subarctic plants are in fact octaploids. These extremely large spores found in the northern latitudes have, for the most part, the rugose architecture which is characteristic of a common variant of *C. fragilis*. However, a few collections have also been found in which the large spores have the echinate architecture of typical *C. fragilis*.

The importance of polyploidy in the flora of northern and high altitude regions has been presented by several workers. Tischler (1935) presented the cytological information dealing with the flora of Schleswig-Holstein. He found that, of the species which extend northward, sixty percent are polyploid. On the other hand, the species extending southward are only twenty-seven percent polyploids. Flovik (1940), in reporting the polyploid situation in the flora of Spitzbergen, stated that eighty percent of the species are polyploid. Cain (1944) in discussing the problem of polyploidy comments:

Flovik interprets these figures as evidence of a tendency toward the fact that increased chromosome number increases adaptability to extreme habitats, such as arctic and alpine conditions, and that polyploidy appears to have played an important role in the origin of forms which have been able to colonize cold regions.

This is probably the correct explanation for the distribution of polyploidy in *Cystopteris* in the northern hemisphere.

HYBRIDIZATION

The subject of hybridization is of great importance in a study of the genus *Cystopteris* for it is in the attempt to classify plants of this probable origin that much confusion has resulted in the past. Hybrids have generally been referred to the species which they most closely resemble and have been named thus as either varieties or forms. Inclusion of these plants with those typical of the various species has naturally tended to a wider extension of the apparent diversity of the individual species and to obscure their real nature. Thus it becomes necessary to segregate these hybrid elements from the parental species and to give them distinct designations.

There are three general phenomena which seem to have had a profound influence on the evolutionary trends within the genus *Cystopteris*. They are (1) autopolyploidy, (2) introgression, and (3) allopolyploidy. As autopolyploidy has been considered in some detail in the section on chromosomes, only brief mention of it will be made here as necessary.

Introgressive Hybridization

The concept of introgressive hybridization has become widely accepted in the last two decades and new species of organisms, both plant and, to a lesser extent, animal, are constantly being reported in which this phenomenon occurs. Anderson (1949, 1953) and Stebbins (1950) have discussed it in some detail. Introgression results from the hybridization of two closely related species in a region where the two species overlap in their ranges. The offspring may or may not be partially sterile depending on the genetic similarity of the two parental genomes. The point is that whatever fertility is present tends to form a bridge between the species over which genetic characteristics of one species can be transmitted into the population of the second species. Thus as Stebbins (1950) has stated:

Introgressive hybridization, whatever may be its importance in modifying and amplifying the variation pattern of certain individual species, is nevertheless by its very nature not a way of producing new morphological or physiological characteristics, and therefore of pro-

gressive evolution. It merely produces convergence between previously more distinct species.

There is strong evidence of introgressive hybridization within the "*Cystopteris fragilis* complex." This group has been methodically sidestepped by taxonomists in the past who have simply lumped together all populations which superficially resembled *C. fragilis*.

The most obvious character which separates non-introgressant *Cystopteris fragilis* and its related species from the rest of the genus is the extension of its veins into teeth at the pinna margin. If this criterion were used for species distinction, however, one would be obliged to rule out a large segment of the traditional *C. fragilis* sensu lato in which all the veins extend into depressions at the pinna margin. Litardière (1912), among other European botanists, has recognized this distinction in anatomy by setting up a subspecies *C. fragilis* ssp. *diaphana* (Bory) Litard. for the latter condition.

I believe that we are dealing here with two distinct species. Not only are the vein terminations different, but there are two additional anatomical characters which support this contention, namely (1) the shapes of the upper epidermal cells, and (2) the outlines of the indusial cells. The upper epidermal cells of *Cystopteris fragilis* are deeply lobed (Pl. 2, fig. B 2) while those of *C. diaphana* are rather uniformly straight-walled or merely undulating (Pl. 9, B 2). Introgressant populations possess varying degrees of epidermal cell lobing showing intermediacy between the two parental species. The indusial cells of *Cystopteris fragilis* are long and relatively narrow (Pl. 2, fig. D). Toward maturity the indusium frequently becomes lacerate at the apex. Much of this is apparently due to separation along the length of the cells as the sorus develops since the young indusia I have examined are relatively entire. *Cystopteris diaphana*, on the other hand, possesses indusia with shorter and relatively broader cells; the indusium remains relatively entire in the later stages and encircles the receptacle more broadly. In addition, other differentiating features, namely the development of sporangial stalks and the margin of the gametophytes, have been described in the section dealing with morphology. Thus, in indusial as well as other anatomical characters, *C. diaphana* resembles more closely the condition found in the rest of the subgenus *Cystopteris* even though it is superficially similar to *C. fragilis*.

Cystopteris fragilis and *C. diaphana* have their own distinct geographic ranges in which the above anatomical characters correlate for the most part, but there are intermediates to be found, especially where their ranges overlap or come in close proximity. In these areas the populations become difficult to identify. This situation results from the fact that these plants are intermediate in their diagnostic characteristics. The correlation of

species characters thus breaks down in the regions of overlap and diverse combinations result, and occasional intermediate specimens are found even at some distance from the actual zones of geographical proximity.

The most probable explanation for these intermediate populations is that gene flow takes place freely between *Cystopteris fragilis* and *C. diaphana* where their gametophytes are growing in close proximity. A close genetic relationship of these two species is suggested by the fact that there is no apparent reduction in the fertility of the intergrades.

The presence of *Cystopteris* intergrades, in areas distant from the overlapping region of the putative parents, may well be a point of serious concern to those who have observed and studied introgression within the flowering plants. However, until introgression is better understood in homosporous plants, intermediate populations within the flowering plants should not be stereotyped and used as a model to be applied to introgression within other large plant groups. The reason for this objection is primarily mechanical as an examination of the respective life cycles will indicate.

The seed of the angiosperms is, in general, a relatively heavy, substantial structure. Thus it would, in the main, drop to the ground soon after release from the ovary. As a result, the introgressant population might perhaps expand slowly at the periphery of the overlap area while still maintaining a continuum through which backcrossing could occur repeatedly.

The dissemination propagule (spore) of the ferns presents a totally different aspect which could result in an entirely different distribution pattern. The spore of *Cystopteris* is relatively small (ca. 30-50 μ) and maintains its viability up to a year or more. The populations of *Cystopteris* in the overlap zones of *C. fragilis* and *C. diaphana* are essentially montane (e.g. Mexico, Canary Islands, eastern Africa, etc.) which would increase the ease with which the spores could be introduced into the prevailing air currents. Thus spores produced by intermediate individuals in the overlap region could be disseminated to distant areas rather easily depending on the whims of atmospheric movements. These spores might (or might not) eventually produce large intermediate populations at a great distance from the original introgressive region. This concept would explain the frequent sporadic occurrences of *C. diaphana* and *C. diaphana* \times *fragilis* beyond their expected ranges. The latter taxon, for example, is represented by the plant, currently known as *C. fragilis* var. *mackayi*, which presents a uniform morphology throughout the eastern and midwestern United States.

The condition in the "*Cystopteris fragilis* complex," therefore, is not necessarily the result of "worldwide introgression" as might be concluded from a cursory examination of the distribution map (Pl. 23). It could be

equally well the result of the dissemination of spores which were produced by intermediate individuals in the region of overlap.

A question logically follows an acceptance of such a hypothesis. Has there been any subsequent mixing of genetic material between these disjunct intermediate populations and those of the prevalent parent in the region? This question will probably not be answered with any degree of assurance until extensive hybridization experiments are carried out between populations of "pure" *Cystopteris diaphana* and *C. fragilis* to test the degree of similarity in their respective genomes. It is conceivable that the arctic populations of *C. fragilis* in the interior of North America and Asia, for example, may be sufficiently distinct, due to their apparent isolation from the *C. diaphana* element, to result in sterile hybrids when crossed. Such a line of investigation would, of course, have to be based on hybridization between parents with the same chromosome number as polyploid series are present within these two taxa.

Allopolyploidy

The occurrence of hybrids involving species of *Cystopteris* with genetically distinct genomes has been implied or partially demonstrated by several botanical investigators in the past. At least one of these reports is very dubious.¹ A very likely interspecific hybrid in the genus *Cystopteris* has been described by Christ (1900) based on a collection by Shuttleworth at Creux du Van (in the Jura Mountains of western Switzerland) in August 1834. His evidence, though based entirely on gross morphology, does show an intermediacy between *C. fragilis* and *C. montana*. A detailed discussion of this hybrid appears in the section dealing with the taxonomy of the genus.

Weatherby (1926) described *Cystopteris fragilis* var. *laurentiana* as a large member of the species. Although he did not ascribe hybrid origin to it, he did allude to its greater size and blunt pinnules, "characters which, Prof. Fernald states, give it in the field the aspect of a *C. bulbifera* without the long apex of the frond."

¹ Parmentier (1900) published an account of an apparent hybrid between *Cystopteris fragilis* and *Asplenium trichomanes* which he named *C. Blindi*. His evidence is entirely based on the anatomy and gross morphology of a sterile plant. The only morphological evidence which he cites to suggest *A. trichomanes* is the small pinna size. Anatomically, his evidence dealing with pinnae (mesophyll and epidermis) could apply to both *Cystopteris* and *Asplenium*. Perhaps the best case for hybridity in his investigation is the shape of the vascular strands in the petiole which apparently resembles that in *Asplenium*. However, his two figures illustrating this character may not be from comparable positions. The figure illustrating the *C. fragilis* condition has two separate traces while the one depicting *Asplenium* shows the traces already joined. Thus it is probably best, until the chromosome situation can be investigated, to consider this taxon merely as one of historical interest.

In 1944 Wherry published on a locality in Berks County, Pennsylvania where *Cystopteris protrusa* and *C. fragilis* var. *mackayi* grew at the base of a cliff. Farther up the cliff plants were found which possessed glandular indusia and occasionally bulblets, characters in common with *C. bulbifera*. When these plants were submitted to Dr. Weatherby for an opinion, he suggested hybridization between *C. bulbifera* and *C. fragilis*. An interesting feature of this locality was that *C. bulbifera* was not known to grow nearer than fifteen miles from this station. Wherry suggested that this might be another case similar to those mentioned by Wagner (1943) where spores from a remote source provide gametes to form a hybrid in a habitat where the incoming species could not exist.

Wagner (1944) reported another occurrence of this apparent hybrid *Cystopteris* at Catoctin Furnace, Frederick County, Maryland. Since these initial publications have made botanists aware of this hybrid combination, numerous localities have been reported.

Shaver (1950) described as a new species, *Cystopteris tennesseensis* and specified the putative parents as *Cystopteris fragilis* var. *protrusa* \times *C. bulbifera*. He also listed several characters which showed the intermediate nature of this taxon between the two species. In the same year McGregor (1950) published on the diversity of this hybrid in the central United States, primarily Kansas and Missouri although he proposed a new combination *C. fragilis* var. *tennesseensis*. He regarded this variety "to be of hybrid origin but it now is a self-perpetuating plant which has become established over a considerable area." This conclusion was reached because of the absence of *C. bulbifera* over a large part of the hybrid range in Kansas and Missouri. He also elevated Weatherby's *C. fragilis* form *simulans* to the varietal level, and indicated its close relation to var. *tennesseensis* because of the occasional presence of bulblets.

The first cytological evidence on the *Cystopteris bulbifera* hybrids was contributed by Wagner (1955). He found that these populations segregated into two groups, those with a chromosome number of $n = 84$ and Michigan populations with $n = 126$. During the same year Hagenah (1955) reported finding the Michigan hybrid in four counties. However, he did not feel that these populations should be attributed to *C. tennesseensis* without further study. Wagner and Hagenah (1956b) reaffirmed their position that the Michigan populations are not identical with *Cystopteris tennesseensis* and suggested "that they may represent an undescribed taxon." I have found that the anatomical and morphological characters of the Michigan hybrids match those of *C. fragilis* var. *laurentiana* and have thus deemed it necessary to make the new combination, *C. \times laurentiana*.

In extrapolating to parental taxa which would agree with the characteristics of these hybrids one can find species which fit them rather closely. In the case of *C. × tennesseensis* ($n = 84$) Shaver was evidently right in his selection of the parental species so far as my investigations can show. The chromosome numbers of both *C. bulbifera* (Britton 1953) and *C. protrusa* (Wagner & Hagenah 1956) have been established as $n = 42$. Since the chromosome complements of the parental genomes are balanced numerically, there appears to be a more or less equal distribution of parental characters in the hybrid.

Cystopteris × laurentiana ($n = 126$), on the other hand, leans toward one parent in the majority of characteristics. This phenomenon can be explained by analyzing the probable genome constitution of this hybrid. *Cystopteris bulbifera* ($2n$), of necessity, would be one parent (supplying among other characters the laminar propagules which occasionally occur on the hybrid). For the other parent, a tetraploid taxon would be required. There are two prime candidates which could probably have served as a parent of this hybrid: (1) *C. fragilis* and (2) the commonly cited and rather uniform *C. fragilis* var. *mackayi* (which I now believe to be a result of *C. diaphana* introgression).

Both putative parents are found throughout the range of *Cystopteris × laurentiana*. Characteristics in addition to bulblets which are indicative of *C. bulbifera* are the details of blade cutting, the somewhat tapered luxuriant frond, the sparsely glandular indusium. Trends toward *C. fragilis* are the increasingly incised pinnules, the linear cells comprising the indusium and the more irregularly lobed epidermal cells. Since the *C. fragilis* genome is represented twice whereas there is only one complement of *C. bulbifera*, it may well be assumed that the exaggeration of *C. fragilis* characteristics is due largely to the overbalance of *C. fragilis* chromosomes.

The abundance of these *Cystopteris bulbifera* hybrids as compared with other species hybrids within the genus is probably largely due to the fact that they possess, in the majority of specimens, a distinctive feature associating them with *C. bulbifera*, namely the vegetative propagule, the bulblet. It is definitely in the realm of possibility that most, if not all sympatric species within the subgenus *Cystopteris* hybridize among themselves where their ranges overlap. However, because of the subtle differences available to identify these hybrids, they are placed with one or the other parent. An example of this problem is the status of *Cystopteris × alpina* in Europe. This taxon has been treated, by European authors as either a subspecies (Luerssen 1889) or a variety (Milde 1867) of *C. fragilis*. Some have even treated *C. diaphana* as synonymous with *C. fragilis* ssp. *alpina*. This treatment is perhaps excusable as some forms of *C. diaphana* do resemble *C. × alpina* macroscopically.

Manton (1950) determined the chromosome number of *C. alpina* (from Switzerland) to be $n = 126$ (6X). I have measured spores from several European collections and find that they are regularly within the 6X size range. In order to decide what the putative parents of this hybrid were, there are two combinations of genomes which should be considered. It could be *C. fragilis* (2X) \times *C. montana* (4X). This possibility should not be ruled out even though I have been unable to find a European collection of *C. fragilis* possessing spores within the diploid size range. However, this hybrid could have been formed at a time when the diploid *C. fragilis* existed in Europe and is now a fertile plant which is maintaining itself by spore reproduction. The other possible combination, which I favor, is that in which *C. fragilis* is the 4X parent with *C. montana* as the 2X parent. This would be the more probable cross because the European *C. fragilis* is primarily 4n or 6n while some *C. montana* collections have been studied which have spores of the 2n range. If this is, in fact, the correct parentage of *C. \times alpina*, it is somewhat analogous to *C. \times laurentiana* in that the characters of *C. fragilis* are expressed more completely in the hybrid than *C. montana*. The only apparent *C. montana* characters which are reflected in the hybrid are the cutting of the pinnules with veins mostly entering emarginations, and in the rather broad stipe scales. In all other respects it more resembles *C. fragilis*.

Another probable hybrid is *Cystopteris kansuana* which is known to me only from the type specimen. It possesses most of the macroscopic characteristics of *C. fragilis*. It also has rather long indusial cells which are indicative of this species. It differs, on the other hand, in the long, delicate stipe, the vein endings entering emarginations, and in the presence of clathrate scales. In these latter three features it resembles *C. sudetica* var. *moupinensis* and the other Asiatic derivatives of *C. sudetica*. It is impossible to postulate with any more certainty the exact origin of this taxon because the sori on the type specimen are immature and do not show the indusial and other structures at maturity. The few mature spores which were observed, however, were entirely aborted. Thus *C. kansuana* is very possibly a sterile hybrid in which chromosome doubling has not occurred.

GEOGRAPHICAL DISTRIBUTION AND HABITAT

The difficulty of obtaining critical data on habitats hampers the individual who tries to evaluate a group of plants primarily from herbarium specimens. The present study involves just such a situation for, with the exception of the author's field observations in the eastern United States,

information has been accumulated largely from floras covering various geographic areas.

The members of the genus *Cystopteris* are primarily found in association with rock surfaces, either on rock faces, crevices, or on talus slopes. In Mackinac County, Michigan, *C. fragilis* has been observed growing on the sides of cracks in limestone pavement.

Wherry (1920) describes *Cystopteris fragilis* from a variety of situations such as "ledges of sandstone, schist and shale, as well as of limestone rocks, and also in talus and in woods entirely apart from any rocks." Typical *C. fragilis* appears to be limited almost entirely to epipetric situations. However, *C. protrusa*, of the eastern United States, which is closely related to *C. fragilis*, has never been reported growing on rock to my knowledge. It is found in rich woods with a loamy soil. *Cystopteris fragilis* var. *mackayi* (the apparent product of introgression between *C. fragilis* and *C. diaphana*) has a wider tolerance, growing on rocks as well as in soil. *Cystopteris douglasii* of Hawaii is also associated with rocks, growing in crevices and along the bases of cliffs.

Cystopteris bulbifera is more specific in its requirements, growing mostly in neutral soils associated with limestone. However, in Michigan it is found to grow luxuriantly in rich, moist *Thuja* swamps and in moist woods apparently with no contact with rock surfaces. *Cystopteris montana*, *C. sudetica* and its Asian derivative *C. pellucida* are apparently confined to epipetric situations. On herbarium labels the statement is repeatedly made that these plants were collected from rocks (calcareous rocks predominantly).

Little information is known to me concerning the habitat of *Cystopteris tenuisecta* and *C. japonica*. One herbarium label of the latter species states that the plant was growing in a beech forest. From this one might assume that it was not in association with rocks. Living material of this species has been received from Japan and the soil residue on the roots proved to have a pH of between 3.5 and 4.0. If this was the true pH in the natural habitat, it is by far the most acid condition encountered for the genus in this study, the remainder of the genus ranging from 6.0-8.0.

The genus *Cystopteris* is cosmopolitan in distribution although it is primarily restricted to temperate regions in the higher latitudes in both northern and southern hemispheres. However some mountain systems within the tropics possess sufficient altitude to produce temperate conditions and along these ranges the genus is well represented.

Cystopteris fragilis has the widest geographic range within the genus and is one of the few fern species which approach a cosmopolitan distribution. It attains its most wide-spread range in the boreal regions, extending through Europe and most of Asia and North America. Thus this species

is truly circumboreal. In addition, there are regions in the southern hemisphere where *C. fragilis* occurs quite disjunctly from its great northern range. New Zealand, Kerguelen Island (in the southern Indian Ocean) and the southern tip of South America possess populations with a very similar gross morphology. The closely related *C. douglasii* is endemic in the Hawaiian Islands.

Typical *Cystopteris protrusa*, with the deltoid blade plan, appears to be restricted to the Appalachian Mountain system, primarily in Tennessee and North Carolina. Toward the western and northern extent of its range (Missouri and Minnesota respectively) the blade plan becomes modified predominantly to the ovoid shape characteristic of *C. fragilis*. *Cystopteris bulbifera* presents a more ample distribution from Newfoundland to Manitoba and southward to Georgia and Arizona.

Cystopteris montana ranges strictly in the boreal regions. In the western hemisphere it is rather frequent in Canada and extends from Labrador to Alaska. The United States material of this species comes from two general regions. Glacier National Park, Montana, might be expected to harbor this species as the park is on the Canadian border. The other region is perhaps of more interest because of its apparently disjunct location. This is in the Sawatch Mountains of Colorado where it occurs at an altitude of about 10,000 feet. It is possible that there are intermediate localities in the mountains forming the Continental Divide which link this station with the bulk of the population in Canada. In Europe *C. montana* is widespread in the Scandinavian countries. It occurs in Scotland and is prevalent in the mountainous regions of central Europe. With the exception of a collection from Syktyvkar and one which may be from the Caucasus, I have not seen this species from the USSR. It occurs in north-west India and in Kansu Province, China. Hooker (1868) states that it occurs also in Kamtchatka but no material has been available to me from this region.

Cystopteris sudetica is closely related to *C. montana* but has a more restricted distribution. It is most abundant in the mountains of Hungary and Czechoslovakia but also extends northwestward to Norway. To the east it occurs in the Caucasus Mountains and in western Russia. Its variety *moupinensis* has been collected in several provinces in central China. *Cystopteris pellucida* is restricted to central and eastern China but this apparent distribution is probably due to the paucity of collections.

Cystopteris diaphana, which in the past has been included in the polymorphous species *C. fragilis*, has an interesting disjunct distribution. Being present in its typical form (with glandular indusia) in the Canary Islands, Belgian Congo and northeastern Tanganyika Territory, this species is widespread from Mexico through South America in the mountain ranges.

Much of the New World material, however, lacks the indusial glands. This African-American distribution should not be surprising, however. As recently as 1958 Brown has stated: "One species, *Woodsia montevidensis*, occurs in the Drakensberg of Natal and in the Transvaal in South Africa. This species is also found in South America." Cain (1944) discusses this particular distribution using Steyermark's work (1932) on the genus *Menodora* as an example, among others. Cain continues:

He [Steyermark] believes the most logical explanation to result from the postulation of a land bridge across the south Atlantic which was obliterated by the Upper Cretaceous. The geologists allow such a land connection (Devonian, through Jurassic to Upper Cretaceous), but the theory of continental displacement should be considered as a possibility along with the "lost continent" idea.

The members of the subgenus *Acystopteris* are confined to the southeastern region of Asia. *Cystopteris tenuisecta* ranges from northeast India south to Java and eastward through southern China to Honshu, Japan. The more restricted *C. japonica* occurs primarily in Japan but has been collected in Szechwan province, China.

A logical postlude to an analysis of distribution patterns within a group of organisms is to deduce a picture of the probable migration routes involved. This involves considering not merely distributional phenomena, however. The determination of the primitive elements and a correlation of their geography with that of the more specialized members of the group must be attempted.

There are two species groups which are candidates for being the primitive members (as analyzed in the section on species relationships) of the genus *Cystopteris*. Of these the subgenus *Acystopteris*, which includes *C. tenuisecta* and *C. japonica*, inhabits southeast Asia. *Cystopteris protrusa*, with its headquarters in the Appalachian Mountains of eastern United States, is the primitive element within the subgenus *Cystopteris* section *Cystopteris*. In its typical form it has the deltoid blade plan which is characteristic of the bulk of the genus. Such a disjunct distribution of the primitive elements is most easily explained by postulating that the genus *Cystopteris* evolved during the Carboniferous period when Gondwanaland presented an extensive land mass in the southern hemisphere. The subgenus *Acystopteris* probably became distinct early in the evolution of the genus. Initiated within the northeastern region of Gondwanaland, it later spread from northeastern India toward the east and south.

The progenitor of *C. protrusa* may also have followed an eastward route from north Gondwanaland and extended from eastern Asia to eastern North America. This hypothesis should not be very startling as it is well known that the floras of the two regions have many floristic elements in common.

Apparently the Appalachian Mountain system is the only remaining outpost for this ancestral stock. The section *Emarginatae* of subgenus *Cystopteris* probably evolved in northern Gondwanaland with the resulting elements taking two routes. The *C. montana-sudetica* element, with its present center in central Europe, very likely migrated through northwestern India toward the west. The other element, namely *C. diaphana*, established its extensive range in the central and western region of Gondwanaland.

Cystopteris fragilis very likely developed rather early from the progenitor of *C. protrusa* and had a wide geographic range in Gondwanaland. Subsequently the north temperate regions were added to the range of *C. fragilis* while the land mass of the "southern continent" was being reduced. All in all, the southern element of *C. fragilis*, now represented in Kerguelen Island, New Zealand, and the southern tip of South America, exhibits common features which are more primitive than its boreal counterpart.

SPECIES RELATIONSHIPS

In order to establish the probable relationships among the species of *Cystopteris* it has been necessary to assemble the data on morphology and anatomy which have been described in a previous section. These data are presented graphically by means of a chart containing concentric radii. The radii represent the total of specializations of the various species, and lines connect those species that possess characters in common. At certain points on the chart "missing links" are postulated in order to account for advanced tendencies common to certain species. Thus this diagram is based on the concept of the "common ground plan" (and it is adapted from a method developed by Dr. Warren H. Wagner, Jr. for his taxonomy courses at the University of Michigan).

In some of the characters selected for this presentation, the decision between primitive versus specialized conditions was obvious. In other characters, however, the tendencies were not clear and thus these characters had to be correlated with those possessing obvious trends. In still other characters no such correlation was possible and these are included on the chart merely to show similarities within species groups.

The twelve characters which were used in the demonstration of species relationships were selected because they either showed obvious trends and/or appeared to be stable in their expression within the various species. A table of specializations (Table 4) was constructed to show the evaluation of the primitive versus the derived condition of each character. The primitive condition was given a value of 0.0 while the derived expression of each

TABLE 4. *Specializations in Cystopteris.*

A. Rhizome long repent (0) to compact (1)
B. Blade pattern deltoid (0) to blade basally contracted (1)
C. Blade not apically attenuate (0) to attenuate (1)
D. Veins extending into marginal teeth (0) to veins into marginal depressions (1)
E. Undulating epidermal cell walls (0); shallow lobes (0.5); deep irregular lobes (1)
F. Cells of scales lacking secondary lateral cell walls (0) to thickened lateral cell walls (1)
G-H. Attenuate indusial cells (G) versus short cells (H)
I. Indusium glandular (0) to non-glandular (1)
J. Accessory indusial hairs absent (0) to present (1)
K. Foliar bulblets absent (0) to present (1)
L-M. Multicellular non-glandular hairs (L) versus multicellular glandular hairs (M)
N-P. Echinate spore (N); rugose (0); spines with highly dissected cross-sectional plan (P)

character received a value of 1.0. Intermediate expressions (where applicable) received a value of 0.5. These numbers were then totaled for each species and plotted on the chart. Thus *Cystopteris tenuisecta* with a total specialization of 1.0 would be considered the most primitive member of the genus while *C. fragilis* with a combined index of 5.0 ranks as the most divergent. The reasoning behind the evaluation of each of the twelve characters is summarized below:

A. RHIZOME HABIT. Within the genus *Cystopteris* the long repent rhizome with easily recognized internodes is the rule. In *C. fragilis* and to a lesser extent *C. bulbifera*, however, the stipe bases invest the rhizome so closely that the internodes may not be readily observed. This results from a more compact though still repent rhizome, and is considered to be a derived condition.

B. BLADE OUTLINE. The generalized outline for the genus *Cystopteris* is that of a broadly deltoid blade, i.e., with the basal pinnae the broadest. However, two species, namely *C. fragilis* and *C. diaphana*, have evolved a more or less ovate outline by reduction in the length of the basal pinnae. In addition, a large segment of the *C. protrusa* populations tend toward this outline.

C. APICAL BLADE ATTENUATION. The blade organization typical of the genus in general is a gradual reduction in the size of pinnae toward the apex. This tapering is developed to an extreme in *Cystopteris bulbifera* where the reduction in pinna size progresses over a greater number of pinnae thus resulting in an attenuate blade apex.

D. VENATION PATTERN. In evaluating this character it has been necessary to examine representatives of apparently closely related genera such as *Dryopteris* and *Athyrium* as a guide in determining the primitive condition. In these genera the veins are directed toward marginal teeth. This feature also exists in *Cystopteris protrusa* and *C. fragilis*. The subgenus *Cystopteris* section *Emarginatae*, however, has the veins extending into

emarginations, a distinctive feature among ferns in general. This latter condition is thus considered to be derived.

E. ADAXIAL EPIDERMAL CELL WALLS. Undulating cell walls are correlated with those species of *Cystopteris* which are primitive in several other characters and are thus thought to be the primitive state. Deeply lobed cells are associated with the more specialized taxa.

F. SCALES WITH THICKENED LATERAL CELL WALLS. This type of scale is referred to as being "clathrate." It is a characteristic feature of the fern genus *Asplenium*, among others. Within *Cystopteris*, however, it occurs only in *C. sudetica* and its Asian associate *C. pellucida*.

G-H. INDUSIAL CELLS. Attenuate indusial cells (G) are limited to subgenus *Cystopteris* section *Cystopteris*. The remainder of the genus is characterized by the shorter and more rectangular cells (H).

I. INDUSIAL GLANDS. The glandular indusium is a prominent feature within the genus *Cystopteris* and is construed to be the primitive condition. However, these glands have been lost within each of the evolutionary lines. Both *C. diaphana* and *C. fragilis* show an interesting trend in regard to this character which possibly has some relation to the expansion of their respective ranges. While glandular indusia are universal in the African material of *C. diaphana*, glands are predominantly absent in New World populations. A similar segregation of this character may be observed in *C. fragilis* where the southern element possesses glands while the boreal element apparently lacks these glands completely.

J. ACCESSORY INDUSIAL HAIRS. These multicellular structures are attached to the outer surface of the indusium. They most frequently occur as single hairs but occasionally a more massive aggregation of cells resembling a second indusium is produced. These hairs have been observed solely in *Cystopteris fragilis* and *C. douglasii*.

K. FOLIAR BULBLETS. These vegetative reproducing structures occur, within the genus *Cystopteris*, only in *C. bulbifera* and thus their presence is construed to be a specialized feature.

L-M. MULTICELLULAR HAIRS. Non-glandular multicellular hairs (L) are restricted to subgenus *Acystopteris*. The subgenus *Cystopteris* possesses only glandular multicellular hairs (M).

N-P. SPORE ARCHITECTURE. The echinate spore (N) is found throughout the subgenus *Cystopteris* while the rugose spore (O) is limited to segments of *C. fragilis*, primarily in the north temperate zone. Spores with highly dissected projections in cross section (P) are confined to the subgenus *Acystopteris*.

An examination of Plate 1 shows that there are two distinct lines of development arising from a prototype which was probably reminiscent of the modern *Cystopteris protrusa*. Subgenus *Acystopteris* resembles the

remainder of the genus in chromosome number and in the position of the indusium. In other respects, such as spore architecture and multicellular hair type, however, this subgenus has become very distinct.

The subgenus *Cystopteris* has evolved along two main lines which are contrasted by such features as vein position, epidermal cells and indusial cells. There are also preliminary indications that these two lines, which are treated as sections of the genus in this work, differ in the marginal profile of the gametophyte.

Within the section *Emarginatae*, the terminal elements of the evolutionary line, namely *C. montana*, *C. sudetica*, *C. pellucida* and *C. bulbifera*, maintain their distinctness throughout their respective ranges and as such are not a problem in the taxonomy of the genus.

Cystopteris diaphana, the fifth member of section *Emarginatae*, presents an entirely different trend for this species apparently mixes extensively with members of section *Cystopteris* (*C. fragilis* and *C. protrusa*). In Plate 1 the shaded area represents the region of apparent interspecific introgression. If a representative collection of *Cystopteris* from North America were plotted on this chart, one would probably find a nearly complete spectrum of variation ranging from the typical plants of *C. fragilis*, *C. protrusa* and *C. diaphana* to various degrees of mixing. The main problem in the "*C. fragilis* complex" then lies in the classification of the intermediate populations.

By critically examining the populations of the "*C. fragilis* complex" from various parts of the North American continent, one can detect certain forms which are relatively distinct in a given region. An example of such a taxon is *Cystopteris fragilis* var. *mackayi* which maintains a distinctive appearance in much of eastern North America. This plant exhibits an intermediate condition between *C. diaphana* and *C. fragilis* in such features as vein position (the veins extending into both marginal teeth and emarginations), epidermal cells and in the shape and organization of the indusium. Other elements, especially from Europe, also have been observed which have a relatively uniform appearance. In the case of such distinctive forms, one might feel obligated to assign a varietal or some other subspecific status. However, when one looks at the whole picture, it becomes almost impossible to define the limits of taxonomic categories where one is dealing not only with these distinct regional elements but also with more subtle differences in varying intensities on a worldwide scale as is demonstrated in Plate 23.

How then can varieties and forms be logically separated when there are various levels and intensities of genetic mixture as well as the more distinctive elements? This is the problem which has been encountered in the study of the "*C. fragilis* complex" and this is the phenomenon which

has apparently led to much of the very extensive nomenclature placed in synonymy in this work. The only apparent way to handle this situation is to regard the three taxa (*C. fragilis*, *C. protrusa*, and *C. diaphana*) as part of a complex including intermediate populations in which only the three extremes are designated as distinct species. The intermediates then, no matter what the degree of similarity to any one of the extremes may be, are then assigned to the complex either as *C. diaphana* \times *fragilis* or as *C. diaphana* \times *protrusa* depending on the expression of characters.

Taking into consideration the preceding discussion, some authorities may be critical of the stand taken here, namely to maintain a species status for the three extremes of the "*C. fragilis* complex." It might be more prudent to treat these three species as being merely extremes of one widely fluctuating species. Perhaps, because of the worldwide variation pattern and the great extent of intergradation, a better classification would be to consider the extremes as geographical subspecies. This treatment, however, would still not solve the problem relating to the handling of the intermediate populations.

I do not favor this approach in the particular situation at hand even though it would be the logical solution perhaps in other comparable groups of organisms. We are apparently dealing here with a complex in which the extremes, if considered separately, would logically be given specific recognition in any comparable group of plants. *Cystopteris diaphana*, for example, has a great deal more in common with section *Emarginatae* than section *Cystopteris* with respect to its anatomical characteristics. The problem then narrows down to the probability that *C. diaphana* has a genome composition which is very similar to that found in the section *Cystopteris*. A possible explanation for this apparently close genetic similarity may be the maintenance of an ancient gene pool within these species groups whereas the rest of the genus has undergone more extensive genetic modification.

No matter what nomenclatural rank may be assigned to the extremes in the "*C. fragilis* complex" by a given taxonomist, it is quite evident that we are dealing here with a group of plants that have a close genetic relationship. Thus the present study is an excellent example of the problem of assigning categories to a complex taxonomic situation.

TAXONOMIC REVISION

This study includes a detailed treatment recognizing ten species, five varieties and six hybrids or intergrades within the genus *Cystopteris*. Several species for which authentic material has not been obtainable have

been omitted or temporarily referred to other taxa on the basis of the original description.

Furthermore two subgenera are recognized within the genus *Cystopteris*. This division is made necessary because of the inclusion of two Asian species which have some common features with the genus but are totally different in other characters. Also for the first time within the genus *Cystopteris*, sectional categories have been introduced to bring out apparent relationships within the genus. These subdivisions have been especially valuable in the rearrangement of elements which in the past have been relegated to the "catchall" species, *C. fragilis*.

The diagnostic key has been constructed to make use of as many macroscopic characters as possible. However, in some cases a dissecting microscope or even a compound microscope must be utilized to identify a specimen accurately.

Cystopteris

Cystopteris Bernhardt, Schrad. Neu. Journ. 1(2): 26. 1806. (non. cons.).
Internat. Bot. Congress, Cambridge (1930).

Filicula Seguiér, Pl. Veron. Suppl. 55. 1754.

Filix Adanson, Fam. d. Pl. 2: 20. 1763.

Cystea Smith Engl. Fl. 4: 260, 284. 1828.

Cyste Dulac, Fl. Haute-Pyrenees 33. 1867.

Small to medium sized ferns primarily of rocky and other epipetric situations but a few species entirely terrestrial, the leaves occurring separately or appearing tufted on rhizome. *Rhizome* compact to wide-creeping, invested with ovate to lanceolate scales. *Stipe* shorter to longer than the blade, stramineous to dark pigmented. *Blade* deltoid or deltoid-attenuate to ovate-lanceolate, bi- to quadripinnatifid; 5-50 cm. long and 2-25 cm. wide; primary pinnae deltoid-lanceolate to ovate-lanceolate, 4-50 pairs, the basal pairs shortly petiolulate, the upper pairs becoming gradually smaller and less dissected; pinnules anadromic. *Lamina* herbaceous to somewhat coriaceous; segment margins lined by jagged cells, ultimate lobes with projecting teeth or depressed emarginations; veins free, entering either teeth or emarginations. *Sorus* dorsal on vein, discrete to sometimes appearing confluent at maturity; indusium attached under the receptacle toward the costa, its free apex arching over the sorus toward the margin of the pinna, ovate-lanceolate to broadly cup-shaped at maturity; sporangia with well developed stalks (except in typical *C. diaphana*), annulus of 13-16 thickened cells (occasionally up to 21); spores bilateral, yellow to dark-brown, echinate or rugose or with short and ridged warts, 27-53 μ long. Basic chromosome number $x = 42$.

Distribution. Worldwide except Antarctica.

Type species. *Cystopteris fragilis* (L.) Bernh.

*Diagnostic Key to the Subgenera, Sections and Species
of Cystopteris*

1. Blade lacking multicellular non-glandular hairs; multicellular glandular hairs present in varying degree; spores echinate or rugose, dark brown.....Subgenus *Cystopteris*.
2. Veins directed into teeth.....Section *Cystopteris*.
3. Indusium attached around one-third the circumference of the receptacle
 4. Rhizome short creeping with approximate nodes; indusium large and conspicuous; average spore size 32-53 μ1. *C. fragilis*
(introgresses with *diaphana*;
hybridizes with *bulbifera* and *montana*)
 4. Rhizome wide creeping with distinct internodes; indusium delicate and occasionally fugacious; average spore size 27-32 μ2. *C. protrusa*
(introgresses with *diaphana*)
3. Indusium attached around one-half the circumference of the receptacle.....3. *C. douglasii*
2. Veins directed into emarginations.....Section *Emarginatae*
5. Leaf deltoid, or deltoid-attenuate with lowest pinnae the longest; rhizome cord-like with long internodes
 6. Basal pinna with the lowest inferior pinnule longer than the superior pinnule.....4. *C. montana*
 6. Basal pinna with the lowest inferior pinnule the same length as or shorter than the superior pinnule
 7. Scales of stipe and rhizome clathrate; foliar bulblets absent on blade axes; blade approximately deltoid
 8. Indusium attached one-half or more of the distance around the receptacle.....5. *C. pellucida*
 8. Indusium attached about one-third of the distance around the receptacle.....6. *C. sudetica*
 7. Scales of stipe and rhizome not clathrate; bulblets present on blade axes; blade apically attenuate.....7. *C. bulbifera*
(hybridizes with *protrusa* and *fragilis*)
 5. Leaf ovate-lanceolate with basal pinnae equal to or shorter than the next pinnae; rhizome more robust, with shortened internodes.....8. *C. diaphana*
(introgresses with *fragilis* and *protrusa*)
1. Blade invested with large multicellular non-glandular hairs; multicellular glandular hairs absent; spores with ridged warts, yellow.....Subgenus *Acystopteris*
9. Stipe and rachis with a shiny ebony pigment; unicellular glands absent on lamina and indusium.....9. *C. japonica*
9. Stipe and rachis stramineous or light brown; unicellular glands present on lamina and indusium.....10. *C. tenuisecta*

Subgenus Cystopteris

Small to medium ferns, with deltoid to lanceolate blades; scales of rhizome and stipe glandular or glabrous; stipes shorter to longer than blade; upper stipe, rachis and minor axes with multicellular glandular

hairs; blade bi- to quadripinnatifid; indusium generally cup-shaped at maturity; spores bilateral, dark brown, with echinate or rugose architecture.

Type species. *Cystopteris fragilis* (L.) Bernh.

Two sections are recognized within subgenus *Cystopteris*, namely section *Cystopteris* and section *Emarginatae*.

A. Section *Cystopteris*.

Veins extending into teeth at the pinna margin; indusium ovate to linear, the free margin frequently lacerate, indusial cells long and narrow (except *C. protrusa* in which the cells approach a rectangular outline); adaxial epidermal cells with deep, irregular lobes.

Type species. *Cystopteris fragilis* (L.) Bernh.

This section contains three species: *Cystopteris fragilis*, *C. protrusa* and *C. douglasii*.

1a. *Cystopteris fragilis* (L.) Bernh. var. *fragilis*

Polypodium "F. fragile" (a misprint) L. Sp. Pl. 1091. 1753.

Polypodium fragile L. Fl. Suecica, ed. 2. 374. 1755.

Polypodium fragile var. *angustatum* Hoffm. Roem. et Uster. Mag. IX, Pt. 33. Pl. 1. 1790.

Filix fragilis (L.) Gilib. Exerc. Phyt. 558. 1792.

Cyathea fragilis (L.) J. Sm. Mem. Acad. Turin, 5: 417. 1793.

Polypodium dentatum Dickson, Fasc. Pl. Crypt. Brit. 3: no. 1. pl. 7. 1793.

Polypodium anthriscifolium Hoffm. Deutschl. Flora 2: 9. 1795.

Polypodium cynapifolium Hoffm. *ibid.*

Cyathea anthriscifolia (Hoffm.) Roth, Tent. Fl. Germ. 3: 98. 1800.

Cyathea cynapifolia (Hoffm.) Roth, *ibid.*

Aspidium fragile (L.) Sw. Journ. Bot. Schrad. 1800 (2): 40. 1801.

Athyrium fragile (L.) Spreng. Anleit. 3: 136. 1804.

Cystopteris fragilis (L.) Bernh. Neu. Journ. Bot. Schrad. 1(2): 26. pl. 2. f. 9. 1806.

Aspidium dentatum (Dick.) Sw. Syn. Fil. 59. 1806.

Cyclopteris fragilis (L.) Gray, Nat. Arr. Br. Pl. 2: 9. 1821.

Athyrium dentatum (Dick.) Gray, *ibid.* 11.

Cystopteris dentata (Dick.) Desvaux, Prod. Fam. Foug. 6: 263. 1827.

Cystopteris orientalis Desvaux, *ibid.* 264.

Cystea fragilis (L.) Sm. Eng. Fl. 4: 289. 1828.

Cystea dentata (Dick.) Sm. *ibid.* 287.

Cystea angustata Sm. *ibid.* 288.

Cystopteris fragilis var. *angustata* (Hoffm.) Link, Fil. Sp. 46. 1841.

Cystopteris fragilis b. *pinnatipartita* Koch, Syn. Fl. Germ. and Helv. Ed 2. 980. 1845.

Cystopteris fragilis b. *pinnatipartita* 1. *anthriscifolia* (Hoffm.) Koch, *ibid.*

Cystopteris fragilis b. *pinnatipartita* 2. *cynapifolia* (Hoffm.) Koch, *ibid.*

Cystopteris fragilis b. *pinnatipartita* 3. *angustata* (Sm.) Koch, *ibid.*

Cystopteris fragilis var. *vulgaris* Hooker, Sp. Fil. 1: 197. 1846.

Cystopteris fragilis var. *dentata* (Dick.) Hooker, *ibid.* 198.

Cystopteris dickieana Sim, Gardeners' Journ. 308. 1848.

Cystopteris fragilis var. *genuina* Bernoulli, Gefäßspfl. der Schweiz. 42. 1857.

Cystopteris fragilis var. *acutidentata* Döll, Fl. Baden 1: 43. 1857.

- Cystopteris fragilis* var. *rupestris* Neilr. Fl. N. Oest. 13. 1857.
Cystopteris fragilis A. *fragilis* var. *lobulato-dentata* Milde, Sporenpl. 68. 1865.
Cystopteris fragilis A. *fragilis* var. *pinnapartita* a. *anthriscifolia* (Hoffm.) Milde, *ibid.*
Cystopteris fragilis A. *fragilis* var. *pinnapartita* b. *cynapifolia* (Hoffm.) Milde, *ibid.*
Cystopteris fragilis A. *fragilis* var. *pinnapartita* c. *angustata* (Sm.) Milde, *ibid.*
Cyste fragilis Dulac. Fl. Hautes-Pyrenees. 33. 1867.
Cystopteris baenitzii Dorfler in Baenitz, Herb. Eur. n. 6510. 1891.
Cystopteris fragilis subsp. *eu-fragilis* var. *Baenitzii* (Dorfl.) Warnst. in Aschers. Graebn. Syn. Mit. Eur. Fl. 1: 17. 1896.
Cystopteris fragilis var. *anthriscifolia* subvar. *favrati* Christ, Farnk. Schw. 156. 1900.
Cystopteris fragilis var. *dentata* subvar. *tavelii* Christ, *ibid.* 158.
Cystopteris fragilis var. *dentata* subvar. *woodsiioides* Christ, *ibid.*
Cystopteris polymorpha Bubani, Fl. Pyr. 4: 431. 1901.
Cystopteris fragilis var. *dickieana* (Sim) Lindberg., Medd. Soc. Fauna et Flora Fennica. 32: 21-24. 1905.
Cystopteris fragilis subsp. *dickieana* (Sim) Hylander, Uppsala Univ. Arsskr. 1945 (7): 59. 1945.

Rhizome short creeping, internodes very short, leaves and old stipe bases approximate, clustered near rhizome apex; scales lanceolate, reddish-brown, abundant near apex, glabrous. *Stipe* shorter than blade, stramineous to lustrous dark brown, with lanceolate scales at base. *Blade* bipinnate to tripinnatifid, ovate-lanceolate, up to 30 cm. long and 12 cm. wide; rachis and minor axes with scattered uni- and multicellular glandular hairs; primary pinnae ovate to ovate-lanceolate, subopposite to alternate, from 1-8 cm. long and 0.5-4.0 cm. wide; basal secondary pinnae shortly petiolulate, the remainder adnate, ovate to lanceolate, with obtuse to acute apices, apices of lobes terminated by rounded or acute teeth into which veins are directed. *Sori* round, discrete to overlapping at maturity; indusium ovate to lanceolate, mostly with lacerate apex, glabrous, cells long attenuate with conspicuous accessory indusial hairs; sporangium with well-developed stalk; spores echinate, dark brown, size 32-53 μ . Chromosome numbers, $n = 84, 126, 168$. (Plate 2)

Distribution. Panboreal, into Mexico, eastern Africa, Ceylon.

Type. Not seen. Copeland (1929) states that the type specimen is in the herbarium of the Linnean Society, London. However, Stearn of the British Museum states (personal communication with R. L. Hauke, 1957) that none of the current specimens of *C. fragilis* in the Linnaean Herbarium were available when the original description was written.

Linnaeus did refer to an illustration in Plukenet's *Phytographie*, however, and Stearn further stated that the type of this illustration is H. S. (Herb. Sloan) 96, Folio 40. If no other type has been designated, this would be the logical specimen to choose.

Discussion. The specific epithet "F. fragile" is quite obviously an error as was pointed out by Weatherby (1926) in his discussion of the problem. This same error has obviously resulted in the formation of the binomial *Filix fragilis*.

Cystopteris dentata is merely a variation of *C. fragilis* in which the ultimate lobes are rounded and the marginal teeth are not acute. Link's

description of *C. rhaetica* places this species as a form of limited distribution in central Europe.

The plants of *Cystopteris dickieana* from the type locality of Aberdeen, Scotland (illustrated by Newman, British Ferns, 1954), are distinctive macroscopically in that the pinnae arise in close proximity to each other so that there is abundant overlapping. These plants apparently retained their macroscopic characteristics in culture (Sowerby, 1859). The only other feature which distinguishes this fern from *C. fragilis* var. *fragilis* is the spore architecture and intermediate conditions have been observed between the rugose spore and echinate spore. As this spore type within *C. fragilis* has a wide geographic range and there are apparent transitional spores, it seems worthy only of designation as a spore form within *C. fragilis*. The imbricate pinnae of the type collection has not been found to be correlated with the spore condition.

A specimen of the type collection of *Cystopteris baenitzii* has been examined and the plants are typical *C. fragilis* var. *fragilis* but with the rugose spores, like those of Dickie's plant.

The abundance of synonyms reflects the diversity of *Cystopteris fragilis* var. *fragilis*. In addition, this species, which is abundant in Europe, has been studied in some detail, resulting in new names and recombinations of old names. Some of the binomials included in my synonymy of this variety may actually represent plants in which introgression with *C. diaphana* has occurred. As authentic specimens have not been available, however, these names have been included under *C. fragilis* var. *fragilis*. Luerksen (1889) attempted a partial synonymy of binomials for this species which seems to be, in the main, accurate. I have, however, removed some names which do not belong there according to my interpretation of var. *fragilis*.

1b. *Cystopteris fragilis* var. *apiiformis* (Gandoger) C. Chr.

Cystopteris apiiformis Gandoger, Bull. Soc. France 60: 28. 1913.

Cystopteris apiiformis = *C. fragilis* var., C. Chr. Ind. Fil. Suppl. 1913-1916.

Similar to *Cystopteris fragilis* var. *fragilis* but indusium glandular; and veins mostly not extending to margin. (Plate 19)

Distribution. New Zealand, southern South America and adjacent islands, Kerguelen Island.

Type. "Ins. Falkland, prope West F. Roy Cove. Skottsberg n. 61." An isotype is in S-PA.

Discussion. Christensen quite obviously intended to make the varietal combination although he worded it as found in the synonymy. *Cystopteris novae-zealandiae* Armstrong and *C. laciniatus* Colenso probably belong here

but as authentic material has not been seen they are not included in the synonymy.

The bulk of the New Zealand specimens have a very characteristic appearance, the bipinnate fronds being much attenuated and the pinnae widely separated, with teeth very shallow. The South American material has broader, more ample fronds which occasionally approach a tripinnatifid condition. The Kerguelen Island population, while still possessing indusial glands, has veins which reach the margins of the pinnae, thus approaching more closely the typical variety.

In these three regions of the southern hemisphere, therefore, *Cystopteris fragilis* is represented by three populations of a variety which have significant features in common. It is postulated that this variety is primitive within the species because of the presence of indusial glands. The vein condition is reminiscent of that found in many species of *Dryopteris* and is universal in the genus *Woodsia* (Brown, 1958).

1c. *Cystopteris fragilis* var. *huteri* Hausman, ex Milde Fil. Eur. 149. 1867.

Similar to *Cystopteris fragilis* var. *fragilis* but with lamina copiously invested with unicellular glands especially on the margins; rachis and frequently the minor axes with long uniseriate multicellular hairs, commonly capped by a dark brown globose gland cell; indusium remaining glabrous. (Plate 19)

Distribution. Limited to the mountainous regions of western and central Europe.

Type. Not seen. "Tirol: Pusterthal. In rup. dolomit. (Huter)."
The specimens at hand agree closely with the original description which I have seen.

Discussion. Specimens from the type region of Tirol are very uniform, with a dissected appearance somewhat resembling that of *C. × alpina* macroscopically but lacking emarginate teeth. It is a very distinctive segregate of *C. fragilis* with a greatly restricted range.

2. *Cystopteris protrusa* (Weath.) Blasdell comb. nov.

Cystopteris fragilis var. *protrusa* Weath. Rhod. 37: 373. 1935.

Rhizome wide-creeping with distinct internodes, apex protruding 2-4 cm. beyond current season's leaves; scales lanceolate, sparse. *Stipe* shorter than blade, stramineous; scales sparse at base. *Blade* bipinnatifid to bipinnate, deltoid to ovate lanceolate, up to 22 cm. long and 12 cm. wide; minor axes with scattered uni- and multicellular glands; primary pinnae subopposite to alternate, petiolulate, ovate to ovate-lanceolate; secondary pinnae at base of blade frequently short petiolulate, pinnatifid into oblong, obtuse lobes; veins typically running into marginal teeth. *Sori* round, discrete to occasionally overlapping at maturity; indusium minute, delicate, occasionally apparently fugacious, ovate, entire at apex, glabrous, with somewhat elongate cells, accessory indusial hairs not observed; spores echinate, dark brown, size 27-32 μ . Chromosome number $n = 42$. (Plate 3)

Distribution. New York to Georgia, westward to Wisconsin and Arkansas.

Type. Tennessee, Knoxville, June 5, 1898. Ruth 564 (GH!).

Discussion. *Cystopteris protrusa* is a very distinct species of eastern United States and has features which are considered primitive within the genus. It possesses a creeping rhizome with the apex protruding far beyond the current growth. This species is also the only known member of section *Cystopteris* which possesses the diploid chromosome number.

While *Cystopteris protrusa* occurs in its typical form (deltoid blades) primarily in the Appalachian Mountain system, its form in populations to the west becomes very similar to that of *C. fragilis* var. *fragilis*. All the characters except blade pattern, however, resemble those of *C. protrusa*.

Cystopteris protrusa is considered to be a parent of the putative hybrid *C. × tennesseensis*. There is also some evidence of apparent introgression between *C. protrusa* and *C. diaphana* which is indicated most frequently by the presence of both types of vein termination.

3. *Cystopteris douglasii* Hooker, Sp. Fil. 1: 200. 1846.

Cystopteris sandwicensis Brack., Expl. Exp. 16: 234. 1854.

Rhizome short creeping, internodes short, resulting in clumping of leaves near apex, sparsely invested with brown lanceolate scales. *Stipe* shorter than blade, stramineous to light brown, scales lanceolate, only at base of stipe. *Blade* bipinnatifid to bipinnate, deltoid to ovate-lanceolate, up to 25 cm. long and 12 cm. wide; rachis and minor axes sparsely invested with uni- and multicellular glandular hairs; primary pinnae shortly petiolulate, subopposite to alternate, broad-ovate; secondary segments not petioled, ovate, with dentate serrations some of which are emarginate, some of veins may enter emarginations. *Sori* round, discrete to overlapping at maturity; indusium cup-shaped, broadly attached under receptacle, glabrous, indusial cells somewhat elongate, invested with accessory indusial hairs; spores dark brown, echinate, size 43-53 μ . Chromosome number $n = ca. 168$. (Plate 4)

Distribution. Hawaiian Islands.

Type. Not seen. It is "Sandwich Islands, D. Douglas, n. 51" and is probably at K.

Discussion. *Cystopteris douglasii* is close to *C. fragilis* and is endemic to the Hawaiian Islands. Superficially it resembles *C. bulbifera* with its twice pinnate lanceolate fronds but it is not as highly dissected. The indusium of *C. douglasii* is rather broadly attached and its cells are somewhat shorter than those in *C. fragilis*. However, the accessory indusial hairs are common to both species.

While typical *C. douglasii* has an ovate-lanceolate blade there is a form with rather wide, sub-deltoid blades which has been described as *C. sandwicensis*. Except for a slight increase in dissection, however, the type specimen (Kaala Mt., Wainai, Sandwich Islands, Wilkes Exped. 1838-42) shows no obvious difference from *C. douglasii*. They are accord-

ingly being maintained as one species. Since the above work was carried out, further spore observations in this species indicate that there may be another polyploid level represented in the range of $4n$ or $6n$.

B. Section Emarginatae

Section *Emarginatae* Blasdell sectio novum.

Cystopteris with veins extending into depressions at the pinna margin; indusium cup- or fingernail-shaped, the free margin relatively entire, indusial cells roughly rectangular in outline; adaxial epidermal cells with regular walls or merely shallow, regular lobes.

Type species. *Cystopteris montana* (Lam.) Bernh.

Sectio *Emarginatae* Blasdell sectio novum.

Cystopteris venulis in depressiones prope marginem pinnae excurrentibus; indusio calyciformi aut unguiformi, margine libero plus magis integro, cellulis indusii circumscriptione fere rectangulari; cellulis adaxialibus epidermalibus circumscriptione regulari aut lobis tantum haud profundis, regularibus. Species typica; *Cystopteris montana* (Lam.) Bernh.

Section *Emarginatae* is set up to delimit a segment of subgenus *Cystopteris* with the following characters in common: vein position, indusial structure and adaxial epidermal cell outline. This section consists of five species: *Cystopteris montana*, *C. pellucida*, *C. sudetica*, *C. bulbifera* and *C. diaphana*.

4. *Cystopteris montana* (Lam.) Bernh. Neu. Journ. Bot. Schrad. 1(2):26. 1806.

Polypodium montanum Lam. Fl. Franc. 1: 23. 1788.

Cyathea montana (Lam.) J. Sm. Mém. Acad. Turin 5: 417. 1793.

Aspidium montanum (Lam.) Sw. Journ. Bot. Schrad. 1800 (2): 42. 1801.

Athyrium montanum (Lam.) Rohl. ex Spreng. Anleit. 3: 143. 1804.

Cystopteris allioni Newman, The Phytologist 1851. app. XXV.

Cystopteris myrrhidifolia Newman, Hist. of Brit. Ferns Ed. III. 97. 1854.

Cyste montana (Lam.) Dulac, Fl. Hautes-Pyrenees 33. 1867.

Polypodium myrrhidifolium Vill. ex Gilibert, Syst. Plant. Eur. I: 114. 1875.

Filix montana (Lam.) Underw. Our Nat. Ferns, Ed. VI, 119. 1900.

Filicula montana (Lam.) Farwell, Am. Mid. Nat. 12: 252. 1931.

Rhizome cord-like, up to 3 mm. in diameter, wide-creeping, internodes extensive, up to 4.0 cm. long, with leaves borne separately, apex invested with large light brown ovate-lanceolate scales. *Stipe* characteristically longer than the blade, occasionally up to 3 times as long, stramineous, invested with large light brown ovate-lanceolate scales up to 6 mm. long and 3 mm. wide with glandular margin. *Blade* quadripinnatifid, broadly deltoid, up to 15 cm. long and 19 cm. wide, the two basal pinnae longer than blade length but frequently arched toward blade apex resulting in a more equilateral deltoid blade; primary pinnae subopposite to alternate, short-petiolulate, the lowest pair longest and the upper pinnae becoming successively smaller, the basal pinnae unsymmetrically triangular resulting from the lengthening of the inferior costal pinnule; tertiary segments pinnatifid with emarginations into which the ultimate veins are directed. *Sori* round, discrete to overlapping at maturity; indusium shallowly cup-

shaped, cells roughly rectangular, invested with primarily marginal unicellular glands; spores dark brown, echinate, size 27-42 μ . Chromosome number $n = 42, 84$. (Plate 5)

Distribution. China, northern India, USSR, Europe, Canada and the United States.

Type. Not seen. The original description which I have examined agrees with the available specimens of this species.

Discussion. The similarities between *Cystopteris montana* and *C. sudetica* are rather imposing. The features which are characteristic of *C. montana*, however, are the greater size of the inferior rachal pinnules as compared with the superior pinnules of the basal pinnae. *Cystopteris montana* also lacks the clathrate scales which are characteristic of *C. sudetica*. There are also fewer glands on the indusia of *C. montana* than in *C. sudetica* and they are limited primarily to the margins.

It is suggested that *Cystopteris montana* has been involved in the production of two described hybrids, namely *C. fragilis* \times *montana* and *C. alpina*. The evidence for these views is strictly morphological and anatomical.

5. *Cystopteris pellucida* (Franch.) Ching ex C. Chr. Ind. Supply. III. 67. 1934.

Aspidium pellucidum Franch. Nouv. Arch. Mus. II 10: 119. 1887.

Dryopteris pellucida (Franch.) C. Chr. Ind. 283. 1905.

Rhizome creeping, internodes extensive, scales clathrate, brown, eglandular, sparse. *Stipe* up to 2 times as long as blade, light green to stramineous, with clathrate scales at base. *Blade* tripinnatifid to tripinnate, deltoid to deltoid-lanceolate, up to 25 cm. long and 13 cm. wide, the lower pinnae frequently directed toward blade apex; basal pinnae short-petiolulate, ovate lanceolate, up to 9 cm. long and 4 cm. wide; secondary pinnae pinnatifid to pinnate, ovate, with emarginations into which the ultimate veins are directed. *Sori* round, discrete to slightly overlapping at maturity; indusium cup-shaped, attached up to 2/3 of the circumference of the receptacle, cells roughly rectangular, glabrous; spores echinate, dark brown, size 27-32 μ . Chromosome number $n = 42$. (Plate 6)

Distribution. Yunnan and Moupin provinces, China.

Type. Not seen. "Moupine, in silvis humidis umbrosis, David, Aug 1869." It is probably located in P. The original description has been studied and agrees closely with the specimens at hand.

Discussion. As one of several Asian species which appear to be closely related to *Cystopteris sudetica* this fern has a rather restricted distribution. It resembles *C. sudetica* var. *sudetica* in blade outline and in the possession of clathrate scales. It differs in the eglandular indusium and in the broad attachment of the indusium to the receptacle. Another feature is the reduction in dissection of this plant as compared with that in *C. sudetica*. A specimen collected by David in 1870 has blades which, while still broadest at the base, have a more lanceolate outline than the other specimens seen.

6a. *Cystopteris sudetica* var. *sudetica*

Cystopteris sudetica A. Br. et Milde, Jahresber. scheles. Ges. 1855: 92.

Cystopteris leucosoria Schur, Oest. Bot. Zeit. 8: 328. 1858.

Cystopteris leucospora Schur, *ibid.*

Cystopteris sudetica var. *vulgaris* Milde, Sporenpl. 71. 1865.

Cystopteris sudetica var. *leptophylla* Milde, *ibid.*

Cystopteris sudetica var. *platyphylla* Milde, *ibid.*

Cystopteris braunii Milde, in lit. ex Milde, *ibid.*

Cystopteris silesiaca A. Br. in lit. ex Milde, *ibid.*

Rhizome slender, up to 2 mm. in diameter, wide-creeping, internodes up to 4 cm. long with leaves occurring singly; scales clathrate, most conspicuous near apex. *Stipe* longer than blade, being frequently 2 to 3 times as long, stramineous; clathrate scales up to 3 mm. long and 2 mm. wide, with glandular margins, scattered toward base of stipe. *Blade* tripinnate to quadripinnatifid, broadly deltoid, up to 19 cm. long and 20 cm. wide (the 2 basal pinnae longer than blade length but generally curved toward blade apex); rachis and minor axes with occasional unicellular and multicellular glandular hairs; primary pinnae predominantly alternate, short petiolulate, the lowest pair longest, the upper pinnae being successively smaller, terminating in a pinnatifid apex, ovate lanceolate; secondary pinnae ovate, inferior pinnule of basal pinna the same size as superior pinnule, secondary pinnae approximate and frequently overlapping; tertiary segments of lower pinnae pinnatifid or merely toothed, with apices of teeth emarginate; vein endings directed into emarginations. *Sori* round, discrete or rarely overlapping when mature, dorsal on vein; indusium cup-shaped, cells roughly rectangular, invested with unicellular glands; spores with echinate architecture, dark brown, 27-32 μ . Chromosome number $n = 42$. (Plate 7)

Distribution. Norway and western Russia but primarily concentrated in the mountainous regions of central Europe.

Type. Not seen. The original description has been examined and agrees with the available specimens from central Europe.

Discussion. The superficial morphology of *Cystopteris sudetica* resembles very closely that found in *C. montana* and, indeed, these two species appear to be closely related. They have in common the long cord-like rhizome with extended internodes. They also have the same deltoid blade plan and similar features of the indusium. They differ, however, in two respects. *Cystopteris sudetica* lacks the extended inferior costal pinnule which is so characteristic of the basal pinnae of *C. montana*. Also *C. sudetica* var. *sudetica* has the distinctive clathrate scales which also occur in its Asian relatives. From *C. sudetica* var. *moupinensis* it differs in its greater dissection and in the presence of indusial glands.

6b. *Cystopteris sudetica* var. *moupinensis* (Franch.) Blasdell comb. nov.

Cystopteris moupinensis Franch. Nouv. Arch. Mus. II 10: 111. 1887.

Cystopteris sphaerocarpa Hayata, Ic. Pl. Form. 4: 144. f. 84. 1914.

Cystopteris modesta Ching, Bull. Fan Mem. Inst. Biol. 10: 5-6. 1940.

Differing from *Cystopteris sudetica* var. *sudetica* in less dissection (tripinnatifid to tripinnate) of the blade and in the lack of glands on the indusium. (Plate 19)

Distribution. Region of Moupine, Yunnan, Sikang, Kansu, Shensi and Szechuan provinces, China.

Type. Not seen. "Moupine, in rupibus adumbratis" David, Aug. 1869. This specimen is probably in P.

Discussion. The placement of *Cystopteris sphaerocarpa* here is based partially on a photograph of the type specimen indicating a close identity to *C. sudetica* var. *moupinensis*. Hayata, in his discussion, refers only to a slight difference in dissection in contrasting the two taxa.

Cystopteris modesta differs from *C. sudetica* var. *moupinensis* in increased dissection and larger indusia. Also noted in Ching's discussion is the fact that "the apices of the segments are always reflexed, covering part of the sori in the manner of *Hypolepis*." He further comments that this condition may be due to the dryness of the season. It seems best to refer *Cystopteris modesta* to the present variety unless authentic material can be examined and the differences be shown to be more substantial than those described.

7. *Cystopteris bulbifera* (L.) Bernh. Schrad. Neu. Journ. 1 (2): 10. 1806.

Polypodium bulbiferum L. Sp. Pl. 2: 1091. 1753.

Aspidium bulbiferum (L.) Sw. Schrad Journ. 1800 (2): 41. 1801.

Nephrodium bulbiferum (L.) Michx. Fl. bor. Am. 2: 268. 1803.

Aspidium atomarium Muhl. ex Willd. Sp. Pl. 5: 279. 1810.

Athyrium atomarium (Muhl.) Pr. Rel. Haenk. 1: 40. 1825.

Cystopteris atomaria (Muhl.) Pr. Tent. 93. 1836.

Cystopteris bulbifera var. *flagelliformis* Lawson, Edinb. New Philos. Journ. 19: 280. 1864.

Cystopteris bulbifera var. *horizontalis* Lawson, *ibid.*

Cystea bulbifera (L.) Watt, Can. Nat. II. 13: 160. 1867.

Filix bulbiferum (L.) Und. Our Nat. Ferns Ed. VI. 119. 1900.

Cystopteris bulbifera forma *horizontalis* (Lawson) Gilbert, List N. Am. Pterid. 16. 1901.

Filicula bulbifera (L.) Farwell, Am. Mid. Nat. 12: 251. 1931.

Filicula bulbifera var. *horizontalis* (Lawson) Farwell, *ibid.*

Rhizome creeping, with short internodes, heavily invested with old stipe bases, scales lanceolate, abundant at apex of rhizome. *Stipe* much shorter than blade length, pink to stramineous, scales limited to base. *Blade* bipinnate to tripinnatifid, attenuate-deltoid, up to 5 ft. long and 5 in. wide at base; rachis and minor axes producing scattered fleshy vegetative propagules (bulblets) and invested with uni- and multicellular glandular hairs; primary pinnae subopposite to alternate, up to 30 pairs, short-petiolulate, ovate-lanceolate to oblong, up to 7.5 cm. long and 5.0 cm. wide; secondary pinnae sessile, pinnatifid, with small rounded emarginate teeth, ultimate veins directed into emarginations. *Sori* round, discrete; indusium cup-shaped, broadly attached under the receptacle, cells short rectangular, typically invested with unicellular glandular hairs; spores dark brown, echinate, size 27-32 μ . Chromosome number $n = 42$. (Plate 8)

Distribution. Newfoundland to Manitoba, south to Georgia and central Arizona, Guadalupe Mts., New Mexico.

Type. Not seen. As is the case with *Cystopteris fragilis*, a type was not cited in the original description. However, as reference is given to Plu-

kenet's *Phytographie*, this illustration would be the logical type of the species.

Discussion. This is a very distinct species primarily of central and eastern United States and Canada. Its attenuate tapering frond, broadly attached indusia and the occurrence of vegetative propagules on the axes are the prime diagnostic features. The bulblets are most frequently glabrous except for a few multicellular glandular hairs. However, occasionally specimens are found in which the bulblets are provided with light brown scales. The indusia, while typically glandular, are occasionally glabrous.

Cystopteris bulbifera is evidently a parent of the putative hybrids, *C. × tennesseensis* and *C. × laurentiana*. Since *C. bulbifera* occurs throughout the ranges of these hybrids, the respective ranges of these intermediates are determined primarily by the distribution of the other parents, diploid *C. protrusa* versus the tetraploid *C. fragilis*.

8. *Cystopteris diaphana* (Bory) Blasdell comb. nov.

Polypodium diaphanum Bory, Voyage Iles Mers Afr. I. 328. 1804.

Athyrium fumarioides Presl, Rel. Haenk. I. 39. 1811.

Cystopteris canariensis Presl, Tent. Pterid. 93. 1836.

Cystopteris fragilis var. *nigrescens* Hook. Sp. Fil. 1: 198. 1846.

Cystopteris azorica Fee, Gen. Fil. 300. 1850-52.

Cystopteris fragilis var. *azorica* (Fée) Moore, Ind. Fil. 282, 1857-62.

Cystopteris fragilis var. *sempervirens* Moore, *ibid.*

Cystopteris fragilis subsp. *alpina* var. *canariensis* (Presl) Milde, Fil. Eur. 152. 1867.

Cystopteris fragilis subsp. *regia* var. *canariensis* (Presl) Aschers. Synop. Mit. Eur. Fl. 1: 18. 1896.

Cystopteris fragilis subsp. *canariensis* (Presl) Christ, Farnkr. Schweiz. 158. 1900.

Asplenium diaphanum Lojaccono, Fl. Sic. 3: 402, tab. VI, fig. 4. 1909.

Cystopteris fragilis subsp. *diaphana* (Bory) Litard., Bull. Soc. Bot. Deux-Sevres, 88. 1911-12.

Rhizome short creeping, internodes short, leaves somewhat clumped near apex, only sparsely invested with dark brown lanceolate scales except at apex, scales occasionally with marginal glands. *Stipe* shorter than the blade, stramineous to medium brown, with some scales at base. *Blade* bipinnate to tripinnate, ovate-lanceolate, up to 30 cm. long and 14 cm. broad; rachis and minor axes with scattered uni- and multicellular glandular hairs; primary pinnae subopposite to alternate, basal pinnae short petiolulate, ovate-lanceolate, obtuse; secondary pinnae obtuse, with emarginations, veins running into emarginations. *Sorus* round, discrete to running together when mature; indusium finger-nail- to cup-shaped, with entire rounded apex, cells roughly rectangular, glandular to glabrous; sporangia with much shortened stalks; spores dark brown, echinate, spore size 27-48 μ . Chromosome number $n = 42, 84, 126$. (Plate 9)

Distribution. Canary Islands, Tanganyika Territory, Mexico, South America.

Type. Not seen. The original description was formulated from plants collected on Reunion Island and agrees with both the African and the South American specimens I have seen.

Discussion. This species, in the past, has been combined with *Cystopteris fragilis* and has been designated by various infraspecific categories. The most recent treatment has been that by Litardière (1912) in which *C. diaphana* was given a subspecific status based primarily on the vein condition and the glandular indusia. He also outlined the distribution of this element which is dominantly southern.

The resemblance of *Cystopteris fragilis* to *C. diaphana* is superficially very great since they both have the ovate-lanceolate type of blade. *Cystopteris diaphana*, however, has certain anatomical features which are quite distinct. Besides the vein characters, *C. diaphana* has adaxial epidermal cells which have straight or merely undulating walls and are somewhat rectangular as opposed to the deeply lobed cells of *C. fragilis*. Also the indusial cells are rather short and rectangular as contrasted with the attenuate cells of *C. fragilis*. Finally, the sporangial stalk of *C. diaphana* is very much reduced (except in certain introgressant populations) so that the sporangium appears essentially sessile. Careful dissections, however, show the stalk cells which are much shortened. The remainder of the species in the genus possess well developed sporangial stalks.

While these characters remain quite distinct where *Cystopteris diaphana* is isolated from *C. fragilis*, they do not correlate well where the ranges of these two species overlap. Apparently large scale gene exchange occurs where these species occur sympatrically.

Subgenus Acystopteris

Subgenus *Acystopteris* (Nakai) Blasdell stat. nov.

Acystopteris Nakai, Bot. Mag. Tokyo. 47: 180. 1933. (pro gen.).

Medium sized ferns with deltoid blades; scales with glandular margins on the stipe base and rhizome apex; stipes nearly equalling length of blade, invested with colorless multicellular non-glandular hairs; blade at least tripinnatifid; indusium merely a small flap subtending sorus (not cup-shaped); spores bilateral, yellow, warts of exospore much dissected in cross section.

Type species. *Cystopteris japonica* Luerksen.

Subgenus *Acystopteris* includes two species: *Cystopteris japonica* and *C. tenuisecta*.

9. *Cystopteris japonica* Luerksen, Bot. Jahr. f. Syst. 4: 363. 1883.

Acystopteris japonica Nakai, Bot. Mag. Tokyo 47: 180. 1933.

Cystopteris japonica var. *taiwaniana* Tagawa, Act. Phytotax. Geobot. 4: 51-57. 1935.

Rhizome creeping, up to 6 mm. in diameter, internodes distinct but short, resulting in grouping of leaves near apex; scales ovate-lanceolate with glandular margins, dark brown, predominantly near rhizome apex. *Stipe* and rachis (and sometimes costa bases)

a shiny black color, with lanceolate, brown, glandular-margined scales throughout the stipe; stipe length approaching length of blade. *Blade* tripinnate, deltoid, up to 35 cm. long and 30 cm. wide, lower pinnae frequently curved toward blade apex, rachis and minor axes provided with multicellular non-glandular hairs; primary pinnae subopposite in lower half of blade, bipinnate, subsessile, long lanceolate, upper pinnae lanceolate and simply pinnate; secondary pinnae opposite to alternate, sessile, elongate-lanceolate; veins of ultimate segments pinnately organized with most veins running into marginal teeth. *Sori* round, discrete, single on the anterior vein branch of the ultimate segments (except for basal pinnae) thus forming two rows parallel with costa of secondary pinna, pale brown; indusium round-ovate, completely obscured in the mature sorus, glabrous, cells short rectangular; spores yellowish, thickly invested with short ridged warts, size 28-37 μ . Chromosome number = 42, 84?. (Plate 10)

Distribution. Kweichow and Szechwan provinces, China to Honshu, Japan.

Type. Not seen. "Kiusiu, Osumi, Hezukumura (Tachiro)." It may have been in the herbarium at Leipzig and if so was destroyed in the Second World War. The specimens at hand agree closely with Luerssen's original description of the species.

Discussion. This species and the closely related *Cystopteris tenuisecta* are quite distinct from the remainder of the genus having in common only the position of the sorus and the basic chromosome number. They have the distinctive features of spore architecture, multicellular non-glandular hairs and epidermal cells on a more diminutive size scale.

Cystopteris japonica differs from *C. tenuisecta* in the possession of a glossy black stipe and rachis. This dark pigment may even extend into the axes of the pinnae. Another diagnostic character is the absence of glands on the indusium. The indusium is very minute and would not appear to serve extensively in the protection of the young sorus.

10. *Cystopteris tenuisecta* (Bl.) Mett., Ann. Lugd. Bat. 1: 241. 1864.

Aspidium tenuisectum Bl. Enum. Plant. Javae. Fasc. II. Filices. 130. 1828.

Alsophila tenuisecta Bl. ex Moore Ind. Fil. 58. 1857-62.

Athyrium tenuisectum (Bl.) Moore, *ibid.* 188.

Asplenium (Athyrium) tenuisectum Hooker, Sp. Fil. 3: 222. 1860.

Lastrea setosa Bedd. Ferns Br. Ind. t. 262. 1869.

Cystopteris setosa Bedd. *ibid.* t. 312.

Davallia setosa (Bedd.) Baker Syn. Fil. 468. 1874.

Cystopteris formosana Hayata, Ic. Plant. Form. 143-146. 1914.

Acystopteris tenuisecta Tagawa, Acta Phytotax. Geobot. 7: 73. 1938.

Rhizome creeping, robust, internodes short but distinct, resulting in grouping of leaves near apex; scales ovate-lanceolate, glandular-margined, most prevalent near rhizome apex. *Stipe* glossy, stramineous, with lanceolate, glandular-margined, brown scales scattered throughout, stipe approaching length of blade. *Blade* tripinnate to quadripinnatifid, deltoid, up to 50 cm. long and 25 cm. broad; rachis and minor axes invested with multicellular non-glandular hairs; primary pinnae subopposite in the lower half of the blade and bipinnate, long lanceolate; upper pinnae lanceolate, pinnate, alternate; secondary pinnae opposite to alternate, sessile, elongate-lanceolate; veins of ultimate segments pinnately organized with most veins running into marginal teeth. *Sori* round, discrete, single on the anterior vein of the ultimate segments thus forming 2

rows parallel to the ultimate costae, pale brown; indusium round-ovate, cells short rectangular, invested with unicellular glands; spores yellowish, thickly covered with short ridged warts, size 28-32 μ . Chromosome number $n = 42$. (Plate 11)

Distribution. Northeast India eastward to Honshu, Japan, southward to Java and the Philippine Islands.

Type. "Crecit in sylvis temperatis insulae Java. Blume." (L!).

Discussion. This species is quite evidently closely related to *Cystopteris japonica*. Its primary distinctive features are the presence of glands on the indusium and in the lack of dark pigment on the primary axes of the leaf.

The description by Beddome of *Lastrea setosa* was based on rather poor material. Later in the same publication he transferred this plant to *Cystopteris* based on more adequate material.

Cystopteris formosana is placed here on the basis of the original description. Hayata states in his discussion of the species that it is perhaps a smaller form of *C. setosa* (now referred to *C. tenuisecta*).

Hybrids

1. *Cystopteris* \times *tennesseensis* Shaver (pro spec.).

Cystopteris fragilis f. *simulans* Weatherby, Rhodora 37: 376. 1935.

Cystopteris tennesseensis Shaver, Journ. Tenn. Acad. Sci. 25 (2): 107. 1950.

Cystopteris fragilis var. *tennesseensis* (Shaver) McGregor, Am. Fern Journ. 40: 202. 1950.

Cystopteris fragilis var. *simulans* (Weath.) McGregor, Am. Fern Journ. *ibid*.

Rhizome creeping, internodes short with leaves tufted near apex, apex invested with numerous lanceolate scales. *Stipe* mostly dark brown at base gradually becoming stramineous toward blade, predominantly shorter than blade. *Blade* bi- to tripinnatifid, deltoid to deltoid-lanceolate, up to 31 cm. long and 18 cm. wide; minor axes with scattered uni- and multicellular glandular hairs, bulblets present or absent on rachis; primary pinnae subopposite to alternate, short petiolulate, broadly ovate; secondary pinnae mostly petiolulate toward base of blade but broadly attached above, obtuse, cut into lobes which are also obtuse, with marginal teeth and emarginations; veins directed both into teeth and emarginations. *Sori* round, discrete to occasionally coenosoral; indusium cup-shaped with truncate apex, rather broadly attached under receptacle, cells roughly rectangular, with or without unicellular glands; spores dark brown, echinate, size 32-42 μ . Chromosome number $n = 84$. (Plate 12)

Distribution. Maryland south to North Carolina, west to Kansas and Oklahoma.

Type. Not seen. "Quarry, Round Lick Creek, near the Cumberland River, Rome, Smith Co., Tennessee. Shaver no. 7885." I have seen numerous collections by Shaver of this plant and they agree closely with specimens throughout the range described above.

Discussion. This putative hybrid appears to combine the characters of *Cystopteris protrusa* and *C. bulbifera*. The features which are diagnostic of *C. bulbifera* are the broad frond base and the frequent occurrence of

bulblets as well as occasional glands on the indusium. It also usually has the acuminate (but not long attenuate) apex of *C. protrusa*. Only rarely does the leaf show a tendency to become attenuate. The putative parents are both diploids, resulting in a tetraploid hybrid which is the case with *C. × tennesseensis*. It is interesting to note that *C. × tennesseensis* has not been reported outside the range of *C. protrusa*. Shaver (1950) was the first to publish the parentage of this hybrid although a hybrid origin had been suggested by Weatherby (in Wherry, 1944) and Wagner (1944).

Cystopteris fragilis form *simulans* is quite evidently referable to this hybrid. McGregor (1950) acknowledges their close relationship but maintains them as two varieties of *C. fragilis*. They both occupy the same geographic regions and are so similar that it is thought best to unite them. The lack of glands in some specimens may possibly be explained by the fact that some specimens of *C. bulbifera* (the presumed parent which supplies the glands to the hybrid) are eglandular.

2. *Cystopteris × laurentiana* (Weath.) Blasdell comb. novum

Cystopteris fragilis var. *laurentiana* Weatherby, *Rhodora*, 28: 129. 1926.

Rhizome creeping, with short internodes, leaves tufted near apex; scales lanceolate, prominent near apex. *Stipe* shorter than the blade, light brown to red-tinged. *Blade* tripinnatifid, ovate-attenuate, up to 34 cm. long and 13 cm. wide; rachis occasionally with bulblets, minor axes with scattered uni- and multicellular glandular hairs; primary pinnae subopposite to alternate, short petiolulate, broadly ovate; secondary pinnae obtuse and frequently their segments also; veins directed both into teeth and into emarginations. *Sori* round, discrete to occasionally overlapping; indusium ovate-lanceolate, frequently with lacerate apex, with elongate cells, provided with scattered unicellular glands (primarily toward base); spores dark brown, echinate, size 38-48 μ . Chromosome number $n = 126$. (Plate 13)

Distribution. Quebec and Newfoundland, west through the Great Lakes region to Wisconsin.

Type. "Limestone-conglomerate cliffs, headland north of Baptiste Michaud's, Bic, Rimouski Co., Quebec." *Fernald & Collins*, July 18, 1904. (GH!).

Discussion. This plant was recognized by Fernald (Weatherby, 1926) as distinct from *Cystopteris fragilis* var. *fragilis* by its greater size and blunt pinnules, features which he states gives it in the field the aspect of a *C. bulbifera* without the long apex of the frond.

Cystopteris × laurentiana appears to be a hybrid between *C. fragilis* and *C. bulbifera*. A discussion of it appears in the section on "Hybridization" above.

It is interesting to note that *Cystopteris × laurentiana* has been reported only from regions within the ranges of the tetraploids *C. fragilis* var. *fragilis* and the apparent introgressant "*C. fragilis* var. *mackayi*." It

has not as yet been found in regions occupied by *C. protrusa* which is a diploid.

The resemblance of this hybrid to *Cystopteris fragilis* is so close that it is sometimes difficult to distinguish the two plants. In northern Michigan it often occurs, however, with a wealth of bulblets on the abaxial blade axes. These Michigan populations have been described by Wagner and Hagenah (1956). Unfortunately, over a large part of its range, bulblets occur only rarely. In such cases the diagnostic features are primarily the presence of scattered glands on the indusium, the nature of the vein endings, and the usually large plant, and a spore size within the 6n range.

3. *Cystopteris* \times *alpina* (Wulfen) Desv. (pro. spec.).

Polypodium alpinum Wulfen, ex Jacq. Collect II, 171. 1788.

Aspidium alpinum Sw. in Schrad. Journ. d. Bot. 1800, II. 42.

Cyathea alpina Roth, Tent. Fl. Germ. III. 99. 1800.

Cystopteris alpina Desv. Mém. Soc. Linn. Paris, 6: 264. 1827.

Cystea alpina Sm. Engl. Fl. 4: 291. 1828.

Cystopteris fragilis var. *alpina* Koch, Syn. Fl. Germ. Ed. 2. 980. 1845.

Cystopteris fragilis subsp. *alpina* (Wulfen) Hartm. Excurs. Fl. 152. 1846.

Cystopteris fragilis \times *montana* Christ, Farnkr. d. Schweiz, 162, f. 28. 1900.

Rhizome short creeping, internodes short with leaves tufted near apex, apex invested with ovate lanceolate scales. *Stipe* stramineous to dark brown, frequently approaching length of blade. *Blade* tripinnate to quadripinnatifid, ovate-lanceolate, up to 21 cm. long and 7.5 cm. wide; minor axes with scattered multicellular glandular hairs; basal pinna pair mostly shorter than succeeding pair, ovate; secondary and tertiary pinna axes winged, the ultimate lobes having either teeth or emarginations commonly with unsymmetrical lateral lobes; veins running into both teeth and emarginations. *Sori* round, discrete; indusium ovate to lanceolate, glabrous, with attenuate cells; spores dark brown, echinate, size 38-48 μ . Chromosome number $n = 126$. (Plate 14)

Distribution. Mountainous regions of central Europe.

Type. Not seen.

Discussion. This plant is probably the most distinct of the elements which has been attributed to *Cystopteris fragilis* in Europe. This is shown by the relative uniformity in the synonymy. *Cystopteris* \times *alpina* resembles *C. fragilis* in the majority of the diagnostic features and thus it is not surprising that past workers have placed it in infraspecific categories of the latter species. The dissection of the blade and the presence of some veins which are directed into emarginations are the only obvious characters which indicate the parentage of *C. montana*. The hexaploid spore size of *C. \times alpina* also lends to the hypothesis of hybrid origin. These problems have been discussed in the section on hybridization.

The conception of *Cystopteris fragilis* \times *montana* Christ is based entirely on the original description and figure by Christ. It is deemed important, however, to bring a consideration of this plant into the broad taxonomy of the genus *Cystopteris* because an intermediacy between *C*

fragilis and *C. montana* appears to exist. In the present treatment this plant is considered to be synonymous with *C. × alpina* although different genome combinations may be involved.

An examination of the original description brings one to the conclusion that features characteristic of *Cystopteris fragilis* are of somewhat more importance than those of *C. montana*. The claim of *C. montana* to parentage here lies primarily on the length of the stipe which is the same as the blade and on the basal pinnae which are the longest on the blade. Christ also states that the minuteness and distribution of the sori is similar to that in *C. montana*. *Cystopteris fragilis*, on the other hand, is represented by characters such as a short rhizome, pinnules with short toothed lobes and veins running into the tips. Thus this proposed hybrid, while it is made quite plausible by the description and figure, needs more study before a decision is made as to its authenticity.

4. *Cystopteris × kansuana* C. Chr. (pro. spec.).

Cystopteris kansuana C. Chr. Journ. Wash. Acad. Sci. 17: 499. 1927.

Rhizome short creeping, with leaves tufted near apex, scales clathrate, ovate-lanceolate, sparse. *Stipe* length nearly equal to length of blade, castaneous, delicate. *Blade* bipinnate, lanceolate, tapering to a caudate apex, up to 8 cm. long and 2 cm. broad; primary pinnae opposite to somewhat alternate, distant, ovate, short petiolulate; basal pinnules unequilateral, pinnules with veins extending into emarginations. *Sori* round, discrete; indusium linear, with attenuate cells, glabrous; spores immature but appear aborted. (Plate 19)

Distribution. Type locality.

Type. La Chang K'ou, near Sining, Kansu province, China. *Ching* 631. (US!).

Discussion. This plant is considered to be a hybrid (apparently sterile) between *Cystopteris fragilis* and *C. sudetica* var. *moupinensis* because of the apparent combination of characters of these two species in *C. × kansuana*. It possesses the relatively compact rhizome and the blade shape of *C. fragilis*. However, it shows the vein position and the clathrate scales of *C. sudetica* and its related Asian taxa.

5. *Cystopteris diaphana × fragilis* complex

Cyathea regia Forster, Sym. Syn. 194. 1798.

Aspidium regium Sw. Schrad. Journ. 1800 (2): 41. 1801.

Nephrodium tenue Michx. Fl. Bor. Am. 2: 269. 1803.

Athyrium regium Spreng. Anleit 3: 139. 1804.

Aspidium tenue (Michx.) Sw. Syn. Fil. 58. 1806.

Athyrium tenue (Michx.) Presl, Rel. Haenk. 1: 39. 1825.

Cystopteris regia (Sw.) Desv. Mem. Soc. Linn. Paris 6: 264. 1827.

Cystopteris tenuis (Michx.) Desv. ibid. 263.

Cystea regia (For.) Sm. Eng. Fl. Ed. 2. 4: 289. 1828.

Cystopteris fragilis B *alpina* var. *regia* Milde, Sporenpl. 69. 1865.

Cystopteris fragilis var. *mackayii* Lawson, Fern Fl. Can. 233. 1889.

Cystopteris filix-fragilis var. *tenuis* (Michx.) Farwell, Ann. Rep. Mich. Acad. Sci. 6: 200. 1904.

Cystopteris filix-fragilis var. *mackayii* (Lawson) Farwell, Am. Fern. Journ. 27: 14. 1937.

Distribution. Widespread, occurring both where the ranges of *C. fragilis* and *C. diaphana* are in close proximity as well as at some distance from the parents.

Discussion. I believe that all of the synonyms listed above represent intermediates of one form or another between the two extremes *C. diaphana* and *C. fragilis*. The genotypes of these species are presumably similar, or once were similar in the past, in their composition (as might be suspected also on the basis of their similar aspect), for not only where the ranges of the two species are in contact is there evidence of intergradation, but the intergrades are evidently sufficiently viable that they often occur separate from the parents. The assumed exchange of genetic material, therefore, does not appear to have any effect on fertility of the offspring. All *C. fragilis* known today is polyploid; the diploid still remains only in *C. diaphana*, and this species also has 4X and 6X forms. The apparent intermediates are all 4X or 6X, according to spore size.

The expression of this apparent introgression may be observed in three contrasting characters which correlate well in specimens of each species. They are vein position, shape of adaxial epidermal cells and shape of the indusium and its cells.

The putative introgressant individuals exhibit no apparent correlation in regard to the diagnostic characters. Each character seems to be independent of the others and to be expressed in varying ways in different plants.

Accurate taxonomic designation of these apparent introgressants is difficult when one is dealing with large collections. Ideally one should indicate in an annotation the degree of expression of a given species in the introgressant plant. However, the only macroscopic character which may be readily used for this purpose is the vein position. One would then be accused of using "one-character taxonomy" without regard for the expression of the other characters. In practically all examples I studied, evidence of intermediacy in the other characters that separate *C. diaphana* and *C. fragilis* were found. I believe, therefore, that vein position is a reliable indicator of intermediacy.

I have made no attempt to express the relative degree of parental expression but have used the only nomenclatural device that I could in this unusual situation, namely to use the blanket formula *Cystopteris diaphana* × *fragilis*. All of the introgressant plants have the veins entering both teeth and emarginations but in varying ratios.

Since the completion of the foregoing work, new cytological evidence suggests that there may be another interpretation possible for "*C. fragilis* var. *mackayii*" which is a tetraploid. This evidence, obtained by Warren H. Wagner Jr., suggests the possibility that *Cystopteris fragilis* var. *mackayi* may be an ancient segregate resulting from hybridization between two diploid species such as *C. diaphana* and *C. protrusa*. The difference in genome composition may thus explain the ability of "*mackayi*" to maintain its distinctness even when occurring in close proximity to *C. fragilis*, a situation which exists in the extreme northeastern United States and in southeastern Canada.

6. *Cystopteris diaphana* \times *protrusa* complex

Distribution. Throughout most of the range of *Cystopteris protrusa*.

Discussion. Apparent introgressant specimens have been observed through the range of *Cystopteris protrusa*. Characteristics of these plants are similar to those described in the above discussion of *C. diaphana* \times *fragilis* with the difference that here we are dealing with diploid plants instead of the tetraploid and hexaploid populations of *C. diaphana* \times *fragilis*.

SUMMARY

1. The history of the fern genus *Cystopteris* shows that the interpretation of inter-relationships of its species and varieties presents many problems. To contribute to the solution of these problems, this investigation was made, utilizing a number of techniques designed for obtaining and correlating new morphological, anatomical, and cytological data.

2. Spore studies in the genus revealed three general types of spore architecture which correlate closely with the taxonomic delimitation of subgenera. One of these spore types has not been illustrated previously, and intermediate forms were noted between the other two types for the first time.

3. The sizes of spores were found to correlate closely with levels of polyploidy, and thus it was possible to estimate chromosome numbers in the genus where actual counts were not feasible.

4. Preliminary studies of gametophytes indicated differences which may prove to be of taxonomic significance in the future when more extensive surveys are made.

5. Analysis of various anatomical features of the mature sporophytes revealed many new facts which bear on interspecific relationships. The

structures which proved most important were the rhizome scales, the adaxial cells of the leaf epidermis, the laminar trichomes and the indusium.

6. Cytological investigations by previous workers and the present investigator show that there are four polyploid levels in the genus. Three of the chromosome numbers found in this study involve taxa never before reported, and previous findings for a number of species are confirmed by new observations.

7. The role of interspecific hybridization in creating variation in *Cystopteris* has been examined, and it is shown that two mechanisms may be involved, namely allopolyploidy and introgression. Both are believed to account for the traditionally confused concept of the members of the "*Cystopteris fragilis* complex."

8. The world distribution of the members of this genus was determined, and explanations are suggested for the current disjunct distributions of certain of the taxa.

9. Evolution and relationships within the genus were postulated on the basis of a correlation of twelve characters. The species were plotted on a concentric chart using those nine characters which could most readily be assessed as advancements. The position of the species on the chart suggests their probable derivations and groups them according to their common ground plans.

10. As a result of these studies, a taxonomic revision is proposed which divides the genus *Cystopteris* into two subgenera, one of them with two sections. Included is a key to the divisions of the genus and to the ten species which are recognized. Descriptions and discussions of each of the species as well as their probable hybrids are presented, with figures to depict their technical characters.

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GH	Gray Herbarium of Harvard University, Cambridge, Massachusetts.
L	Rijksherbarium, Nonnensteeg, Leiden, Netherlands.
P	Museum National d's Histoire Naturelle, Paris, France.
PH	Academy of Natural Sciences, Philadelphia, Pennsylvania.
R	Divisao de Botanica do Museu National, Rio de Janeiro, Brazil.
S-PA	Paleobotanical Department, Swedish Museum of Natural History, Stockholm.
TENN	University of Tennessee, Knoxville.
US	U. S. National Herbarium, Smithsonian Institution, Washington, D. C.
WELT	The Dominion Museum, Wellington, New Zealand.

Latin diagnoses were prepared by Professor R. A. Pack of the University of Michigan, Ann Arbor, Michigan.

APPENDIX

List of Specimen Citations

(The herbarium abbreviations are those proposed by Lanjouw and Stafleu 1956)

1a. *Cystopteris fragilis* (L.) Bernh. var. *fragilis*

SELECTED SPECIMENS:

CANADA.—ALBERTA.—Head of Smoky River, *Hollister* 8 (US); Shaganappi, Calgary, *Moodie*, June 21, 1913 (US); Jasper Park, Cabin Creek, *Macoun* 98124 (US); Rosedale, *Moodie* 987 (US); Waterton Lakes National Park, Waterton, *Hermann* 13078 (US); Chipewyan, *Raup and Abbe* 4688 (US); Lake Mamawi, *Raup and Abbe* 4400 (S-PA). BRITISH COLUMBIA.—Canyon at Carbonate, Selkirk Mountains, *Heacock*, 2 Jul 1904 (US); Queen Charlotte Islands, *Osgood*, 1900 (US); Upper Ingonika River, Cassiar Dist., *Preble and Mixter* 690 (US); 3 miles SW of Malakwa, *Hermann* 12932 (US); Big Bend Dist., Selkirk Mts., *Shaw* 1002 (PH); Lake Mamawi, *Raup and Abbe* 4400 (S-PA). ELLESMERE ISLAND.—Neyprecht Island, *Stein* 178 (US). LABRADOR.—Killinek Island, *Walker* 755 (PH); Battle Harbor, *Williamson*, 6-13 Aug 1911 (PH); Mugford Island, *Palmer*, 27 Aug 1929 (PH); Ungara, *Turner* 673 (US); West Turnavik, *Bartlett* 2 (US). MANITOBA.—Lake Winnipeg, *Macoun*, Aug 1884. NORTH-WEST TERRITORIES.—District of Mackenzie, Yellowknife, *Cody and McCanse* 3559 (US); Port Radium, Great Bear Lake, *Shacklette* 2900 (US); District of Franklin, Frobisher Bay, Sylvania Grinnell River, *Collins* 43a (US); Melville Peninsula, Ross Bay, *Cody* 1512 (US). ONTARIO.—0.5 mi. S of Bond Lake, York Co., *Soper and Dale* 4149 (US); Lookout Ridge, Algonquin Park, *Wherry*, 26 Aug 1934 (PH); Batchawa Falls, Algoma district, *Taylor et al.* 170 (S-PA); Rockcliffe near Ottawa, *Malte*, 7 Aug 1923 (S-PA). QUEBEC.—Pointe Rouleau, Lake Mistassini, *Rousseau and Rouleau* 663 (US); Grand Cascapedia, Gaspé, *Hart* 12 (US); SW of Bic, Rimouski Co., *Clausen and Trapido* 2836 (US). SASKATCHEWAN.—Lake Athabaska, Charlotte Pt., *Raup* 6234 (S-PA). YUKON.—Moosehide Mt., Dawson, *Calder* 2964 (US); Wood-chopper Creek, *Collier* 102 (US); 50 mi. above Stewart River, *Tarleton* 151 (US); SE of Lewis, White Pass and Yukon R.R., *Schmid* 48 (PH); Rampart House, Yukon-Alaska Border, *Loan* 693 (S-PA).

GREENLAND.—Head of Søndre Strømfjord, *Erlanson* 2420 (US); Cape Hatherton, *Koelz* 201 (US); Scoresby Sund, *Hartz*, 16 Aug 1891 (US); Kaiser-Franz-Josephs-Fjord, *Buchenau*, Feb. 1895 (US); Godhavn, Kleist, 16 Aug 1904 (S-PA, US); Qagssiarssuk, *Porsild*, 10 Aug 1925 (US); Etah, *Ekblaw* 12 (US); Englishmen's Harbor, Disco Island, *Erlanson* 2870 (US); Grant Fjord off Clavering Fjord, *Bartlett* 429 (TENN, US); Ymerön, Mt. Celsius, *Jarvik*, 31 Jul 1947 (S-PA); Umanak, *Ekman*, 30 Aug 1923 (S-PA); Regio Julianehaab, *Lagerkranz*, 6 Sep 1946 (S-PA); Regio Angmagssalik, *Lagerkranz*, 28 Jul 1946 (S-PA).

GUATEMALA.—Dept. of Huehuetenango, vicinity of Chemal, *Steyermark* 50263 (US); Vicinity of Tunima, *Steyermark* 48411 (US).

ICELAND.—Reykjavik, *Scamman* 1207 (US); Kjosarsysla, Hvalfjörður, Byrnjudalsarfoss, *Love, A. & D.*, 13 Sep 1948 (S-PA); Hofsfjall, *Davidsson*, 14 Aug 1897 (S-PA); Sedisfjörður, *Kjellberg*, 26 Jun 1915 (S-PA); Siglufjörður, *Lagerkranz*, 4 Aug 1928 (S-PA).

MEXICO—CHIAPAS.—Acotepec, *Rovirosa* 1054 (PH). COAHUILA.—Villa Acuna, *Wynd & Mueller* 521 (US). GUERRERO.—West of Petlacala, *Mexia* 9068 (US). MICHOACAN.—Vicinity of Uruapan, *Leeds* 231 (PH, US). MORELOS.—Cuernavaca, *Deam*, 7 Jul 1900 (US). PUEBLA.—Popocatepetl, *Rose & Hay* 5989 (US).

UNITED STATES.—ARIZONA.—Coconino Co.: Oak Creek Canyon, *Phillips* 2968

(US). Gila Co.: Workman Creek, *Little* 4301 (US). Pima Co.: Mt. Lemmon, Tucson, *Shreve*, 1 Oct 1917 (S-PA). CALIFORNIA.—Alpine Co.: Pigeon Flat, *Hoover* 5355 (US). Amador Co.: Elsie's Creek, *Hansen* 1460 (US). Butte Co.: Iron Canon, *Austin* 1866 (US). Calaveras Co.: Moran Creek, *Ranzoni*, Aug 1946 (US). Inyo Co.: Sierra Nevada, *Coville & Funston* 2127 (US). Lassen Co.: Susanville, *Jones*, 25 Jun 1897 (US). Madera Co.: Bass Lake, *Storer* 235 (US). Mono Co.: Potato Creek, *Alexander & Kellog* 4516 (US). Nevada Co.: Donner Pass, *Heller*, 17 Aug 1903 (US). Plumas Co.: Lassen Forest, *Eggleston* 7236 (US). San Bernardino Co.: San Bernardino, *Vasey*, Aug 1880 (PH). San Diego Co.: Smith Mt., San Diego, *Orcutt*, Jul 1882 (PH). Santa Clara Co.: Congress Springs, near Saratoga, *Pendleton* 1348 (US). Shasta Co.: Hat Creek, *Hall & Babcock* 4267 (S-PA). Tulare Co.: N of Mineral King, *Wherry*, 23 Jun 1940 (PH). Tuolumne Co.: Eagle Meadow, *Hoover* 1529 (US). COLORADO.—Clear Creek Co.: Berthond Pass, near Georgetown, *Sheldon* 244 (US). Douglas Co.: Franktown, *Wherry*, 17 Jun 1937 (PH). El Paso Co.: W of Palmer Lake, *Wherry*, 26 Jun 1937 (PH). Garfield Co.: trail to Flat Top, *Hermann* 5538 (PH). Gilpin Co.: Tolland, *Palmer* 31392 (S-PA). Gunnison Co.: NW of Crested Butte, *Wherry*, 17 Jul 1937 (PH). Hinsdale Co.: Spring Creek Rd., 8½ mi. S of Pass, *Wherry*, 13 Jul 1937 (PH). Larimer Co.: 9 mi. S of Estes Park, *Benner* 7737 (PH). Mineral Co.: Wagon Wheel Gap, *Wherry*, 12 Jul 1937 (PH). Ouray Co.: Box Canyon, Ouray, *Wherry*, 18 Jul 1937 (PH). Rio Grande Co.: opposite Del Norte, *Wherry*, 12 Jul 1937 (PH). CONNECTICUT.—New Haven Co.: New Haven, *Allen*, 1 Jun 1878 (US). IDAHO.—Bear Lake Co.: Montpelier, *Wherry*, 17 Jun 1931 (PH). Blaine Co.: 5 mi. N of Ketchum, *Henderson* 3264 (US). Boise Co.: on Lowman-Atlanta Rd., *Hitchcock & Muhlick* 10046 (US). Custer Co.: Ryan Peak, *Hitchcock & Muhlick* 10587 (US). Elmore Co.: 10 mi. W of Featherville, *Hitchcock & Muhlick* 10368 (US). Idaho Co.: Heaven's Gate, *Jones, Q.* 218 (US). Latah Co.: Thatuna Hills, *Dillon* 576 (S-PA). Nez Perces Co.: valley of Peter Creek, *Sandberg et al.* 1047 (S-PA, US). Owyhee Co.: East Bruneau, *Nelson & Macbride* 1905 (S-PA, US). Valley Co.: Brundage Mt., *Davis* 2927 (PH). MAINE.—Hancock Co.: Mt. Desert Island, *Wherry*, 21 Aug 1935 (PH). MASSACHUSETTS.—Worcester Co.: Mt. Wachusett, Princeton, *Collins*, 17 Jul 1893 (US). MICHIGAN.—Keweenaw Co.: Lake Bailey, *Hermann* 7739 (US). MINNESOTA.—Lake Co.: East Beaver Bay bluff, *Lakela* 13577 (US). MONTANA.—Gallatin Co.: Lone Mt., Bozeman, *Blankinship* 640 (PH). Lake Co.: Mission Mts., *Kirkwood* 1001 (US). Madison Co.: Devil's Lane, Gravelly Range, *Hitchcock & Muhlick*, 19 Jul 1945 (PH). Meagher Co.: Little Belt Mts., near the Pass, *Flodman* 15 (US). Missoula Co.: O'Keefe's Canyon, near Missoula, *MacDougal* 211 (US). Park Co.: Livingston, *Scheuber*, 10 Jul 1901 (US). Sweet Grass Co.: Wreck Creek, *Eggleston* 7979 (US). NEBRASKA.—Dawes Co.: Belmont, *Webber* 230 (US). Thomas Co.: near Plummer Ford, Dismal River, *Rydberg* 1452 (US). NEVADA.—Clark Co.: Charleston Mts., Little Falls, *Clokey* 8255 (S-PA, TENN, US). Elko Co.: Ruby Mts., *Train* 337 (US). NEW MEXICO.—Grant Co.: Hillsboro Peak, *Metcalfe* 1201 (US). San Miguel Co.: Las Vegas, *Vasey*, Jul 1881 (US). Sierra Co.: Animas Canyon, *Pilsbry*, 10-18 Sep 1915 (PH). NORTH DAKOTA.—Benson Co.: Fort Totten, *Bergman* 1903 (US). Golden Valley Co.: Sentinel Butte, *Clausen* 8217 (US). OKLAHOMA.—Cimmaron Co.: Kenton, *Stevens* 496 (US). OREGON.—Hood River Co.: Mt. Hood, Mirror Lake, *Thompson* 3578 (S-PA). Jackson Co.: near Ashland, *Applegate* 2179a (US). Klamath Co.: Crater Lake National Park, *Coville* 1380 (US). Lake Co.: Lake Albert, *Eggleston* 7145 (US). Union Co.: Lake Anthony, *Wherry*, 3 Jul 1931 (PH). Wasco Co.: Dalles of Columbia River, *Eaton, D. C.*, n.d. (PH). PENNSYLVANIA.—Beaver Co.: Dutchmans Run, *Shafer*, 9 Jul 1885 (PH). SOUTH DAKOTA.—Lawrence Co.: Little Spearfish Canyon, *Over* 13840 (PH). Meade Co.: Piedmont and Little Elk Creek, *Rydberg* 1198 (US). Washabaugh Co.: Bear Creek, *Over* 1681 (US). UTAH.—Beaver Co.: east of Beaver, *Pennell et al.* 22827 (PH). Duchesne Co.: Mt. Emmons, *Hermann* 5092 (PH). Emery Co.: Wasatch Mts., *Pennell et al.* 22693 (PH). Sanpete Co.: Lake Canyon, Manti, *Tidestrom* 1889 (US). Summit Co.: Lamotte Peak, *Hermann* 5979 (PH). Utah Co.: Provo, *Goodding* 1140 (US). Washington Co.: Pine Valley, *Pennell & Schaeffer* 21826 (PH). WASHINGTON.—

Chelan Co.: Blewett Pass, *Thompson*, 28 Apr 1940 (PH). Clallam Co.: Olympic Mts., *Elmer* 2812 (US). Douglas Co.: Egbert Spring, *Sandberg & Leiberg* 351 (US). Kittitas Co.: Mt. Stuart, *Elmer* 1219 (US). Stevens Co.: Mt. Carleton, *Kreager*, 18 Jul 1902 (US). Whitman Co.: Rock Lake, *Beattie & Lawrence*, 28-30 May 1904 (PH). Yakima Co.: Cleman Mt., *Thompson*, 28 Apr 1940 (PH). WISCONSIN.—Door Co.: Egg Harbor, *Schnatten*, Jul 1882 (US). Iron Co.: Hurley, *Random*, 30 May 1896 (US). WYOMING.—Albany Co.: South Sybille, *Nelson* 7374 (US). Big Horn Co.: South Paintrock Creek, *Williams* 3146 (US). Crook Co.: 5 mi. N. of Sundance, *Porter* 5358 (PH). Fremont Co.: W of Lander, *Porter* 5588 (PH, US). Johnson Co.: near Buffalo, S Fork of Clear Creek, *Williams*, 3 Aug 1898 (US). Lincoln Co.: Afton, *Payson & Armstrong*, 24 Jun 1923 (PH). Teton Co.: Hoback Canyon, *Porter* 1157 (S-PA). Washakie Co.: upper Lee Creek, Big Horn Mts., *Pennell & Shaeffer* 24330 (PH). ALASKA.—Sadlerochit River, *Spetzman* 1184 (US); Nome, *Flett* 1508 (US); Mitrofanina Bay, Alaska Peninsula, *Griggs*, 20 Jul 1913 (US); Umiat, Colville River, *Spetzman* 2205 (US); Lake Peters (E of Canning River), *Spetzman* 1402 (US); Yakutat, *Stair*, 14 Jul 1945 (PH); Rapids Lodge, 138 mi. S of Fairbanks, *Scamman* 4 (S-PA). Aleutian Islands: Dutch Harbor, Unalaska, *Flett* 1517 (US); Glacier Valley, Unalaska, *Jepson* 250 (US); Great Sitka, *Llano* 1194b (US); Attu Island, *Llano* 1393a (US); False Pass, Unimak Island, *Eyerdam* 2111 (S-PA). Pribilof Islands.: St. Paul Island, *Palmer* 181 (US); St. Paul Island, *True & Prentiss* 41 (US); St. George Island, *True & Prentiss* 61 (US).

ASIA (INCLUDING SOVIET UNION)

AFGHANISTAN.—Kurram Valley, *Aitchison*, Dec 1879 (S-PA).

CEYLON.—Sudspitze, *Smith* (S-PA).

CHINA.—Kansu.: Lan Ze Cheon K'ou, near Sining, *Ching* 592 (US). Shansi.: Cieh-hsiuh district, Cho-mei-shan, *H. Smith*, Oct 1924 (S-PA); Yuan-chu district, Ye-cho-shan, *H. Smith*, 18 Jul 1924 (S-PA). Sinkiang.: Bogdo, Fu-Shn-Shan, *Hummel*, 15 Jun 1928 (S-PA); Bogdo, Ozun-ava, *Hummel*, 7 Jun 1928 (S-PA). Szechuan.: Karloug, *Smith*, 3 Aug 1922 (S-PA); Tsipula, *Smith*, 26 Aug 1922 (S-PA); Dongrergo, *Smith*, 9 Aug 1922 (S-PA); Hsioch-shan, *Smith*, 19 Jul 1922 (S-PA). Tibet: Ladak, Dah, *no coll.* (S-PA); Balti, Skardo, *no coll.* (US).

JAPAN.—Hondo, Azusayama, in Shinano, *Ohwi* 249 (L, S-PA, US); Sakhalin Island, Mereyo, *Faurie* 305 (S-PA); Shinano, Mt. Toyoguchi, *Hamegata* 3439 (US).

IRAN.—Kuhikakaghan, Mazenderan, *Koelz* 16386 (US); Dimalu, Mazenderan, *Koelz* 16551 (US); Bardu Forest, Khorassan, *Koelz* 16762 (US); Kerman province, Kerman, *Bornmuller* 4487 (PH).

IRAQ.—Arl Gird Dag, *Gillett* 12357 (US); Sefin Dag, *Gillett* 8152 (US); Ser Kurawa, *Gillett* 9771 (US).

MONGOLIA.—Honger obbo, *Eriksson* 281 (US); Kentei Mts., at source of Tola, Mensa and Iro rivers, *Ikonnikov-Galitzky*, 1 Aug 1929 (S-PA); Ara-Khangai district, Khanchai, *Nabrob*, 3 Aug 1926 (S-PA).

INDIA.—Simla, *Collett*, Oct 1885 (S-PA). KASHMIR.—Bok, Zanskar, *Koelz* 2964 (L, S-PA); Ka La, Ladak, *Koelz* 2508m (L); Gilgit (Balti or Little Tibet), *Winterbottom*, 8 Aug 1847 (L); Srinagar, Tangmarg, *Hummel*, 29 Mar 1953 (S-PA); Gulmarg, *Stewart*, 26 Jul 1926 (PH); Padam, Zaskar, *Koelz* 5750 (US); Mune, Zaskar, *Koelz* 5730 (US); Pahlgam, *Stewart* 21897B (US); Pensi La, Zanskar, *Koelz* 2934k (US); Tragbal, *Stewart* 4719 (US); Sonaniarg, *Stewart* 3461 (US).

PAKISTAN.—Swat, between Maina and Ilam Mts., *Rodin* 5469 (US); Lahul, Kangra, *Koelz* 5190 (US); Sisu, Lahul, *Koelz* 648 (US); Changla Gab, Murree Hills, *Stewart* 4061a (US); Chamba, Sach Pass, *Stewart* 2610 (US); Chamba, Alwas, *Stewart* 2420 (US); Chitral, Lowari Pass, *Harriss* 16885 (S-PA); Chitral, Barum Gol, above Shokor Shal, *Wendelbo*, 19 Jun 1950 (S-PA).

UNION OF SOVIET SOCIALIST REPUBLICS.—Azerbaijdzhan, Caucasus Mts., *Karjagin*, 26 Jul 1935 (US); Caucasus, Stavropol, *Novopokrovsky & Turkevich*, 26

Jun 1915 (S-PA); Tiflis (Tbilisi), *Kousnetzoff*, 18 Jul 1890 (S-PA); Caucasus, Majkop, *Mecmynoh*, 27 Aug 1911 (S-PA); Armenia, near Lemenowka, *Fomin*, 4 Jul 1929 (S-PA); Ukraine, Czerkassy, Korsua, *Pidophiczka*, Jul 1924 (S-PA); Karelia, *Hulten*, 29 Jun 1927 (S-PA); Moskau, *Zickendrath*, 29 Jun 1900 (S-PA); Moskau, Kunzewo, *Zickendrath*, 26 Sep 1894 (S-PA); Ingriae [between Lake Lodoga & Lake Peipus], *Borisova*, 6 Jul 1927 (S-PA); Estonia, between Keila and Joa, *Lundstrom*, Jul 1922 (S-PA); Latvia, Vidzeme, Priekuli, *Starcs*, 25 Aug 1924 (S-PA); Königsberg, Frederickstein, *Baenitz*, 6 Aug 1881 (S-PA); Pskow, near river Welikaja, *Andrejew*, 30 Aug 1900 (S-PA); Tomsk, Zmeinogorsk, *Iljin*, 29 Jun 1909 (L); Semipalatinsk, *Schipezinsky*, 19 May 1914 (S-PA); Altai, Buchtarminsko, *Meyer*, n.d. (S-PA); Zabaikalski, Mangischlak-halvon, *Dubianskii*, 8 May 1906 (S-PA); Schilka [Transbaikalia], *Turszaninow*, n.d. (S-PA); Songarei, Alatan, *Schrenk*, 6 Jun 1842 (S-PA). Vladimir, Kardbanowo, *Zickendrath*, 25 Jun 1894 (S-PA); Regio transiliensis (Vjernyi district, near lake Issyk), *Titov*, 13 Sep 1915 (S-PA); Charkov, Zmievska, *Miljotin*, 13 Jul 1912 (S-PA); Nova Zemlia, sinus Karmakulski, *Ekstam*, 16 Aug 1901 (S-PA); Nova Zemlia, Mal. Kaimakul, *Ekstam*, 3 Sep 1901 (S-PA); Nova Zemlia, Machiggin, Blomstre, *Lyrge*, 3 Aug. 1921 (S-PA). SIBERIA.—Jakutsk, Bulun, *Nilsson*, 1898 (S-PA); Jakutsk, Kumach-Sur, *Nilsson*, 24 Jul 1898 (S-PA); Jakutsk, Balaganach, *Nilsson*, 27 Jun 1898 (S-PA); Jenisei, Stolba, *Arnell*, 1 Jul 1876 (S-PA); Jenisei, Mjelnitza, *Brenner*, 12 Jul 1876 (S-PA); Jenisei, Uskimys, *Arnell*, 5 Jul 1876 (S-PA); valley of river Lena, Natara, *Nilsson-Ehle*, 22 Jun 1898 (S-PA) KAMCHATKA.—Bogatyrjovk (Avatscha Bay), *Hulten*, 16 Jul 1920 (S-PA); Cape Koslof, *Malaise*, Jun 1923 (S-PA); Unkanaktjeks, Golyginas flodsystem, *Hulten*, 20 Aug 1922 (S-PA). KURIL ISLANDS.—Paramushir Tokari, *Bergman*, 5 Sep 1930 (S-PA).

TURKEY.—Zudschas Dagh, *Cyren*, 4 Jun 1927 (S-PA); Bithynisha Olympen, *Cyren*, 15 Jun 1927 (S-PA); Cilicico-Kurdicum, Karduchia, *Mukus*, *Kotschy*, Sep 1859 (S-PA); Anatolis, *Wiedermann*, n.d. (S-PA).

EUROPE (EXCLUDING SOVIET UNION)

AUSTRIA.—Tirol, Braunesk, Leimbach, *Wolf*, n.d. (L); Badgastein, *Splitgerber*, Jun 1862 (L); Gmunden, *Dorfler*, n.d. (S-PA); Styria, *Agardh*, 1827 (S-PA); Gostling, *Kummerle*, 28 Sep 1905 (S-PA).

BELGIUM.—Namur, Gedinne, *Gravet*, 6 Jul 1884 (L); Malmedy, *Kern*, Aug 1939 (L); Spa, *Thielens*, Aug 1862 (L); Namen, *Thielens*, Aug 1861 (L); Namur, Nafrature, *Gravet*, 29 Jul 1886 (L); Namur, Ouhimont, *Gravet*, 26 Aug 1867 (L); Dinant, *Gravet*, 10 Jul 1871 (L).

BRITISH ISLES.—SCOTLAND.—S. Aberdeen, Morrone Hill near Braemar, *Hoogland*, 17 Jul 1948 (L); Perth, near Crienlauch, *Hoogland*, 30 Jun 1948 (L); Orkney Islands, Hoy, *Johnston*, 6 Aug 1924 (S-PA).

BULGARIA.—Mt. Vitosa, Zlatni-Mostove, *Vihodzevssky*, 1 Aug 1952 (S-PA).

CZECHOSLOVAKIA.—Bohemia, *Skarnitzl*, 14 Aug 1903 (S-PA); Bohemia, Telsdorf, *Rosendahl*, Jul 1910 (S-PA); Moravia, Brno, *Bily*, 2 Aug 1934 (S-PA).

DENMARK.—Skjor, Boegerbregne, *Möller*, May 1894 (S-PA); Sjaelland Island, *Thomsen*, 4 Jun 1870 (L); Faeroes, Stromo, Kirkebo, Thorshavn, *Feilberg & Rostrup*, 16 Jul 1867 (S-PA).

FINLAND.—Aland, Eckero, *Möller*, 16 Jul 1928 (S-PA); Kuusamo, Paanajarvi, *Backman*, 1 Jul 1902 (S-PA); Sydvaranger, Elvenes, *Norrman*, 2 Aug 1937 (S-PA); Aland, Sund, Bomarsund, *Möller*, 18 Jul 1928 (S-PA); Karelia, Sunku, Arsenovalok, *Sparre*, 5 Jul 1942 (S-PA); Tavastia, Lammi, *Backman*, Aug 1909 (S-PA).

FRANCE.—Isere, Platernoz, *Milliat & Aines* 214 (P); Puy de Dome, Mont-Dore, *Ozanon*, 26 Jul 1884 (P); Vosges, pres du la cascade de la Serva, *Silbermann*, Oct 1865 (P); Haute-Savoie, Bourguignon-les-Coufflaus, *Bertrand*, Aug 1891 (P); Cantal, bois de Messilac, *de Puyfol*, 22 Jun 1889 (S-PA); Drome, foret de Taou, *Gombault*, 24 May 1924 (S-PA); Corsica, Fort Vizzavona *Hemmendorff*, 25 Jun 1924 (S-PA).

GERMANY.—Westfalen, Witten, *Schemmann*, Jun 1907 (L, S-PA); Baden, Heidel-

berg, *Voigtlaender-Tetzner*, 7 Jun 1907 (S-PA); Thuringen, Jena, *Dietrick*, 3 Aug 1832 (S-PA); Sachsen, Zwickau, *Lehmann*, 13 Jun 1902 (S-PA); Neanderthal prope Dusseldorf, *de Friese*, n.d. (L); Brandenburg, Neuruppin, *Warnosorf*, Jul 1891 (S-PA); Bayern, Oberpfalz, Velburg, *Prechtelsbauer*, Aug 1901 (S-PA); Bayern, Oberstdorf, *Krieger*, Aug 1906 (S-PA).

GREECE.—region of Parnassos Mt., *Guicciardi*, Jul 1855 (L).

HUNGARY.—Posoniensis, *Baumler*, Jul 1911 (S-PA); Lika-Kobava, *Kummerle*, 27 Jul 1929 (S-PA); Tozsony, *Tozsony, Baumler*, May 1878 (S-PA); Szepes, *Filarszky*, Jul 1906 (S-PA); Gomor, *Richter*, 20 Aug 1898 (S-PA).

ITALY.—Etrusca, NW of Rome, *Maggio*, 1882 (L); Mountains Merano (S. Tirol), *Enander*, 15 Sep 1925 (S-PA); Liguria uber Tenda, *Bicknell*, Jul 1901 (S-PA); Toscana, *Ascherson & Reinhardt*, 19 Jul 1863 (S-PA); Emilia, Modena, *Vaccari*, Aug 1886 (S-PA); Piedmont, Cottian Alps, *Rostan*, 1880 (S-PA); Toscana, Monte Falterona, *Corradi*, 4 Aug 1946 (L); Sicily, Mt. Aetna, *Splitgerber*, 27 May 1833 (L); Sicily, Mt. Aetna, *Huet du Pavillon*, 12 Jul 1855 (L).

LUXEMBOURG.—Berdorf, *van Steenis*, 28 Jun 1924 (L); Echternach, *van Steenis*, 25 Jun 1924 (L); Orval [?], *Gravet*, 18 May 1857 (L).

NETHERLANDS.—Ijsland, Husafell, *de Lange-Luyten*, 27 Jul 1932 (L).

NORWAY.—Kongsvold (Dovre Fjeld), *Baenitz*, 26 Jul-13 Aug 1891 (L); Troms, Salagen, *Norrman*, 10 Aug 1938 (S-PA); Dombas, Hareggur, *Gunnarsson*, 19 Aug 1929 (S-PA); Nordfjorden, *Malmgren*, 10 Aug 1868 (S-PA); Skamberget, *Mattiorit*, 27 Jul 1882 (S-PA); Cap Thorsten, *Nath*, 1870 (S-PA); Isfjorden, Kap Boheman, *no coll.*, 30 Jul 1896 (S-PA); Tempelbay, *Mathorst*, 25 Jul 1882 (S-PA).

POLAND.—Silesia, Gorlitz, *Baenitz*, 1860 (S-PA); Silesia, Breslau, *Callier*, 8 Sep 1925 (S-PA); Elk, *Savio*, 21 May 1888 (L); Danzig, *Klatt*, 3 Jun 1841 (S-PA); Riesengebirge, Agneteudorf, *Tescheow*, Aug 1909 (S-PA).

ROMANIA.—Transsilvania, district of Fagaras, *Buia et al.*, 13 Aug 1936 (S-PA); Transilvania, *Barth*, 6 Jun 1908 (S-PA).

SWEDEN.—Vestrogotland, Toarps, *Olson*, 2 Jun 1914 (S-PA); Torne Lappmark, Abisko, Nuolja, *Rosendahl*, Jul 1910 (S-PA); Ostergotland, Omberg, Alvastra, *Dahlstedt*, 14 Jul 1881 (S-PA); Stockholm, Naska, *Thedenius*, 1852 (S-PA); Jamtland, Froson, *Rosendahl*, Aug 1912 (S-PA); Skaraborg, Smedstorfs, *Thunsee*, 26 Jun 1908 (S-PA); Blekinge, Nattraby, *Arrhenius*, 3 Aug 1927 (S-PA); Oland Island, Borgholm, *Munthe*, 18 Aug 1901 (S-PA); Gotland Island, Ljugarn, *Skarman*, Jul 1895 (S-PA); Smaland, Madesjo, *Medelius*, 28 Jun 1910 (S-PA); Nerike, Palsboda, *Sjoholno*, 1888 (S-PA); Harjedalen, Tannas, *Selling*, 4 Jul 1946 (S-PA).

SWITZERLAND.—Vaud, Pont de Nant, *Masson*, Aug 1886 (US); Wallis, Zennalt, *Birger*, 21 Jun 1925 (S-PA); Lugano, *Birger*, 31 May 1925 (S-PA); Berne, Blumenthal, *Rosendahl*, Jun 1903 (S-PA); Wallis, Alpe de Cleuson, *Wolf*, Sep 1904 (S-PA); Grisons (Graubunden), *Hooker*, 1862 (S-PA); Wandt, *Wilezek & Wirtgen*, 19 Aug 1902 (S-PA); Fribourg, between Charmey and Cerniat, *Brunner*, 13 Jul 1950 (L).

JUGOSLAVIA.—Bosnia, Vlasie Plateau, *Brandis*, 23 Aug 1897 (S-PA); Montenegro, Landzak, *Nuravjev*, 8 Jun 1930 (S-PA); Bosniz, Sarajevo, *Murbeck*, 11 Jun 1889 (S-PA); Montenegro, *Rohlens*, n.d. (S-PA).

1b. *Cystopteris fragilis* var. *apiiformis* (Gandoger) C. Chr.

SELECTED SPECIMENS:

NEW ZEALAND.—Upcot, Awateri Valley, Marlbro, *Petrie*, Feb. 1922 (WELT); Bealey, Canterbury, *Kirk*, 1883 (US, WELT); W part of Amurilo, W of Moorison, *Petrie*, n.d. (WELT); Clutha Valley, S from Alexandra, *Petrie*, Nov 1893 (WELT); Upper Waimakariri, South Island, *Kirk*, n.d. (WELT); Isolated Hill, Marlbro, *Alston*, 25 Apr 1915 (WELT); Central Otago, *Petrie*, n.d. (WELT); Castle Hill, *Kirk*, 24 Jan 1891 (WELT); Amuri, *Kirk*, n.d. (WELT); Nelson, *Pant*, n.d. (WELT); Tre-

lisick, Canterbury, *Kirk*, Jan 1896 (WELT); Mingha Valley, *Oliver*, 15 Jan 1928 (WELT); Otago Province, head of Lake Waikaitipu, *Walker* 4688 (US).

ARGENTINA.—Patagonia.: Baguales, *Borge* 102 (S-PA); Tweedie, *Borge* 211 (S-PA); Lago Argentino, *Furlong* 8 (US); Magalhaens Land, *Andersson*, 1852 (S-PA); Nahuel Huapi, *Buchtien*, 14 Feb 1905 (US).

CHILE.—Territory Magallanes, Last Hope Inlet, *Mexia* 7991 (S-PA, US); Aysen province, E of Coihaique, *Correll* C123 (US).

FALKLAND ISLANDS.—Roy Cove, *Skottsberg* 61 (ISOTYPE, S-PA).

SOUTH GEORGIA.—*Mosthaff*, 18 Mar 1883 (S-PA).

KERGUELEN ISLAND.—*Kidder*, 24 Dec 1874 (US); *Kidder*, 10 Dec 1874 (US); *Haumann*, 17 Nov 1874 (US); *Eaton*, 26 Feb 1875 (S-PA).

1c. *Cystopteris fragilis* var. *huteri* Hausman

SPECIMENS EXAMINED:

AUSTRIA.—Tirol.: *Rosenstock*, 29 Sep 1901 (S-PA); *Rosenstock*, 29 Jul 1901 (S-PA); *Rosenstock*, 27 Jul 1901 (L).

BELGIUM.—Ardennes Mts., Libramont, *Hostie*, 3 Jul 1938 (P).

HUNGARY.—Montes Magas Tatra, *Kummerle & Timko*, 7 Jul 1916 (S-PA).

ITALY.—S Tirol, *Gross*, 19 Jul 1933 (US); Bormio, *Soderlund*, 2 Aug 1921 (S-PA).

SWITZERLAND.—Berne Oberland, Kandersteg, *Tavel*, 14 Aug 1917 (S-PA).

2. *Cystopteris protrusa* (Weath.) Blasdell

SELECTED SPECIMENS:

UNITED STATES.—ARKANSAS.—Logan Co.: Magazine Mt., *Wherry*, 30 Apr 1934 (PH). Washington Co.: N of Fayetteville, *Wherry*, 6 May 1925 (US). ALABAMA.—Tuscaloosa Co.: 8 miles above Tuscaloosa, *Harper* 3047 (PH). GEORGIA.—Rabun Co.: near summit of Black Rock Mt., *Correll* 6617 (US). ILLINOIS.—Champaign Co.: Urbana, *Gates* 1946 (US). Du Page Co.: rich woods near Roselle, *Chase* 9427 (US). Peoria Co.: Princeville, *Chase*, 28 May 1896 (PH). Richland Co.: Bird Haven, near Olney, *Ridgway* 3035 (PH). INDIANA.—Posey Co.: Nash's Woods, *Cain*, 12 Jul 1932 (TENN). Wells Co.: Woods 3/4 miles N of Bluffton, *Deam*, 3 Jul 1907 (PH). IOWA.—Allamakee Co.: S side of Yellow River, *Wherry*, 1 Jun 1937 (PH). Clayton Co.: S of McGregor, *Wherry*, 1 Jun 1937 (PH). Mitchell Co.: 3 mi. SW of Osage, *Wherry*, 2 Jun 1937 (PH). KENTUCKY.—Edmonson Co.: Vicinity of Mammoth Cave, *Palmer*, May 1899 (US). Harlan Co.: Little Black Mt., *McCoy*, 26 Aug 1934 (PH). Kenton Co.: Taylon ravine, *Lea*, 3 Jun 1840 (PH). Madison Co.: E of Berea, *Smith, L. B. et al.* 3604 (US). MICHIGAN.—Oakland Co.: Section 4 Southfield Twp., *Hagenah* 877 (US). Washtenaw Co.: Huron River Drive, Ann Arbor Twp., *Wagner* 8073 (MICH). MISSISSIPPI.—Westside, *Tracy* 1399 (US). MISSOURI.—Marion Co.: Hannibal, Mark Twains' Cave, *Davis*, 9 Jul 1909 (PH). Stoddard Co.: Crowley's Ridge, near Messler, *Palmer* 34847 (PH). NEW YORK.—Richmond Co.: Staten Island, Bloodroot Valley, *Dowell* 3884 (US). NORTH CAROLINA.—Alleghany Co.: near Twin Oaks, *Correll & McDowell* 10821 (US). Avery Co.: 1/2 mi. S of Cranberry, *Wherry*, 17 Jul 1938 (PH). Buncombe Co.: 3 mi. SE of Beech, *Wherry*, 1 Jun 1939 (PH). Jackson Co.: E of Glenville, *Godfrey & O'Connell* 51976 (US). Oconee Co.: Tomassee Knob, *House* 2092 (US). Swain Co.: Nantahala Gorge, *Leeds* 474 (PH). Transylvania Co.: 5 mi. S of Toxaway Station, *Wherry & McVaugh*, 12 Jul 1936 (PH). Yadkin Co.: near Lime Rock along the Yadkin River, *Correll & McDowell* 10964 (US). OHIO.—Hamilton Co.: ad ripas fluminis Ohio, prope "North Bend," *Short*, n.d. (PH). Lorain Co.: Pittsfield, *Ricksecker*, 5 Jul 1894 (US). PENNSYLVANIA.—Allegheny Co.: *Hatry*, 11 May 1902 (US). Bedford Co.: 1/2 mi. SW of Sulphur Springs, *Berkheimer* 1254 (PH). Centre Co.: 2 mi. SW of Woodward, *Wahl* 1468 (PH). Dauphin Co.: Harrisburg, *Williamson*, 1 June ? (PH). Greene

Co.: 1 $\frac{3}{4}$ mi. E of Waynesburg, *Wherry & Leeds* 3501 (PH). Lycoming Co.: 1 mi. NW of Montoursville, *Wherry*, 2 Jun 1941 (PH). York Co.: York Furnace, Lower Susquehanna River, *Stone*, 19 May 1906 (PH). TENNESSEE.—Bedford Co.: near Normandy, *Shaver* 10455 (TENN). Blount Co.: 1 mile from Kinzel Springs Hotel, *Shaver* 10230 (TENN). Clay Co.: 2.1 mi. W of Celina, *Shaver* 10513 (TENN). Cocke Co.: 16 mi. E of Newport, *Shaver* 10213 (TENN). Coffee Co.: Rutledge Falls near Tullahoma, *Sharp* 4745 (TENN). Franklin Co.: near Suwanee, *Harlow*, n.d. (US). Giles Co.: near Milky Way Farm, W of U.S. 31, *Shaver* 10469 (TENN). Hawkins Co.: E of Kyles Ford, *Shaver* 10212 (TENN). Hickman Co.: 8.1 mi. E from road 100, *Shaver* 9162 (TENN). Knox Co.: Wooded talus slope, Gallagher Ferry, *Shaver* 10494 (TENN). Lewis Co.: 4.1 mi. N of Hohenwald, *Shaver* 10208 (TENN). Lincoln Co.: Teal Hollow, near Kelso, *Shaver* 10450 (TENN). Loudon Co.: limestone bluff by Clinch River, *Shaver* 10500 (TENN). Macon Co.: 5.9 mi. E of LaFayette, *Shaver* 10481 (TENN). Marion Co.: 1 mi. from Ladds Station, *Shaver* 10233 (TENN). Maury Co.: 2 mi. W of Hampshire, *Shaver* 10203 (TENN). Montgomery Co.: Porter's Bluff, *Shanks* 2032 (TENN). Obion Co.: near Reelfoot Lake, *Avery* NN28 (TENN). Pickett Co.: 1.9 mi. NW of Forbus, *Shaver* 10509 (TENN). Shelby Co.: Shelby Forest Park, *Sharp* 10415 (TENN). Obion Co.: near Reelfoot Lake, *Avery* NN28 (TENN). Pickett Co.: 1.9 mi. Co.: 2 to 3 mi. S of Watertown, *Shaver* 10488 (TENN). VIRGINIA.—Fairfax Co.: Potomac side, *Langley, Palmer*, 19 May 1901 (PH). Loudoun Co.: 1 to 2 mi. below Harpers Ferry, *Benedict* 2886 (PH). WEST VIRGINIA.—Fayette Co.: 1 mi. N of Gauley Bridge, *Wherry*, 23 Jul 1935 (PH). Grant Co.: 1 $\frac{1}{2}$ mi. NE of Petersburg, *Wherry*, 12 Apr 1936 (PH). Greenbrier Co.: 1 $\frac{1}{2}$ mi. SW of Renich P.O., *Wherry*, 20 Jul 1938 (PH). Mingo Co.: 1 mi. N of Nolan, *Wherry*, 12 Jul 1938 (PH). Ohio Co.: 7 mi. E of Wheeling, *MacElwee*, n.d. (PH). Ritchie Co.: Laurel Junction, *Smith*, 12 Sep 1879 (US). WISCONSIN.—Grant Co.: 15 mi. NW of Bloomington, *Tryon & Tryon* 4346 (TENN, US).

3. *Cystopteris douglasii* Hooker

SPECIMENS EXAMINED:

HAWAII.—*Baldwin*, n.d. (PH). HAWAII.—Mauna Kea, n.d. (S-PA); Mauna Kea, *Faurie* 159 (S-PA). KAUAI.—Waimea, *Faurie* 157 (S-PA). MAUI.—Kaleakala Crater, *Wagner* 5261 (UC); Haleakala, *Mann & Brigham* 480 (US); *Lichtenthaler*, n.d. (US); East Maui, *U.S. S. Pacific Expl. Exped.* 1838-42 (US); Haleakala, *Faurie* 158 (S-PA).

4. *Cystopteris montana* (Lam.) Bernh.

SELECTED SPECIMENS:

NORTH AMERICA:

ALASKA.—McKinley National Park, W of Wonder Lake, *Mexia* 2188 (PH); Anchorage, *York* X122 (PH); Teller Reindeer Station, Port Clarence, *Walpole* 1956 (US); Seward Peninsula, W of Krusgamapa River, *Collier*, 1900 (US); 5 mi. N of Nome City, *Fleet* 1507 (US); Fort Gibbon, *Heideman* 79 (US); Livengood, about 80 mi. NNW of Fairbanks, *Scamman* 4879 (US); Brooks Range, NW of Walker Lake, upper Kopuk River, *Jordal* 3971 (US); Port Vita, Raspberry Island, Kodiak group, *Eyerdam* 3917 (US); Wiseman, on Middle Fork of the Koyukuk River, *Scamman* 2180 (US); Alaska Range, Healy on west side of Nenana Valley, *Porsild* 317 (US).

CANADA.—ALBERTA.—Lake Louise, *Brown* 711 (PH); Slave Lake District, Atauwau River (Salteau), *Brinkman* 4211 (US). BRITISH COLUMBIA.—Yoho Valley, Selkirk Mts., *Shaw* 586 (PH); Big Bend Highway, near Kinbasket Lake, *Eastham* 9292 (US); Selkirk Mts., woods near Fish Lake, *Shaw* 1210 (PH, US). LABRADOR.—Straits of Belle Isle, Blanc Sablon, *Fernald & Wiegand* 2333 (PH, US); Rama, *Sticker* 374 (US); Attikamagen Lake, Iron Arm, *Harper* 3565 (US). NEWFOUNDLAND.—Straits of Belle Isle, Savage Cove, *Fernald et al.* 26153 (PH, US). ONTARIO.—Royston Park, Owen Sound, *Macoun*, 1876 (PH); Fort William, *Williamson* 2337

(PH); E of Port Arthur, *Williamson*, n.d. (PH). QUEBEC.—Gaspé Co.: trail from the Forks of the River Ste. Anne des Monts to Table-topped Mountain, *Fernald & Collins* 290 (PH); Mt. Albert, *Fernald et al.* 25373 (PH, US); Lake Mistassini, *Rousseau & Rouleau* 856 (US). YUKON.—Klondike, Indian Divide, *Tarleton* 152c (US); Melozi River, *Collier* 135 (US); Dawson, *Eastwood* 453 (US); Canol Rd., Mile 55-60 Quiet Lake, *Porsild & Breitung* 11107 (US).

GREENLAND.—S. f. Kiagtut, Tunugdliarfik-Fjord, 61°10' N., *Porsild & Porsild*, 10 Aug 1925 (US).

UNITED STATES.—COLORADO.—Sawatch Range, Mt. Antero Spur, *Brandege*, Jul 1880 (PH, US); Summit Co.: 2 mi. by road N of Hoosier Pass, *Wherry*, 11 Aug 1937 (PH, US). MONTANA.—Gruenight [?] Pass, Glacier National Park, *Rugg*, Jul 1932 (US).

EURASIA:

AUSTRIA.—Voralberg, *Barkman* 3566 (L); Tirol, between Matrei & Kloster, *Hal-lier*, 30 May 1890 (L); Kärnten, *Rustofry*, 11 Aug 1877 (L); Carinthia, *Hoppe*, n.d. (L); near Gmunden, *Dorfler*, 23 Jul 1888 (L, S-PA); Alps of Salisburg, *Mendil*, n.d. (US); Styria, Murau, *Fest*, Jul 1900 (US).

CHINA.—KANSU.—near Pingfan, *Ching* 572 (US); Ta Hwa, near Pingfan, *Ching* 553 (US); Tai-tong-ho, *Licent*, 19 Aug 1918 (P).

CZECHOSLOVAKIA.—Slovakia, on calcareous cliffs along moist ravines, *Suza*, 13 Jun 1930 (US); Slovakia septentrionalis, montes Bielske Tatry, *Domin & Krajina*, 10 Jul 1929 (PH, US).

FINLAND.—Sakkabani, *Krok*, 11 Jul 1898 (S-PA); Kuusamo, Paanajarvi, *Montell*, 4 Jul 1898 (S-PA); Lapponia ponojensis, Katschkowka, *Kihlman*, 24 Jul 1889 (S-PA).

FRANCE.—AIN.—Jura Mts., between Faucille and Mijoux, *Machalet*, 10 Aug 1856 (P). DROME.—Lus-la-Croix, *Chatenier*, 26 Aug 1890 (P). HAUTES-PYRENEES.—Cascade de Splumons pres Cauterets, *Vallot*, Jul 1885 (P). ISERE.—Choroland, *Milliat*, 15 Aug 1939 (P).

GERMANY.—near Salzburg, Austria, *Schott*, n.d. (US); Baiern, *Magnus*, 11 Aug 1874 (US); Bavaria, Berchtesgaden, *Ball*, 1890 (US).

HUNGARY.—Csik, near Gyilkosto, *Boros*, 24 Jul 1941 (S-PA).

INDIA.—Kashmir, Sonamarg, *Stewart* 6868 (US); Kumaun, Ralam Glacier, *Duthie* 3647 (US); Western Nepal, Budhi Village, *Duthie* 6274 (US).

ITALY.—Mt. Sciliar, above Siusi, NE of Bolzano, *Chrysler* 2895 (PH).

NORWAY.—Dovre, Kongsvold, *Wallin*, 7 Aug 1883 (S-PA); Troms, Gratangen, *Norrman*, 6 Aug 1938 (S-PA); Nordland, Saltdalen, Solvagbind, *Asplud*, 30 Jul 1937 (S-PA); Gudbrandsdalen, Ringsbos, *Zetterstedt*, 22 Jun 1870 (US).

SWEDEN.—Jamtland, Tannforsen, *Rosendahl*, 8 Jul 1910 (S-PA); Angermanland, Tasjo, *Cedergren*, 13 Jul 1927 (S-PA); Dalarna, Orsa, *Rosendahl*, Jul 1912 (S-PA); Harjedalen, Tannas, *Engstedt*, 31 Jul 1932 (S-PA); Asele Lappmark, Dorotea, *Samuelsson*, 26 Aug 1926 (S-PA); Lycksele Lappmark, Backnas, *Nordenstam*, 13 Jul 1936 (S-PA); Pite Lappmark, Arjeplog, *Wistrand*, 13 Jul 1947 (S-PA); Lappland, Jukkasjarvi, Abisko, *Samuelsson & Zander*, 14 Aug 1927 (L, S-PA).

SWITZERLAND.—Unterwalden, between Grasenberg and Engenberg, *Cramer*, Jul 1859 (L); Waadt, *Wirtgen* 329 (L); Vaud, Pays-d'Enhaut, *Villaret*, 17 Aug 1952 (US); Glarus, prope Stachelberg, *Ball*, Jul 1857 (US); Bern, Rosenlauri, *Ball*, 12 Aug 1857 (US); Bonavalettaz (Gruyere), *Castella*, 3 Aug 1906 (US).

UNION OF SOVIET SOCIALIST REPUBLICS.—Caucasus, *Busch*, 28 Aug 1933 (PH); Syktyvkar district, Komi, *Andreev*, 14 Aug 1909 (US).

5. *Cystopteris pellucida* (Franch) Ching

SPECIMENS EXAMINED:

CHINA.—MOUPIN.—(Thibet oriental), *David*, 1870 (P). YUNNAN.—*Delavay*, n.d. (P); in ravines, *Ducloux* 169 (P).

6a. *Cystopteris sudetica* A. Br. et Milde var. *sudetica*

SELECTED SPECIMENS:

CZECHOSLOVAKIA.—MORAVIA.—Ostsudeten-Altvatergebirge, Freiwalden, *Laus*, Aug 1935 (S-PA); near Holesov, *Gogela*, n.d. (S-PA).

HUNGARY.—Szepes, Hohen-Tatra, *Nyarady*, 5 Sep 1911 (S-PA); Piennineupass (Karpathen), *Ullepitsch*, Jul 1890 (S-PA); Maramaros, Borsabanya, *Boros*, 17 Jul 1942 (S-PA); Gomor, in valle Stracenensi, *Richter*, 11 Jul 1901 (S-PA, US).

NORWAY.—GUDBRANDSDALEN.—Nordra Fron, *Samuelsson & Zander*, 22 Jul 1934 (US); Kongsli, *Wall*, 22 Jul 1934 (S-PA).

POLAND.—Carpathians, Korvielisko, *Sagorski*, Jul 1887 (S-PA); Silesia, Jesenik (Gesénke) near Reiweisen, *Laus*, Sep 1915 (S-PA); Allemagne, Silesie, Sudetes, *Laus*, Jul 1935 (S-PA).

ROMANIA.—Transilvania, Bihor district, *Pop*, 29 Aug 1935 (S-PA, US); Bucovina, near Pojana-Stampi (Eastern Carpathians), *Dorfler*, 1855 (L).

UNION OF SOVIET SOCIALIST REPUBLICS.—Tomsk, Kuznezow 675 (S-PA); Wolagda, *Zickendrath*, 18 Jul 1893 (S-PA).

6b. *Cystopteris sudetica* var. *moupinensis* (Franch.) Blasdel

SPECIMENS EXAMINED:

CHINA.—KANSU.—Sin-long-chan et Ma-ho-chan, *Licent* 4288 (P). MOUPIN.—*David*, 1870 (P). SHENSI.—Tai-pei-shan, *Purdom* 63 (S-PA, US). SIKANG.—between Taining (Ngata) and Taofu (Dawo), *Smith* 12098 (S-PA). SZECHUAN.—Karloug, *Smith* 4227 (S-PA); Dongrergo, *Smith* 3628 (S-PA).

7. *Cystopteris bulbifera* (L.) Bernh.

SELECTED SPECIMENS:

CANADA.—NEW BRUNSWICK.—Fairville, *Fowler*, 26 Jul 1877 (US). NEW-FOUNDLAND.—Boone Bay, Shag Cliff, *Fernald et al.* 1121 (PH); Middle Arm, Bay of Islands, *Fernald et al.* 1120 (PH); Lower Humber Valley, between Marble Mountain and Humbermouth, *Fernald et al.* 1119 (PH); Highlands of St. John, W face of Bard Harbor Hill, *Fernald & Long* 27206 (PH). NOVA SCOTIA.—Gypsum area, Brooklyn, *McLellan*, 18 Jun 1938 (US); Victoria Co.: Port Bevis, *Fernald & Long* 19473 (PH). ONTARIO.—Bruce Peninsula, Umbrella Lake, *Krotkov* 9582 (US); Niagara Falls Glen, *Fisher*, 6 Aug 1901 (PH); Toronto, Don Valley, *Armstrong*, 25 Jul 1891 (US); Algoma District, Batchawana Falls, *Taylor et al.* 165 (US). Brant Co.: 2 mi. E of Ayr, *Soper and Dale* 4121 (US). Carleton Co.: Ottawa District, NW of Stanley Corners, *Senn et al.* 181 (TENN). Durham Co.: 7.5 mi. S of Lindsay, *Soper & Dale* 3867 (US). Grey Co.: 3 mi. NW of Owen Sound, *Wherry*, 20 Jun 1934 (PH). Leeds Co.: Kitley Twp., *Senn* 1665 (US). Peterborough Co.: ½ mi. NW of Westwood, *Wherry*, 5 Sep 1932 (PH). QUEBEC.—Beauce Co.: 3 mi. N of Leeds Station, *Wherry*, 24 Aug 1935 (PH). Gaspé Co.: W of Perce, *Henry* 1753 (PH). Barnston, near Stanstead, *Lucien & Sylvestre* 1540 (US); Georgeville, *Churchill*, 13 Aug 1886 (US); La Trappe, *Louis-Marie*, 1 Sep 1931 (PH); L'Ile d'Anticosti, *Marie-Victorin & Rolland-Germain* 24620 (PH, US); Oka, *Adrien* 1273 (PH).

UNITED STATES.—ALABAMA.—Colbert Co.: near Sheffield, *Mohr*, 8 Jun 1892 (US). Dade Co.: 9 mi. W of Trenton, *Howell*, 23 Jun 1913 (US). Madison Co.: in the vicinity of Huntsville, *Pollard & Maxon* 390 (US). Marshall Co.: Guntersville, *Howell* 817 (US). St. Clair Co.: St. Clair Spring near Ashville, *Mohr*, Jul 1880 (US). ARKANSAS.—Benton Co.: near Garfield, *Palmer* 44466 (US). Marion Co.: Bull Shoals Dam Reservoir, *Demaree* 29280 (PH). ARIZONA.—Coconino Co.: Oak Creek, 18 mi. SW of Flagstaff, *Goldman* 2188 (US). CONNECTICUT.—Canaan Mt., *Leggett*, Jul 1865 (PH). New Haven Co.: New Haven, *Safford* 397 (US). GEORGIA.—Floyd Co.: 3 mi. SW of Rome, *Duncan & Hardin* 15246 (US). ILLI-

NOIS.—Cook Co.: Lemont, *Hill* 1152 (PH). Jo Daviess Co.: $\frac{1}{4}$ mi. S of Council Hill, *Lansing* 4146 (PH). Tazewell Co.: 5 mi. N of East Peoria, *Chase* 12739 (US). Will Co.: Lockport, *Skeels* 621 (US). INDIANA.—Crawford Co.: 6 mi. S of Leavenworth, *Tryon* 4434 (TENN, US). Harrison Co.: 3 mi. E of Elisabeth, *Deam* 20554 (US). Huntington Co.: $\frac{1}{4}$ mi. E of Andrews Stop along Wabash Valley Traction line, *Deam*, 7 Jul 1907 (PH). Lawrence Co.: Spring Mill State Park, *Cain* 6387 (TENN). Montgomery Co.: Pine Hills, *Friesner* 9711 (TENN). Putnam Co.: 3 mi. W of Groveland, *Friesner* 7086 (TENN). IOWA.—Clayton Co.: 8 mi. S of Guttenburg, *Wherry*, 1 Jun 1937 (PH). Clinton Co.: Clinton, *Pammel* 238 (US). Dubuque Co.: $2\frac{1}{2}$ mi. NW of Durango, *Wherry*, 1 Jun 1937 (PH). Fayette Co.: Shaded lime-rocks, *Fink* 446 (US). Poweshiek Co.: Grinnell, *Jones* 1876 (PH). KENTUCKY.—Carter Co.: near Cascade Caverns, *Smith et al.* 3451 (US). Edmonson Co.: Mammoth Cave National Park, *Lix* 54 (US). Fayette Co.: Lexington, *Short*, n. d. (PH). Pulaski Co.: near Cedar Grove, *Wherry & Pennell* 13783 (PH). Warren Co.: Bowling Green, cave entrances, *Price*, Jun 1893 (PH). MAINE.—Aroostook Co.: McKiels Br., Allaguash River, *Fellows* 112 (PH). Franklin Co.: woods near Farmington, *Chamberlain & Knowlton*, 2 Sep 1904 (US). Penobscot Co.: Cedar swamp, *Lee, Steinmetz* 259 (US). Somerset Co.: woods on slopes of Green Mountain, *St. John & Nichols* 2068 (US). MARYLAND.—Washington Co.: Anietam, *Freeman*, 2 Aug 1936 (US). MASSACHUSETTS.—Berkshire Co.: vicinity of Tyringham, *Vail*, 18 Jul 1897 (PH). Franklin Co.: Roaring Brook, *Leverett, Adams*, 15 Aug 1870 (PH). Hampshire Co.: Shady woods, *Amherst, Clark*, Jul 1881 (PH). MICHIGAN.—Alger Co.: 8 mi. S of AuTrain, *Wherry & Leeds* 3377 (PH). Berrien Co.: 4 mi. N of Buchanan, *Wherry*, 9 Sep 1944 (PH). Cheboygan Co.: Cheboygan, *Kofoed*, 20 Aug 1890 (TENN). Crawford Co.: vicinity of Grayling, *Piper*, Jul 1922 (US). Eaton Co.: near Grand Ledge Clay Company quarry, *Wagner* 8078 (MICH). Grand Traverse Co.: along Boardman River NE of Kingsley, *Hagenah* 1342 (US). Ionia Co.: 4 mi. W of Lyons, *Wagner* 8080 (MICH). Kalkaska Co.: 2 mi. S. of Kalkaska on US-131, *Hagenah* 1313 (US). Kent Co.: S of Carlisle, *Wherry*, 25 June 1933 (PH, US). Mackinac Co.: Mackinac Island, *Hicks*, 30 Jun 1889 (US). Oakland Co.: Farmington, *Farwell* 6064 (US). Ontonagon Co.: Porcupine Mts., *Wherry & Leeds* 3341 (PH). St. Clair Co.: near Port Huron, *Dodge*, 26 Jul 1896 (TENN, US). MINNESOTA.—Clearwater Co.: Boholl Trail, *Grant* 3343 (US). Winona Co.: Winona, *Holzinger*, 10 Aug 1888 (US). MISSOURI.—Benton Co.: Limestone bluffs of Osage River, *Palmer* 35968 (US). Callaway Co.: Fulton, *Greger*, Jul 1896 (US). Laclede Co.: along Gasconade River, N of Hazel Green, *Steyermark* 8076 (US). Marion Co.: Hannibal, *Davis*, 6 Jul 1909 (PH). Phelps Co.: "Slaughter Sink" near Arlington, *Palmer & Steyermark* 41394 (PH, US). Ralls Co.: 2 mi. N of New London, *Wherry*, 8 Jul 1935 (PH). Shelby Co.: limestone creek bluffs, near Bethel, *Palmer & Steyermark* 40899 (PH). Stoddard Co.: Crowley's Ridge, near Painton, *Palmer* 34903 (PH). Washington Co.: near Bliss, *Steyermark* 7031 (US). NEW HAMPSHIRE.—Cheshire Co.: Keene, *Milligan*, Jul 1884 (US). NEW JERSEY.—Bergen Co.: Closter, *Austin*, n.d. (US). Sussex Co.: E of Newton, *Dowell* 5024 (US). Warren Co.: Cedar Lake, SW of Blirstown, *Smith*, 25 Aug 1895 (PH). NEW MEXICO.—Canyon above Grey's Ranch, Guadalupe Mts., *Goodding*, 29 Aug 1937 (US). NEW YORK.—Broome Co.: Day's Glen, vicinity of Lisle, *Dowell* 4140 (US). Clinton Co.: Valcour Island, *Bain & Smith* 2963 (US). Dutchess Co.: vicinity of Clove, *Standley & Bollman* 11880 (US). Essex Co.: Ausable Chasm, *Leeds* 55 (PH). Greene Co.: ravine SE from Haines Falls, *Wherry*, 25 Jun 1946 (PH). Herkimer Co.: Old Forge, Limekiln Creek, *Dowell* 4477 (US). Madison Co.: vicinity of Oneida, *Maxon*, 24 Jun 1895 (US). Monroe Co.: Telephone Road, East Henrietta, *Matthews* 4392 (PH). Niagara Co.: Niagara Falls, *Shurtleff*, n.d. (US). Onondaga Co.: near Syracuse, *Myers*, n.d. (US). Schenectady Co.: *Fisher*, Oct 1896 (PH). Schoharie Co.: Sharon Springs, *House* 19547 (US). Schuyler Co.: Watkins Glen, *Rau*, 8 Sep 1871 (PH). Tompkins Co.: Six Mile Creek, Ithaca, *Eames & MacDaniels* 3382 (US). Ulster Co.: vicinity of Shandaken, *Miller*, 16 Aug 1901 (US). Washington Co.: 1 mi. E of Argyle, *Schaeffer*

2191 (PH). Wyoming Co.: Wyoming, *Hartnell*, 13 Jun 1903 (PH). Yates Co.: Penn Yan, *Hartnell*, n.d. (PH). NORTH CAROLINA.—Madison Co.: 4 mi. W of Hot Springs, *Oosting* 35305 (PH, US). Swain Co.: Blowing Springs, Nathahale Gorge, *Blomquist & Anderson* 1653 (PH). OHIO.—Clark Co.: 5 mi. W of Springfield, *Leeds* 3189 (PH). Erie Co.: Swifts' Hollow, Vermilion River, *Grover*, 13 Jul 1900 (US). Geauga Co.: Thompson, *Werner*, 27 Sep 1885 (US). Hamilton Co.: *Mohr*, n.d. (US). Loraine Co.: Elyria, *Steele*, Jul 1874 (US). Ross Co.: Point Creek, *Brown*, 23 May 1953 (MICH). Sandusky Co.: vicinity of Freemont City, *Leonard* 2118 (US). PENNSYLVANIA.—Allegheny Co.: Moon Twp., *Hatry*, 18 May 1902 (PH, US). Beaver Co.: Crows Run, *Shafer*, 31 Jul 1885 (PH). Blair Co.: Limestone cliffs at Arch Spring, *Canan*, 1941 (PH). Bradford Co.: Troy, *Bartram*, 19-20 Jul 1913 (PH). Center Co.: 1½ mi. S. of Bellefonte, *Leeds* 3567 (PH). Clinton Co.: 3 mi. SW of Hyner, *Wherry*, 1 Jun 1941 (PH). Columbia Co.: ½ mi. SW of Catawissa, *Wherry*, 29 Jul 1938 (PH). Dauphin Co.: entrance to Indian Echo Cave, S of Hummelstown, *Wherry*, 30 Jun 1934 (PH). Fayette Co.: Ohiopyle, *Brown et al.* 132 (PH). Franklin Co.: Mercersburg, *Porter*, 27 Oct 1845 (PH). Greene Co.: near Crabapple, *Myers*, 7 Jul 1935 (PH). Huntingdon Co.: near Alexandria, *Porter*, Jul 1845 (PH). Laikar Co.: *Turning*, Aug 1906 (PH). Lancaster Co.: near Lancaster, *Small*, 15 Jul 1890 (US). Lawrence Co.: above Rock Point, *Jennings*, 26 Jul 1909 (PH). Mifflin Co.: ½ mi. S of Honey Creek, *Wherry*, 13 Aug 1942 (PH). Monroe Co.: stream at Ross-common, *Rau*, 21 Jul 1878 (PH). Northampton Co.: 1 mi. E of Kreidersville, *Schaeffer* 13930 (US). Pike Co.: Bushkill Falls, *Brown*, 30 May 1897 (PH). Susquehanna Co.: near Ararat, *Saunders*, 8-20 Jul 1900 (PH). Tioga Co.: 2 mi. NW of Kennedy, *Leeds* 580 (PH). Union Co.: 1 mi. W of White Deer, *Wherry*, 16 Apr 1938 (PH). Wayne Co.: 2 mi. N of L. Shehauken, *Dix*, Jul 1936 (PH). Wyoming Co.: ½ mi. SE of Tunkhannock, *Pretz* 7255 (PH). YORK Co.: near Philadelphia, *Crawford*, 2 Jul 1904 (PH). TENNESSEE.—Anderson Co.: E of Clinch River, *Shaver* 10302 (TENN). Bledsoe Co.: below Low Gap, *Shanks et al.* 4474 (TENN). Bedford Co.: near Normandy, *Shaver* 10457 (TENN). Blount Co.: NE end of Jones Bend, *Shaver* 10639 (TENN). Bradley Co.: 3.3 mi. E of Charleston, *Shaver* 10146 (TENN). Campbell Co.: Cedar Creek, *Sharp et al.* 3353 (TENN). Cannon Co.: 7 mi. NE of Woodbury, *Shaver* 10219 (TENN). Cheatham Co.: Craggie Hope, *Svenson* 4208 (PH). Claiborne Co.: west side of Clinch River, *Shaver* 10469 (TENN). Clay Co.: W of Cumberland River and Celina, *Shaver* 10552 (TENN). Coe Co.: N of Newport, *Shaver* 10395 (TENN). Coffee Co.: near Tullahoma, *Sharp et al.* 4748 (TENN). Cumberland Co.: Ozone Falls, *Shanks et al.* 13823 (TENN). Fentress Co.: 8 mi. N of Jamestown, *Shaver* 10262 (TENN). Grainger Co.: Tampico, *Morrison & Brown* 82 (TENN). Greene Co.: near Chaney, *Shaver* 10693 (TENN). Hamblen Co.: 4 mi. N of Morristown, *Wherry*, 24 Aug 1937 (PH). Hamilton Co.: N of Red Bank, *Shaver* 10630 (TENN). Hawkins Co.: Chestnut Ridge, *Wolfe* 489 (TENN). Humphreys Co.: 6 mi. N of Waverly, *Shaver* 10538 (TENN). Jefferson Co.: north-facing bluffs down the Holston River, *Shaver* 10684 (TENN). Johnson Co.: 8 mi. N of Mountain City, *Shaver* 10381 (TENN). Knox Co.: Baker's Bluff, *Rice* 411 (TENN). Lawrence Co.: W of Lawrenceburg, *Wherry*, 22 Aug 1937 (PH). Loudon Co.: near Hickory Creek, *Shaver* 10499 (TENN). Marion Co.: Battle Creek, *Sharp & Underwood* 2520 (TENN). Meigs Co.: NW of Decatur, *Shaver* 10606 (TENN). Montgomery Co.: W of Ringgold, *Shanks* 970 (TENN). Rhea Co.: near the Tennessee River, *Shaver* 10590 (TENN). Roane Co.: Harriman Bluffs, *Sharp & Underwood* 2053 (TENN). Robertson Co.: road from Joelton to Greenbrier, *Shaver* 4307 (TENN). Rutherford Co.: Snail Shell Cave, *DeSelm* 977 (D, TENN). Sevier Co.: Cherokee Orchard, *Rice* 411 (TENN). Smith Co.: 1.8 mi. N of Chestnut Mound, *Shaver* 10138 (TENN). Union Co.: .9 mi. N of the Knox Co. line, *Shaver* 10669 (TENN). Van Buren Co.: E of Spencer, *Shaver* 10576 (TENN). Washington Co.: NW of Philadelphia, *Shaver* 10653 (TENN). Wayne Co.: SE of Waynesboro, *Sharp et al.* 9612 (TENN). White Co.: W of Sparta, *Shanks et al.* 5013 (TENN). UTAH.—Elk Mountains, *Rydberg & Garrett* 9343 (US). VERMONT.—Bennington Co.: Dorset, *Terry*, 29 Aug 1905 (US). Caledonia Co.:

Barnet, *Stevens*, 14 Jul 1892 (US). Chittenden Co.: Richmond, *Doray*, 28 Jun 1944 (US). Cumberland Co.: Pownal, *Knowlton*, 14 Jun 1918 (PH). Lamoille Co.: Eden, *Knowlton*, 20 Jul 1916 (PH). Orleans Co.: Willoughby, *Knowlton*, 24 Aug 1918 (PH). Rutland Co.: Burlington, *Jones & Eggleston*, 4 Aug 1893 (US). Windsor Co.: Woodstock, *Kittredge*, 13 Aug 1920 (PH). WEST VIRGINIA.—Fayette Co.: Quinmemont, *Pollard & Maxon* 10 (US). Greenbrier Co.: SW of Renick P. O., *Wherry*, 10 Jul 1938 (PH). Jefferson Co.: Harper's Ferry, *Henshaw*, 4 Jul 1884 (US). Mercer Co.: NE of Bluefield, *Wherry*, 18 July 1938 (PH). Monroe Co.: near Greenville, *Morris* 1026 (US). Pendleton Co.: Mouth of Seneca, *Leeds* 264 (PH). Randolph Co.: SE of Huttonsville, *Wherry*, 7 Jul 1938 (PH). VIRGINIA.—Alleghany Co.: NE of Covington, *Wherry*, 27 Aug 1938 (PH). Bath Co.: Jackson River Gorge, *Henry* 2181 (PH). Craig Co.: Potts Creek Valley, *Steele* 174 (US). Fairfax Co.: Potomac Bluff, Langley, *Palmer*, 13 Jul 1902 (PH). Frederick Co.: Shenandoah, *Cresson* 108 (PH). Giles Co.: Harveys Cave Sinkhole, *Iltis* 1882 (TENN). Highland Co.: N of Franklin, *Leeds* 263 (PH). Lee Co.: E of Pennington Gap, *Leeds* 176 (PH). Montgomery Co.: 2 mi. E of East Radford, *Adams & Wherry* 2259 (PH). Patrick Co.: north approach to Pinnacles of Dan, *Wherry*, 5 Sep 1946 (PH). Rock Bridge Co.: Natural Bridge, *Sowden*, 9 Jun 1923 (PH). Russell Co.: W of Dickensonville, *Leeds* 477 (PH). Smyth Co.: near Marion, *Small*, 22 May 1892 (PH, US). Washington Co.: 2 mi. NE of Bristol, *Wherry*, 8 Jun 1934 (PH). Wythe Co.: S of Eagle, *Wherry*, 14 Jul 1936 (PH). WISCONSIN.—Brown Co.: DePere, *Kellogg*, 4 Jul 1888 (US). Door Co.: Ephraim, *Millspauch* 3954 (US). Polk Co.: at Osceola, *Tryon & Tryon* 4339 (TENN, US). Sauk Co.: near Merrimac, *Wherry & Leeds* 3306 (PH). Trempealeau Co.: Trempealeau, *Fassett* 4098 (PH).

8. *Cystopteris diaphana* (Bory) Blasdell

SELECTED SPECIMENS:

NORTH AMERICA

COSTA RICA.—Coliblanco, *Maxon* 312 (US); Cartago, Cartago, *Cooper*, Apr 1888 (US); San Jose, Las Nubes, *Standley* 38357 (US); Region of Zarcero, *Smith*, n.d. (US).

GUATEMALA.—Chimaltenango, Santa Elena, *Skutch* 290 (US). Chiquimula, Volcan Ipala, *Steyermark* 30559 (US). Guatemala, *Smith* 2424 (US). San Marcos, Volcan Tajumulco, *Steyermark* 36783 (US).

HAITI.—Petionville, *Ekman* 1436 (US).

JAMAICA.—trail from St. Helens Gap to Latimer River, *Maxon & Killip* 901 (US); summit of Blue Mountain Peak, *Maxon* 1400 (US).

MEXICO.—Chiapas, San Cristobal, *Munch* 60 (US). Chichuahua, Sierre Madre, *Nelson* 6146 (US). Distrito-Federal, Guajimalpa, *Matuda* 20994 (US). Durango, Metates, N of Cueva, *Pennell* 18437 (PH). Jalisco, above Jazmin, *McVaugh* 10065 (US). Mexico, Popo Park, *Hitchcock*, 4-8 Aug 1910 (US). Michoacan, vicinity of Morelia, *Arsene* 6899 (US). Morelos, El Parque, *Orcutt* 3845 (US). Nayarit, territory of Tepic, *Rose* 2207 (US). Oaxaca, Sierra de San Felipe, *Smith* 2065 (US). Puebla, Hueyotlipan, *Arsene*, 15 Jun 1908 (US). Vera Cruz, Orizaba, *Copeland* 35a (US).

PANAMA.—vicinity of El Boquete, Chiriqui, *Maxon* 5238 (US). Quebrada Velo Volcano, *Woodson & Schery* 245 (US).

SOUTH AMERICA

ARGENTINA.—Catamarca, Belen, *Sleumer & Vervoorst* 2462 (US). Cordoba, Sierra Chica, *Osten*, 9 May 1917 (S-PA). Tucuman, Burroyaco, *Venturi* 8026 (S-PA).

BOLIVIA.—Unduavi, Nordyungas, *Buchtien* 2671 (S-PA). Larecaja, Sorata, *Man- don*, Jul 1857 (S-PA). La Paz, Incaihaca, *Asplund* 3746 (US). Near Pelichuco, *Williams* 2615 (US).

BRAZIL.—Santa Catarina, Riozinho, *Smith & Klein* 7889 (US). Rio Grande do Sul, Sao Leopoldo, *Dutra* 213 (R).

CHILE.—Santiago, San Cristobel, *Hastings* 105 (US).

COLUMBIA.—Caldas, Paramo del Quindio, *Pennell & Hazen* 12118 (US). Cundinamarca, 18 km. E of Cabrera, *Fosberg* 20764 (US). El Cauca, Coconuco, *Killip* 6845 (US). Narino, W of Ipiales, *Ewan* 16106 (US).

ECUADOR.—Azuay, E of Cuenca, *Correll* E355 (US). Bolivar, on road from Guaranda to Ambato, *Correll* E441 (US). Cotopaxi, *Haught* 2930 (US). Imbabura, Mariano Acosta, *Wiggins* 10287 (US). Pichincha, near Quito, *Sydow*, 30 Sep 1937 (S-PA, US). Tungurahua, 15 km. above Ambato, *Correll* E307 (US).

PERU.—Lucumayo Valley, *Cook & Gilbert*, 19 Jun 1915 (US). Calca, Cuzco, Vilcambamba, *Vargas* 4004a (US). Ollantaytambo, *Cook & Gilbert* 742 (US). Rio Blanco, *Macbride & Featherstone* 703 (US).

VENEZUELA.—Sucre, Cerro Turumuquire, *Steyermark* 62552 (US). Merida, S. Rafael de Mucuchies, *Pittier* 12914 (US). Merida, Mucuruba, *Gehriger* 303 (US).

AFRICA AND EUROPE

ABYSSINIA.—*Schimper*, n.d. (L).

BELGIAN CONGO.—Kivu, Volcan Mikeno, *Humbert* 8006 (US).

CANARY ISLANDS.—Gran Canaria, San Mateo, *Asplund* 85 (S-PA). La Palma, *Bornmüller*, 24 Apr 1901 (S-PA). Tenerife, Bco del Rio, *Pitard*, Feb 1906 (L, S-PA). Tenerife, La Perdona la madre del agua, *Burchard* 30 (S-PA).

MADEIRA ISLAND.—Funchal, *Sederholm*, 30 Dec 1884 (S-PA).

NATAL.—*Wood*, n.d. (S-PA).

PORTUGAL.—Lusitania, Estremadura, near Capuchos, *Rainha* 8849 (US).

TANGANYIKA TERRITORY.—Kilimandjaro, *Daubenberger*, Apr 1906 (L, S-PA).

9. *Cystopteris japonica* Lssn.

SELECTED SPECIMENS:

CHINA.—Kouy-Tsheow, *Cavalerie*, 4 Sep 1902 (L, S-PA). Szechuan, Ta-hsiangling, *Smith* 2124 (S-PA).

JAPAN.—Honshu.: Nara, N of Zenkiguti, *Tagawa* 5842 (US); Musashi, Nagurimura, *Hamegata* 2904 (US); Hyogo, Koranotaki, *Satiyomura*, *Tagawa* 6485 (US); Shikoku.: Mt. Yologura, Takaokagun, Kochi-ken, *Uno* 2611 (US). Nanokawa, Tosa, Sikok, *Watanabe*, 11 Jul 1892 (P).

10. *Cystopteris tenuisecta* (Bl.) Mett.

SELECTED SPECIMENS:

BORNEO.—Mt. Kinabalu, *Clemens*, 28 Jun 1933 (L).

CEYLON.—*Parish*, 1868 (P).

CHINA.—Yunnan.: Mengtze, *Hancock*, 1893-5 (US); Shweli River drainage basin, E of Tengyueh, *Rock* 7722 (US).

INDIA.—Assam, Cherrapunji, Khasi Hills, *Mann*, Sep 1888 (L). Sikkim, *Thomson*, n.d. (US). Manipur, *Buysman* 2908 (P).

JAPAN.—mountains of Yoshino, *Faurie* 220, Sep. 1913 (S-PA).

INDOCHINA.—Tonkin, *Petelot*, Jul 1920 (P).

JAVA.—Mt. Gede, Kandang badak, *Danser*, 17 Dec 1925 (L).

MALAYA.—Pahang, Cameron Highlands, *Holtum*, 10 May 1936 (US).

PHILIPPINE ISLANDS.—Luzon, Pauri, *Merrill* 8381 (L).

SUMATRA.—Gojor, *Van Daalen*, 1904 (L).

TAIWAN.—Arisan, *Faurie* 661 (S-PA). Bunkikiyo, *Faurie* 387 (S-PA).

HYBRIDS

1. *Cystopteris* × *tennesseensis* Shaver

SELECTED SPECIMENS:

ARKANSAS.—Benton Co.: Martins Bluff, *McGregor* 3722 (US). Randolph Co.: Revenden Springs, *Demaree* 29202 (PH). KANSAS.—Bourbon Co.: 2 mi. S of Uniontown, *McGregor* 1778 (US). Chautauqua Co.: near Sedan, *Palmer* 41805 (US). Montgomery Co.: 8 mi. W of Sycamore, *McGregor* 2399 (US). Wilson Co.: 2 mi. W of Neodesha, *McGregor* 3404 (US). KENTUCKY.—Edmonson Co.: Mammoth Cave National Park, *Lix* 29 (US). Hardin Co.: Vertres, *Wherry & Pennell* 13632 (PH). Powell Co.: Natural Bridge, *McCoy*, 23 Jun 1934 (PH). MISSOURI.—Greene Co.: vicinity of Willard, *Standley* 9650 (US). McDonald Co.: 3 mi. NE of Noel, *McGregor* 3641 (US). Morgan Co.: N of Florence, *Wherry*, 26 May 1940 (PH). Pike Co.: 11 mi. NNW of Bowling Green, *Wherry*, 8 Jul 1935 (PH). NORTH CAROLINA.—Craven Co.: E of Fort Barnwell, *Radford* 5618 (US). OKLAHOMA.—Delaware Co.: *McGregor* 3749 (US). Pontotoc Co.: 4 mi. SE of Ada, *Waterfall* 8385 (PH). TENNESSEE.—DeKalb Co.: between Dowelltown and Smithville, *Shaver* 10505 (TENN, US). Giles Co.: near Waco, *Shaver* 10220 (TENN, US). Grundy Co.: road to Beersheba Springs, *Shaver* 10188 (TENN). Hardin Co.: east of Olive Hill, *Shaver* 10533 (TENN). Hickman Co.: Centerville, *Shaver* 10526 (TENN, US). Lewis Co.: 4 mi. N of Hohenwald, *Shaver* 10222 (TENN). Lincoln Co.: 10 mi. S of Fayetteville, *Shaver* 10280 (TENN). Macon Co.: 6 mi. E of Lafayette, *Shaver* 10555 (TENN). Marshall Co.: road from Cornersville toward Diana, *Shaver* 10460 (TENN). Overton Co.: 3 mi. SE of Livingston, *Shaver* 10550 (TENN). Perry Co.: 11 mi. W of Lewis Co. line, *Shaver* 10215 (TENN). Smith Co.: Rome, *Shaver* 10427 (Type locality, TENN, US). Trousdale Co.: 4 mi. NE of Hartsville, *Shaver* 10485 (US). Wayne Co.: Forty-nine Creek, *Shaver* 10531 (TENN). TEXAS.—Culberson Co.: Guadalupe Mts., Devils Canyon, *Moore & Steyermark* 3561 (US).

2. *Cystopteris* × *laurentiana* (Weath.) Blasdell

SELECTED SPECIMENS:

CANADA.—NEWFOUNDLAND.—Port au Port, *Kennedy* 90 (GH); Mt. Moriah, *Fernald et al.* 26152 (PH, US); W. Arm, Bonne Bay, *Fernald et al.* 1123 (PH); Highlands of St. John, *Fernald et al.* 27214 (PH). NOVA SCOTIA.—Cape Breton Island, *Nichols* 678 (GH). ONTARIO.—Manitoulin Island, *Pease & Ogden* 24,997 (US); 15 mi. E of Port Arthur, *Tryon & Faber* 4919 (US). Bruce Peninsula, Dyer Bay, *Pease & Ogden* 24,871 (US); Brinkman's Corners, *Taylor* 6129 (US). Thunder Bay District, at International Bridge, *Carton* 1859 (US). QUEBEC.—Gaspé Co.: Cap Pleureuse, *Fernald & Weatherby* 2402 (US); Cap-Rosier, *Marie-Victorin* 17040 (GH, US); Petite Tourelle, *Marie-Victorin et al.* 3897 (US). Beauce Co.: 3 mi. N of Leeds Station, *Wherry*, 24 Aug 1935 (PH). Rimouski Co.: Bic, *Bartram & Long* 259 (PH); headland north of Baptiste Michaud's, Bic, *Collins & Fernald*, 18 Jul 1904 (TYPE, GH). Iles de la Madeleine.: Cap-aux-Meules, *Marie-Victorin* 9333 (GH). Ile Nue, *Marie-Victorin & Rolland-Germain* 24618 (GH). Matane Co.: near base of Mt. Nicolabert, *Joffre, Fernald & Pease* 24790 (GH).

UNITED STATES.—MINNESOTA.—Lake Co.: Manitou Falls, *Tryon et al.* 4894 (US). PENNSYLVANIA.—Centre Co.: 3 mi. NNE of Pennsylvania State College, *Wahl* 1449 (PH). Pike Co.: Kimbles Station, *Wherry*, 24 Jun 1936 (PH).

3. *Cystopteris* × *alpina* (Wulfen) Desv.

SELECTED SPECIMENS:

ALBANIA.—“Prokletija,” *Dorfler*, 18 Jul 1914 (S-PA).

AUSTRIA.—S Tyrol, *Rosenstock*, Jul 1897 (L). Carinthia, *Suringar*, n.d. (L). Salzburg, *Sauter*, n.d. (L).

FRANCE.—Haute Savoie, Mt. Vergy, *Bourgeau*, 27 Jul 1873 (P). Savoy, *Suringar*, 1865 (L). Basses-Alpes, L'Arche, *no coll.* (S-PA).

GERMANY.—Bayern Partenkirchen, *Harz*, 10 Sep 1920 (S-PA). Bayern, Oberstdorf, *no coll.* Jul 1920 (S-PA). Sachsen, *no coll.* (S-PA).

GREECE.—Mt. Parnassos, *Orphanodes*, 30 Jul 1854 (S-PA). Peloponnesus, Achaia in mt. "Chelmos" (Aroania), *Bornmüller*, 19 Jun 1926.

HUNGARY.—Lika-Kibava Croatiae, *Filarszky & Kummerle*, 4 Jul 1911 (S-PA) Jatri, *Pawdbroch*, 15 Jul 1922 (S-PA).

ITALY.—Piedmont, Cottian Alps, *Rostan*, 1880 (S-PA). Lombardy, Val di Pona, *Levier*, Jul 1867 (S-PA). Dolomites Mts., Colfosco, *Werdermann & Meyer*, 5 Aug 1956 (US). Sicily, Mt. Aetna, *Huet du Pavillon*, 12 Jul 1855 (L).

JUGOSLAVIA.—Montenegro ad Cirova Pecina, Mt. Durmitov, *Muryev*, 27 Jun 1930 (S-PA).

SWITZERLAND.—Glarus, *Sinia*, 9 Aug 1927 (L). Vaud, *Masson*, 11 Jul 1876 (S-PA). Valais, *Wilezek*, 17 Jul 1905 (S-PA). Waadt, *Kuhlmann & Wirtgen*, n.d. (S-PA). Unterwalden, *Samuelsson*, 10 Jul 1921 (S-PA).

4. *Cystopteris diaphana* × *fragilis* complex

SELECTED SPECIMENS:

NORTH AMERICA

ALASKA.—Mt. McKinley National Park, *Nelson* 4100 (US); Skagway, *Eastwood* 749 (US). Cook Inlet, *Coville & Kearney* 2437 (US); Cape Nome, *Blaisdell*, 1900 (US); Kodiak Isl., Olga Bay, *Looff*, Aug 1938 (US). Aleutian Islands.: Sitka, Mt. Venstovoi, *Evermann* 233 (US); St. Paul Island, *Townsend*, Aug 1893 (US); Umnak Island, *Nikolski*, *Hulten* 7134 (US); Attu Island, Holtz Bay, *Schaack* 360 (US); Unalaska, *Turner & Rust*, 1879-81 (PH).

CANADA.—ALBERTA.—Waterton Lakes National Park, *Breitung* 16091 (US); Fort Chipewyan, *Raup* 6053 (US); Lake Louise, *Brown* 717 (PH). BRITISH COLUMBIA.—Vancouver Island, vicinity of Victoria, *Macoun* 545 (US); near Fish Lake, *Shaw* 1211 (US); Brackendale, Squamish River, *Macoun* 92740 (US). LABRADOR.—Battle Harbor, *Waghorne*, 30 Aug 1891 (US). NEW BRUNSWICK.—Gloucester Co., Caraquet, *Dore & Gorham* 45796 (US); Kent Co., cliffs of Bon Ami, *Fowler*, 25 Aug 1866 (PH). NEWFOUNDLAND.—region of Ingornachoix Bay, Gargamelle Cove, *Fernald et al.* 1122 (PH, US); Avalon Peninsula, Placentia, *Williamson* 364 (PH); Bay of Islands, *Eames & Godfrey* 5776 (PH); Straits of Belle Isle, Big Brook, *Pease & Griscom* 27209 (PH); Brig Bay, *Fernald et al.* 26151 (PH). ONTARIO.—Grey Co., Owen Sound, *McColl*, Sep 1919 (S-PA, US); Thunder Bay District, 11 mi. NE of Port Arthur, *Garton* 1320 (US); Durham Co., 8 mi. S of Lindsay, *Soper & Dale* 3873 (US); Sault Ste. Marie, *Hermann* 7264 (PH). QUEBEC.—Matane Co., Mt. Logan, *Fernald & Pease* 24784 (US); Gaspé Co., Bonaventure Island, off Perce, *Storer* 270 (US); Rimouski Co., Bic, *Churchill*, 15 Jul 1905 (PH); Labelle Co., Nominigüe, *Heroux & Roy*, 15 Jul 1932 (PH); McGregor Lake, near Ottawa, *Malte*, 13 Jun 1923 (S-PA); James Bay, Charlton Island, *Porsild* 4277 (S-PA). YUKON.—Yukon River, 3 mi. above Fortymile River, *Collier* 23 (US).

COSTA RICA.—Irazu Volcano, *Lankester* 655 (US).

DOMINICAN REPUBLIC.—San Juan, Sabana Neuva, *Howard* 9112 (US).

GREENLAND.—Disco, Godhaven, *Porsild*, 10-20 Sep 1922 (US); Ymer Island, *Seidenfaden* 380 (S-PA); head of Søndre Strømfjord, *Erlanson* 2430 (US); Tugtup Agtakorfiá, Julianehaab District, *Gordon*, Aug 1923 (PH); North Star Bay, University Ridge, *Ekblaw* 11 (S-PA).

GUATEMALA.—Dept. Alta Verapaz, Coban, *Tuerckheim* 8630 (US).

HAITI.—gorge of River Chota, *Ekman* 5986 (US).

ICELAND.—Laxardal, *Palsson* 4 (PH); Grenujadastad, *Taylor*, 4 Jul 1895 (US);

Hofsskard, *Davidsson*, 19 Aug 1897 (US); Skagafjordur, Keta, *Sorensen*, 1930 (US); Gullbringusysla, Kapellukraun, Lambhagi, *Love*, 11 Sep 1949 (S-PA).

JAMAICA.—near Castleton Botanical Garden, *Underwood* 456 (US); trail from Cinchona to Blue Mt. Peak, *Maxon* 1495 (US); summit of Blue Mountain Peak, *Maxon* 9903 (US).

MEXICO.—Vera Cruz, Mt. Orizaba, *Seaton* 162 (US); Distrito-Federal, Contreras, *Orcutt* 3477 (US); Durango, Metates, north of Cueva, *Pennell* 18404 (US); Hidalgo, S. Miguel Regla, *Lyonnet* 2011 (US); Michoacan, Zacapu, *Leeds* 232 (PH); Jalisco, near Atequizallan, *Correll* 14364 (PH).

UNITED STATES.—ARIZONA.—Apache Co.: Hannagan Meadows, *Phillips* 2812 (US). Cochise Co.: Chuicahua National Forest, *Eggleston* 10791 (US). Coconino Co.: Clover Springs, *Collom* 948 (US). Pima Co.: Happy Valley, *Phillips* 2864 (US).

CALIFORNIA.—Butte Co.: Butte Creek Canyon, *Austin* 244 (US). Fresno Co.: Kings Canyon, *Storer* 182 (US). Mendocino Co.: Ukiah, *Bolander*, Apr 1860 (US). Modoc Co.: Emerson Peak, Warner Mts., *Alexander & Kellogg* 5059 (US). San Bernardino Co.: San Bernardino Mts., *Parish* 3126 (US). Siskiyou Co.: Paradise Lake, Marble Mts., *Alexander & Kellogg* 5865 (US). Sonoma Co.: at foot of Mt. Hood, *Heller*, 26 Jun 1902 (US). Tulare Co.: Bakeoven Meadows, *Howell* 27130 (US).

COLORADO.—Clear Creek Co.: Idaho Springs, *Smith*, 20 Jul 1884 (PH). El Paso Co.: Colorado Springs, *Smith*, 6 Aug 1881 (PH). Mexa Co.: S of Fruita, *Pennell & Schaeffer* 22120 (PH). Montrose Co.: 35 mi. W of Montrose, *Wherry*, 20 Jul 1937 (PH). Routt Co.: NE of Steamboat Springs, *Wherry*, 15 Jun 1937 (PH). San Juan Co.: Red Mt. Pass, *Wherry*, 18 Jul 1937 (PH). San Miguel Co.: 2½ mi. SW of Sam Station, *Wherry*, 19 Jul 1937 (PH). CONNECTICUT.—London Co.: N. Stonington, *Jausson*, 5 Sep 1927 (S-PA). New Haven Co.: Oxford, *Harger* 3769 (PH).

IDAHO.—Bear Lake Co.: Montpelier, *Pennell*, 17 Jun 1931 (PH). Blaine Co.: Poison Creek, Sawtooth National Forest, *Woods & Tidestrom* 2626 (US). Idaho Co.: Lochsa, *Rose* 414 (US). Nez Perces Co.: Lake Waha, *Heller* 3295 (US). Owyhee Co.: 10 mi. E of Silver City, *Davis* 2083 (PH). IOWA.—Cass Co.: near Lewis, *Fay* 5169 (US). Clayton Co.: S of McGregor, *Wherry*, 1 Jun 1937 (PH, US). Emmett Co.: SW of Esterville, *Wherry*, 2 Jun 1937 (PH).

KANSAS.—Douglas Co.: Lawrence, *Stevens*, n.d. (US). MAINE.—Penobscot Co.: Bangor, *Chickering*, Jun 1859 (US). Somerset Co.: Carratunk Falls, *Collins*, 8 Jul 1885 (US). MASSACHUSETTS.—Berkshire Co.: Mt. Washington, *Meredith*, 31 Jul 1922 (PH). Hampshire Co.: Middlefield, *Fernald & Long* 8354 (PH). Worcester Co.: Princeton, Mt. Wachusett, *Collins*, 5 Jul 1893 (US).

MICHIGAN.—Gratiot Co.: Alma, *Davis*, Jul 1889 (US). Houghton Co.: Silver Mountain, *Richards* 2318 (S-PA). Keweenaw Co.: gorge of Eagle River, *Richards* 2057 (S-PA). Polk Co.: St. Croix Falls, *Wherry & Leeds* 3311 (PH). Marquette Co.: E of Ishpeming, *Wherry & Leeds*, 4 Jul 1935 (PH). St. Joseph Co.: Klinger Lake, *Wherry*, 7 Jun 1948 (PH). Washtenaw Co.: Dixboro, *Hermann* 6902 (PH).

MINNESOTA.—Carlton Co.: Midway Creek, *Cronquist* 3853 (S-PA). Cook Co.: S of Clearwater Lake, *Butters & Buell* 464 (US). Washington Co.: 1½ mi. N of Point Douglas, *Moore* 10012 (US). Winona Co.: Dakota, *Mellele*, Aug 1934 (S-PA).

MISSOURI.—Barry Co.: road between Cassville and Galena, *Wilkins* 2529 (PH).

MONTANA.—Glacier Co.: Glacier National Park, Logan Pass, *Benner* 5074 (PH).

NEVADA.—Clark Co.: Charleston Mts., Little Falls, *Clokey* 5373 (US). Elko Co.: Fox Creek Fork, *Train* 786 (PH). Leander Co.: Bunker Hill, *Kennedy* 4179 (PH). Mineral Co.: Cat Creek, *Alexander & Kellogg* 4474 (US).

NEW JERSEY.—Essex Co.: Orange Mts., Newark, *Lyon*, 11 Aug 1896 (US).

NEW MEXICO.—Dona Ana Co.: Organ Mts., *Wooton*, 16 Aug 1895 (US). Lincoln Co.: Ruidoss Creek, *Wooton*, 10 Jul 1895 (US). Otero Co.: Clouderoft, *Viereck*, 29 May 1902 (PH).

Rio Arriba Co.: Chama, *Standley* 6628 (US). San Miguel Co.: Pecos, *Bartlett*, Sep 1904 (US). Santa Fe Co.: 7 mi E of Santa Fe, *Heller*, 7 Jul 1897 (US). Socorro Co.: Mogollon Mts., *Wooton*, 8 Aug 1900 (US).

Union Co.: Sierra Grande, *Standley* 6167 (US). NEW YORK.—Allegany Co.: Alma Hill, *Clausen*, 18 Jun 1939 (US). Tompkins Co.: Six Mile Creek, Ithaca, *Metcalf* 7385 (US).

Washington Co.: Kingsbury, *Burnham*, 13

Aug 1916 (S-PA). NORTH CAROLINA.—Avery Co.: *Wherry*, 24 Aug 1938 (PH). Mitchell Co.: Roan Mt., *Smith*, 13 Jul 1880 (US). Watauga Co.: Grandfather Mt., *Leeds* 58 (PH). NORTH DAKOTA.—Morton Co.: Mandan, *Sarvis* 53 (US). OREGON.—Clackamas Co.: Oregon City, *Foster*, 20 Jun 1906 (PH). Douglas Co.: Nichols Station, *Ward* 31 (US). Klamath Co.: near Keno, *Applegate* 2010 (US). Lake Co.: Big Lake, *Eggleston* 7003 (US). Multnomah Co.: vicinity of Portland, *Palmer* 1493 (US). Union Co.: 15 mi. NW of Elgin, *Wherry*, 2 Jul 1931 (PH). PENNSYLVANIA.—Blair Co.: Hollidaysburg, *Wherry*, 20 Sep 1941 (PH). Bradford Co.: 5 mi. NW of Towanda, *Wherry*, 13 Aug 1935 (PH). Cameron Co.: Sterling Run, *Wherry*, 5 Sep 1940 (PH). Lycoming Co.: Clarksburg, *Wherry*, 2 Jun 1941 (PH). Mercer Co.: Leesburg, *Wherry*, 30 Aug 1939 (PH). Montgomery, Conshohocken, *Banes*, 6 Aug 1891 (S-PA). Pike Co.: Kimbles, *Wherry*, 24 Jun 1936 (PH). Somerset Co.: Petersburg, *Brown & Saunders*, 10 Jul 1898 (PH). Sullivan Co.: Lincoln Falls, *Johnson*, 6 Jul 1924 (PH). Wayne Co.: SE of Scott Center, *Wherry*, 3 Sep 1939 (PH). RHODE ISLAND.—Providence Co.: Diamond Hill, *Palmer* 46746 (US). SOUTH DAKOTA.—Meade Co.: Piedmont & Little Elk Creek, *Rydberg* 1198 (US). TENNESSEE.—Blount Co.: SE of Walland, *Wherry*, 9 Jun 1934 (PH). UTAH.—Grand Co.: Post Canyon, *Graham* 9876 (US). Piute Co.: Marysville, *Jones* 5896 (US). Sanpete Co.: Lake Canyon, Manti, *Tidestrom* 1872 (US). Washington Co.: Zion National Park, *Pennell & Schaeffer* 21682 (PH). VERMONT.—Chittenden Co.: Huntington, *Doray*, Jul 1943 (US). Rutland Co.: Brandon, *Knowlton*, 20 Aug 1899 (US). Washington Co.: Duxbury, *Doray*, 30 Jun 1944 (US). Windham Co.: Townshend, *Wheeler*, 16 Sep 1922 (S-PA). Windsor Co.: Quechee Gulf, *Leeds* 772 (PH). VIRGINIA.—Fauquier Co.: Marlsham, *Allard* 2885 (US). Madison Co.: Stony Man Mt., *Palmer*, 26 Aug 1901 (US). Page Co.: Mount Marshall, *Allard* 771 (US). WASHINGTON.—Asotin Co.: SW of Anatone, *Cronquist* 5716 (S-PA, US). Cowlitz Co.: Castle Rock, *Kellogg & Hartford* 1185 (US). Kittitas Co.: Mt. Stuart, *Thompson*, 16 May 1931 (PH). Okanogan Co.: Muckamuck Lookout, *Thompson* 6992 (PH). Pierce Co.: Eagle Peak, Mt. Rainier National Park, *Jennings* 10011 (US). Skamania Co.: Mt. St. Helens, *Coville* 825 (US). Whatcom Co.: Chuckanut Drive, *Thompson* 5910 (PH). Yakima Co.: Yakima Region, Snipes Creek, *Cotton* 422 (US). WEST VIRGINIA.—Hardy Co.: 7 mi. N of Moorefield, *Wherry*, 12 Apr 1936 (PH). WYOMING.—Albany Co.: 11 mi. E of Laramie, *Wherry*, 9 Jun 1937 (PH). Fremont Co.: Farson-Lander Road, *Porter* 4980 (PH). WISCONSIN.—Trempealeau Co.: Perrot State Park, *Hartley*, 8 Jun 1956 (US). Sauk Co.: near Merrimac, *Wherry & Leeds* 3303 (PH).

SOUTH AMERICA

ARGENTINA.—Nord-Patagonien, San Carlos, *Buchtien* 174 (S-PA). Santa Cruz, Lago Argentino, *Vervoorst* 4379 (S-PA). Neuquen, Arroyo La Estacada, *Barba* 2160 (US). Rio Negro, Cerro Catedral, *Pedersen* 1471 (US). Lago Correntoso, *Pedersen* 229 (US). BOLIVIA.—Oruro, Abaroa, Challapata, *Asplund* 3247 (S-PA). La Paz, Omasugas, Isla del Sol, Yumani, *Asplund* 3617 (S-PA). Pelichuco, *Williams* 2614 (US). Insel Titicaca, *Buchtien* 2804 (US). CHILE.—Valparaiso, Salto-Islen, *Skottsberg* 933 (S-PA). Temuco, *Claude-Joseph* 1893 (US). Santiago, above Rio Colorado, *Hastings* 513 (US). Valdivia, *Buchtien*, Dec 1896 (US). COLOMBIA.—Narino, 6 kilom. above San Jose, *Ewan* 16571 (US). Santander, near Vetaz, *Killip & Smith* 17950 (US). Boyaca, Hacia La Cueva, *Cuatrecasas* 1627 (US). ECUADOR.—El Carchi, El Angel, *Popenoe*, Jun 1921 (US). Pichincha, 5-6 mi. W of Quito, *Steyermark* 52380 (US). JUAN FERNANDEZ.—Mas Afuera, *Skottsberg* 508 (S-PA, US). PERU.—between Juliaca and Cuzco, *Hitchcock* 22440 (US). Arequipa, Lomas de Capae, *Coronado* 40 (US). Puno, Caccarhara, *Pearson* 105 (PH). VENEZUELA.—Merida, Laguna Mucubaji, *Steyermark* 57491 (US).

EURASIA

CHINA.—Shansi, Lu Yah Shan, *Smith* 8134 (S-PA).

CZECHOSLOVAKIA.—Bohemia, Gratzen, *Jaky*, 16 Aug. 1893 (S-PA).

DENMARK.—Lolland, *Lange*, 4 Jun 1848 (S-PA); Moen, Vollerrip, *Jungerster*,

12 Aug 1897 (S-PA). The Faeroes.: Island of Astero, *Simmons*, 17 Aug 1895 (S-PA); Island of Sudero, Vag, *Simmons*, 17 Aug 1895 (S-PA).

FRANCE.—Haute Savoie, Mt. Vergy, *Boissier*, Jul 1859 (S-PA). Savoy, la Thouvriere pres Tignes, *Chermeson & Evrard*, 21 Aug 1913 (P). Pyrenees Orientales, Collioure, *Copineau*, 20 May 1891 (P). Ain, E du Reculet, *Pfister* 1081 (US). Cantal, Vallee du Sinica, *Walter* 459 (P, US). Haute Savoie, Chamonis, *Rey-Pailhade*, n.d. (P). Nievre, Montsauche, *Duffour*, 2 Jun 1915 (P). Mondoubleau (Loir-et-Cher), Sarge, *Desvaux*, 24 May 1848 (P). Haute Saone, Fleurey-le-Faverney, *Bertrand*, Sep 1889 (P). Seine-et-Oise, Magny pres Chateaufort, *Guillotaux*, 12 Jun 1848 (S-PA).

GERMANY.—Baden, Heidelberg, *Lang*, 17 Sep 1869 (S-PA). Sachsen, Lohmen, *Kohl*, 1872 (S-PA); Eisleben, *Eggers*, 27 Aug 1907 (S-PA). Hannover, *Wappenley*, Aug 1866 (S-PA). Mecklenburg, Babelin, *Hahn*, Jun 1906 (S-PA). Brandenburg, Guben, *Baenitz*, n.d. (S-PA).

HUNGARY.—Tozsony, *Baumler*, Sep 1910 (S-PA). Gomor, Murany, *Richter*, 5 Jul 1901 (S-PA).

IRAN.—Khorasan, Mts. of Nishapur, *Gaub*, 23 Jul 1937 (S-PA).

ITALY.—S. Tirol, Mts. of Merano, *Enander*, 10 Sep 1925 (S-PA). Etrusca (Tuscany), *Agosto*, 1862 (S-PA).

LEBANON.—Mizrab supre Arz Er Rab (Cedros), *Samuelsson*, 10 Jun 1932 (S-PA).

NETHERLANDS.—Valkenburg, Zuid-Limburg, *Lako*, Aug 1903 (S-PA).

NORWAY.—Sondhordl, Bommelon, *Andersson*, 13 Jul 1891 (S-PA). Asker, *Vestergren*, 12 Jul 1916 (S-PA).

POLAND.—Bromberg (Bydgoszcz), *Baenitz*, 1864 (S-PA). Sommerfeld (Zemsh), *Baenitz*, Jul 1859 (S-PA).

PORTUGAL.—Sierra da Estrella, *Birger*, 5 Apr 1921 (S-PA). Porto, *Buchtien*, 1891 (US).

SPAIN.—Leon Pena Coroida, *Gandoger*, Jun 1904 (L). Lerida, Monsech de Rubies, *Kretschmer*, 28 May 1926 (S-PA). Navarre, region of Aragon River, *Enander*, 1 Oct 1927 (S-PA).

SWEDEN.—Varmland, Sunne, *Ohlin*, 30 Jul 1920 (S-PA). Stockholm, Runmaro, *Rosendahl*, Jul 1915 (S-PA). Lappland, Jukkasjarvi, *Smith*, 6 Jul 1927 (L, S-PA). Jamtland, Areskutan, *Rosendahl*, 20 Jul 1910 (S-PA).

SWITZERLAND.—Interlaken, *Birger*, 23 Jun 1925 (S-PA). Luzern, Sonnenberg, *Birger*, 23 May 1925 (S-PA). Lugano, *Birger*, 12 Jun 1925 (S-PA). Bern, Kandersteg, *Tavel*, 27 Aug 1916 (S-PA). Valais, Erbignon, *no coll.* (US). Gimmelswald, *Keller*, 9 Jul 1893 (PH).

SYRIA.—Arissa, *Ehrenberg*, May-Jun 1820-26 (L). Mont Amanus, *Haradjian*, Aug 1906 (S-PA). Berut, *Ehrenberg*, 18 May 1824 (S-PA).

UNION OF SOVIET SOCIALIST REPUBLICS.—Lapponia murmanica, Rynda, *Hulten*, 1 Aug 1927 (S-PA). "Iter Ireutense ad fl. Lena et Kirenga," *Kusnezow*, 1910 (S-PA). Moskau, Kunzowo, *Balcunw*, 9 Jul 1901 (S-PA). Estonia, Ostseeinsel Dago bei Tardas, *Kupffer*, 8 Aug 1903 (S-PA); Wormso, Magnushof, *Gröntved*, 15 Jul 1926 (S-PA). Livland, Osteeinsel ösel, *Kupffer*, 10 Aug 1907 (S-PA). Kamtehatka.: Lake Asabatch, *Malaise*, Aug 1925 (S-PA); Bolschajas flodsystem, *Hulten*, 12 Sep 1921 (S-PA); near Petropavlovsk, *Mertius*, n.d. (S-PA); Savoiko, *Eyerdam*, 27 Jul 1928 (S-PA).

AFRICA AND ASSOCIATED ISLANDS

AZORES.—Tayal, *Brown* 328 (PH, US).

BELGIAN EAST AFRICA.—Mt. Kenia, *Mearns* 1442 (US).

CANARY ISLANDS.—Gran Canaria, *Rosendahl*, Jan 1913 (S-PA). Tenerife, Agua Garcia, *Cyren*, 12 Jun 1929 (S-PA).

MADEIRA.—Funchal, *Bornmuller*, 22 Mar 1900 (S-PA).

MOROCCO.—Azib de Tiebka, *Balls B2568* (S-PA).

5. *Cystopteris diaphana* × *protrusa* complex

SPECIMENS EXAMINED:

GEORGIA.—Gilmer Co.: 8 mi. E of Chatsworth, *Pyron & McVaugh* 2955 (US).
ILLINOIS.—Richland Co.: 2½ mi. N. of Olney, *Ridgway*, 7 Jul 1910 (US). IN-
DIANA.—Howard Co.: 1 mi. E of Burlington, *Deam* 56983 (PH). Parke Co.: 3 mi.
SE of Mansfield, *Tryon* 4289 (TENN, US). Wells Co.: Chester Twp., *Deam*, 26 Jun
1904 (US). IOWA.—Poweshiek Co.: Grinnell, *no coll.* (TENN). Winneshiek Co.:
¾ mi. W of Decorah, *Wherry*, 1 Jun 1937 (PH). KENTUCKY.—Graves Co.: 2½ mi.
NE of Water Valley, *Wherry*, 11 Jul 1935 (PH). Hardin Co.: Vertrees, *Wherry &*
Pennell 13632 (PH). LOUISIANA.—West Feliciana Co.: 1 mi. W of Plettenberg,
Correll 10472 (US). MICHIGAN.—Van Buren Co.: 2½ mi. E of Bangor on M-43,
Hagenah 1372 (US). MISSOURI.—Harrison Co.: near Eagleton, *Palmer & Steyer-*
mark 41350 (PH). Reynolds Co.: Centerville, *Eggert*, 22 Jun 1879 (US). NE-
BRASKA.—Saunders Co.: Ashland, *Williams*, 18 Aug 1888 (US). NORTH CARO-
LINA.—Ashe Co.: S of Jefferson, *Wherry*, 14 Jul 1936 (PH). Haywood Co.: Waynes-
ville, *Barksdale*, 1 Aug 1936 (PH). Jackson Co.: Saco Falls, 2 mi. SW Saco Gap,
Anderson 1446 (PH). NEW MEXICO.—Lincoln Co.: above Ruidoso Creek, *Wilkins*
2365 (PH). OHIO.—Franklin Co.: Columbus, *no coll.* (PH). Lorain Co.: Oberlin,
Grover, 10 Jul 1900 (US). Trumbull Co.: NE of Brookfield, *Whittenberger*, 10 Sep
1939 (PH). OKLAHOMA.—Murray Co.: Arbuckle Mts., Davis, *Emig* 467 (US).
PENNSYLVANIA.—Franklin Co.: Mercersburg, *Porter*, 20 May 1845 (PH). TEN-
NESSEE.—Bradley Co.: below road from Benton Station to Charleston, *Shaver* 10228
(TENN). Cannon Co.: 8 mi. NE of Woodbury, *Shaver* 10206 (TENN). Cumberland
Co.: 3 mi N of the Bledsoe Co. line, *Shaver* 10225 (TENN). Grainger Co.: 6 mi. E
of the Claiborne Co. line, *Shaver* 10211 (TENN). Hamilton Co.: N of Red Bank,
Shaver 10633 (TENN). McNairy Co.: S of Selmer, *Shaver* 10204 (TENN). Moore
Co.: N of Lynchburg, *Shaver* 10447 (TENN). Unicoi Co.: Bluff near Unaka Springs,
Shaver 10380 (TENN). Van Buren Co.: E. of Spencer, *Shaver* 10575 (TENN).
VIRGINIA.—8 mi. SW of Jonesville, *Wherry*, 11 Jul 1938 (PH). Smyth Co.: near
Marion, *Britton & Fail*, 13 Jun 1892 (PH). WEST VIRGINIA.—Cabell Co.: Pleasant
Valley, *Gilbert* 860 (PH, TENN). Fayette Co.: *Nuttall*, 1890-98 (PH). Monongalia
Co.: Cheat River, Morgantown, *Hatry*, 6 Jul 1902 (PH). Wirt Co.: 1 mi. above Pales-
tine, *Bartholomew* W1941-1035 (TENN).

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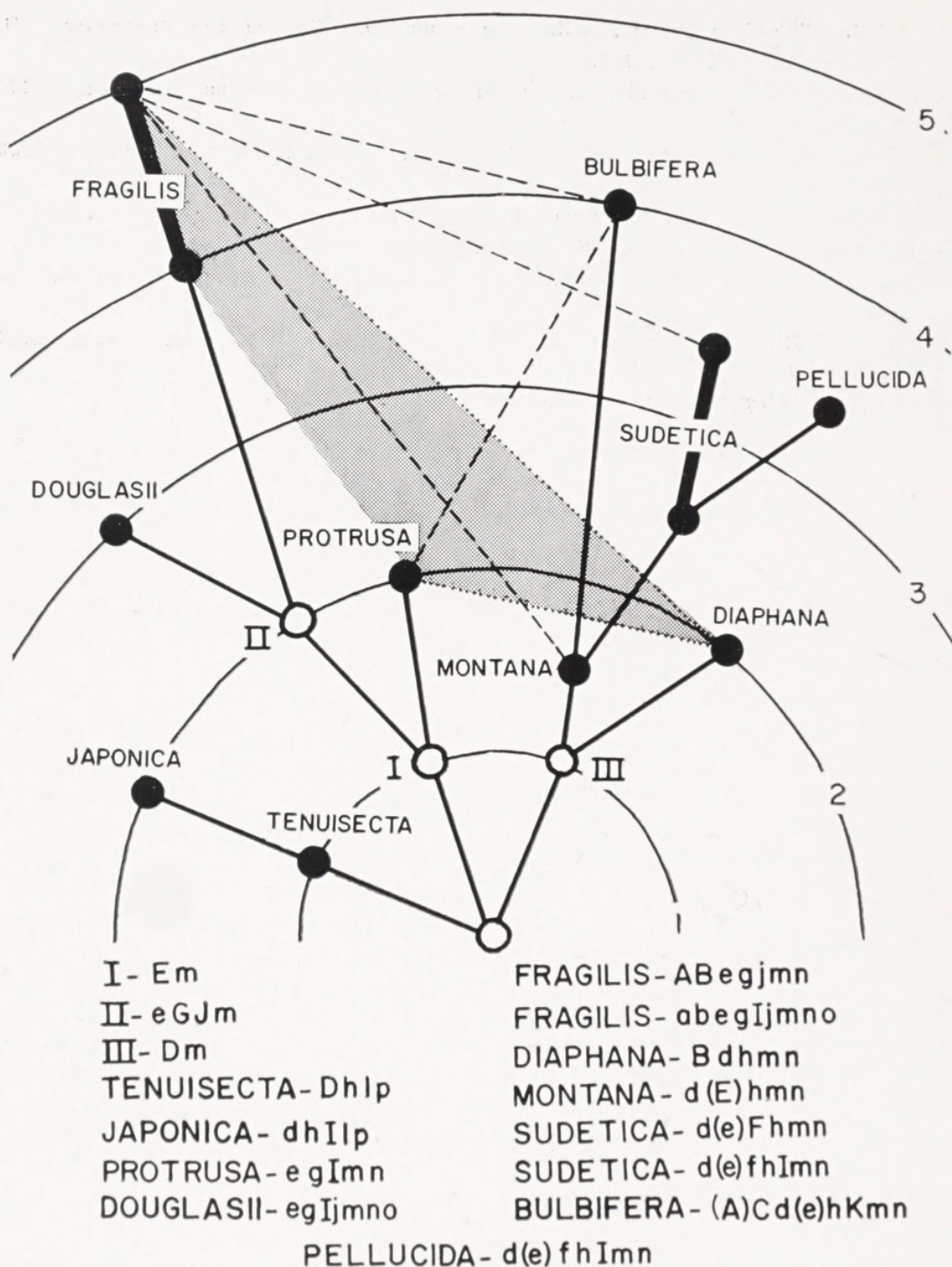


PLATE 1

EVOLUTIONARY TENDENCIES IN *CYSTOPTERIS*

Black dots are species, open circles presumed ancestral types. Solid lines indicate paths of evolution, dashed lines represent allopolyploids, and shaded region indicates taxa which are involved in apparent introgression. Upper case letters show the first occurrence of an advanced character in an evolutionary line; lower case letters indicate subsequent occurrence of advanced characters in the lines. Letters in parentheses represent intermediate conditions.

Characters. A. Rhizome organization. B. Blade pattern. C. Blade attenuation. D. Vein position. E. Adaxial epidermal cell wall outline. F. Scales with lateral cell wall thickenings. G-H. Indusial cells (No obvious trend). G. Attenuate. H. Short. I. Glandularity of indusium. J. Accessory indusial hairs. K. Foliar bulblets. L-M. Multicellular hairs (No obvious trend). L. Non-glandular. M. Glandular. N-P. Spore architecture (No obvious trend). N. Echinate. O. Rugose. P. Spines with irregular cross sections.

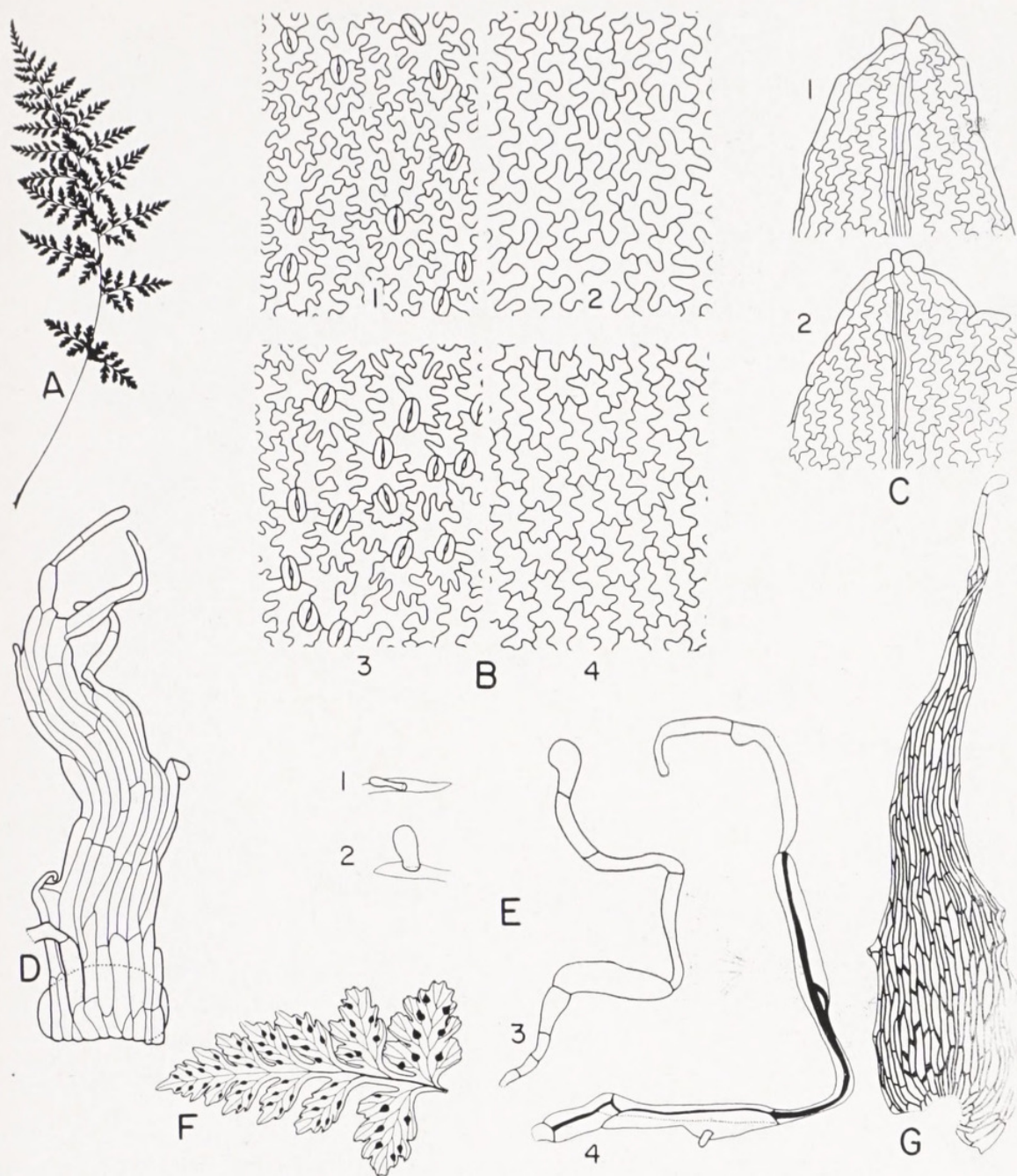


PLATE 2

CYSTOPTERIS FRAGILIS (L.) BERNH.

Fig. A. Silhouette of blade. Germany, Merxmüller, Aug. 1956. (living material. Grown at U. of Michigan Botanical Gardens). B. Epidermal cells. 1-2. Greenland, Bartlett 459a (US). 3-4. Sadlerochit River, Alaska, Spetzman 1184 (US). C. Marginal laminar cells. 1. Fort Yukon, Alaska, Russell, 8-12 Aug. 1889 (US). 2. Vicinity of Cape Lisburne, Alaska, Washburne, Jul. 1904 (US). D. Indusium. Fort Yukon, Alaska, Russell, 8-12 Aug. 1889 (US). E. Hairs and hair-like scales. F. Pinna. Sadlerochit River, Alaska (US). G. Scale of rhizome. Northwest Territories, Canada, Porsild 5194 (S-PA). The scale of each drawing is indicated on Plate 3.



PLATE 3

CYSTOPTERIS PROTRUSA (WEATH.) BLASDELL

Fig. A. Silhouette of blade. Near Chelsea, Michigan, *Blasdell* 277. B. Epidermal cells. 1-2. Near Chelsea, Michigan, *Blasdell* 277. C. Marginal laminar cells. Sulphur Springs, Pennsylvania, *Berkimer* 1254 (PH). D. Indusium. Near Chelsea, Michigan, *Blasdell* 277. E. Hairs. F. Pinna. Dexter Township, Michigan, *Wagner* 8075 (MICH). G. Scale of rhizome. Nolan, West Virginia, *Wherry*, 12 Jul. 1938 (PH).

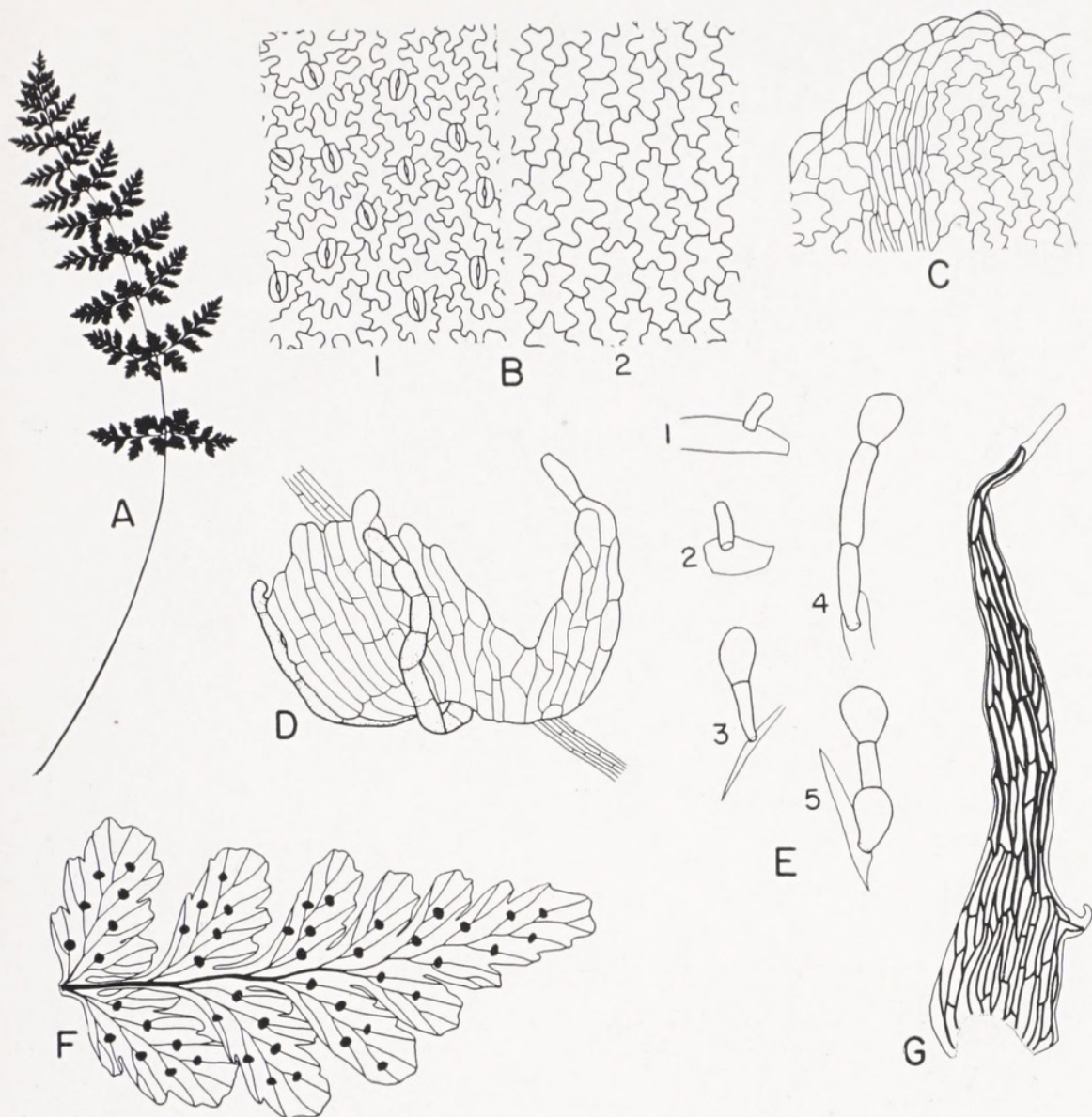


PLATE 4

CYSTOPTERIS DOUGLASII HOOK.

Fig. A. Silhouette of blade. Mauna Kea, Hawaii, *Horner*, 31 Jul. 1956 (from plants grown at the U. of Michigan Botanical Gardens). B. Epidermal cells. Hawaii, *Baldwin*, n.d. (PH). C. Marginal laminar cells. Haleakala Crater, Maui, T. H., *Hitchcock* 14966 (US). D. Indusium. Maui, Hawaii, *Mann & Brigham* 480 (US). E. Hairs. F. Pinna. Maui, Hawaii, *Mann & Brigham* 480 (US). G. Scale of rhizome. Haleakala Crater, Maui, *Wagner* 5261 (UC). The scale of each drawing is indicated on Plate 3.

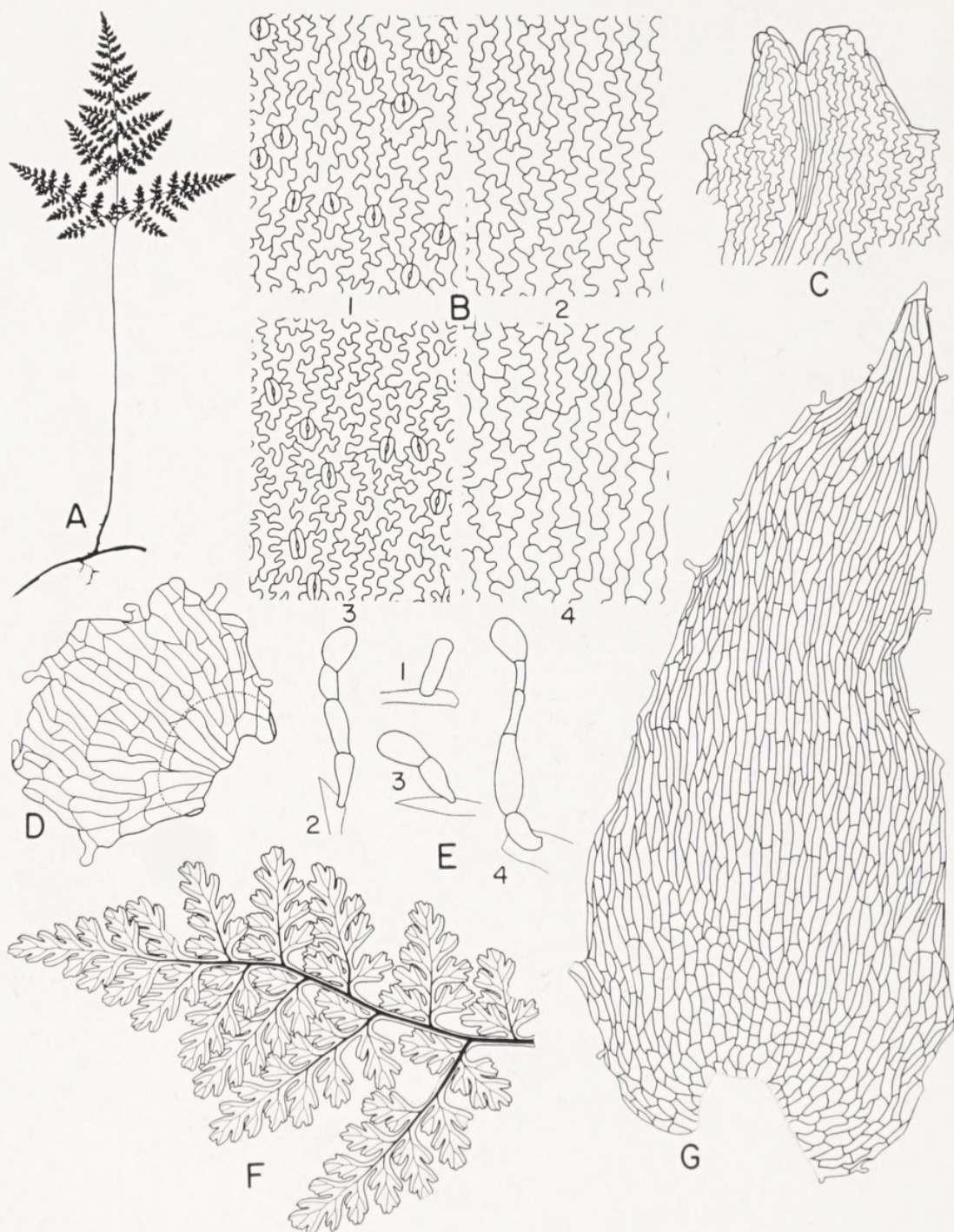


PLATE 5

CYSTOPTERIS MONTANA (LAM.) BERNH.

Fig. A. Silhouette of blade. Tyndero, Norway, *Blomquist*, 16 Aug. 1936 (S-PA). B. Epidermal cells. 1-2. Fish Lake, British Columbia, *Shaw* 1210 (US). 3-4. Yukon River, Alaska, *Palmer* 70 (US). C. Marginal laminar cells. Swiss Tyrol, *Langkoff*, *Macfarlane*, 9 Jul. 1906 (PH). D. Indusium. Yukon River, Alaska, *Palmer* 70 (US). E. Hairs. F. Pinna. Nome, Alaska, *Powers* 90 (US). G. Scale of rhizome. Jamtland, Switzerland, *Osterlind*, 30 Jul. 1935 (US). The scale of each drawing is indicated on Plate 3.

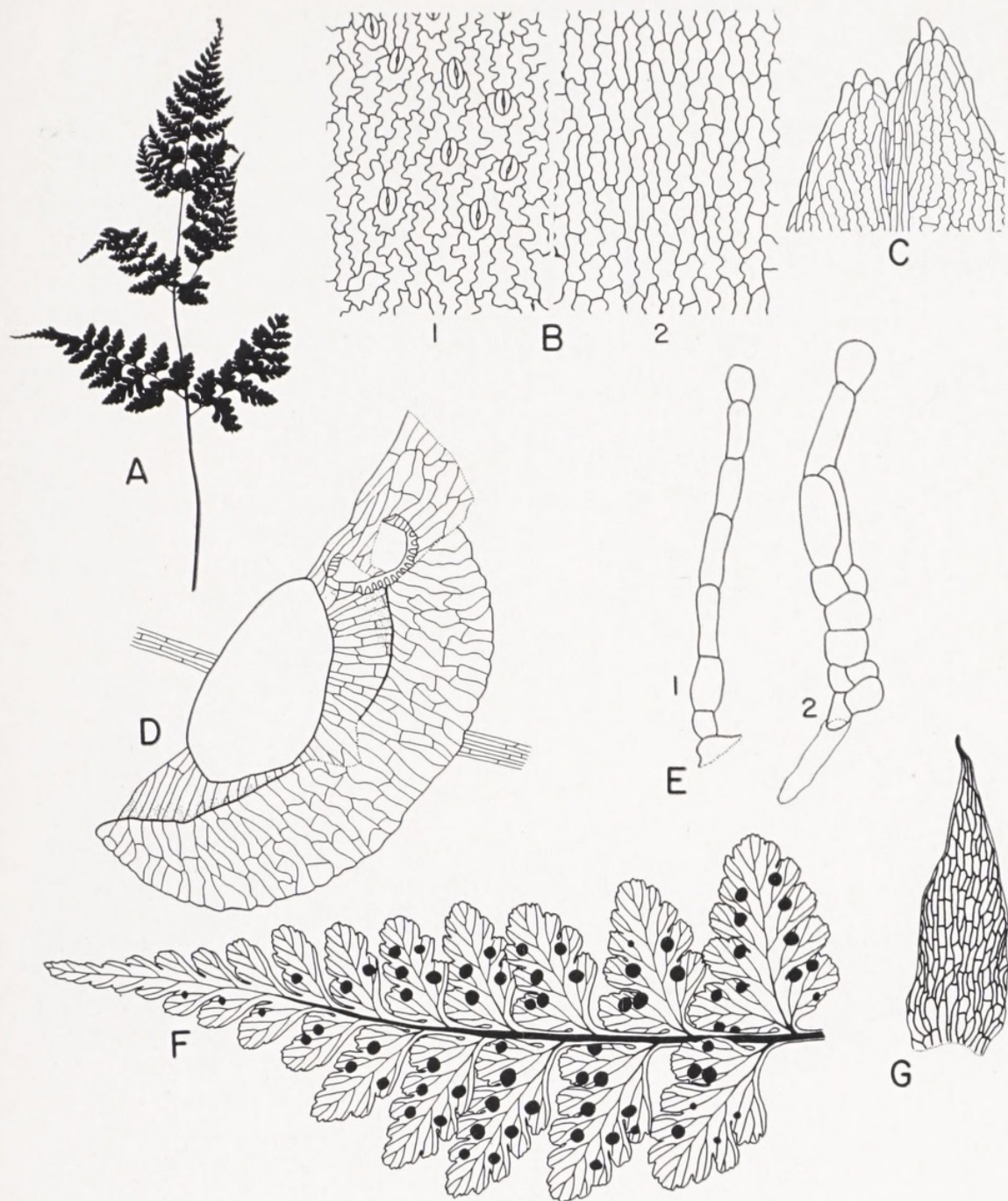


PLATE 6

CYSTOPTERIS PELLUCIDA (FRANCH.) CHING

Fig. A. Silhouette of blade. Yunnan, *Ducloux*, 29 Aug. 1909 (P). B. Epidermal cells. Yunnan, *Ducloux*, 29 Aug. 1909 (P). C. Marginal laminar cells. Yunnan, China, *Delavay*, n.d. (P). D. Indusium. Yunnan, China, *Ducloux*, 29 Aug. 1909 (P). E. Hairs. F. Pinna. Yunnan, China, *Ducloux*, 29 Aug. 1909 (P). G. Scale of rhizome. Yunnan, China, *Delavay*, n.d. (P). The scale of each drawing is indicated on Plate 3.

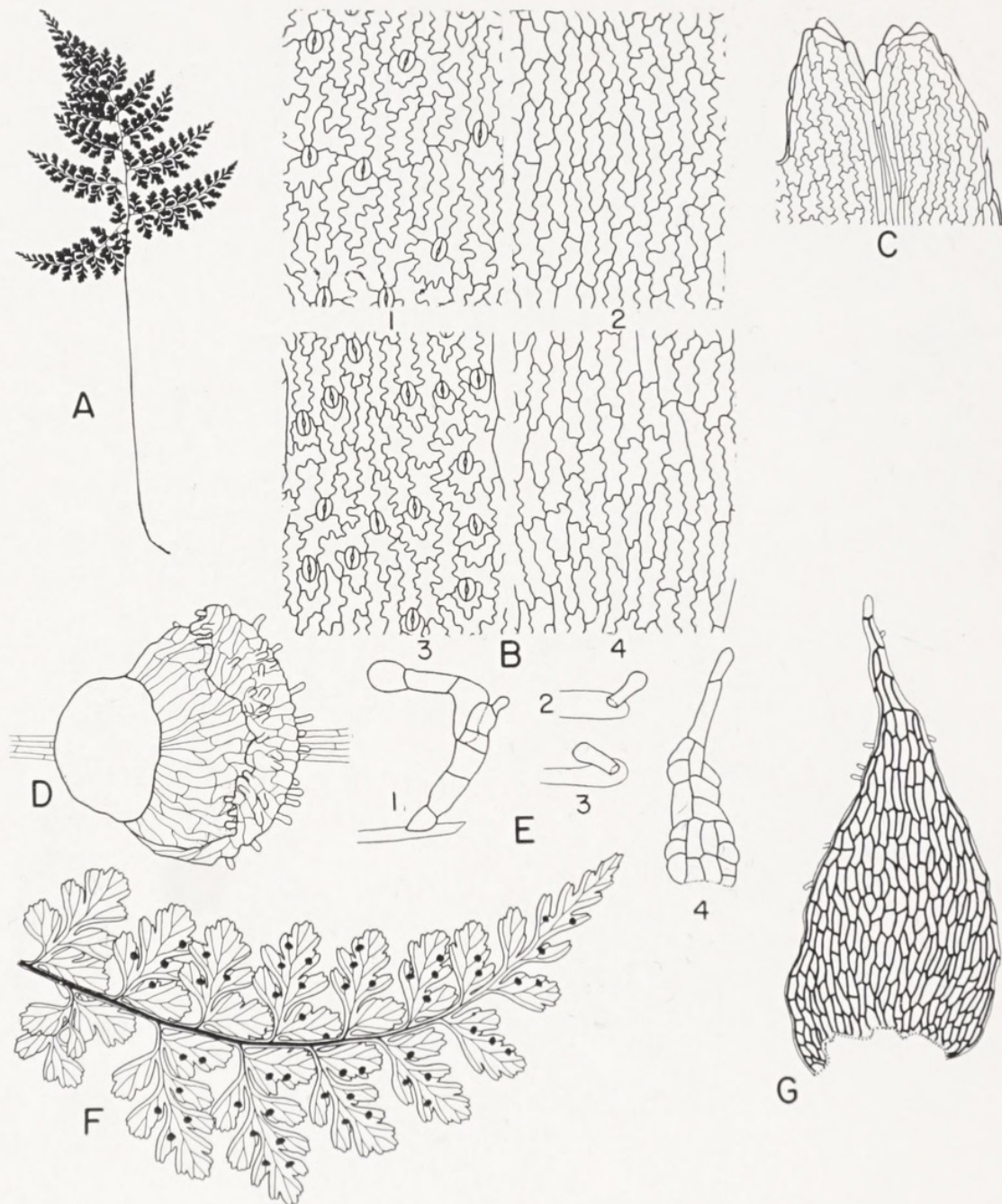


PLATE 7

CYSTOPTERIS SUDETICA A. BR. ET MILDE

Fig. A. Silhouette of blade. Gomor, Hungary, *Richter*, 12 Aug. 1900 (S-PA). B. Epidermal cells. 1-2. *C. sudetica* var. *sudetica*, Moravia, Czechoslovakia, *Laus*, Aug. 1935 (S-PA). 3-4. *C. sudetica* var. *moupinensis*, Szechuan, China, *Smith* 4227 (S-PA). C. Marginal laminar cells. Silesia, Poland, *Laus*, 7 Jul. 1933 (S-PA). D. Indusium. Transylvania, Romania, *Pop*, 29 Aug. 1935 (S-PA). E. Hairs. F. Pinna. Pinninenpass, Hungary, *Ullepitsch*, 20 Jun. 1890 (S-PA). G. Scale of rhizome. Szepes, Hungary, *Gyorffy*, Jul. 1907 (US). The scale of each drawing is indicated on Plate 3.

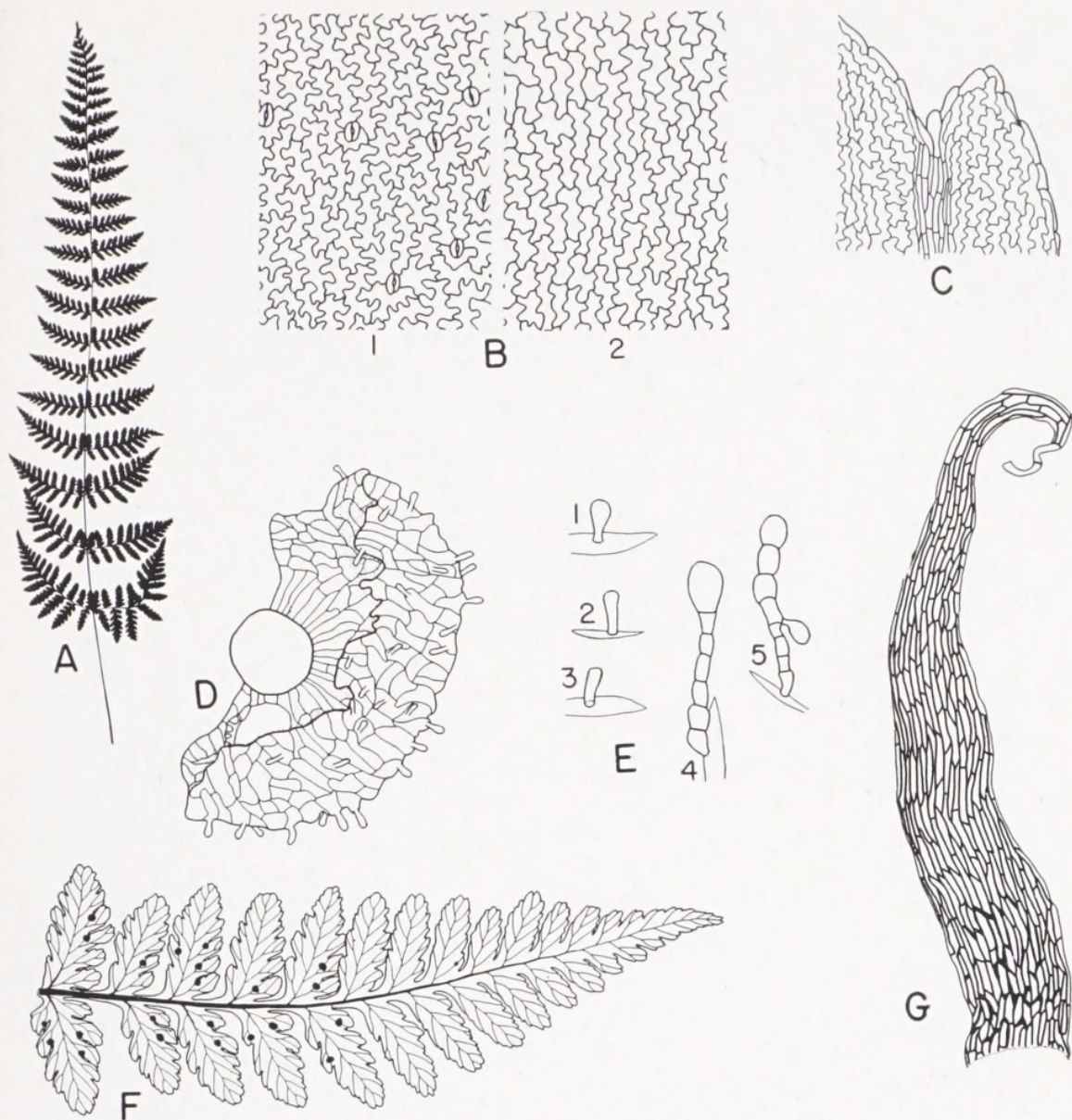


PLATE 8

CYSTOPTERIS BULBIFERA (L.) BERNH.

Fig. A. Silhouette of blade. Becks Woods, near Plymouth, Michigan, *Blasdel*, 18 Jul. 1958 (MICH). B. Epidermal cells. Grand Ledge, Michigan, *Wagner* 8078 (MICH). C. Marginal laminar cells. Oka, Quebec, *Adrien* 1273 (PH). D. Indusium. Ephraim, Wisconsin, *Millsbaugh* 3954 (US). E. Hairs. F. Pinna. Grand Ledge, Michigan, *Wagner* 8078 (MICH). G. Scale of rhizome. Grand Ledge, Michigan, *Wagner* 8078 (MICH). The scale of each drawing is indicated on Plate 3.

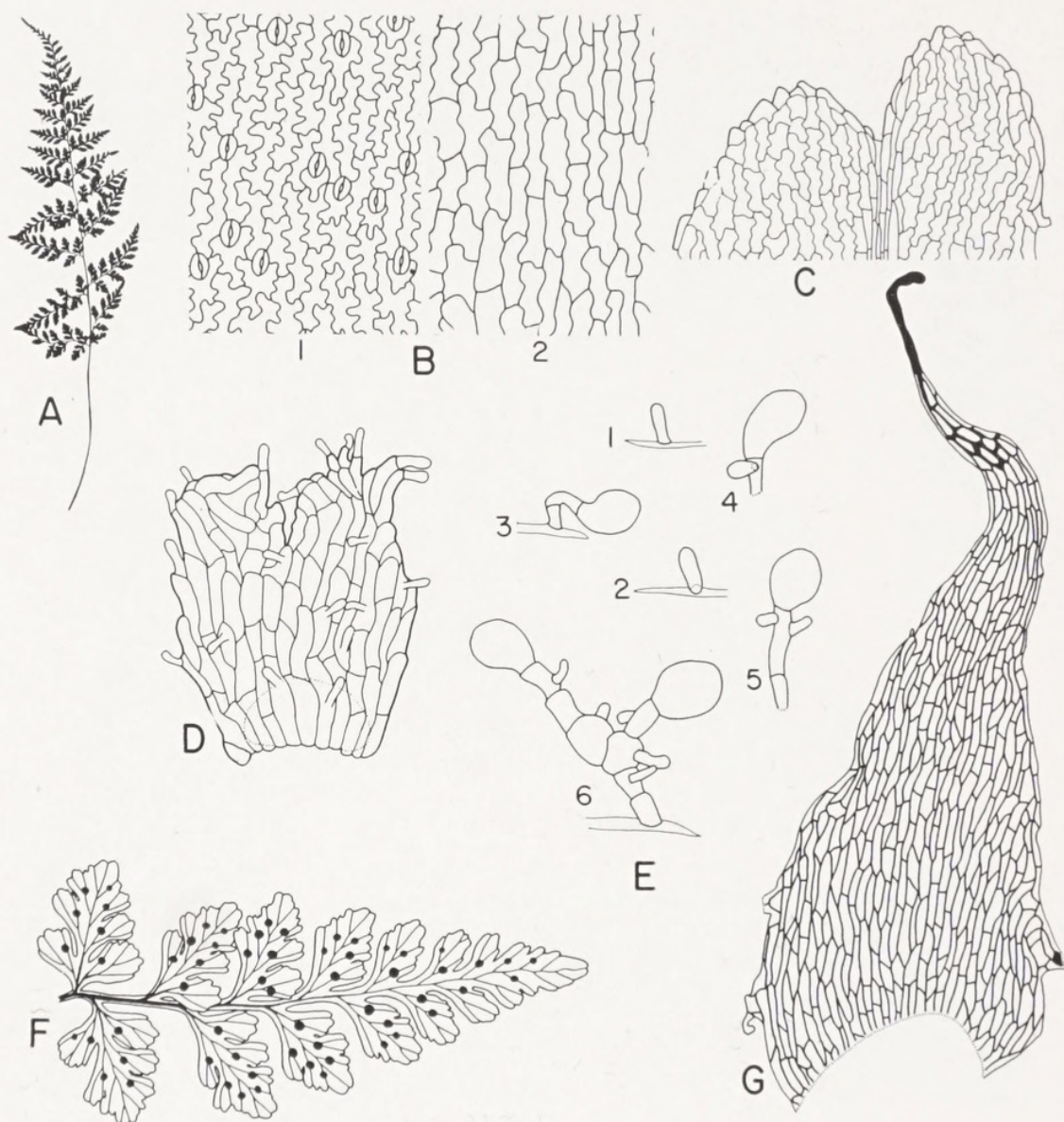


PLATE 9

CYSTOPTERIS DIAPHANA (BORY) BLASDELL

Fig. A. Silhouette of blade. Peru, *Bues* 1004 (US). B. Epidermal cells. Peru, *Bues* 1004 (US). C. Marginal laminar cells. Peru, *Bues* 1004 (US). D. Indusium. Chile, *Joseph* 5591 (US). E. Hairs. F. Pinna. Peru, *Bues* 1004 (US). G. Scale of rhizome. Tucuman, Argentina, *Venturi* 6086 (US). The scale of each drawing is indicated on Plate 3.

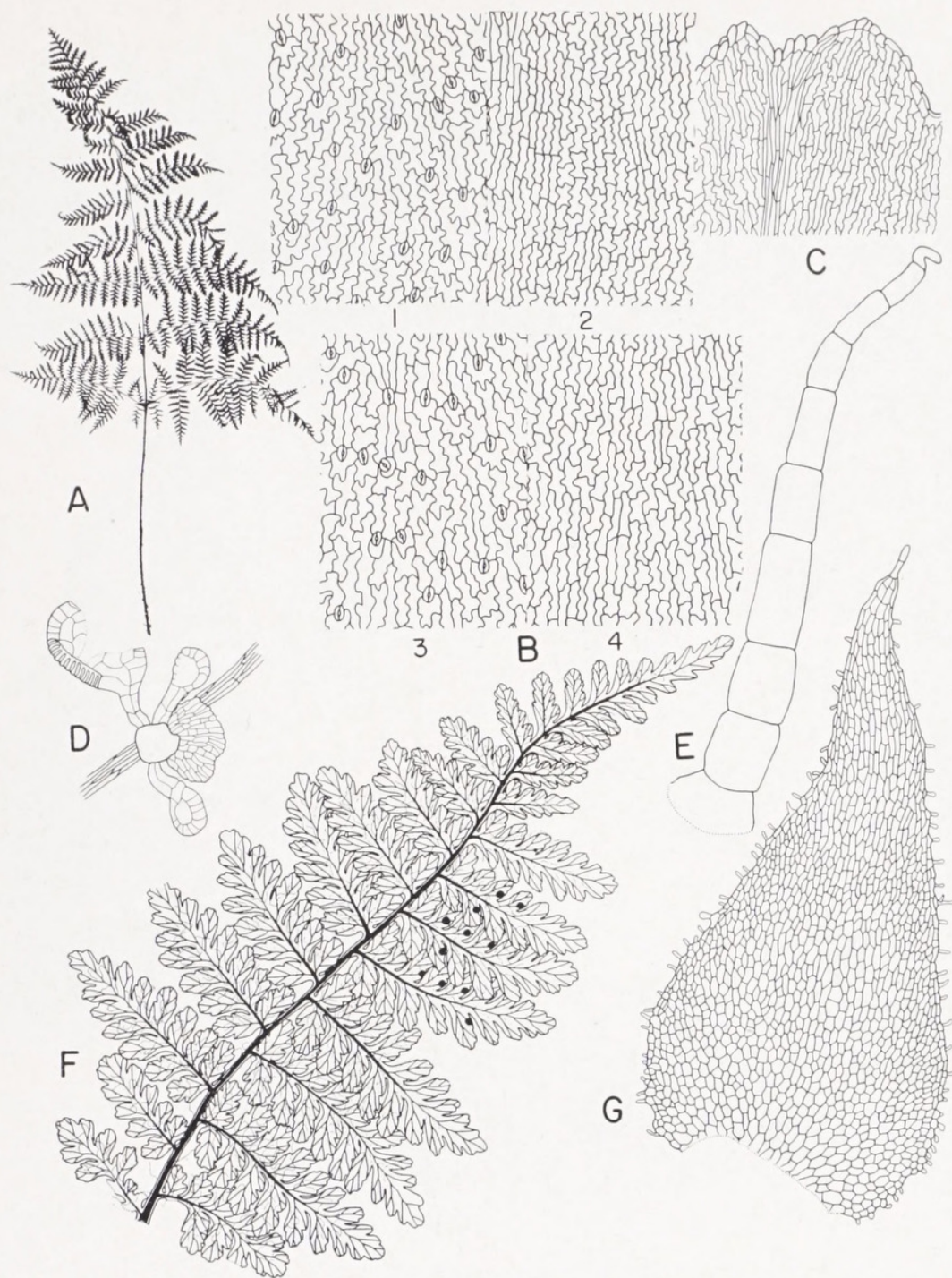


PLATE 10

CYSTOPTERIS JAPONICA LSSN.

Fig. A. Silhouette of blade. Honshu, Japan, *Kurata*, 28 Nov. 1956. B. Epidermal cells. 1-2. Plant with $2n$ spores. Shikoku, Japan, *Uno* 2611 (US). 3-4. Plant with larger spores. Shikoku, Japan, *n.c.* 11 Jul. 1892 (US). C. Marginal laminar cells. Shikoku, Japan, *n.c.* 11 Jul. 1892 (US). D. Indusium. Shikoku, Japan, *Uno* 2611 (US). E. Multicellular non-glandular hair. F. Pinna. Honshu, Japan, *Kurata*, 28 Nov. 1956. G. Scale from stipe base of young frond. Honshu, Japan, *Kurata*, 28 Nov. 1956. The scale of each drawing is indicated on Plate 3.

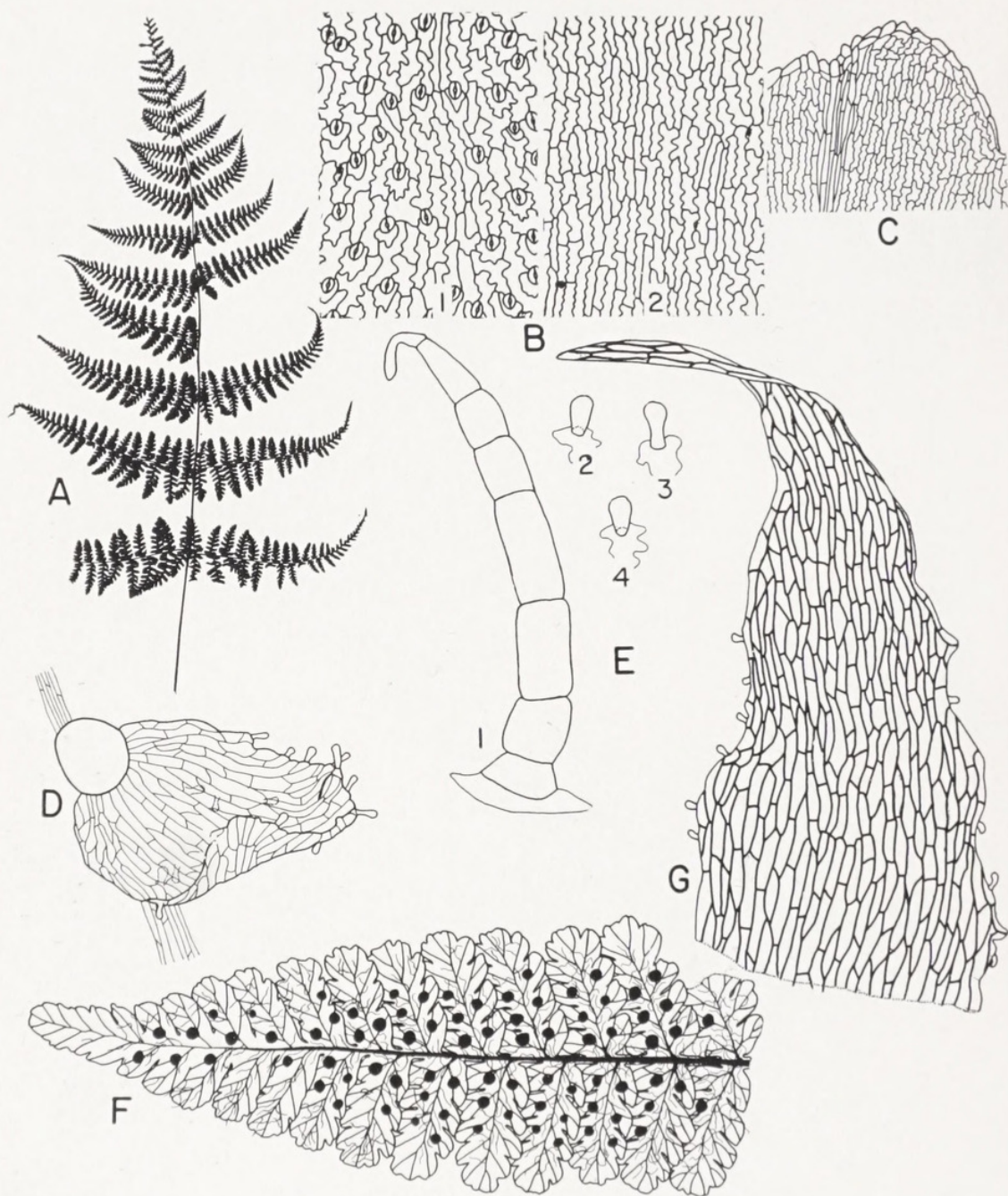


PLATE 11

CYSTOPTERIS TENUISECTA (BL.) METT.

Fig. A. Silhouette of blade. Yunnan, China, *Henry* 11539A (US). B. Epidermal cells. Pahang, Malaya, *Holttum*, 10 May 1936 (US). C. Marginal laminar cells. Assam, *Mann*, Jul. 1890 (S-PA). D. Indusium. Yunnan, China, *Henry* 11539A (US). E. Hairs. 1. Multicellular non-glandular hair. 2-4. Unicellular glandular hairs. F. Pinna. Assam, *Mann*, Jul. 1890 (S-PA). G. Scale of rhizome. Assam, *Mann*, Jul. 1890 (S-PA). The scale of each drawing is indicated on Plate 3.

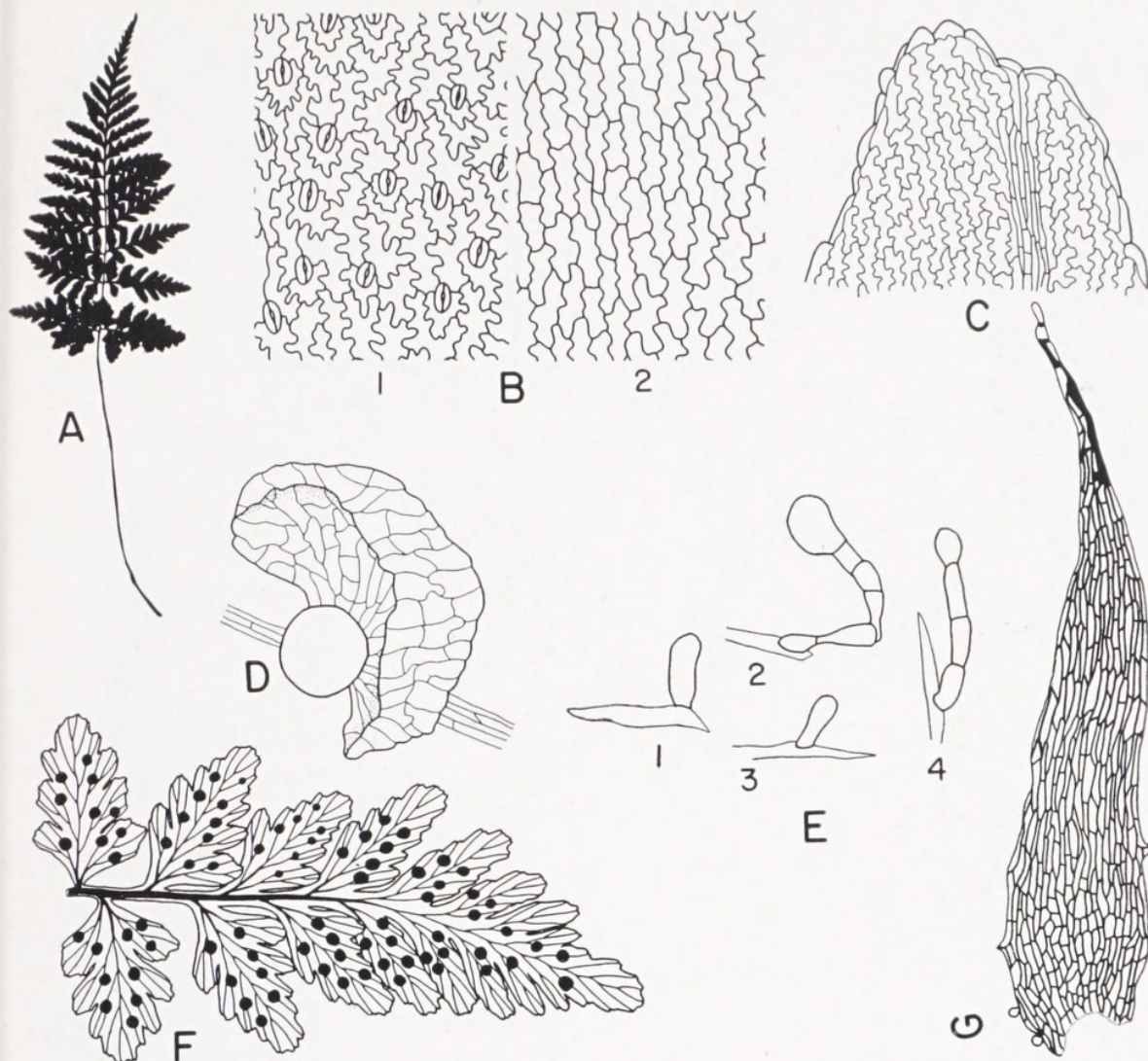


PLATE 12

CYSTOPTERIS X TENNESSEENSIS SHAVER

Fig. A. Silhouette of blade. Marshall Co., Tennessee, *Shaver* 10460 (US). B. Epidermal cells. Martin's Bluff, Arkansas, *McGregor* 3722 (US). C. Marginal laminar cells. Johnson Co., Kansas, *McGregor* 4389 (US). D. Indusium. Livingston, Tennessee, *Shaver* 10553 (TENN). E. Hairs. F. Pinna. *McGregor* 3722. G. Scale of rhizome. Neodesha, Kansas, *McGregor* 3404 (US). The scale of each drawing is indicated on Plate 3.

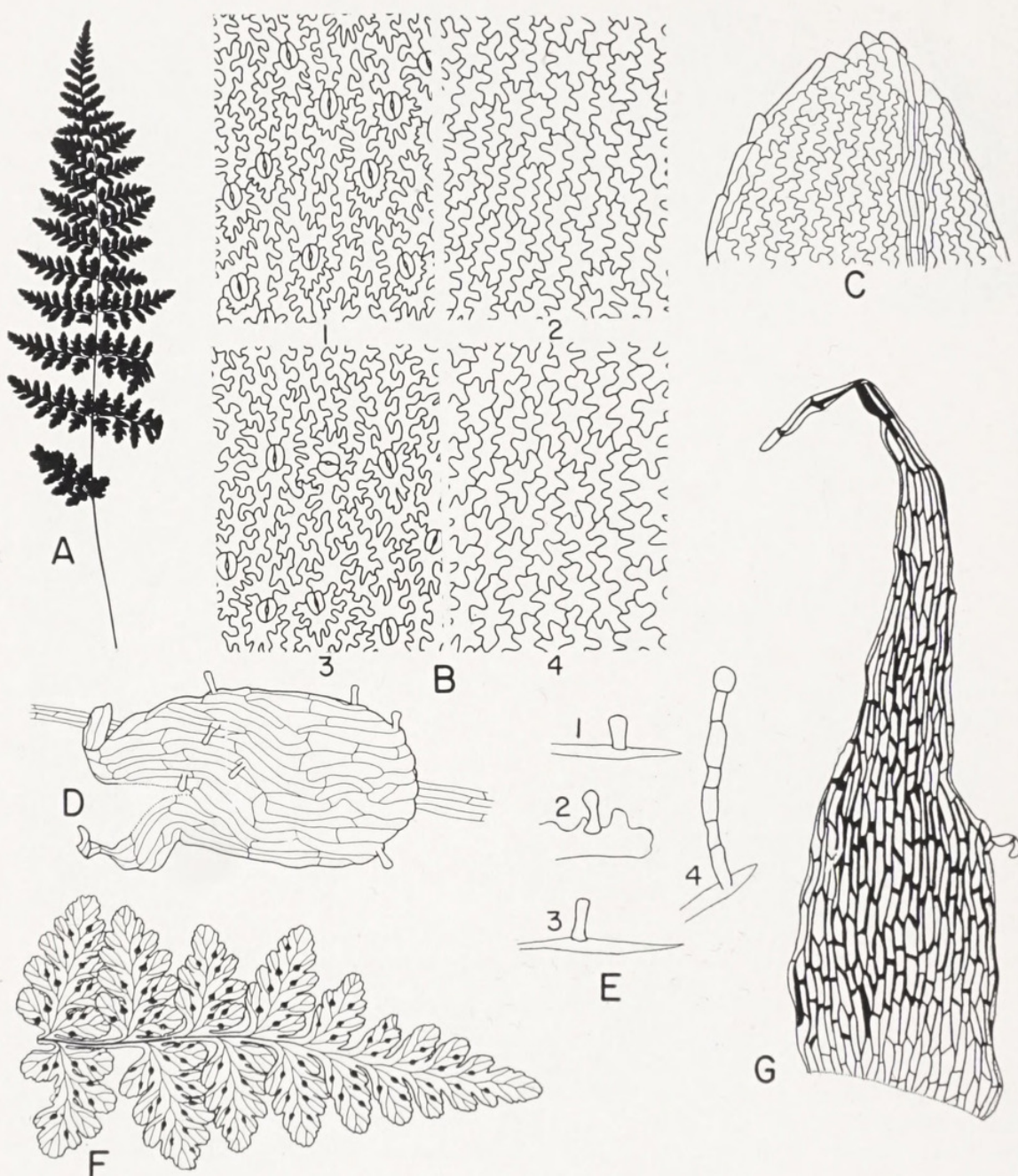


PLATE 13

CYSTOPTERIS X LAURENTIANA (WEATH.) BLASDELL.

Fig. A. Silhouette of blade. Amnicon Falls, Wisconsin, Tryon 4874 (US). B. Epidermal cells. Fayette, Michigan, Hagenah, 19 Jul. 1954 (MICH). 1-2. Plant with normal spores. 3-4. Plant with aborted spores and possibly a backcross to *Cystopteris fragilis*. C. Marginal laminar cells. Lake Co., Minnesota, Tryon & Faber 4896 (US). D. Indusium. Bic, Quebec, Rousseau 26549 (US). E. Hairs. F. Pinna. Bruce Peninsula, Ontario, Taylor 6129 (US). G. Scale of rhizome. Taylor 6129. The scale of each drawing is indicated on Plate 3.

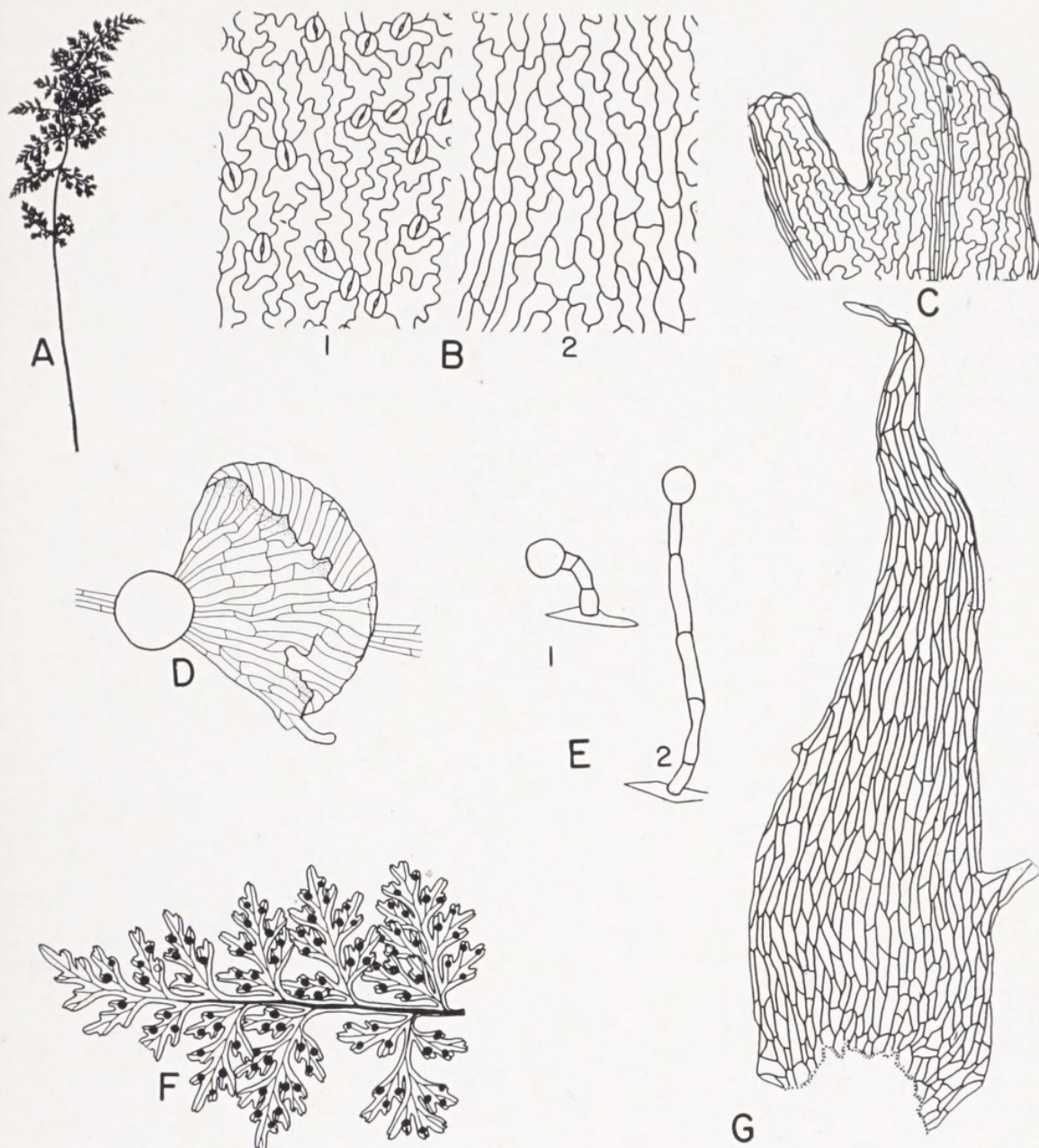


PLATE 14

CYSTOPTERIS X ALPINA (WULFEN) DESV.

Fig. A. Silhouette of blade. Bavarian Alps, Germany, *Shultes* (L). B. Epidermal cells. Carinth, Switzerland, *Suringar*, 1865 (L). C. Marginal laminar cells, *Suringar*, 1865. D. Indusium. *Savoie*, Switzerland (L). E. Hairs. F. Pinna. *Suringar*, 1865. G. Scale of rhizome. Savoy, France, *Bourgeau*, 27 Jul. 1873 (L). The scale of each drawing is indicated on Plate 3.

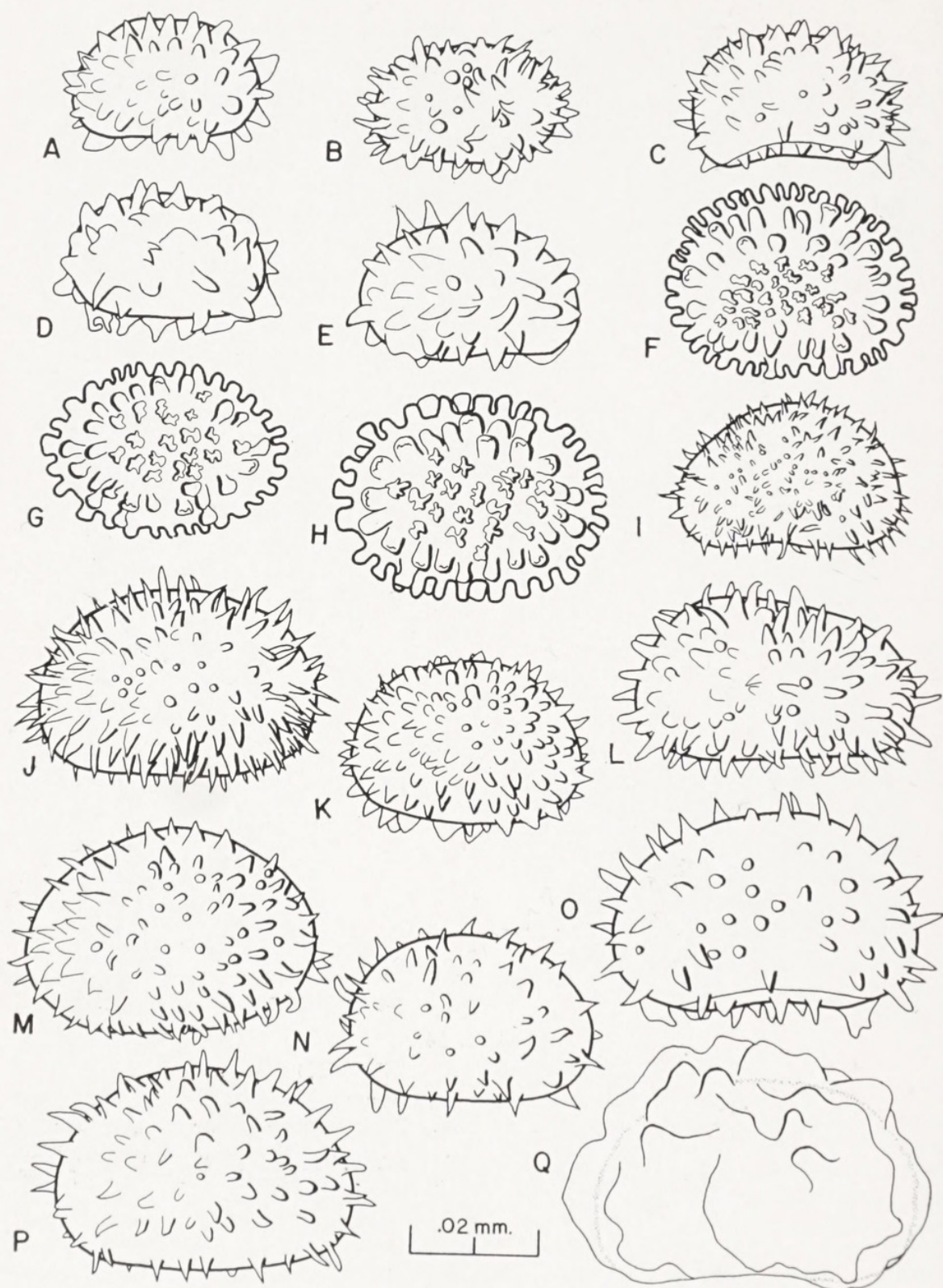


PLATE 15
SPORES IN CYSTOPTERIS

Fig. A. *C. bulbifera*. B. *C. protrusa*. C. *C. sudetica*. D, E. *C. montana*. F. *C. tenuisecta*. G, H. *C. japonica*. I, J. *C. diaphana*. K. *C. X tennesseensis*. L, M. *C. X laurentiana*. N, P. *C. fragilis*. O. *C. douglasii*. Q. *C. fragilis* (rugose spore).

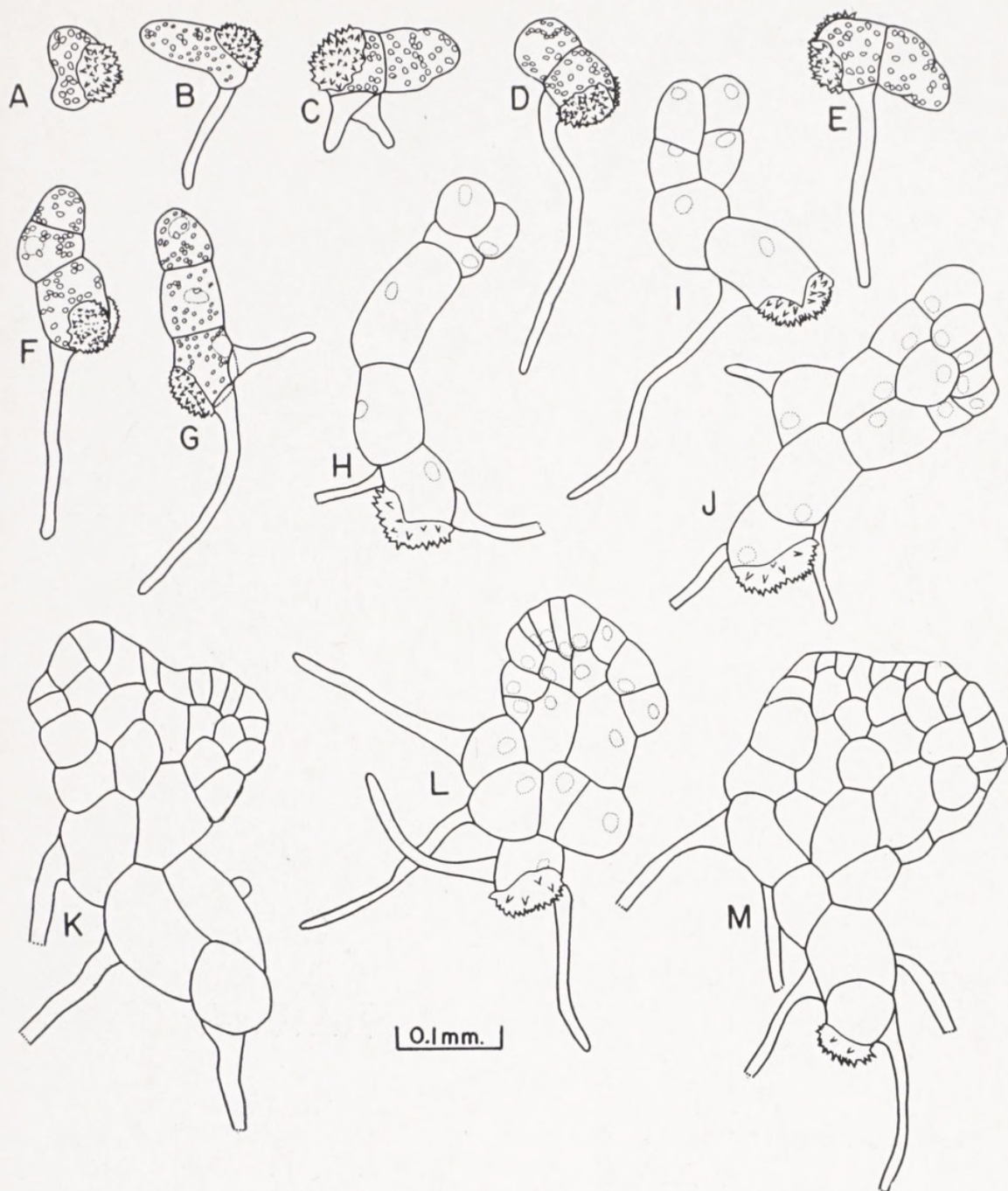


PLATE 16

GAMETOPHYTE DEVELOPMENT IN *CYSTOPTERIS*

Gametophytes of *C. douglasii*. Fig. A-G. Filamentous stage. H-M. Cell plate stage.

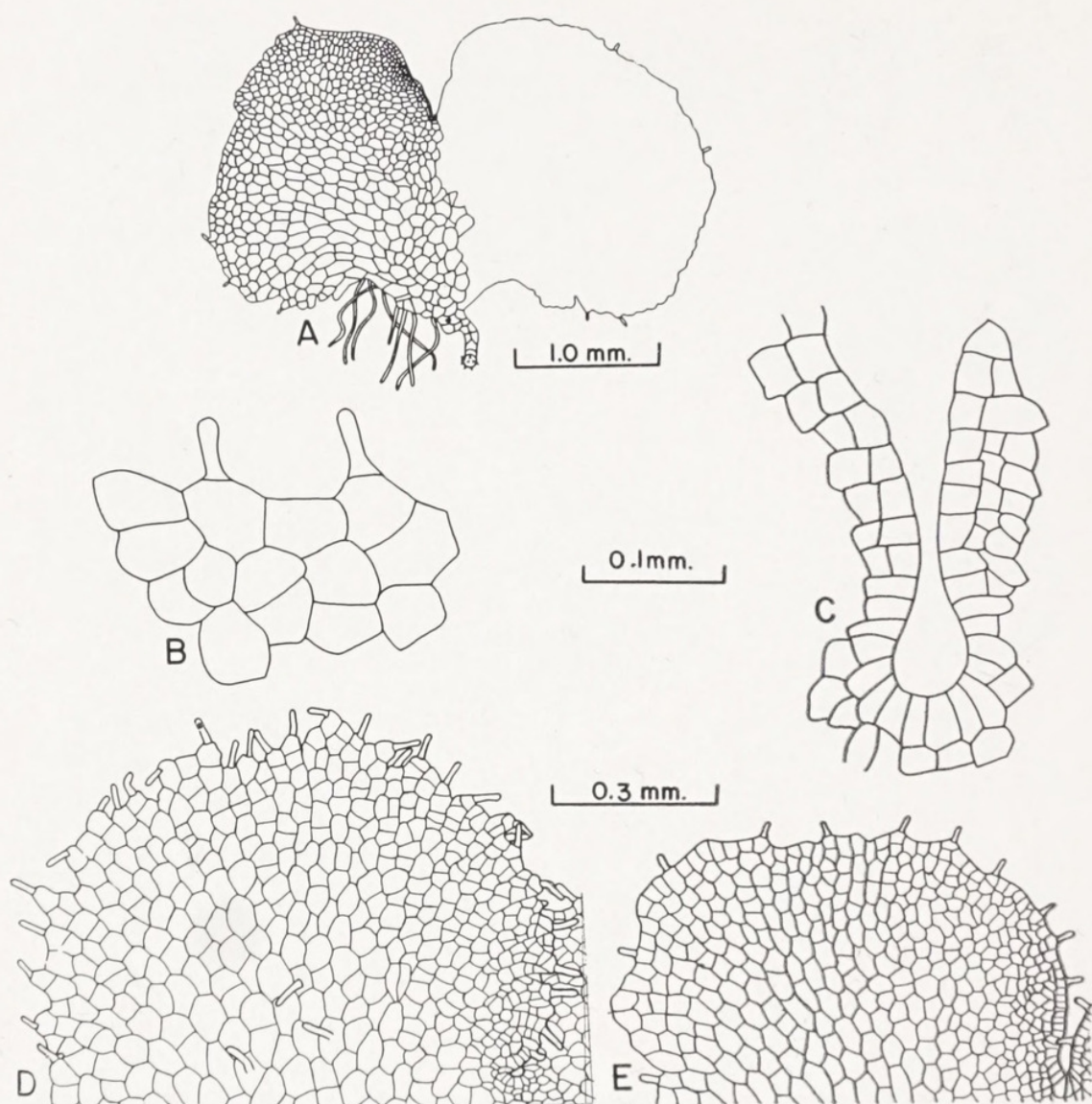


PLATE 17

MATURE GAMETOPHYTE IN *CYSTOPTERIS*

Fig. A. Gametophyte of *C. douglasii*. B. Detail of marginal cells and glands. *C. douglasii*. C. Detail of gametophyte notch. *C. douglasii*. D. Lobe of *C. diaphana* gametophyte showing irregular margin and long glands. E. Lobe of *C. fragilis* gametophyte showing smooth margin and shorter glands.

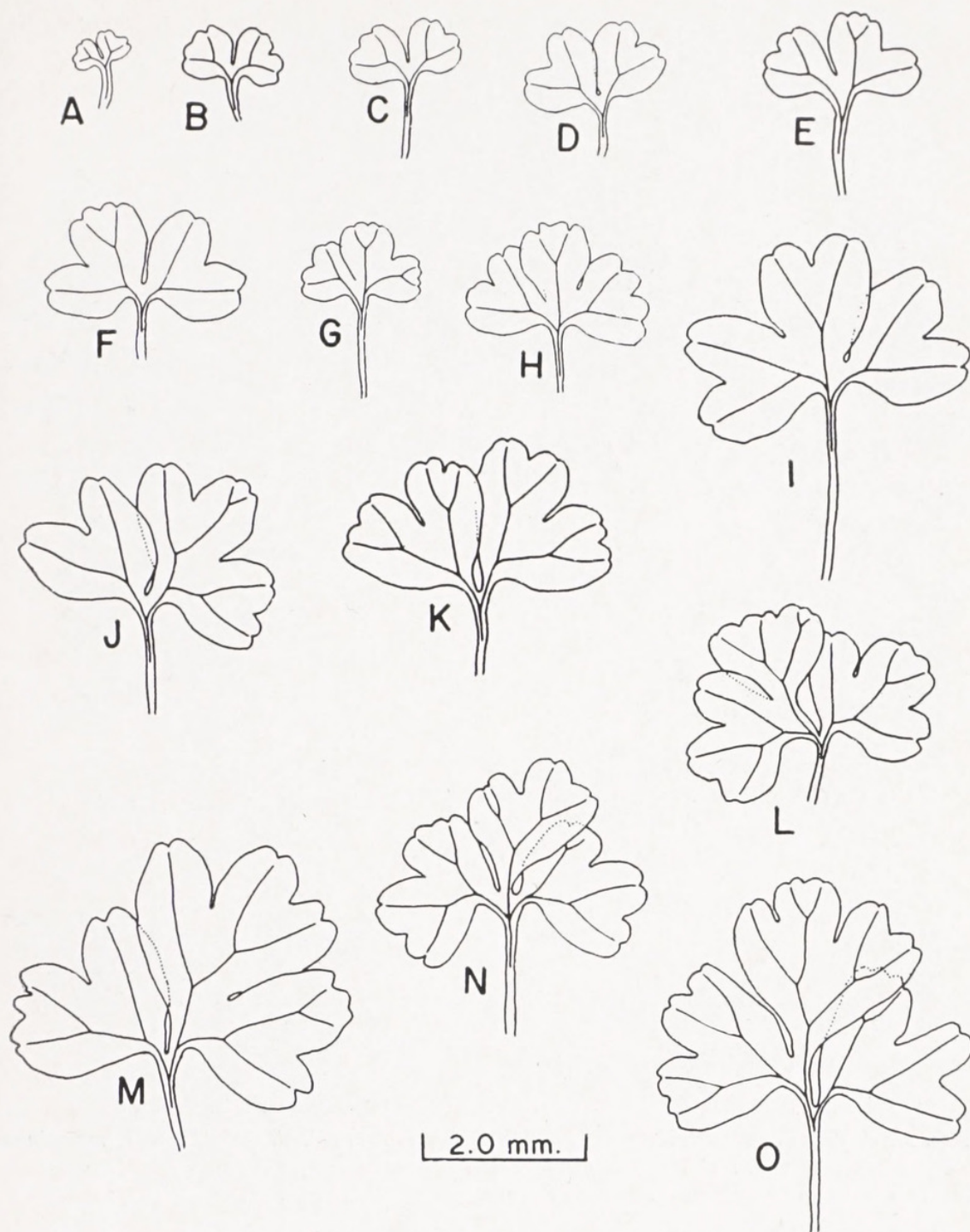


PLATE 18

HETEROBLASTIC SERIES OF SPOROPHYTE LEAVES IN *CYSTOPTERIS*Fig. A-O. Leaves of young sporophyte of *C. bulbifera*.

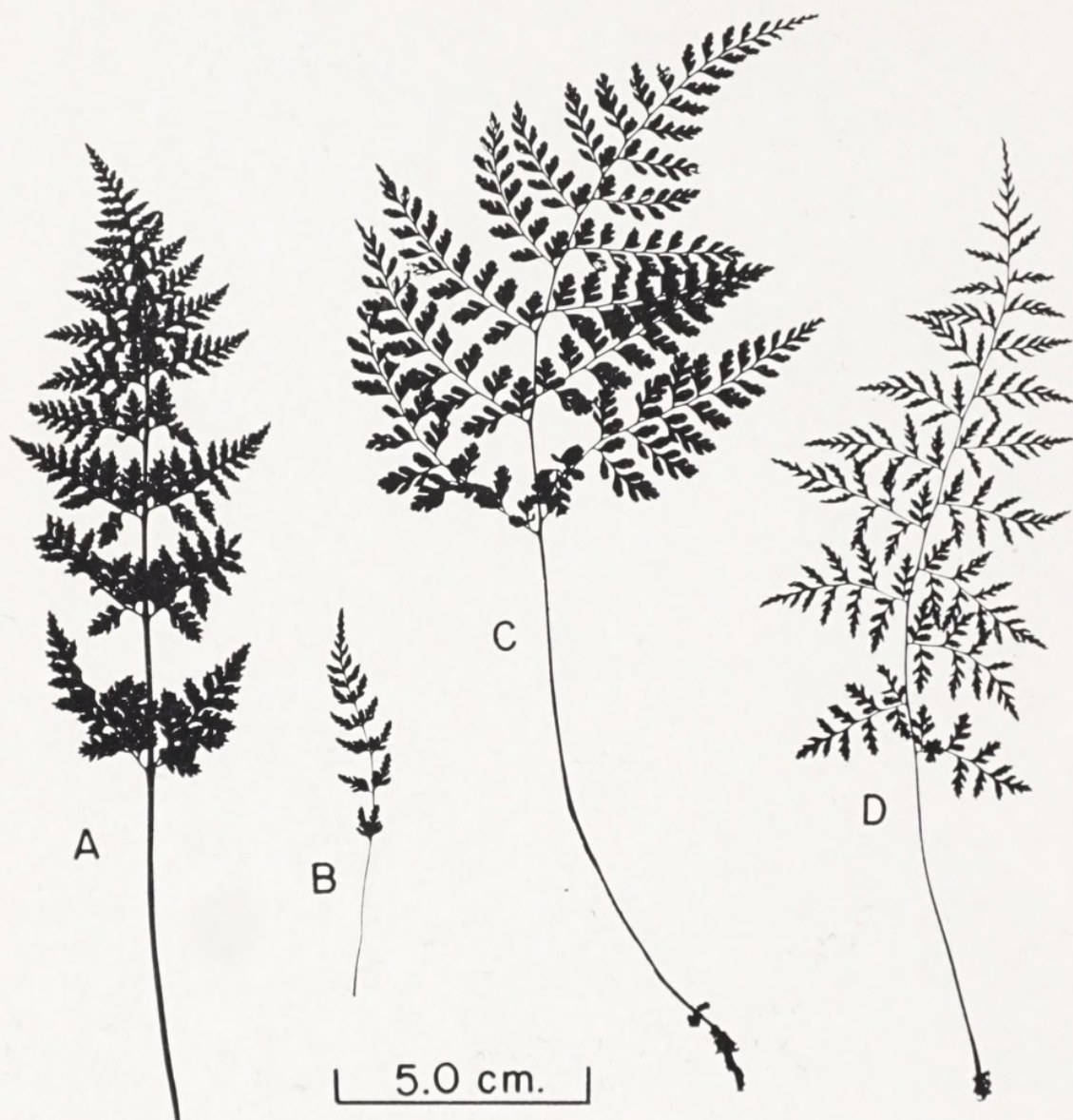


PLATE 19

SILHOUETTES OF MISCELLANEOUS *CYSTOPTERIS* TAXA

Fig. A. *C. fragilis* var. *apiiformis*. B. *C. x kansuana*. C. *C. sudetica* var. *moupinensis*. D. *C. fragilis* var. *huteri*.

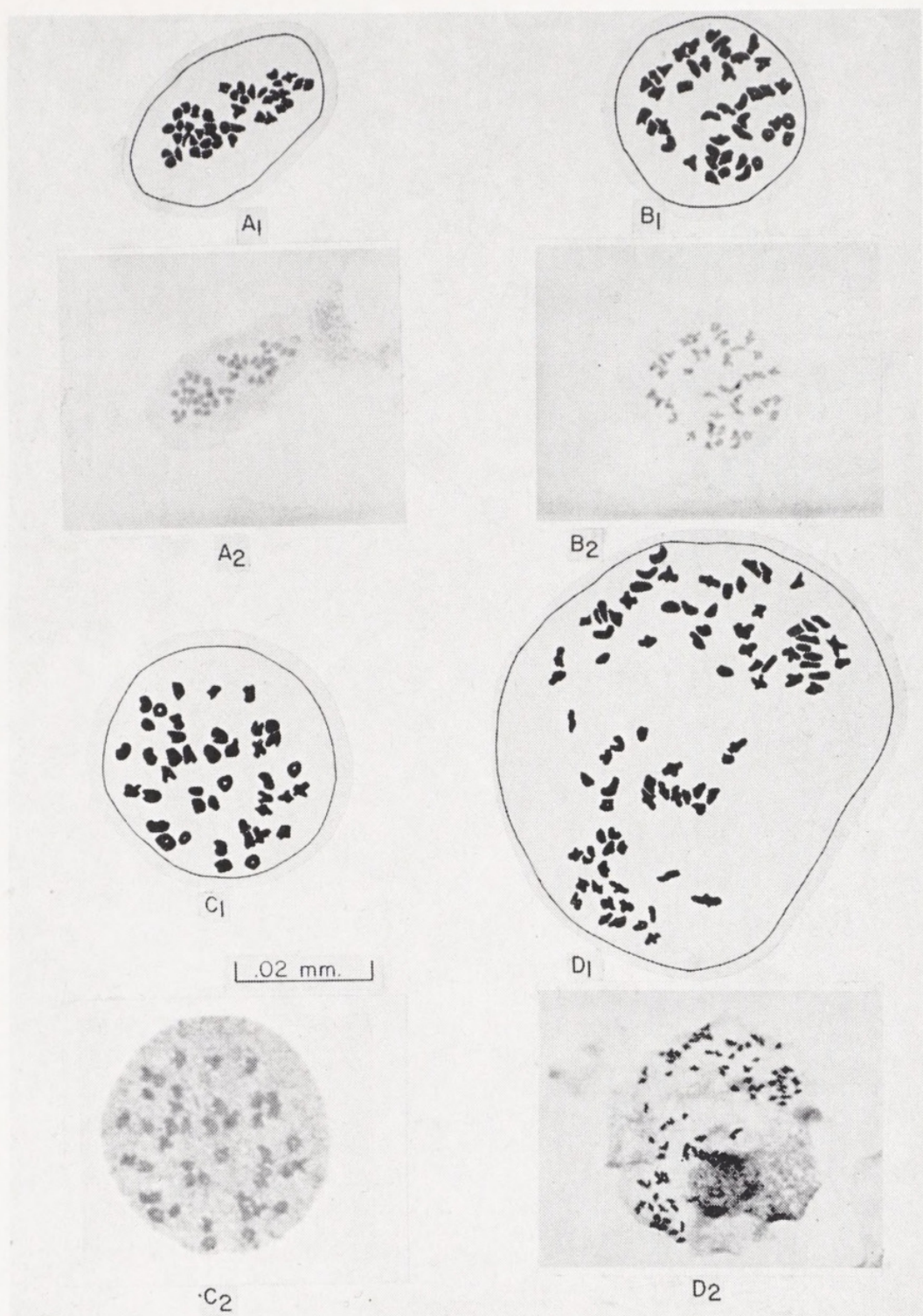


PLATE 20

CYTOLOGICAL SQUASHES IN *CYSTOPTERIS*

Fig. A. 1-2. *C. diaphana* X *protrusa* (Gold Hill, New Mexico, *Castetter* 9596. MICH.) $n = 42$. B. 1-2. *C. protrusa* (Elkmont, Tennessee, *Vannorsdall*, 30 Apr. 1956. MICH). $n = 42$. C. 1-2. *C. diaphana* (Santiago, Chile, *Valenzuela et Vergara*, 13 Oct. 1956. MICH). $n = 42$. D. 1-2. *C. fragilis* (Argentina, Provincia Neuguen, Parque Nacional de Nahual-Huapi, Peninsula Quetrihué, *Diem*, Aug. 1956. MICH). $n = 84$.

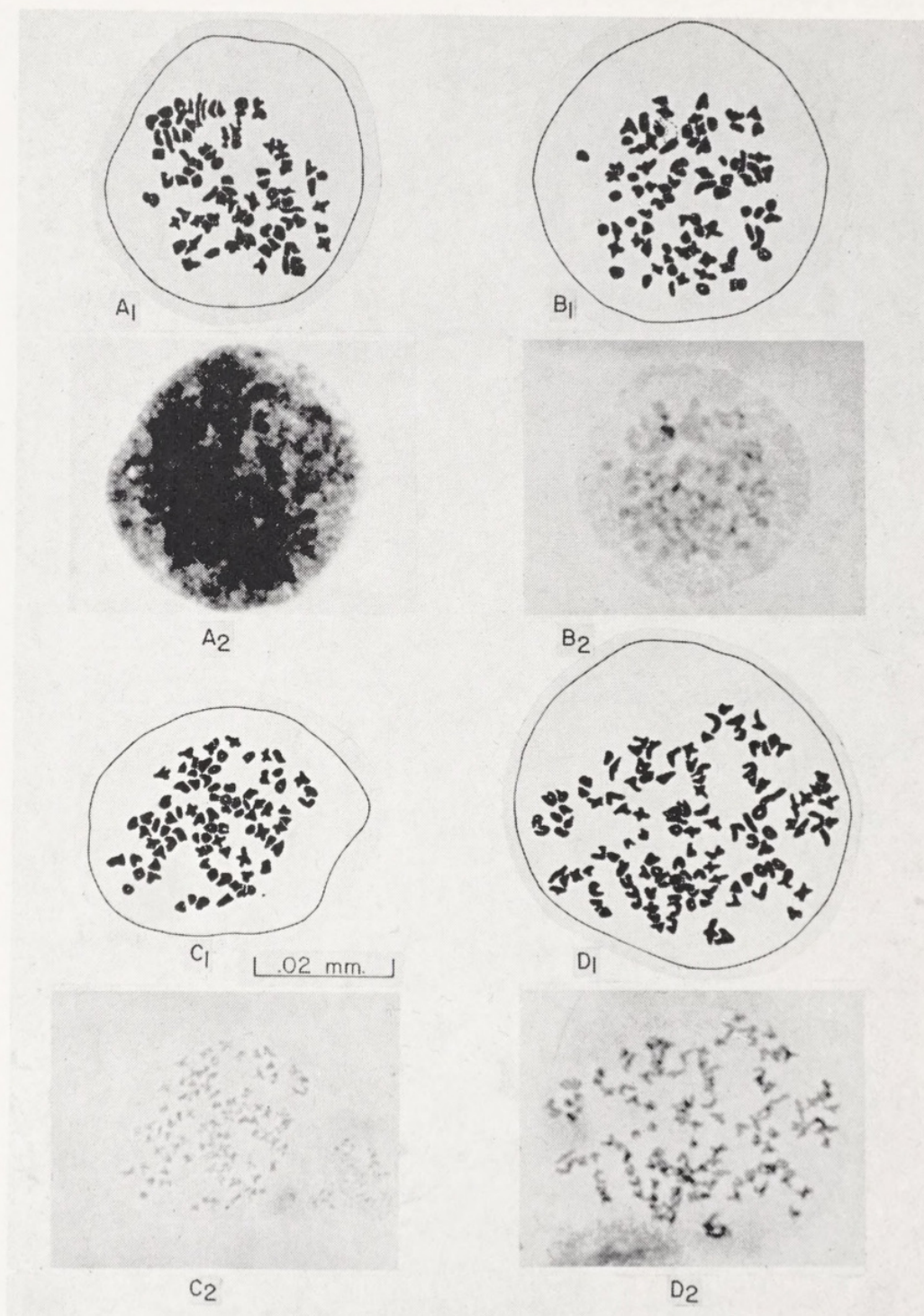


PLATE 21

CYTOLOGICAL SQUASHES IN *CYSTOPTERIS*

Fig. A. 1, 2. *C. fragilis* (Germany, *Merxmüller*, MICH). $n = 84$. B. 1, 2. *C. fragilis* (Yates Center, Woodson Co., Kansas, *McGregor*, MICH). $n = 84$. C. 1, 2. *C. X tennesseensis* (Clear Creek, Fairfield Co., Ohio. *Blasdell* 230 MICH). $n = 84$. D. 1, 2. *C. X laurentiana* (Ishpeming, Michigan, *Blasdell* 194 MICH). $n = 126$.

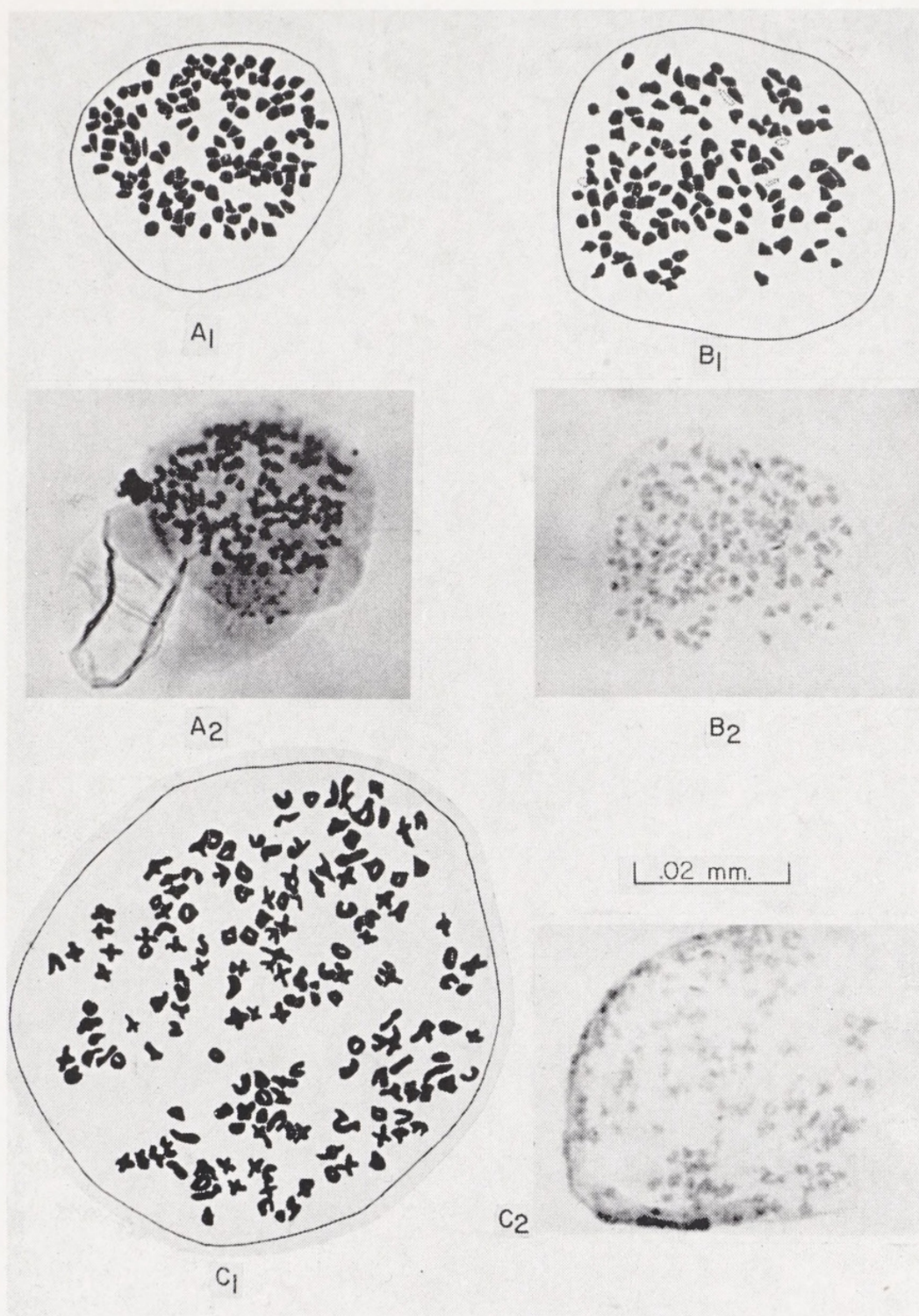


PLATE 22

CYTOLOGICAL SQUASHES IN *CYSTOPTERIS*

Fig. A. 1, 2. *C. fragilis* (Italy, Ehrendorfer. MICH). $n = \text{ca. } 126$. B. 1, 2. *C. diaphana* (Costa Rica, Leon, MICH). $n = 126$. C. 1, 2. *C. douglasii* (Mauna Kea, Hawaii, Horner. MICH). $n = \text{ca. } 168$.

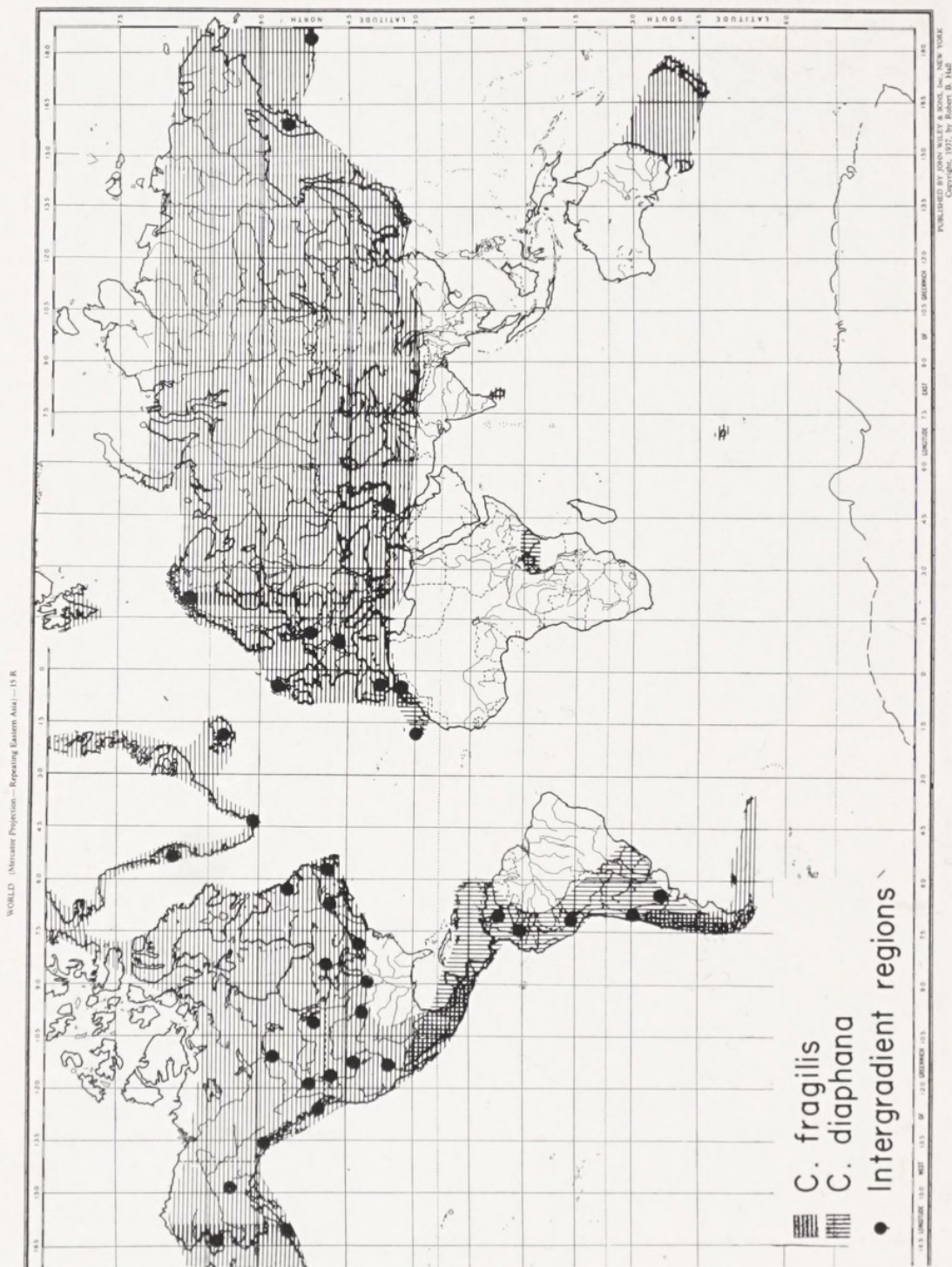


PLATE 23
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