

AN INVESTIGATION OF THE TAXONOMY
OF CHEILANTHES EATONII, C. EATONII
FORMA CASTANEA, AND C. TOMENTOSA

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ABSTRACT

AN INVESTIGATION OF THE TAXONOMY OF CHEILANTHES EATONII, C. EATONII FORMA CASTANEA, AND C. TOMENTOSA

by Julie Hitt

Three xerophytic ferns, Cheilanthes eatonii, C. eatonii f. castanea, and C. tomentosa have many similar characteristics and appear to be closely related. These three taxa were studied primarily by morphological comparison in an attempt to determine their proper taxonomic rank.

Spores from living plants were sterilized and sown both on a mineral salt agar medium and soil for gametophytic study. Spores from living plants and herbarium specimens were acetylated for detailed study. Measurements of the following characters were recorded:

- 1) spore diameter in the equatorial plane
- 2) length of the blade and stipe
- 3) width of the blade
- 4) length and width of the cells of the upper and lower leaf epidermal surfaces
- 5) length and width of the stomates
- 6) length and width of the rhizome, stipe, rachis, and pinna midrib scales

The indusium and sporangium of each taxon were generally compared.

Cheilanthes tomentosa is distinguished from the other two taxa by these characters:

- 1) longer and narrower stipe, rachis, and pinna midrib scales
- 2) longer and broader fronds
- 3) greater blade-length:stipe-length ratio

The scales of C. eatonii and C. eatonii f. castanea have a broad base and gradually taper toward the tip with those of C. eatonii being broader at the base than those of C. eatonii f. castanea. Their frond measurements and blade-length:stipe-length ratio are similar. All three taxa were found to be triploid apogamous hybrids.

Based on constant morphological characters, C. tomentosa and C. eatonii may be properly classified as species. Cheilanthes eatonii f. castanea is classified as a forma because of its close alliance to C. eatonii in morphological characters. These conclusions are also supported by cytological evidence.

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INTRODUCTION

The genus Cheilanthes was originally described by Swartz in 1806 and includes 130-200 species. The systematic position of this genus seems to be in a great state of confusion at present and the boundary of the genus varies according to the authority. This is evident when the position of the genus is compared in various systems of classification. Cheilanthes is usually placed in the Gymnogrammoid fern group of the family Polypodiaceae as designated by Bower (Vol. 3, 1928). The kinship of this group "is based partly on positive characters of external form and internal anatomy: partly upon the rather negative soral characters, and particularly upon the absence of a true indusium, with its corollary, an indefinite soral construction. They may be held to represent a plexus of phyletic lines all traceable back with probability to Ferns with marginal sporangia of larger size than theirs such as the present-day Osmundaceae and Schizaeaceae." More specifically Bower is referring to the advanced members Anemia and Mohria of the Schizaeaceae. The sporangia and vascular systems of the latter two genera are similar to those of Cheilanthes, and Mohria has dermal scales which are found in Cheilanthes and most other Gymnogrammoids. More specifically Cheilanthes is placed in the fourth section of this

group, which includes specialized xerophytic genera, such as Pellaea, Doryopteris, Cheilanthes, Notholaena, Saffordia, and Trachypteris. Bower (Vol, 3, 1928) makes it explicit that the derivation of the Cheilanthoid Ferns from the living Schizaeaceae is not clear-cut, but "the variety and cogency of the comparisons may be held as indicating a reasonable probability of its truth."

Copeland (1947) states that Cheilanthes has long been a "puzzling genus" and places it in the family Pteridaceae. The ancestors of this family may be found in the Schizaeaceae and may involve more than a single line of descent. Concerning Cheilanthes Copeland (1947) contends that the Schizaeaceae ancestry should be an alternate choice with a Dennstaedtioid origin as the other choice. The latter choice would be based on soral affinity found in Hypolepis, Pteris, and Cheilanthes--reflexed margins protecting the sori in all cases. In other words, Cheilanthes was derived from an indusiate ancestor according to this theory. Hypolepis is related to Dennstaedtia with a hispid stipe being common in primitive members of both genera. However, he does recognize that the generic affinities in the group are not well-defined.

Pichi-Sermolli (1957-1960) agrees with Copeland in the possible derivation of Cheilanthes from the Schizaeaceae. He states that "the Gymnogrammoid, Cheilanthoid, Adiantoid and Vittarioid ferns may be held to represent phyletic lines which branched off early from a common stock."

Holttum (1947) supports the possible Schizaeoid ancestry of Cheilanthes. He states: "Several authors have pointed out the resemblance of Cheilanthes and its allies to Mohria, a genus of the Schizaeaceae. Mohria is advanced, as compared with other Schizaeaceae, in having scales instead of hairs, and in its vascular structure. It has single sporangia at its vein-endings, with the margin of the lamina reflexed to cover them as in Cheilanthes. A remarkable primitive ally of Cheilanthes, the genus Sinopteris, also has single terminal sporangia; this may well be an indication of Schizaeoid affinity." Holttum (1947) places Cheilanthes in the subfamily Gymnogrammoideae in the family Adiantaceae, which also includes the subfamily Vittarioideae. He does not support a Pteroid derivation for the Cheilanthoid group, one of his main contentions being the difference in rachis shape. In the Pteroid group "the midribs of the leaflets are deeply grooved with raised edges, these edges being decurrent upon the edges of the groove of the rachis, which is interrupted to receive them." Such a rachis shape does not exist in the Cheilanthoid group.

Christensen (1938) places Cheilanthes in the family Polypodiaceae, subfamily Gymnogrammeoideae. He says the 27 genera in this subfamily "are of uncertain mutual relationship and probably representing more evolutionary lines, but most of them no doubt related to the Pteridoideae, with which they were associated by most authors." Cheilanthes is placed

in the tribe Cheilantheae about which he says: "The 8 genera of this tribe (Adiantopsis, Cheilanthes, Notholaena, Sinopteris, Pellaea, Doryopteris, Saffordia, and Cheilanthopsis) run confusingly together and the classification of the species is quite uncertain."

Diels (1902) also places Cheilanthes in a Pteroid series in Engler and Prantl's classification. In addition, Ching (1940) places Cheilanthes in the family Sinopteridaceae, a Pteroid-Gymnogrammeoid series derivative. This series includes the families Hypolepidaceae, Pteridaceae, Sinopteridaceae, Gymnogrammaceae, Adiantaceae, and Ceratopteridaceae in a direct linear order of derivation.

In addition to the question of the ancestry and classification of Cheilanthes, the specific as well as the generic affinities of the Cheilanthoid group are not well defined as Christensen (1938) and Copeland (1947), among others, have mentioned. The purpose of this research is to study several taxa of Cheilanthes which appear to be closely related in an attempt to determine the correct level of taxonomic classification.

Cheilanthes tomentosa Link and C. eatonii Baker, ex Hook. & Bak. from investigation appear to be two separate species, but C. eatonii Baker f. castanea (Maxon) Correll is a problematical taxon which has been classified both as a species and as a form of C. eatonii. As is evident from an examination of the original descriptions below, these three

taxa have many characteristics in common and are separated only by minute differences.

Cheilanthes tomentosa Link (Link, 1833--English translation by C. V. Morton)

Frond tripinnatifid, the stipes tomentose and scaly-pilose, the pinnae thinly tomentose above and densely tomentose beneath, the crenations minute.

We accept the name Cheilanthes tomentosa for a fern specimen grown from seeds (spores) from Mexico. Fronds 6-8 inches long; stipes and rachis pale green, with a thin tomentum, the hairs flattened and thus scalelike; pinnae scarcely an inch long, triangular in outline, the pinnules crenate-pinnatifid, the crenations minute a line (i.e. 2 mm.) in diameter, tomentose above where soon the green color shines through, very densely tomentose beneath. Indusia greenish, glabrous.

Cheilanthes Eatonii, Baker (Hooker and Baker, 1874)

Stipe tufted, 3-6 inches long, wiry, erect, densely clothed with pale-brown linear subulate scales; frond 3-8 inches long, 1 $\frac{1}{2}$ -2 inches broad, ovate-lanceolate, tripinnatifid; lower pinnae distant, alternate or opposite, deltoid; pinnules linear-oblong, pinnatifid; rachis rigid, covered with scales like the stipe which also cover thickly the midrib of the pinnae beneath; texture coriaceous; upper surface densely clothed with white woolly tomentum, lower also densely matted, the margin of the segments incurved.--C. tomentosa, Hk. Sp. 2. p. 96. (in part), t. 109. A. non Link.

Habitat. Gathered in an expedition from Western Texas to El Paso, New Mexico, October 1849, C. Wright, No. 816.--This differs from C. tomentosa by being coated with distinct scales instead of mere woolly hairs on the stipe, rachis, and midrib of the pinnae beneath, and by being matted with tomentum on the upper surface.

Cheilanthes castanea Maxon, sp. nov. (Maxon, 1919)

Rhizome short-creeping, nodose or short-branching, the divisions 1 to 3 cm. long, less than 1 cm. thick, densely paleaceous, the scales oblique, imbricate, falcate, 3 to 3.5 mm. long, about 0.6 mm. broad at the base, subulate attenuate, rather lax, tawny, with a distinct glossy, dark brown, sclerotic, median stripe extending nearly to the filiform, flexuous tip. Fronds, few, very closely distichous, erect, 16 to 30 cm. long; stipe 9 to 18 cm. long, castaneous, sublustrous beneath a thin covering of appressed to rigidly ascending, pale tawny

scales, the larger of these linear-attenuate, underlaid by minute acicular ones; lamina linear to linear-oblong, long-acuminate, 7 to 17 cm. long, 2 to 4 cm. broad, tripinnate, the rachis similar to the stipe but with larger and more numerous scales; larger pinnae 8 to 12 pairs, spreading (or with age oblique and involute), distant, sessile, deltoid-oblong, acutish, slightly inequilateral; secondary rachises persistently paleaceous, the scales rather large, flaccid, imbricate, linear-deltoid to ovate, long-acuminate, firmly attached at the cordate base, erose-denticulate, tawny; segments of the larger pinnules mostly 3 or 5, oblong, entire, unequal, the terminal ones the longest (up to 4 mm. long), with a cuneate base; segments loosely but copiously tomentose beneath with spirally crispate, light castaneous hairs, glabrate above, the few similar but griseous hairs easily deciduous; segments mostly fertile, the recurved margin gradually thinner, slightly repand, minutely sinuate, pale, hardly forming a proper indusium; sporangia not concealed at maturity, the tomentum separating evenly from the indusiiform margin. Leaf tissue rather rigidly herbaceous, dull grayish green.

Cheilanthes Eatonii Baker forma castanea (Maxon) Correll,
1949 Comb. nov. Cheilanthes castanea Maxon

When extremes of typical C. Eatonii and forma castanea are found they are so distinctive that one would immediately consider them to be specifically different. Unfortunately, very little material of extreme f. castanea exists in herbaria. An overwhelming amount of material does exist, however, which grades into one or the other of these two forms. It is simply an arbitrary matter as to which category they should be relegated. I have placed all plants which have all or part of their fronds tending to be glabrescent on the upper surface of their segments into f. castanea. I have designated those plants with segments hoary and densely tomentose above as the typical form.

Habitat same as that of the typical form.

OCCURRENCE AND HABITAT

The distribution of these taxa is almost the same according to several authors (Wherry, 1961; Fernald, 1950; Morton, 1951; Gleason, 1963; Maxon, 1919) and as indicated by locality data on herbarium specimens. C. tomentosa is found in Mexico, New Mexico, Arizona, Texas, Oklahoma, Missouri, Arkansas, Kansas, Alabama, and Georgia and extends northward to the mountains of western Virginia, North and South Carolina, West Virginia, Tennessee, and Kentucky. This species has the widest distribution of the taxa included in the study, the ranges of the other two being included within this distribution. C. eatonii is found in Mexico, New Mexico, Arizona, Colorado, Utah, Oklahoma, and Texas. Cheilanthes eatonii f. castanea has approximately the same range as C. eatonii except for Colorado and Utah.

These taxa are found primarily in dry areas on wooded hillsides, crevices of rocky slopes and ledges, or often in chaparral. They have been reported as high as 8000 feet in altitude (Morton, 1951).

COMPARATIVE MORPHOLOGY

MATERIALS AND METHODS

For this study approximately 150 specimens from the Texas Research Foundation (LL), 60 specimens from the Smithsonian

Institution (US), and 30 specimens from the Michigan State University Herbarium (MSC) were examined. In addition, living plants of C. eatonii 63-49B, C. eatonii f. castanea 63-28, 63-30, 63-49D, 64-21, C. tomentosa 2048, 63-60, and 64-16 were used as sources of spores and epidermal surfaces of the leaves. Voucher specimens of these plants have been deposited in the Michigan State University Herbarium. All specimens are cited in the appendix. The following characters were recorded:

1. Spores
 - a. Diameter
2. Gametophyte
 - a. General description
 - b. Gametangia
3. Rhizome
 - a. Scales--base and tip
4. Frond
 - a. Stipe
 - 1) length (comparison to blade also)
 - 2) terete or sulcate
 - 3) color
5. Blade
 - a. Length and width
 - b. Shape
 - c. Descriptions of pinnae, pinnules, and ultimate segments
 - d. Cells of the lower and upper leaf epidermides

6. Hairs and scales

a. Stipe

b. Rachis

c. Pinna midrib

7. Indusium and sporangium

a. General description

The methods used in studying the individual characters are included at the beginning of each section under the results and discussion.

RESULTS AND DISCUSSION

SPORES

Fronds containing mature sporangia were collected from living material in the greenhouse. These were placed in a 5% household chlorox solution containing a few drops of Tween 20 (wetting agent) and brushed on both sides for 5-10 seconds with a camel's hair brush. They were then rinsed in water and placed in a plant press between blotters for several days prior to sowing for growth studies. Spores to be studied morphologically were collected from herbarium specimens with forceps and placed in a few cc. of glacial acetic acid. Spore preparations were then made following Erdtman's acetolysis technique (1952). The spores were placed directly into centrifuge tubes containing 5 cc. of acetolysis solution. This solution was prepared by adding drop by drop 1 part concentrated sulfuric acid to 9 parts acetic anhydride (chemically pure). A glass stirring rod was placed in each tube and the tubes were heated for several minutes in a water bath not exceeding 80°C. Once this temperature was reached, the heating was stopped and each tube was stirred before centrifuging for several minutes. After centrifuging, the acetolysis solution was decanted and the spores were rinsed once with glacial acetic acid and once with water, centrifuging

and decanting after each rinse. Since the spores were a very dark brown, they were bleached for easier observation. This was accomplished by pouring a few cc. of household chlorox and leaving until spores became a light brown. Water was added and the spores were then centrifuged, decanted, and rinsed again with water. The spores were then stained with a 1% safranin in 50% alcohol solution and rinsed in water. The spores were suspended in a 1:1 glycerine and water preparation for at least 10 minutes or could be left for a day or so without affecting the spores. When slide preparations were to be made, the spore suspensions were centrifuged and decanted. A drop of the spore residue was placed on a slide on a warming plate. A coverslip was applied and the slide was sealed with Canada balsam or clear fingernail polish.

The diameter of the spores was measured as the greatest distance in the equatorial plane excluding the perispore. Fifty spores from each of five specimens of each taxon were measured. The spores were drawn in the same plane with the aid of a camera lucida.

To determine the number of spores per sporangium a single sporangium which had not dehisced was mounted on a slide in a drop of Hoyer's solution.

The spores of all three taxa appear very similar and no distinguishing characteristics could be observed. The spores are trilete and globose with crassimarginate smooth laesurae (Plate I, Figs. 7-9). They range in color from light tan to

dark brownish-black, the lighter color usually indicating younger spores. Nayar (1963) reports that members of Cheilanthes have an exine which is composed of an inner and outer layer, the endo- and ecto-exine. In the three taxa of this study this demarcation can not be clearly observed. Although there seem to be two distinct layers in some spores, it is not a constant character. The exine is smooth or nearly so in all spores and ranges from 1.5 to 3.5 μ in thickness. The outline of the protoplast is easily observed.

Another layer is present outside the exine which is called the perispore or perine. The exact concept of a perispore has long been a point of confusion. Bower (1963) states:

The plasmodium intrudes between the separating spore-mother-cells forming a rich nutritive medium, which is absorbed in the more primitive ferns in the developing spores; but in certain advanced types it may in part remain as a deposit on the outside of the wall, and is called the perispore (fig. 359). The wall of the spore itself is often marked by characteristic sculpturing which at times gives a basis for systematic comparison; but in this the perispore is more important. Ferns may in fact be divided into two groups according to the presence or absence of a perispore. None is seen in the Eusporangiate Ferns, nor in the Osmundaceae, Schizaeaceae, Hymenophyllaceae, Cyatheaceae, Davalliaceae, or in Ceratopteris. In fact, it is absent from all the more primitive ferns, and of the remaining Leptosporangiates it is wanting in the Vittarieae, Gymnogrammeae, Polypodiaceae, and Pterideae; but it is present in the Asplenieae and Aspidieae. The perispore thus possesses a certain value for comparison; but confidence in it as a safe criterion is shaken by the fact that while it is present in Blechnum and Woodwardia it is absent in the closely related Brainea and Doodia. It is clearly a feature adopted late in descent, and restricted to certain circles of affinity.

However, Harris (1955) goes on to say, after quoting Bower:

It is a common observation that whereas the mature spores of a given species may exhibit a characteristic ornamentation, spores which are not fully mature lack this ornamentation. Between the smooth immature spores and the fully coated mature spores others may be observed which show a partial accretion of the ornamental layer (Fig. 2g and h). If this arises by the gelation of plasmodial substance on the exterior of the spore, it is a perispore as defined by Moll (1934) and other writers. It is possible, then, that the occurrence of a perispore is more general than supposed by Bower.

In some ferns it is difficult to determine whether or not a distinct perispore is present. Therefore, the terms "sculptive" or "winged" spore have been adopted by workers when referring to a layer outside the exine of doubtful origin (Erdtman, 1952, and Harris, 1955). In the three taxa of this study the perispore is well-defined and is usually slightly darker in color than the underlying spore. It is smooth and is approximately 1.5-3.5 μ in thickness. The perispore is usually slightly thicker than the exine, but sometimes both appear to be about the same in thickness.

The diametric measurements of the spores did not prove to be valuable as a distinguishing characteristic (Table I). Graphs of the measurements show C. eatonii f. castanea and C. tomentosa to have a nearly normal curve (Figures 1 and 3) while C. eatonii (Figure 2) tends toward a normal curve with a slight dip near the summit, indicating greater phenotypic variation than the other two taxa. It is to be noted that the measurement range of C. eatonii f. castanea falls within

that of C. eatonii. The sporangia of each taxon contain 32 spores per sporangium. The spores are uniform in appearance and none of them is aborted.

Table I. Spore Diameter

Taxa*	Collector	Collection Number	Diameter (μ)	
			Mean	Range
<u>C. tomentosa</u>	I.W.Knobloch	1953	57.8	(48.0-70.4)
	E.Castetter	63-60	58.9	(44.8-67.2)
	I.W.Knobloch	847	58.6	(51.2-70.4)
	I.W.Knobloch	2048	61.1	(48.0-70.4)
	D.Moore	64-16	61.5	(54.4-73.6)
			57.6=Mean of the means	
<u>C. eatonii</u>	R.M.Stewart	63-49B	59.1	(51.2-73.6)
	R.M.Stewart	1112	55.6	(41.6-67.2)
	I.W.Knobloch	752	51.9	(38.4-70.2)
	D.S.Correll	23291	51.8	(41.6-60.8)
	D.S.Correll & I.M.Johnston	21625	58.3	(41.6-73.6)
			55.3=Mean of the means	
<u>C. eatonii</u> f. <u>castanea</u>	B.H.Warnock	63-28	57.4	(51.2-64.0)
	G.Goodman	64-21	56.2	(51.2-64.0)
	Lefebure	1161	61.2	(48.0-70.4)
	J.K.Baker	63-49D	56.3	(48.0-64.0)
	B.H.Warnock	63-30	59.9	(51.2-67.2)
			58.2=Mean of the means	

* Specimen citations in appendix.

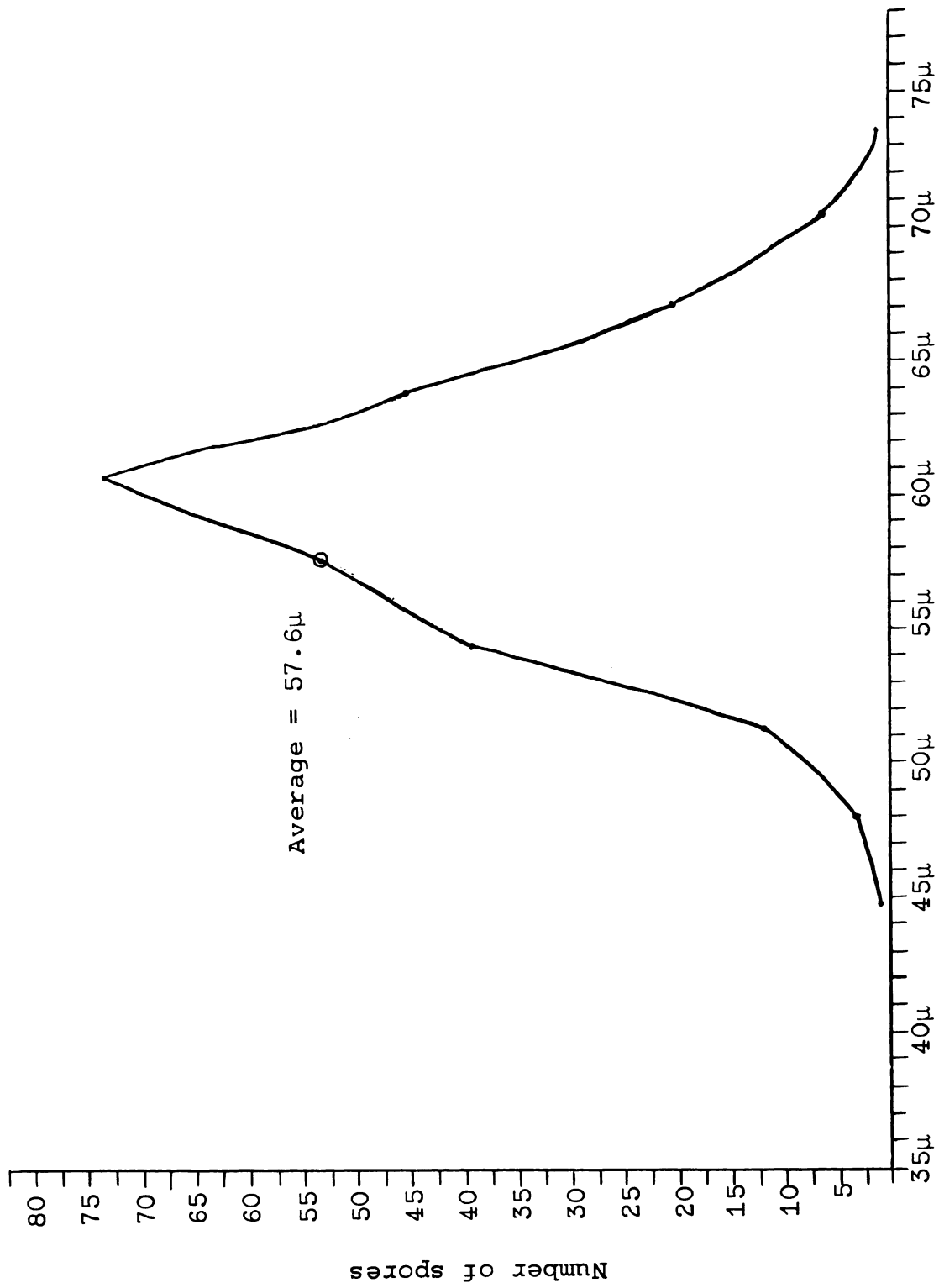


Figure 1. Cheilanthes tomentosa spore diameter.

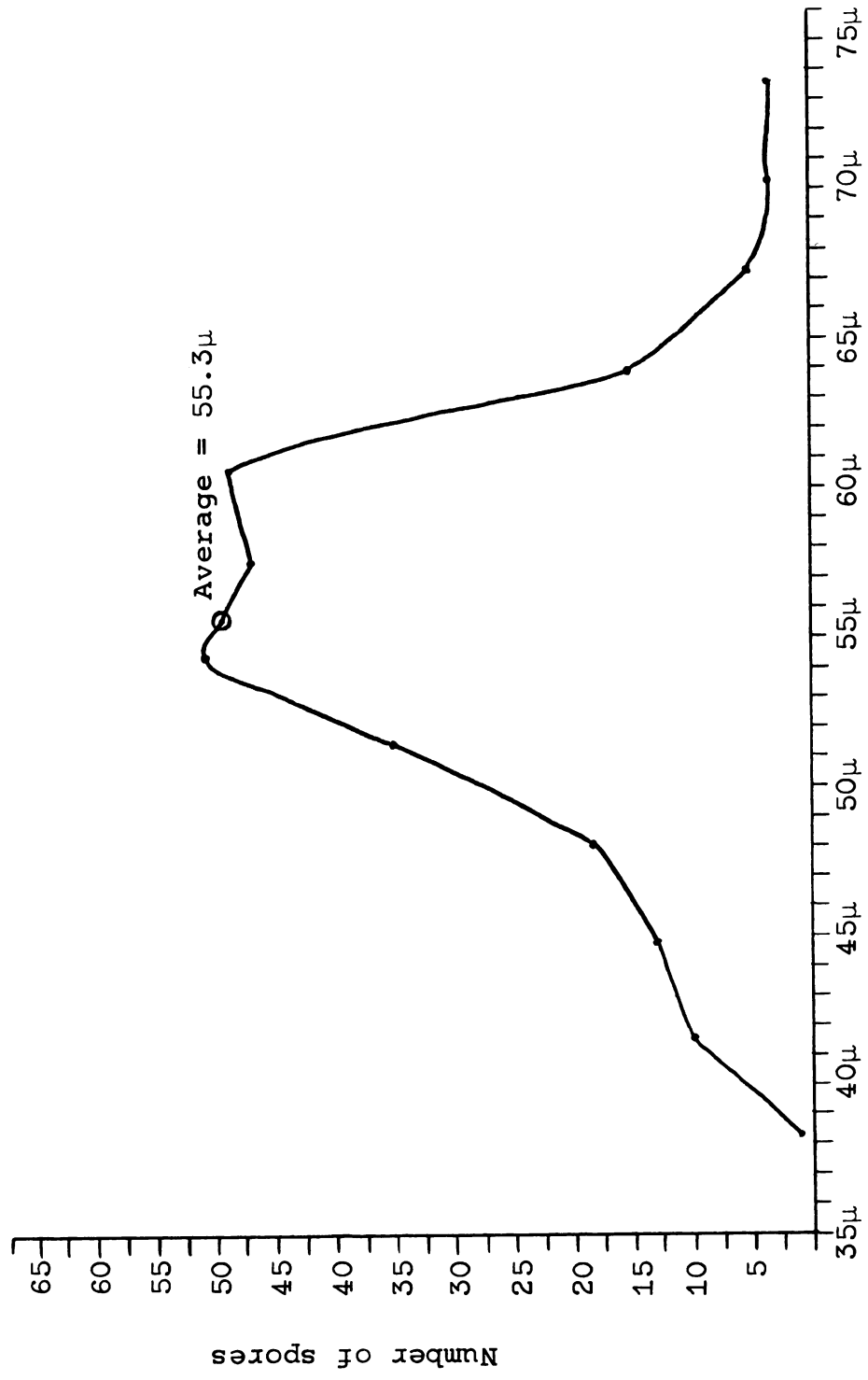


Figure 2. *Cheilanthes eatonii* spore diameter.

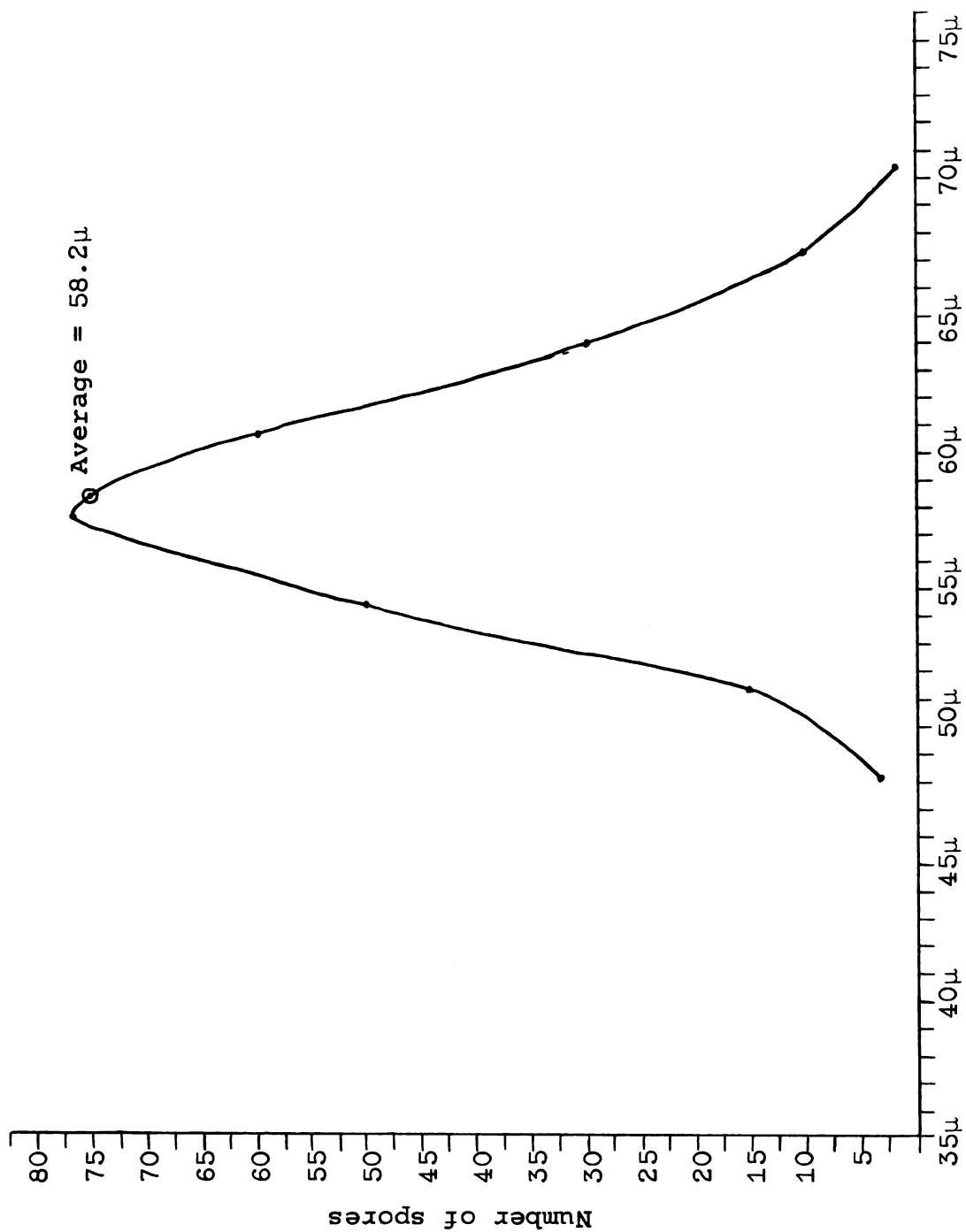


Figure 3. *Cheilanthes eatonii* f. *castanea* spore diameter.

Gametophyte

In early January, 1965, spores for sowing were collected from living material and treated in the same manner described in the spore discussion (p. 10). While the fronds were drying, potting soil was placed in flower pots and autoclaved for one hour under 15 pounds of steam pressure. After the fronds had dried, and the sporangia had dehisced, the spores were collected and approximately half of them sprinkled on the soil. Petri dishes served as covers for the flower pots and these were sealed to the pots with masking tape. The pots were placed under 24-hour fluorescent lighting in trays containing approximately an inch of water.

At the same time a nutrient agar solution was prepared using the following formula (Steeves, et al., 1955):

Knudson's solution of mineral salts

Water (glass redistilled)	100 cc.
$\text{Ca}(\text{NO}_3)_2 \cdot 4\text{H}_2\text{O}$	500 mg.
$\text{MgSO}_4 \cdot 7\text{H}_2\text{O}$	125 mg.
K_2HPO_4	125 mg.

To the above were added 1 cc. of ferric citrate, 1 cc. of trace elements, 50 g. of sucrose, and 1% agar. The solution was heated to melt the agar and poured into 125 ml. Erlenmeyer flasks to a depth of about 3/4 inch. The flasks were stoppered and autoclaved for 20 minutes under 15 pounds of steam pressure. Spores were then sprinkled on the agar medium and the flasks were placed under fluorescent lights.

By the end of January most of the agar cultures were contaminated and of no value. At this time Whittier's (1964) method of spore sterilization was tried. Remaining spores from fronds collected earlier were wet with a 0.1% solution of Tween 80 and placed in a 15% solution of household chlorox for 2 minutes. The spores were collected on filter paper and washed several times with sterile water. The filter papers were placed in envelopes and put between blotters for drying. After drying, the spores were scraped from the filter paper with a sterile knife and placed in a vial containing several cc. of sterile water. The vial contents were transferred aseptically to Knudson's agar medium. The vial contents were transferred aseptically to Knudson's agar medium. One advantage of this method is that it allows for a more even distribution of the spores over the surface medium. At this time no spores of C. eatonii 63-49B were available for sowing and so gametophytes of this plant were not available for study. By the end of February prothalli were evident on soil and agar cultures. As the agar dried in the cultures, the prothalli were transferred aseptically to new culture media by means of a transferring needle. By the end of May young sporophytes were evident and some were preserved in FAA. By the middle of June, sporophytes were evident on the soil cultures.

The gametophytes of C. eatonii f. castanea and C. tomentosa were examined, but no material of C. eatonii was

available as mentioned previously; hence, complete gametophytic comparisons could not be made. Lenette Atkinson (pers. comm.) also supplied additional information and support to the investigator's findings.

The gametophyte of C. tomentosa is usually an elongated plate of cells at first which then broadens into a basically cordate-shaped prothallus with a very broad sinus (Plate II, Figure 1). The margins are slightly irregularly lobed. In many cases, one or both of the thallus wings send out additional filamentous thalli (Plate II, Figure 3), the resulting gametophyte having a bizarre appearance. On the agar cultures the gametophytes grew in clumps with those on the upper surface being of the cordate nature and filamentous ones growing into the agar below (Plate II, Figure 2). The thalli are one cell in thickness except in the central area below the sinus where a cushion of cells several layers thick forms.

The gametophyte of C. eatonii f. castanea is similar to that of the previous taxon except that the margins are more deeply lobed, thus giving the entire thallus a much more irregular appearance than that of C. tomentosa (Plate II, Figure 4). The thalli are often very wavy and somewhat urn-shaped making them difficult to flatten for observation. The filamentous growths of the thallus wings and lower surface may again be noted (Plate II, Figures 5 and 6).

Atkinson (pers. comm.) observed the thalli of C. eatonii to be large cornucopia-shaped structures when grown in fibre-sand.

In C. tomentosa, C. eatonii f. castanea, and C. eatonii (Atkinson, pers. comm.) antheridia are found near the basal end of the prothallus away from the apical notch. These are subspherical and sessile on the thallus or on a one-celled stalk (Plate II, Figure 2; Plate II, Figure 5). No arche-gonia were observed on any thalli. Unicellular rhizoids occur on the underneath surface along the midrib cushion, but no hairs are observed on any of the thalli.

The usefulness of the gametophyte in taxonomic studies is rather doubtful as Wagner (1952) points out: "As has been shown widely in the literature, and as is probably true of all cordate gametophytes of leptosporangiate ferns, the form is exceedingly plastic, varying in accordance with lighting, temperature, nutrition, crowding, and other external conditions." Others, however, find the gametophyte stage of value in their studies.

Apogamy

All three taxa are apogamous. This is indicated by several observations which will be discussed in detail later: 1) a mound or cushion of cells forms on the lower surface below the sinus on the gametophyte which seems to be a pre-requisite for apogamy, 2) each sporangium contains 32

well-formed spores instead of the usual 64 well-formed spores found in sexual species, and 3) no archegonia have been observed on the gametophytes.

Apogamy in ferns may be defined as the production of a sporophyte, the vascular plant of the asexual generation, from the gametophyte, the non-vascular plant of the sexual generation without the occurrence of syngamy (Whittier and Steeves, 1960). There are basically two types of apogamy: obligate and induced. Obligate apogamy refers to the formation of sporophytes from the gametophytic tissue as a necessity because fertilization cannot take place. This necessity results from either the antheridia or the archegonia or both being absent from the gametophyte. Induced or facultative apogamy refers to the formation of sporophytes from gametophytic tissue by controlling the cultural conditions. Under normal conditions these plants would have functional archegonia and antheridia and fertilization could take place to sexually produce the sporophyte.

Whittier (1965) describes the development of sporophytes apogamously in C. tomentosa as follows: "After the cordate prothallus thickens, a small tan area appears in the cushion region behind the apical notch. This color results from a modification of chloroplasts in the meristematic cells of this region. The area increases in size and becomes brown. A mound of dark-green cells with sporophytic hairs is produced from cells of the brown area. From this mound the leaf

appears first, with the root following shortly thereafter." This mound of darkened cells was observed also in the gametophytes investigated in this study. Whittier (1962) and other workers have concluded that a thickened thallial structure must be formed before apogamy can occur.

In apogamy the central cytological problem is that of reconciling the absence of a sexual nuclear fusion with the presence of an apparently normal meiotic process in the development of spores in the sporophyte (Manton, 1950). There must be some compensating process to stabilize the number of chromosomes. Early work on this idea was done by Allen (1914) with Aspidium falcatum Sw. (now Cyrtomium falcatum Presl). He correctly stated that the meiotic process produced spores with the same chromosome number as the parent and that the sporophyte and gametophyte were the same in nuclear content and of the same chromosome number as the parent.

He found sporangia with eight spore mother cells, sixteen spore mother cells, and some intermediates. In 1919 Steil studied intermediate nuclear stages as found in Nephrodium hirtipes Hk. [now Dryopteris atrata (Wall.) Ching]. These stages were the result of incomplete nuclear division immediately preceding meiosis causing the nuclear content of the spore mother cell to be doubled momentarily. This was the key to the compensation mechanism.

Manton (1950) describes the cytological processes taking place in the sporangia of the apogomously-produced sporophyte. The early stages of sporangial development are identical in a sexual or apogamous sporophyte. A very exact set of cell cleavages occurs in what was originally a single superficial cell. A short filament develops, the terminal cell of which undergoes four oblique cleavages. By this means the sporangium wall is separated from the central tetrahedral cell. This central cell next undergoes a set of cleavages which separates the nutritive tapetal layer from the archesporium. The archesporium then undergoes four equal mitoses resulting in a central unit of sixteen cells. These cells enlarge to become spore mother cells which undergo meiosis each giving rise to four spores.

In apogamous ferns the sporangial development is the same until the onset of mitoses in the archesporium. At this stage there are four possibilities for further development:

(1) All four archesporial cleavages may take place and sixteen spore mother cells formed as in the sexual species.

(2) The first three cleavages may be perfect, but the fourth is imperfect. Metaphase starts in the eight archesporial cells as usual with the chromatids attached to the spindle. At anaphase there is no chromatid movement to the poles and no cleavage of cytoplasm. The nucleus becomes a restitution one and eventually becomes a spore mother cell with meiosis occurring and resulting in only 32 spores with the $2n$ number of chromosomes.

(3) A variation of (2) may occur in which the nuclei become irregularly lobed and have partial cross walls resulting in unequal constricted portions. Because the distribution of chromosomes to the constricted portions is random, there is a good chance that the nuclei will be genetically unbalanced and the spores will probably abort.

(4) Two cleavages of the archesporium may be affected resulting in a four-celled state with four large mother cells at meiosis each with four times the normal number of chromosomes. The pairing of chromosomes is restricted to sister chromosomes and the ripe sporangia yield sixteen large spores with twice the chromosome number of the parent. This may have some connection with polyploidy.

The three taxa in this study all have 32 good spores per sporangium, as was previously mentioned, and therefore seem to fit in the second developmental possibility.

Mature Sporophyte

Rhizome

The rhizome scales were mounted on a slide in Hoyer's solution for study. The length was measured from the base to the tip of the scale and the width was measured at the widest point near the base of the scale. Measurements were made using scales from both the base and the tip of the rhizome. The rhizome is very similar in all three taxa in being stout with fronds arising in very close proximity to one another.

It is densely covered with imbricate scales which are linear to linear-lanceolate and tawny-colored. Those at the base usually have a central dark brownish-black stripe which may vary in occupying the central third of the scale up to a short distance from the margin. Scales at the tip may be uniformly tawny or have a small central stripe (Plate I, Figures 1-6). Measurements of the scales show only slight differences among the three taxa (Table II). C. tomentosa has longer, narrower scales which are characteristic of its scales on other parts of the plant to be discussed later.

Table II. Rhizone Scale Measurements

Taxa *	Base L x W (mm)	Tip L x W (mm)	Average of Base and Tip L x W (mm)
<u>C. tomentosa</u>	5.3 x .27	4.5 x .22	5.0 x .25
Range	4.5-6.0 (L)	Range 3.5-6.0 (L)	
"	.15-.34 (W)	" .13-.27 (W)	
<u>C. eatonii</u>	4.5 x .48	3.7 x .32	4.1 x .38
Range	3.2-6.0 (L)	Range 3.0-4.3 (L)	
"	.20-1.39 (W)	" .14-.53 (W)	
<u>C. eatonii</u> f. <u>castanea</u>	4.7 x .49	4.4 x .45	4.5 x .47
Range	4.2-5.2 (L)	Range 4.2-5.2 (L)	
"	.15-1.0 (W)	" .32-.62 (W)	

* Specimen citations in appendix.

Frond

Stipe and Rachis

The stipe of all three taxa is terete and dark reddish-brown to black. The rachis is slightly lighter in color. Knobloch and Volz (in press) recently investigated the anatomy of the stipe and rachis of these three taxa as well as other members of Cheilanthes. They observed the following similarities in the genus:

All stipes and rachises possess an epidermis, a cortex with an endodermis, and a stele. In the latter, one is able to discern varying amounts of pericycle, parenchyma, phloem and xylem. As the axis matures, the basal cells of the epidermis become lignified, their lumina become small, and the cells apparently die; this series of events is of advantage to the plant in that a greater measure of support is gained. Stomates are present, being especially noticeable in the rachis. The cortex is similar in its mode of lignification. The high degree of lignification makes it difficult to obtain untorn sections. The outer cortex in some species becomes more aerenchymatous and chlorophyllous acropetally. The inner cortex or endodermis is a one-celled layer of tissue with easily ruptured radial walls. The stele-cortex ratio changes acropetally with the stele occupying a proportionally smaller area up in the rachis.

The vascular tissues are bounded by a pericycle which varies from one to several cells in depth. The phloem surrounds the centrally-placed xylem and consists of both sieve and parenchyma cells. There are fewer sieve cells on the edges of the xylem than on either the adaxial or abaxial faces. Both xylem and phloem are primary tissues.

Three anatomical areas of the stipe and rachis--the general cross-section, the stele, and the xylem within the stele--were examined and described by Knobloch and Volz (in press) for the taxa in this study as follows:

	<u>C. <i>eatonii</i></u> f. <u><i>castanea</i></u>	<u>C. <i>eatonii</i></u>	<u>C. <i>tomentosa</i></u>
Cross-section	sub-terete below, gradually becomes terete above	sub-terete at very base, changes to terete above and in rachis	base sub- terete, be- comes terete above
Stele	sulcate near the ground	subcate below, sub-sulcate above	sulcate above and below
Xylem	varies from 2- stranded or, at times, weakly X condition at base, to X or butterfly shape upward and into rachis	X or butter- fly shape	initially 2- stranded or weak X shape at base, be- comes strong X or butter- fly shape above and into rachis

As Brown (1964) mentions, the Japanese worker, Ogura, (1938) "considers the 'Cheilanthes-type' of stele to form a transitional stage between the group of ferns that he calls the 'Monostelic' with only one stele in both the stipe and the rachis and 'Distelic' in which the stipe contains two steles that unite further up in the rachis." Thus, this may be part of the explanation for the 2-stranded xylem in some plants.

Blade

The length of the blade was measured from the base of the blade to the tip of the blade and the width was measured at the widest point of the blade. The stipe length was

measured from the base of the blade to the point of attachment of the stipe to the rhizome.

Measurements of the blade length and width as well as the stipe length (Table III) indicate that C. eatonii is usually shorter in length and is intermediate in width when compared to the other two taxa. Since these measurements are based on approximately 45 herbarium specimens of each taxon, the measurements may be slightly smaller than normally found in living plants.

The blade of C. tomentosa is oblong-lanceolate to narrowly lanceolate and bipinnate-pinnatifid to tripinnate-tripinnatifid. The pinnae range from oblong-lanceolate to ovate-oblong with some being narrowly triangular-lanceolate. There are usually from 17 to 27 pairs of pinnae per frond. The pinnules are ovate-oblong to oblong-lanceolate with some being triangular-lanceolate. There are usually from 5 to 14 pairs of pinnules per basal pinna. The oldest pinnule arises on the side of the pinna midrib toward the apex of the frond and is therefore said to be anadromous (Mickel, 1962). The ultimate segments are suborbicular-obovate to elliptic with the terminal segment being larger than the other segments. (Plate III)

The blade of C. eatonii is oblong-lanceolate to narrowly lanceolate and tripinnate with a tripinnate-pinnatifid frond occasionally being observed. The pinnae number from 17 to 20 pairs per frond and are narrowly triangular-lanceolate to

ovate-oblong. The pinnules number from 5 to 9 pairs per basal pinna and are triangular-elliptic to oblong-lanceolate. The oldest pinnule is anadromous. The ultimate segments are suborbicular-obovate to elliptic and the terminal segment is larger than the other segments (Plate IV).

The blade of C. eatonii f. castanea is oblong-lanceolate to narrowly lanceolate and tripinnate. The pinnae are narrowly triangular-lanceolate to triangular-ovate with some being ovate-oblong. The pinnae average from 19 to 27 pairs per frond while the pinnules average from 5 to 9 pairs per basal pinna. The pinnules are narrowly triangular-elliptic to narrowly triangular lanceolate, the oldest one being anadromous. The ultimate segments are suborbicular-obovate, elliptic, or broadly ovate with the terminal segment being larger than the other segments (Plate V).

Table III. Frond Measurements

Taxa *	Blade Length (cm)	Blade Width (cm)	Stipe Length (cm)	Ratio Blade L: Stipe L
<u>C. tomentosa</u>	20.2	3.8	11.6	1.7
<u>C. eatonii</u>	11.7	2.6	9.0	1.3
<u>C. eatonii</u> f. <u>castanea</u>	12.1	2.0	10.6	1.1

* Specimen citations in appendix.

Epidermal Cells

To study the upper epidermal cells, imprints of the leaf surface were made using clear nail polish. All hairs were removed from the surface and a thin layer of nail polish was applied. Approximately one-half hour later or when the nail polish was dry, the imprint was peeled off by means of forceps and a dissecting needle and placed on a slide, imprint side up. A cover slip was applied and the slide sealed. The cells were viewed and drawn by means of a microprojector. In the case of herbarium specimens, the pinnae were soaked in water with a few drops of glycerine in it to soften them. After remaining in the softening solution overnight, the specimens were blotted to remove excess moisture and then treated the same as fresh material. This method was not at all successful on the lower epidermal surface. Instead, an epidermal peel was made and the cells were drawn with the aid of a camera lucida.

The epidermal cells were measured from one end of the longest axis to the other and from one end of the broadest axis to the other. The stomatal measurements were made from the outer border of one guard cell to the outer border of its partner. Measurements were based on an average of 10 cells from each of five plants of each taxon.

There are no tangible differences in the epidermal surfaces of the three taxa (Plates VI and VII). The cells of the upper surface have slightly thicker walls than those of

the lower epidermis and are 9 to 12 μ longer. The thicker walls may be expected since these plants are inhabitants of dry areas. In both surfaces each cell has contact with from 5 to 8 other cells. The cells in both surfaces have moderately convoluted walls giving the general appearance of a jigsaw puzzle (Plates VI and VII). In general, there is a great deal of variation in size and shape of the cells within the same plant. Stomates are found only in the lower epidermis and are uniform in size and shape. There may be a great deal of variation in the measurements from plant to plant as Table IV shows. The explanation according to Wagner (1952) might be as follows: "In view of the well-known capacity of laminar cells to be modified by environmental factors, the characters of the laminar cells are rather difficult to evaluate precisely. That textural differences in the laminae of various ferns are important in taxonomy is well-known, and there is little doubt that, basically, these are genetically fixed."

Knobloch and Volz (1964) have investigated the leaf blade anatomy of these taxa and their findings are summarized on the following page:

Species	<u>C. eatonii</u> f. <u>castanea</u>	<u>C. eatonii</u>	<u>C. tomentosa</u>
Palisade layer	Well-defined layer with few inter-cellular spaces	Cells loosely arranged with numerous spaces; H- and Y-shaped cells common in central palisade region	Central cells rectangular, loosely arranged, and subquadrate in shape on margins of cells; H-shaped cells here and there
Mesophyll layer	Cells loosely arranged and frequently armed	Cells loosely arranged and armed	Cells loosely arranged and armed
Vascular bundle	Large with a bundle sheath; many tracheids; few phloem elements and bundle parenchyma	Bundle sheath underlain with distinct pericycle; xylem area centrally located and greater in area than phloem or parenchyma areas	Prominent bundle sheath; tracheids centrally located; phloem cells few and numerous parenchyma cells

Table IV. Measurements of Epidermal Cells and Stomata

Taxa *	Collector	Collection Number	Upper epidermis (L x W) (μ)	Lower epidermis (L x W) (μ)	Stomates (μ)
<u>C. tomentosa</u>	E. Castetter	63-60	90 x 34	81 x 45	44 x 38
	I. W. Knobloch	2048	96 x 36	66 x 34	45 x 38
	D. Moore	61-16	94 x 41	69 x 34	48 x 38
	I. W. Knobloch	847	69 x 25	74 x 37	46 x 34
	I. W. Knobloch	1966	93 x 33	91 x 43	44 x 36
	Mean of the means		88 x 34	76 x 39	45 x 37
<u>C. eatonii</u>	I. W. Knobloch	752	89 x 38	74 x 41	42 x 32
	R. M. Stewart	63-49B	93 x 37	76 x 40	41 x 34
	I. W. Knobloch	2062	92 x 39	99 x 43	44 x 34
	D. S. Correll and				
	I. M. Johnston	21625	91 x 38	76 x 40	42 x 31
	D. S. Correll	23291	72 x 35	67 x 43	40 x 33
	Mean of the means		87 x 37	78 x 41	42 x 33
<u>C. eatonii</u> f. <u>castanea</u>	B. H. Warnock	63-30	97 x 41	82 x 48	42 x 33
	G. Goodman	64-21	95 x 42	70 x 44	40 x 30
	J. K. Baker	63-49D	103 x 43	95 x 45	41 x 33
	B. H. Warnock	63-28	94 x 42	101 x 42	44 x 36
	Lefebure	1161	99 x 53	82 x 46	47 x 38
	Mean of the means		98 x 44	86 x 45	43 x 34

* Specimen citation in appendix.

Hairs and Scales

Hairs and scales for study were collected from the stipe, rachis, and pinna midrib of the three taxa in this study and mounted on a slide in a drop of Hoyer's solution. Measurements of 30 larger scales from each of the 3 areas were made from each of 4 representative specimens of each taxon. The length was measured from the tip of the scale to the base and the width of the widest part of the scale. The length:width ratio for each taxon was determined from the final measurement averages.

In this study hair is defined as a structure consisting of a single cell or a single row of cells. Scale is defined as a flat plate of cells being two or more cells wide at the base and one cell thick (Foster, 1949).

The rachis of C. eatonii is covered with large scales which have a broad cordate base and gradually taper to a point at the tip (Plate VIII, Figure 8). Comparative measurements are given in Table V. Many smaller scales and several-celled hairs also cover the rachis (Plate IX, Figures 7 and 8). Hairs and smaller scales of the same type are found on the stipe. However, the base of the larger scales located toward the lower part of the rachis and down the stipe becomes narrower and almost truncate. No scales are found on the adaxial surface of the pinna midrib. The abaxial surface of the pinna midrib has very few scales, these being similar in shape to the scales on the apical portion of the

Table V. Larger Scale Measurements

Taxa *	Stipe L x W (mm)	Ratio L:W	Rachis L x W (mm)	Ratio L:W	Pinna Midrib L x W (mm)	Ratio L:W
<u>C. eatonii</u>	2.3 x 0.25	9.4	2.4 x 0.5	4.8	1.7 x 0.6	2.8
	Range 1.6-3.2 (L)		Range 1.4-3.6 (L)		Range 1.0-2.7 (L)	
	" 0.1-0.5 (W)		" 0.2-0.9 (W)		" 0.3-0.9 (W)	
<u>C. eatonii</u>	2.5 x 0.2	12.5	2.7 x 0.4	6.8	1.9 x 0.4	4.8
f. <u>castanea</u>	Range 1.3-3.8 (L)		Range 1.5-4.9 (L)		Range 1.2-3.5 (L)	
	" 0.1-0.5 (W)		" 0.2-0.9 (W)		" 0.2-0.8 (W)	
<u>C. tomentosa</u>	3.0 x 0.1	30.0	3.0 x 0.1	30.0	2.2 x 0.1	22.0
	Range 1.7-4.9 (L)		Range 1.8-5.1 (L)		Range 1.5-3.5 (L)	
	" 0.1-0.2 (W)		" 0.1-0.5 (W)		" 0.1-0.2 (W)	

* Specimen citations in appendix.

rachis. However, it is densely covered with very long narrow hairs composed of several cells (Plate IX, Figure 6). These hairs also form a dense covering on the upper and lower laminar surfaces (Plate IV, Figures 1 and 2). They are usually whitish-grey in color and, hence, give the frond an overall hoary appearance.

In C. eatonii f. castanea the hair and scale arrangement is very similar to that of C. eatonii except that the upper laminar surface is usually glabrescent (Plate V, Figures 1 and 2). The larger scales tend to be longer and taper more gradually than those in C. eatonii (Plate VIII, Figures 4, 5, and 6). The scales and hairs are usually castaneous or rusty in color.

In C. tomentosa the larger scales are not nearly so frequent on the stipe and rachis as in the previous two taxa. The scales on the rachis are narrowly lanceolate with a slightly wider cordate base (Plate VIII, Figure 2). As in the previous two taxa, toward the base of the rachis and down the stipe the base of the larger scales becomes narrower and almost truncate (Plate VIII, Figure 1). The scales on the stipe are narrowly lanceolate to linear. The stipe and rachis are much more densely covered with hairs and smaller scales than in the previous two taxa. No scales are found on the upper surface of the pinna midrib, but a few similar in shape to those on the upper rachis are found on the lower surface (Plate VIII, Figure 3). Both laminar surfaces are

covered with very long narrow hairs, the lower surface being matted and the upper not as densely pubescent. The scales and hairs are usually pale brown to grey in color.

In all three taxa the end cell walls of the hairs are curved and appear to be U-shaped. The terminal cells of the scales also have the same type of cell walls (Plate IX, Figures 1-10; Plate X, Figures 1-5).

Hairs and scales were also examined on young plants about one and a half years old and found to be the same in size and shape as those on the older plants.

Indusium and Sporangium

In all three taxa a false indusium is formed by the reflexed margin of the leaf segments. The margin is continuous and its edge is smooth. Sporangia are borne at the ends of lateral veins. A thorough study of the sporangia was not made, but a preliminary investigation shows the sporangia of all three taxa to be similar and to agree with Nayar's (1963) general description. Here the sporangia are described as:

. . . large, almost globular (or pyriform) in shape and short stalked, the stalk being composed of two or three tiers of short cells. . . . The sporangial wall, though one cell thick, is characteristic in being composed of an exceptionally large number of small cells of more or less regular contours arranged in irregular vertical rows: the stalk abuts on 8-16 wall cells. . . . The annulus is broad, slightly tilted at the base towards one side, protruding prominently from the general surface, 12-15

cells long, and separated conspicuously from the stalk by 2-6 unthickened cell walls. The stomium is broad, lateral, and consists of 6-12 transversely elongated narrow cells. 4-8 thin-walled cells separate the stomium from the annulus and 2-5 from the stalk.

As the sporangia mature and begin to dehisce, the indusial flap is pushed back, allowing the spores to fall free.

SUMMARY AND CONCLUSIONS

Cheilanthes eatonii, C. eatonii f. castanea, and C. tomentosa have the following similarities:

1) The ranges of C. eatonii and C. eatonii f. castanea are similar and are found within the range of C. tomentosa but do not range further east than Texas and Oklahoma.

2) Found in crevices of rocky ledges and cliffs in dry areas.

3) Round trilete spores with a smooth exposure margin, surrounded by a smooth-margined perispore.

4) Apogamous gametophytes.

5) Stipe and rachis anatomy

a) General cross-section sub-terete below, becomes terete above.

b) Stele sulcate below, subsulcate above.

c) Xylem X or butterfly-shaped, sometimes 2-stranded at base.

6) General shape of blade (oblong-lanceolate to narrowly lanceolate), pinnae (triangular-lanceolate to oblong-ovate), pinnules (triangular elliptic to oblong lanceolate), and ultimate segments (suborbicular-obovate to elliptic).

7) Laminar epidermal surfaces with moderately convoluted cell walls and cells varying widely in size and shape.

8) U-shaped cell walls in the hairs and terminal cells of the small scales.

9) Reflexed margin of the leaf segments forming a continuous indusium.

10) Large globose sporangia with 32 turgid spores.

The similarities summarized above make it evident that these three taxa belong in the same genus and are very closely related.

No definite conclusions can be drawn from the preliminary gametophytic study. It does seem that environmental conditions may play a very influential role in determining their form. The environmental effect on obligate apogamy is a questionable one. For example, Whittier (1965) states:

In considering the influence of dryness on fern prothalli, it has been suggested that obligate apogamy may be an adaptation to a xerophytic habit (Hayes, 1924; Stokey, 1948). This is supported by the findings of Lang (1898) and Duncan (1942), who showed that capillary water from the soil was sufficient for prothallial growth but insufficient for fertilization. Sperm require free water for access to the archegonia. Obligate apogamy would obviate the necessity of this water for sporophytic formation. Increases in dryness of the media without surface water did not increase apogamy in these two species of Cheilanthes (C. tomentosa and C. alabamensis). It must be concluded that there is no evidence for enhanced gametophytic growth or for increased initiation of apogamous sporophytes in response to dry media.

The three taxa differ in the following characteristics:

1) Frond measurements--Cheilanthes tomentosa has longer and broader fronds as well as a greater blade-length:stipe-length ratio (1.7) than either C. eatonii (1.3) or C. eatonii f. castanea (1.1). The latter two taxa are very close in

frond measurements and are about 8 cm shorter and $1-1\frac{1}{2}$ cm narrower than C. tomentosa.

2) Scales and hairs--The larger pale brown to grey scales on the fronds of C. tomentosa are more narrowly lanceolate to linear than those on the other two taxa. The larger scales of the other taxa are broader at the base, C. eatonii f. castanea being slightly narrower at the base and tapering more gradually toward the tip than C. eatonii. The scales and hairs of C. eatonii are white or grey, sometimes slightly rusty-colored, while those of C. eatonii f. castanea are a definite medium to dark rusty or castaneous color. The upper surface of the segments of C. eatonii is densely covered with long, narrow hairs while typical C. eatonii f. castanea is glabrescent and C. tomentosa exhibits an intermediate condition.

These differences among the three taxa may be compared simultaneously by means of polygonal graphs (Figures 4-7). These graphs consist of a circle with as many radii as there are characters to be compared (Davidson, 1947), in this case, nine. The characteristics of each taxon are plotted along each radius using an appropriate scale. The plotted points for each taxon are joined and thus a polygon represents each taxon. Similarity of polygon shape indicates close relationship. Essentially parallel lines between adjacent radii indicate a positive correlation while intersecting lines indicate a negative correlation.

From the composite polygonal graph of the three taxa (Figure 4) the following conclusions may be made:

- 1) There is a positive correlation among the scale lengths of all three taxa when compared with one another.
- 2) There is a positive correlation among the scale widths of all three taxa, the correlation between C. eatonii and C. eatonii f. castanea being much higher than that of C. tomentosa with either of these two taxa.
- 3) There is a positive correlation among all three taxa between the blade width and the ratio of the stipe length: blade length.
- 4) There is a positive correlation between the frond length and blade width between C. tomentosa and C. eatonii.
- 5) For the same characteristics there is a positive correlation, although not as great as in 4), between C. tomentosa and C. eatonii f. castanea.
- 6) For the same characteristics there is a negative correlation between C. eatonii and C. eatonii f. castanea.
- 7) There is a negative correlation among all three taxa between the width and length of the stipe scales. This would also be true for the rachis and pinna midrib scales if their length and width radii were adjacent.

From a glance at the individual polygon of each taxon (Figures 5-7) it is evident that the shape of the polygons of C. eatonii and C. eatonii f. castanea are very similar while that of C. tomentosa is quite different. Thus it appears

Figure 4. Composite polygonal graph

- A. - Large scale stipe width, scale 4 units = .1 mm
- B. - Large scale stipe length, scale 1 unit = .1 mm
- C. - Large scale rachis length, scale 1 unit = .1 mm
- D. - Large scale pinna midrib length, scale 1 unit = .1 mm
- E. - Ratio stipe length: blade length, scale 1 unit = .1
- F. - Blade width, scale 3 units = 1 cm
- G. - Frong length, scale 1 unit = 1 cm
- H. - Large scale pinna midrib width, scale 4 units = .1 mm
- I. - Large scale rachis width, scale 4 units = .1 mm

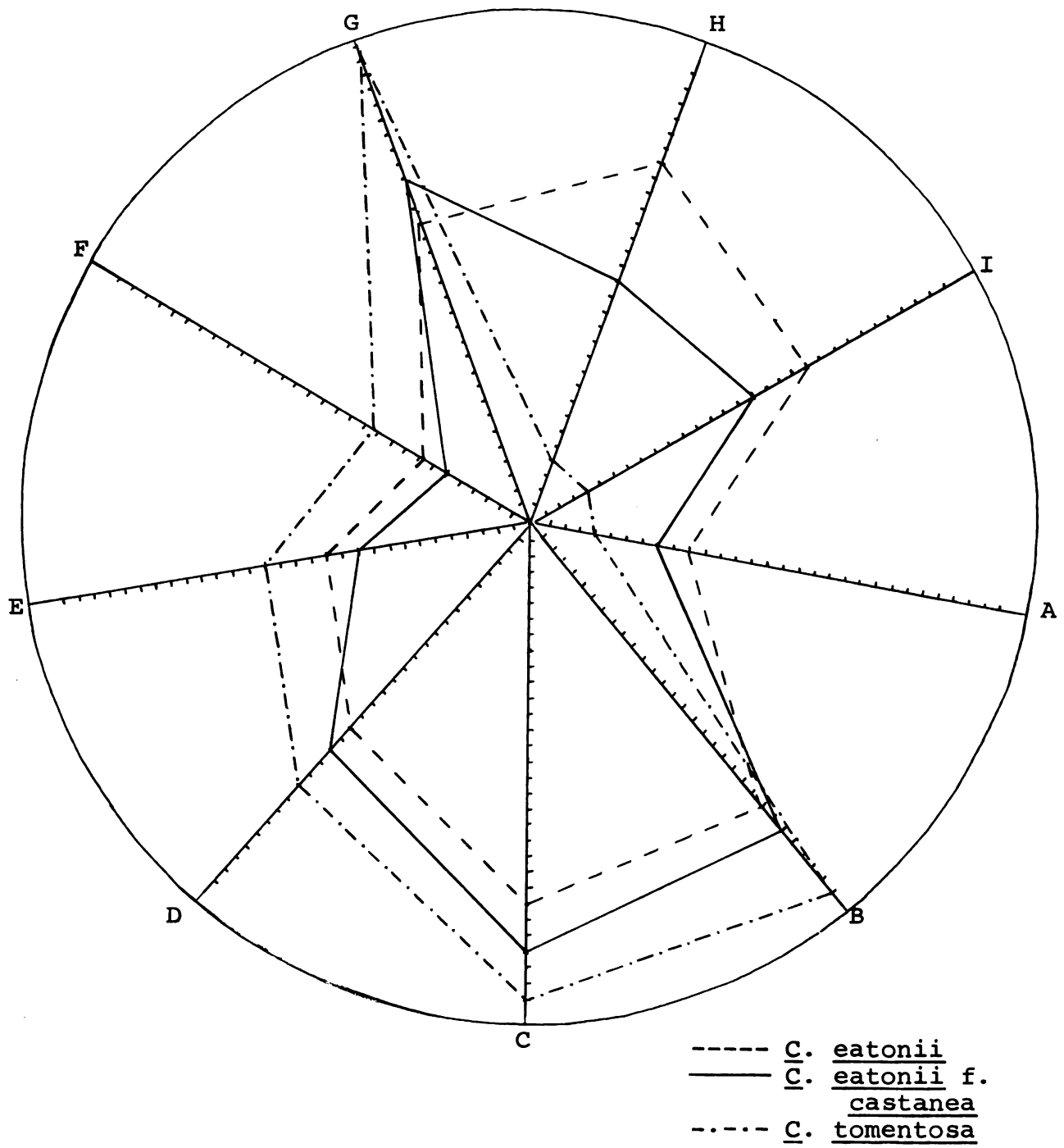


Figure 4

Figure 5. Cheilanthes eatonii polygonal graph

- A. - Large scale stipe width, scale 4 units = .1 mm
- B. - Large scale stipe length, scale 1 unit = .1 mm
- C. - Large scale rachis length, scale 1 unit = .1 mm
- D. - Large scale pinna midrib length, scale 1 unit = .1 mm
- E. - Ratio stipe length: blade length, scale 1 unit = .1
- F. - Blade width, scale 3 units = 1 cm
- G. - Frond length, scale 1 unit = 1 cm
- H. - Large scale pinna midrib width, scale 4 units = .1 mm
- I. - Large scale rachis width, scale 4 units = .1 mm

Figure 6. Cheilanthes eatonii f. castanea polygonal graph

- A. - Large scale stipe width, scale 4 units = .1 mm
- B. - Large scale stipe length, scale 1 unit = .1 mm
- C. - Large scale rachis length, scale 1 unit = .1 mm
- D. - Large scale pinna midrib length, scale 1 unit = .1 mm
- E. - Ratio stipe length: blade length, scale 1 unit = .1
- F. - Blade width, scale 3 units = 1 cm
- G. - Frond length, scale 1 unit = 1 cm
- H. - Large scale pinna midrib width, scale 4 units = .1 mm
- I. - Large scale rachis width, scale 4 units = .1 mm

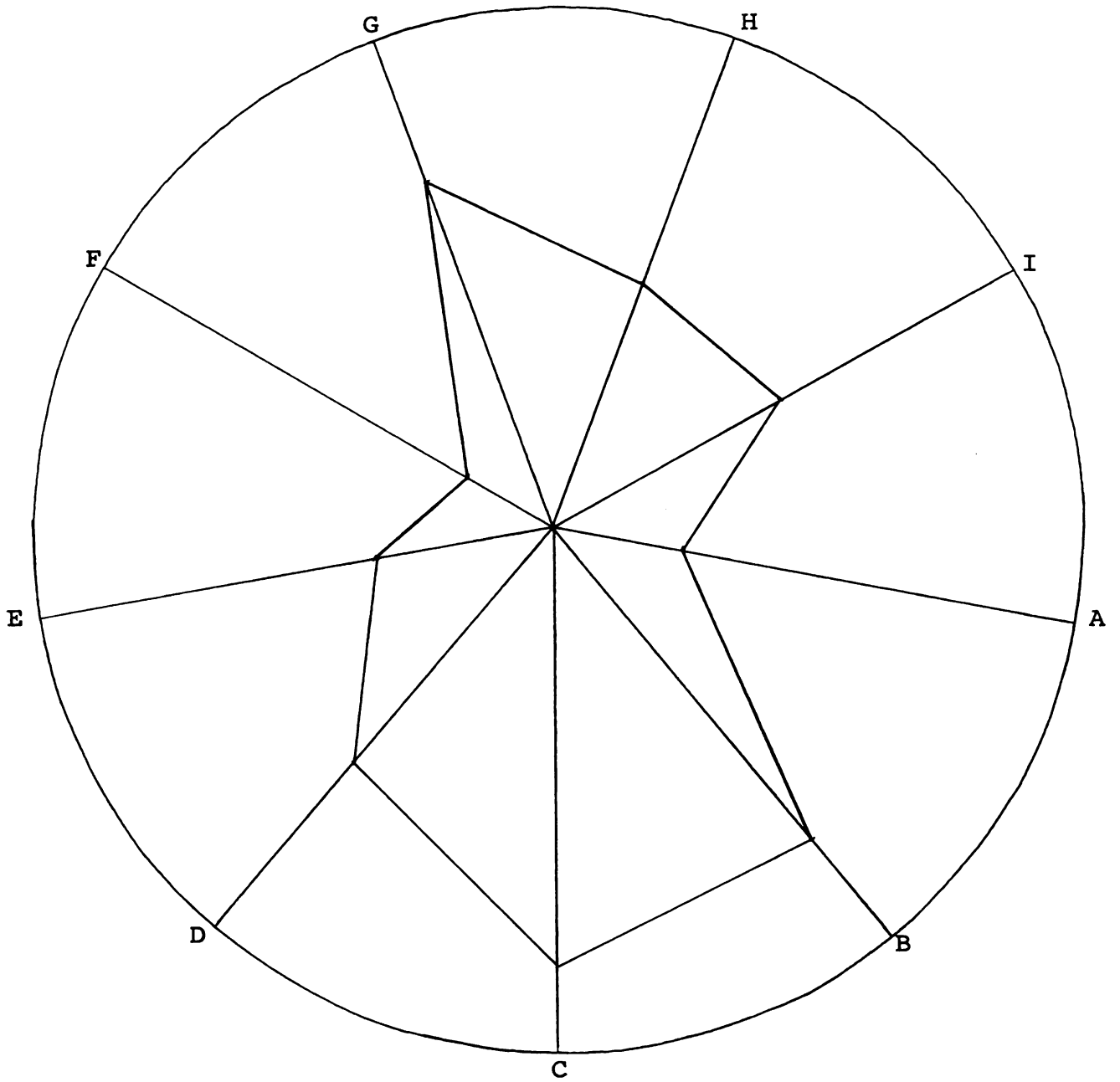


Figure 6

Figure 7. Cheilanthes tomentosa polygonal graph

- A. - Large scale stipe width, scale 4 units = .1 mm
- B. - Large scale stipe length, scale 1 unit = .1 mm
- C. - Large scale rachis length, scale 1 unit = .1 mm
- D. - Large scale pinna midrib length, scale 1 unit = .1 mm
- E. - Ratio stipe length:blade length, scale 1 unit = .1
- F. - Blade width, scale 3 units = 1 cm
- G. - Frond length, scale 1 unit = 1 cm
- H. - Large scale pinna midrib width, scale 4 units = .1 mm
- I. - Large scale rachis width, scale 4 units = .1 mm

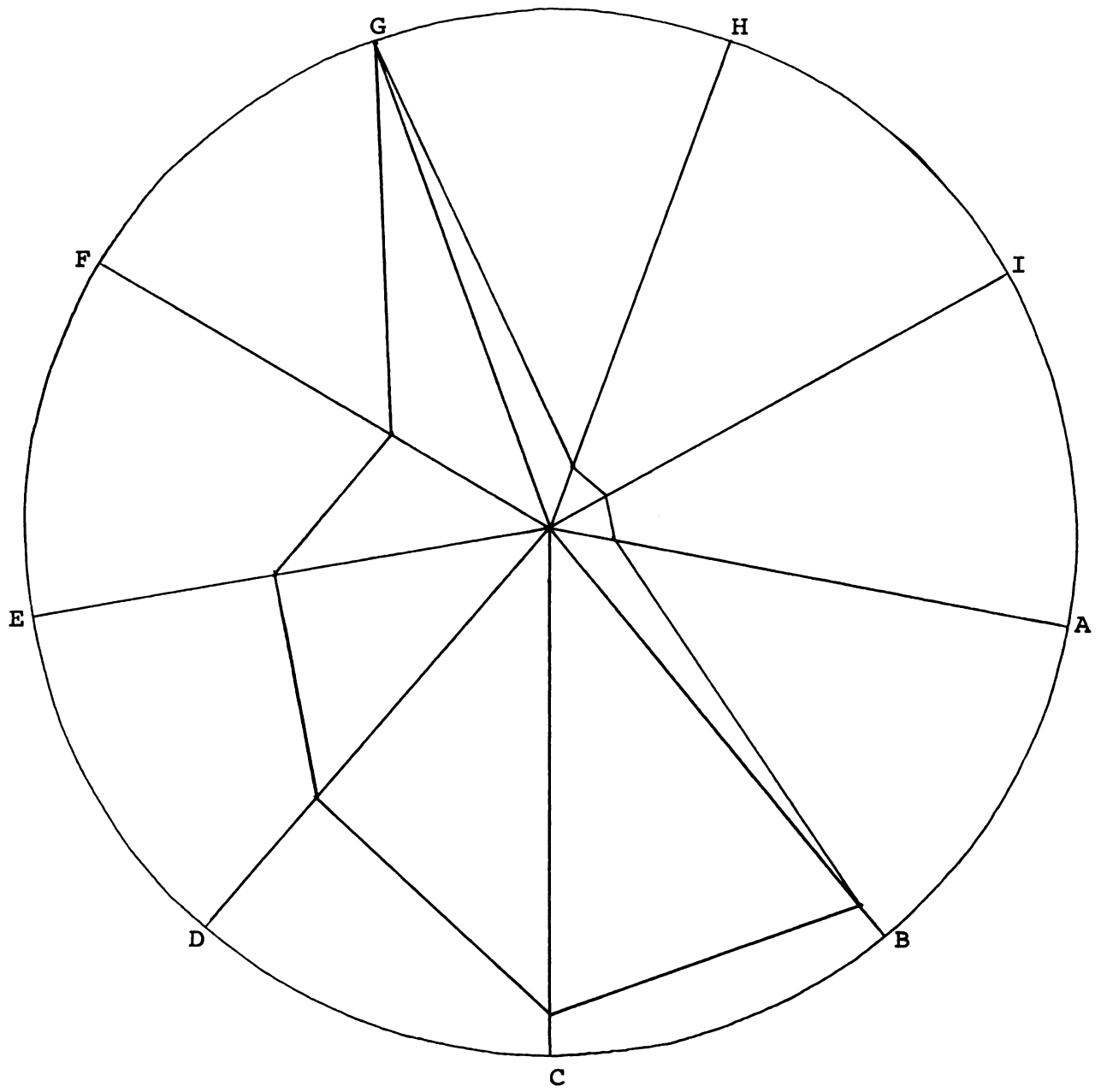


Figure 7

that C. eatonii and C. eatonii f. castanea are very closely related to one another while C. tomentosa is much more distantly related. It seems evident that C. tomentosa can definitely be considered distinct from the other taxa.

C. eatonii appears also to be distinctive enough in its characteristics to be a good species. Maxon (1919) felt that "the characters distinguishing the two species (C. tomentosa and C. eatonii) are constant and quite sufficient for their immediate recognition. He summarized the distinguishing characteristics as follows:

C. tomentosa

Stipe and rachises rather copiously clothed with lax tawny hairs and numerous subflexuous, twisted, nearly filiform, laxly spreading scales, these mostly persistent and at length forming a loose or matted tomentum; broad scales wholly wanting.

Segments copiously but rather loosely tomentose beneath, delicately villous-tomentulose above with long, twisted, flexuous hairs, the segments not bound together by an intricate hairy covering.

Herbaceous margin of the segments deeply recurved, abruptly modified to a rather broad, white, distinctly membraneous proper indusium.

C. eatonii

Stipe, primary rachis, and lower side of secondary rachises imbricate-paleaceous; relatively large, flat, oblong-lanceolate, ascending scales of stipe and primary rachis underlaid by numerous, appressed, minute, acicular, rigid ones; scales of secondary rachises ovate-acuminate, mainly imbricate, flaccid.

Segments densely matted-tomentose beneath, copiously and rather coarsely tomentose above, the entangled hairs of both surfaces closely enveloping and joining the fragile segments.

Herbaceous recurved margin of the segments less abruptly and completely modified, the narrow, whitish, membraneous border forming a very scant true indusium.

There are additional characters found in the greater size of C. tomentosa, its more spreading and dissected pinnae, and the shape, number, and relative position of the segments; but these variable features are so dependent upon age, vegetative vigor, and seasonal condition as to be scarcely of diagnostic importance.

In the paper in which Maxon (1919) originally described C. castanea (C. eatonii f. castanea) he stated:

The relationship of C. castanea is apparently with C. Eatonii, from which species it differs sufficiently in its fewer and several times larger segments, these glabrate above and separate, not closely enveloped and held together by a mass of entangled hairs arising from both surfaces as in C. Eatonii. The scales of the rachises are quite different in character also.

After comparing many specimens of these two taxa, this investigator has found that the character of "fewer and several times larger segments" of C. castanea (C. eatonii f. castanea) is not constant. The segments of this taxon and C. eatonii often appear very similar in size and number of segments. Therefore, this is not a satisfactory character. In addition, the statement that "the scales of the rachises are quite different in character" is a vague statement. As previously mentioned, the scales of C. eatonii and C. eatonii f. castanea are very similar to one another yet both are distinctively different from those of C. tomentosa. The scales of C. eatonii f. castanea appear to be only a variation or modification of those of C. eatonii. Thus, it does not seem that C. castanea merits specific rank but would be better classified as a forma. According to Lawrence (1951) forma "is generally applied to trivial variations occurring among

individuals of populations." Correll (1949) transferred the taxon from the rank of species to that of forma, placing those plants which have "all or part of their fronds tending to be glabrescent on the upper surface of their segments into f. castanea . . . those plants with segments hoary and densely tomentose above as the typical form." The evidence from this study supports Correll's placement of this taxon at the rank of forma.

Further evidence that the two taxa mentioned above should be regarded as parts of a single species is provided by the chromosome numbers which Knobloch (pers. comm.) reports as $2n = 87$ (C. eatonii - Knobloch 63-49B and C. eatonii f. castanea - Knobloch 63-30 and 63-49D). This contrasts with C. tomentosa in which $2n = 90$ (Knobloch, 1966, and unpublished; C. tomentosa - Knobloch 63-60, 64-16, and 2048A). Since the basic number of Cheilanthes is $x = 29$ or 30 (Wagner, 1963), the three taxa in this study must be triploids. It appears likely that each of them is a triploid hybrid resulting from a tetraploid crossing with a diploid. The apogamous reproduction with viable spore production may provide a mechanism for perpetuating the hybrid genotypes. Apogamy, however, is not a simple genetic mechanism of Mendelian inheritance, but involves a balance of morphological, cytological, physiological, and genetical phenomena.

A comparable situation is found in many apomictic angiosperms as Swanson (1952) indicates in the following statement:

From an evolutionary point of view, apomixis presents a complex and exceedingly difficult problem. With hybridization, polyploidy, and apomixis tending to confuse the clear-cut differences between species, the taxonomist is confronted with a problem that is well-nigh insoluble unless cytological data are at hand. This is particularly true since the apomicts, despite the prevalence of maternal inheritance, are highly polymorphic because of the occasional successful sexual reproductions. Many of the sexual offspring of apomicts are weak (Clausen 1954), but each little variant, despite its irregular genic or chromosomal background, possesses the potentiality for preservation, leading to what have been termed agamic complexes. These are found in such genera as Crepis, Taraxacum, Hieracium, Rubus, Potentilla, Poa, and Parthenium, and all are known as taxonomically difficult groups.

Taxonomists have tended to describe these variants as micro-species.

Since C. eatonii and C. eatonii f. castanea reproduce asexually, each individual is genetically isolated from every other one. Therefore, it seems logical that no clear distinction should be made between the two taxa since there may be a slight variation from individual to individual, thus giving a continuum from the typical C. eatonii at one end of the scale to the typical C. eatonii f. castanea at the other end of the scale. These taxa may be part of a hybrid swarm. Sexual species, each probably having distinct characters, have yet to be reported for these two taxa. However, this possibility does exist since several other species in the genus Cheilanthes have been found to have both sexual and asexual members (Knobloch, unpublished).

Several members of Cheilanthes appear to be closely related to the taxa of this study. Cheilanthes wootonii Maxon

has a $2n = 116$ (Knobloch, unpublished) and thus a tetraploid. Its fronds are somewhat similar to the taxa included here. This taxon also has long scales which gradually taper toward the tip and have a broad cordate base. Cheilanthes lanosa (Michx.) D. C. Eaton has a $2n = 30$ and is thus a diploid. It is similar in appearance to C. tomentosa but lacks scales. The rachis, stipe, and pinna midrib are covered with hispidulous articulate hairs. The lower surface of the fronds is pubescent with light brown hairs while the upper surface is only sparsely pubescent. Cheilanthes lindheimeri (J. Smith) Hook. has fronds similar in shape to the taxa of this study and broad-based scales which gradually taper toward the tip. The upper and lower surfaces are matted with long narrow white hairs. Cheilanthes fendleri Hook has scales similar to those of C. eatonii f. castanea and is similar in general frond shape, the upper surface being glabrous.

Cheilanthes wootonii, C. lindheimeri, C. fendleri, and C. lanosa may be involved in the ancestry of the taxa included in this study. Further investigations are needed to provide a better understanding of the role of apogamy and hybridity in the formation of such taxa as C. tomentosa, C. eatonii, and C. eatonii f. castanea.

PLATES

PLATE I

C. tomentosa

FIGS.

1. Rhizome scale - tip
2. Rhizome scale - base

C. eatonii f. castanea

FIGS.

3. Rhizome scale - tip
4. Rhizome scale - base

C. eatonii

FIGS.

5. Rhizome scale - tip
6. Rhizome scale - base

C. eatonii

FIG. 7. Spore

C. tomentosa

FIG. 8. Spore

C. eatonii f. castanea

FIG. 9. spore

PLATE I

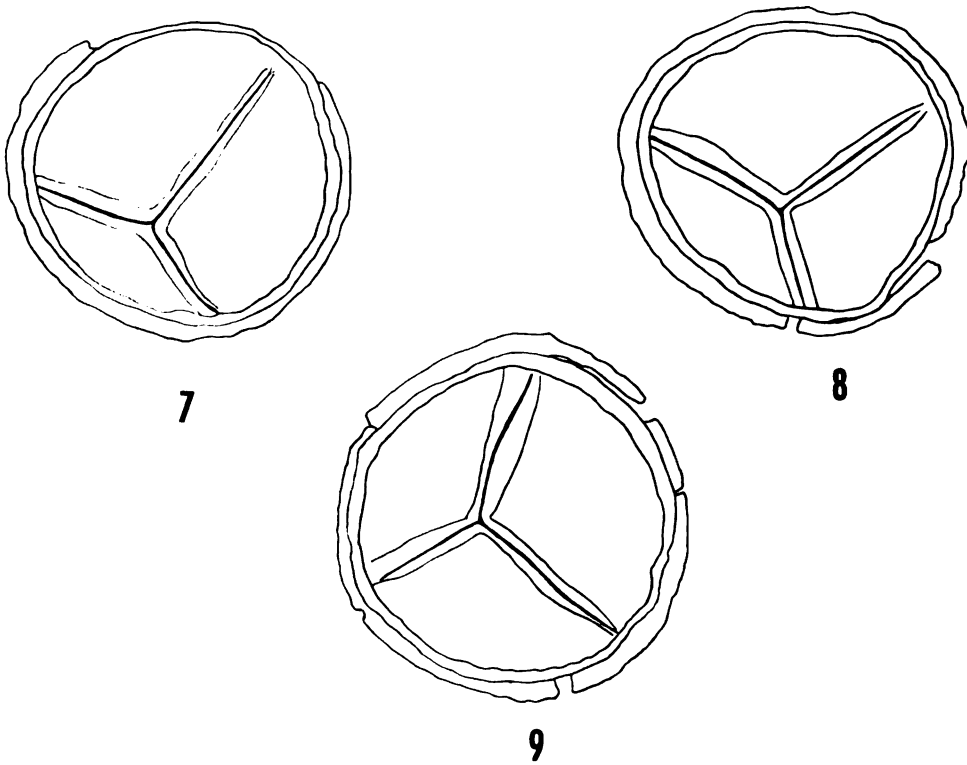
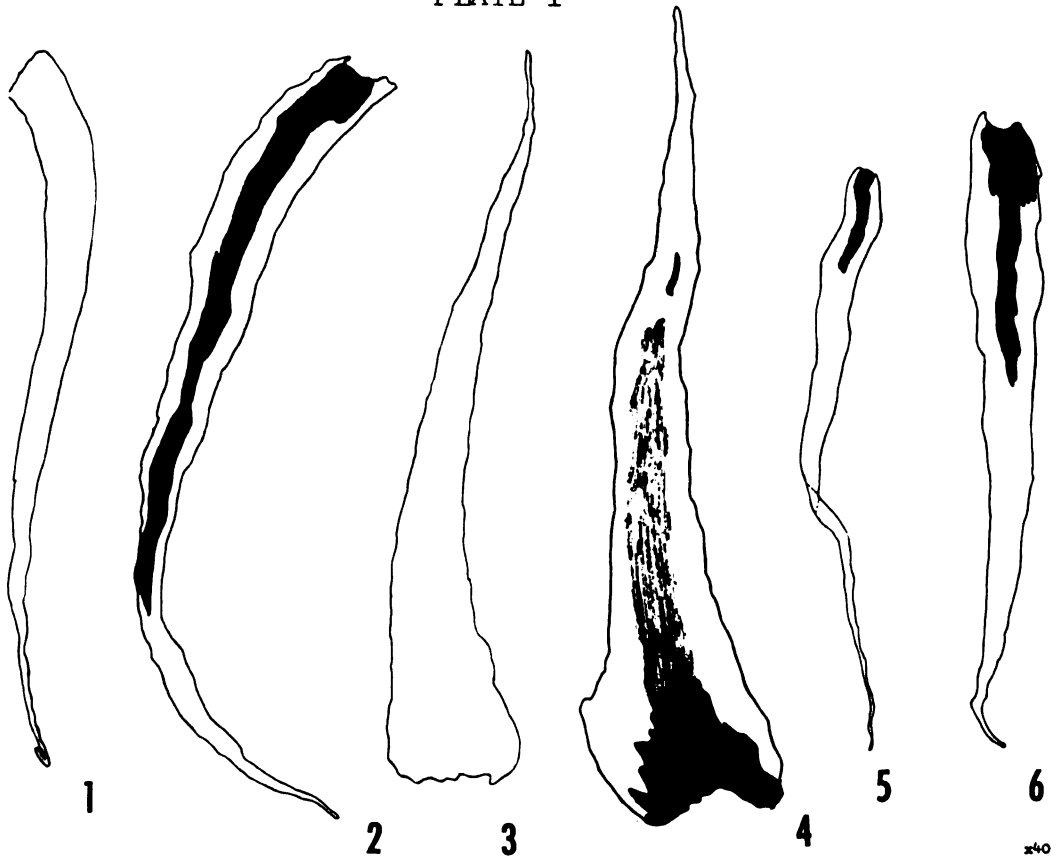
 10μ

PLATE II

C. tomentosa

FIGS.

1. Gametophyte with young apogamous sporophyte
2. Gametophyte with antheridia
3. Wing of thallus with additional filamentous
thalli

C. eatonii f. castanea

FIGS.

4. Gametophyte with young apogamous sporophyte
5. Gametophyte with antheridia
6. Wing of thallus with additional filamentous
thalli

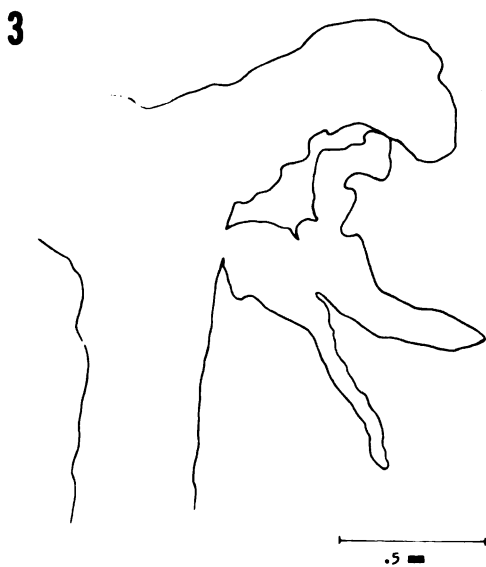
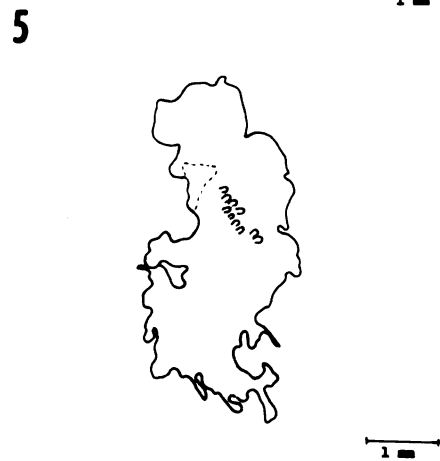
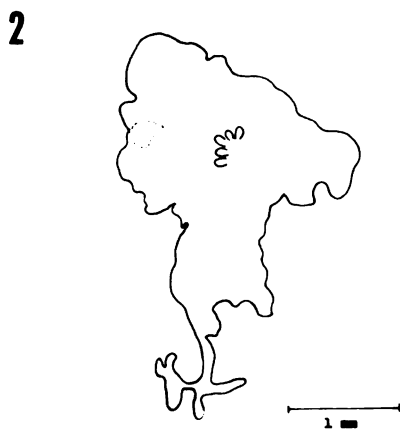
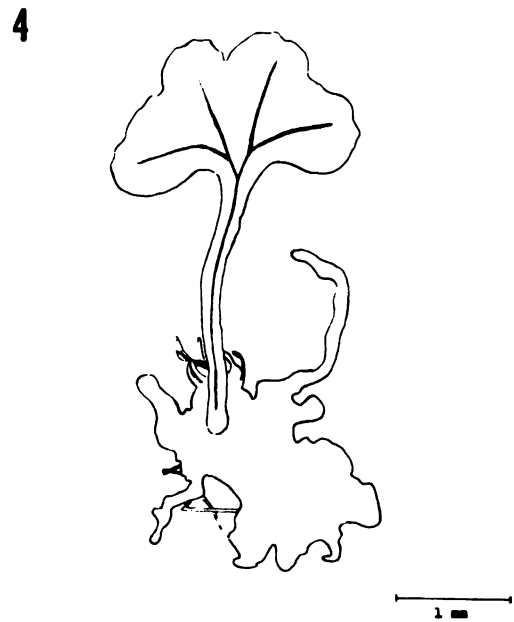
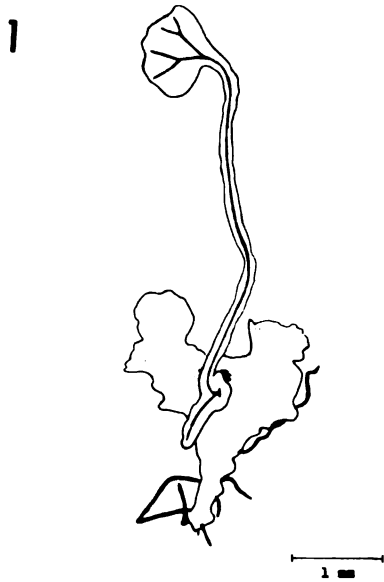


PLATE III

FIGS.

1. Cheilanthus eatonii (Robert M. Stewart 1112)
2. Cheilanthus eatonii (D. S. Correll 23291)

LUNDELL
HERBARIUM

MEXICO: eastern Cordillera
Robert M. Brown, no. 1117 Aug. 9, 1911
Chalchicomula, eastern slope
alt. 5,000 ft.
Specimens on the lower
branches of cliffs, rarely common
Plants of Santa Clara, Mexico, collected in eastern
 foothills of the Sierra de las Cruces.

Figure 1

LUNDELL
HERBARIUM

9.54 cm

Figure 2

PLATE IV

FIGS.

1. Cheilanthes eatonii f. castanea (D. S. Correll 13718A)
2. Cheilanthes eatonii f. castanea (B. H. Warnock 20891)



Figure 1



Figure 2

PLATE V

FIGS.

1. Cheilanthes tomentosa (Rogers McVaugh 8355)
2. Cheilanthes tomentosa (H. B. Parks s. n.)



Figure 1



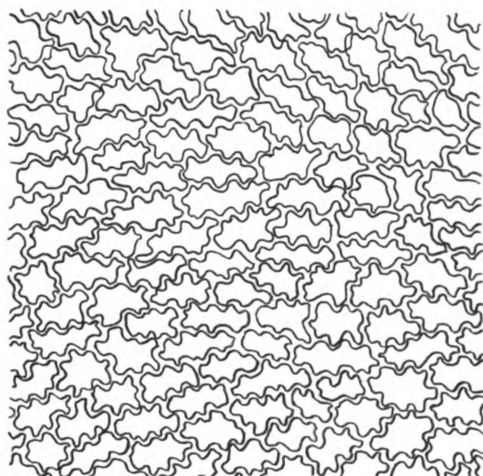
Figure 2

PLATE VI

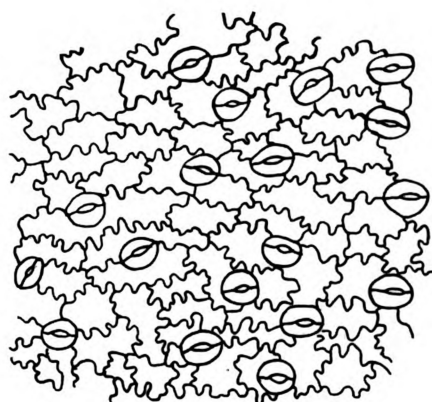
FIGS.

1. C. eatonii (Knobloch 752) upper epidermal cells
2. C. eatonii (Knobloch 752) lower epidermal cells
3. C. eatonii f. castanea (Knobloch 63-30) upper epidermal cells
4. C. eatonii f. castanea (Knobloch 63-30) lower epidermal cells
5. C. tomentosa (Knobloch 63-60) upper epidermal cells
6. C. tomentosa (Knobloch 63-60) lower epidermal cells

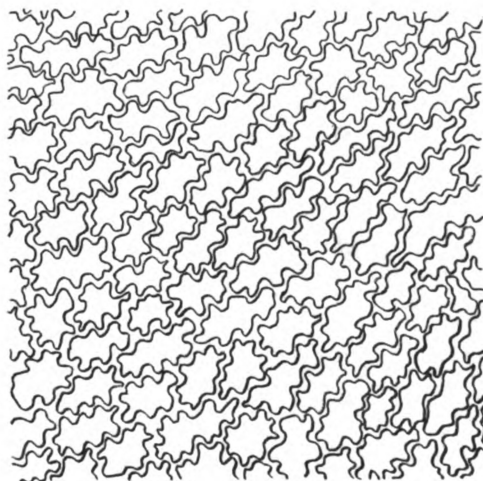
PLATE VI



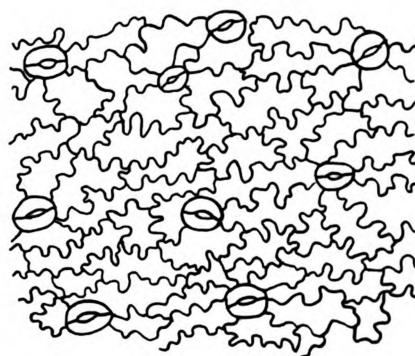
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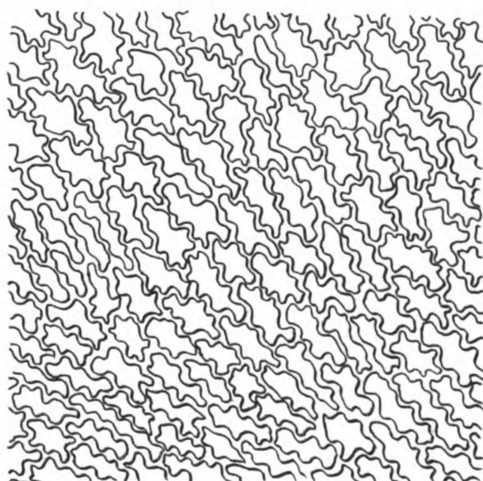
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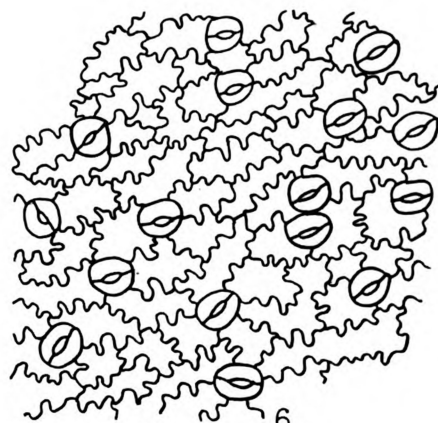
3



4



5



6

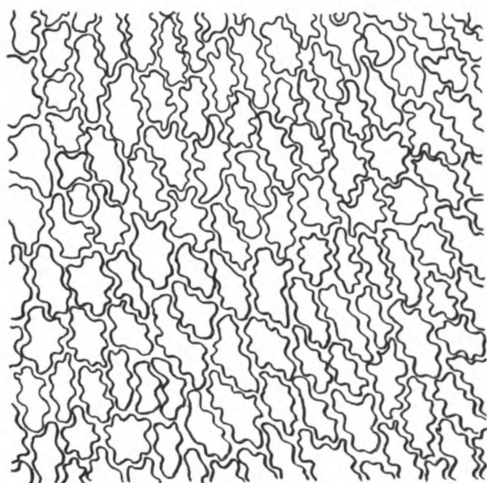
 100μ

PLATE VII

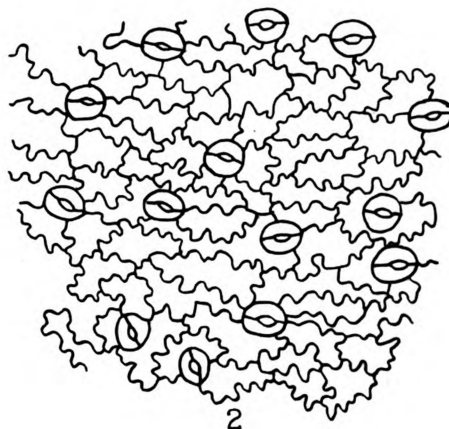
FIGS.

1. C. eatonii (Knobloch 63-49B) upper epidermal cells
2. C. eatonii (Knobloch 63-49B) lower epidermal cells
3. C. eatonii f. castanea (Knobloch 64-21) upper epidermal cells
4. C. eatonii f. castanea (Knobloch 64-21) lower epidermal cells
5. C. tomentosa (Knobloch 2048) upper epidermal cells
6. C. tomentosa (Knobloch 2048) lower epidermal cells

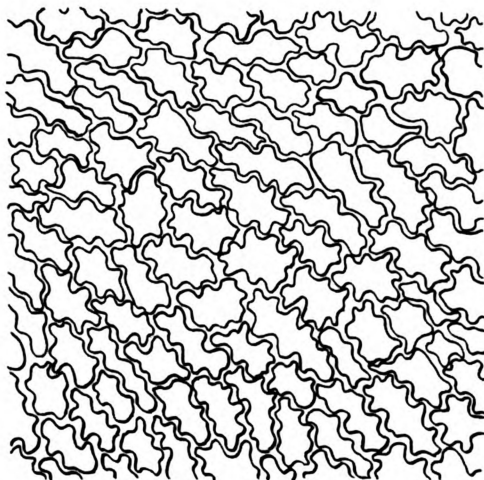
PLATE VII



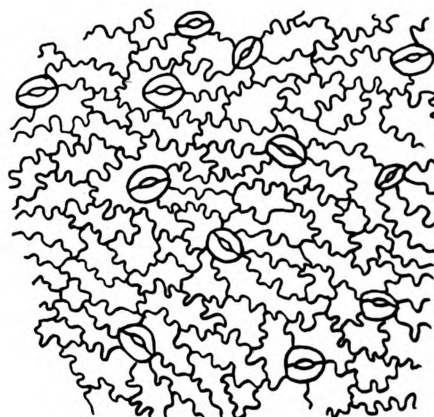
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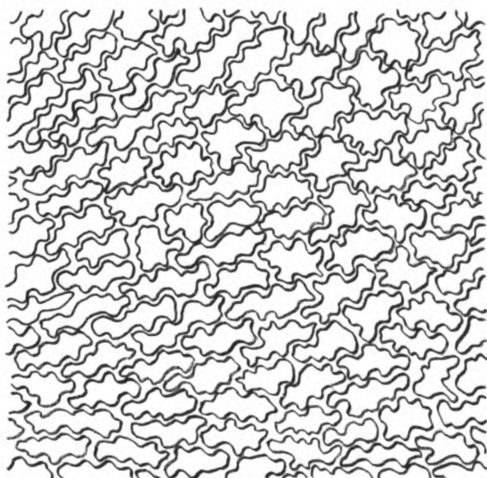
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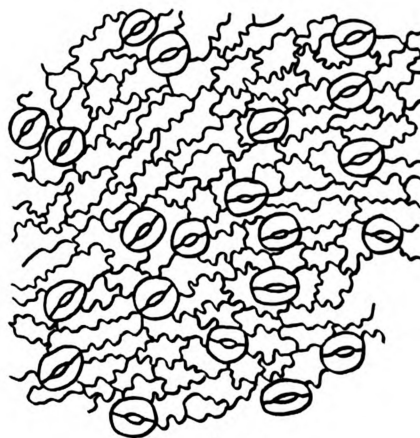
3



4



5



6

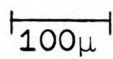
100 μ

PLATE VIII

C. tomentosa

FIGS.

1. Large stipe scale
2. Large rachis scale
3. Pinna midrib scale

C. eatonii f. castanea

FIGS.

4. Large stipe scale
5. Large rachis scale
6. Pinna midrib scale

C. eatonii

FIGS.

7. Large stipe scale
8. Large rachis scale
9. Pinna midrib scale

PLATE VIII

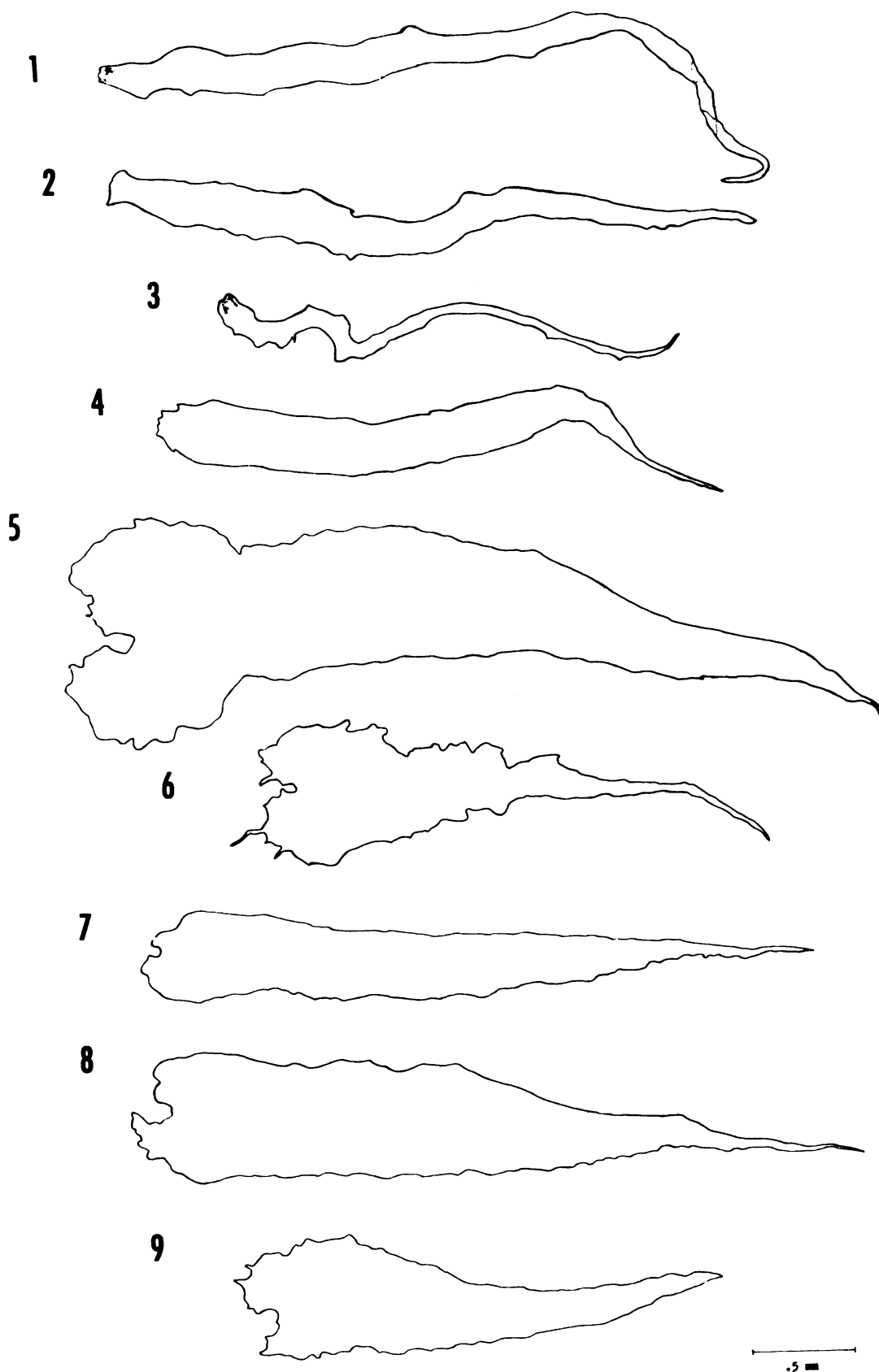


PLATE IX

C. eatonii f. castanea

FIGS.

1. Pinna midrib hair
2. Rachis hair
3. Small rachis hair
4. Stipe hair
5. Small stipe scale

C. eatonii

FIGS.

6. Pinna midrib hair
7. Rachis hair
8. Small rachis hair
9. Stipe hair
10. Small stipe scale

PLATE X

C. tomentosa

FIGS.

1. Small rachis hair
2. Rachis hair
3. Small stipe hair
4. Stipe hair
5. Pinna midrib hair

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APPENDIX

APPENDIX

Specimens examined - Table III, Frond Measurements*

Cheilanthes eatonii

UNITED STATES. Arizona: Cochise Co., limestone hill near Dos Cabezas, W. S. Phillips 2925 (US); Graham Co., Arivaipa Canyon in "The Box," W. S. Phillips 2948 (US).

Colorado: El Paso Co., 17 mi. south of Colorado Springs, dry sandstone ledges east of highway south of Deadman Canyon, E. T. Wherry s. n. (US); Las Animas Co., near Troy, C. M. Rogers 4902 (US).

New Mexico: between Anton Chico and mouth of Gallinas River, J. N. Rose 17674 (US); Sandis Mts., C. L. Herrick 987 (US).

Oklahoma: Cimarron Co., 4 mi. north of Kenton, E. T. Wherry s.n. (US).

Texas: Brewster Co., Chisos Mts., summit of Mt. Emory, D. S. Correll 13685 (LL); mountain side of Green Gulch, C. L. Lundell 13212 (LL); Mt. Emory, D. S. Correll 13647 (LL); Green Gulch, D. S. Correll 13664 (LL); near summit of Mt. Emory, D. S. Correll 13688 (LL); Basin, Chisos Mts., D. S. Correll 13615 (LL); Big Bend National Park, Cattail Falls, D. S. Correll and H. B. Correll 30604 (LL); Basin, Chisos Mts., D. S. Correll 13614 (LL); alpine, G. M. Soxman 231 (US); top of Pulliam Bluff Canyon, B. H. Warnock 1102 (US); Culberson Co., Sierra Diablo Mts., near summit of Victoria Peak, D. S. Correll 13773 (LL); 10 mi. north of Van Horn, Beach Mt., D. S. Correll 13980 (LL); Sierra Diablo Mts., Victoria Canyon, D. S. Correll 13768 (LL); Guadalupe Mts., mt. stream above Pine Springs Camp, D. S. Correll 13884 (LL); El Paso Co., Hueco Mts., Hueco Tanks, D. S. Correll 13792 (LL); base of ledges, Hueco Tanks, D. S. Correll 15095 (LL); Hueco Mts., Hueco Tanks, D. S. Correll 13807 (LL); Hudspeth Co., H. B. Parks s. n. (LL); Sierra Tinaja Pinta, Cornudas Range, D. S. Correll and H. B. Correll 24705A (LL); H. B. Parks s. n. (LL); Jeff Davis Co., Davis Mts., summit of Sawtooth Mt., D. S. Correll 15019 (LL); Morris Co., Daingerfield State Park, D. S. Correll and H. B. Correll 12480 (LL); Presidio Co., 8 mi. NW of Shafter, D. S. Correll 13747, 13738, and 13739 (LL); Val Verde Co., near Langtry, Pump Canyon, D. S. Correll and H. B. Correll 12913 and 12912 (LL); 100 mi. east of El Paso, Guadalupe canyon, C. L. Hitchcock 4314 (LL).

*Table III is listed first because it includes most of the specimens examined for morphological comparisons and, therefore, the specimens repeated are listed only by collector and number in the tables which follow Table III.

MEXICO. Chihuahua: 6 mi. SE of Sacramento, route #45, D. S. Correll and I. M. Johnston 21749 (LL); 5.5 mi. NW of Parral, D. S. Correll and H. S. Gentry 22716 (LL); 8 mi. NW of Parral, Minas Nuevas, D. S. Correll and H. S. Gentry 22749 and 22748 (LL); between Yepomera and Babicora, D. S. Correll and I. M. Johnston 21625 (LL); 15 mi. south of Encinillas, D. S. Correll 23291 (LL); 4 mi. SW of Villa Matqumoros, Sierra de Santa Barbara, D. S. Correll and H. S. Gentry 22788 (LL); 12.7 mi. SW of Chihuahua on road to Cuahtemos, T. Soderstrom 916 (LL).

Coahuila: 16 mi. west of Saltillo, R. C. Rollins and R. M. Tyron 58307 (US); Sierra de San Antonio, canyon at San Antonio de los Alamos, I. M. Johnston and C. H. Muller 903 (LL); Pichacho de San Jose, eastern foothills of Sierra de las Cruces, R. M. Stewart 1112 (LL); 1 mi. south of Carricito north facing ledge of basalt, I. M. Johnston and C. H. Muller 162 (LL).

Durango: Durango and vicinity, E. Palmer 893 (US).

San Luis Potosi: Charcus, C. L. Lundell 5790 (US).

Tamaulipas: Marcela, Stanford, Lauber, and Taylor 2716 (US); 4 kilo. west of Miquihauana in canyon, L. R. Retherford and R. D. Northcraft 676 (US).

Zacatecas: 34 mi. north of Fresnillo, R. C. Rollins and R. M. Tyron 58257 (US); north slopes, E. E. Lloyd s. n. (US).

Cheilanthes eatonii f. castanea

UNITED STATES. Arizona: Cochise Co., Huachuca Mts. Miller Canyon, W. S. Phillips 2801 (US).

New Mexico: Carlsbad Caverns, V. Bailey s. n. (US).

Oklahoma: Canadian Co., Devil's Canyon, E. L. Little, Jr. 3882 (US).

Texas: Brewster Co., Chisos Mts., Green Gulch, D. S. Correll 13662, 13663, and 13667 (LL); Chisos Mts., north slope of Mt. Emory, D. S. Correll 13679, 13682, and 13654 (LL); Chisos Mts., Mt. Emory, in Basin, D. S. Correll 13646 (LL); Chisos Mts., near Basin, D. S. Correll 13642 and 13626 (LL); Chisos Mts., rimrock, C. H. Mueller s. n. (LL); Chisos Mts., Boot Canyon, D. S. Correll 13718A (LL); Chisos Mts., C. H. Mueller 8254 (US); Old Blue Glass Mts., B. H. Warnock 20892 (LL); Glass Mts., Gage Ranch, B. H. Warnock 20891 (LL); NE side Mt. Ord, Gage Estate, 11 mi. south of Alpine, B. H. Warnock and R. McVaugh s. n. (LL); Culberson Co., Guadalupe Mts., SE slope of Pine Top Mt., D. S. Correll 13909 and 13887 (LL); Sierra Diablo Mts., Victoria Canyon, D. S. Correll 13758 (LL); Guadalupe Mts., Guadalupe Canyon, D. S. Correll 13849 (LL); Jeff Davis Co., Davis Mts., Sawtooth Mt., D. S. Correll 15018 (LL); 10 mi. NW of Fort Davis, Sprowles Ranch, D. S. Correll 13560 (LL); Davis Mts., Limpia Canyon, C. L. Lundell and A. A. Lundell 14253 (LL); 10 mi. SE of Fort Davis,

tributary of Musquiz Canyon, D. S. Correll 13491A (LL); Morris Co., Daingerfield State Park, D. S. Correll and H. B. Correll 12438 (LL); Presidio Co., 8 mi. NW of Shafter, vicinity of "Elephant Rocks," D. S. Correll 13748 (LL).

MEXICO. Chihuahua: other side of mts. to west from San Francisco de Oro, Arroyo de Granadeña, T. Soderstrom 885 (LL); 15 mi. south of Encinillas, base of cliffs in canyon of large mt. mass west of route #45, D. S. Correll 23285 (LL).

Coahuila: edges of Carneros Pass, C. G. Pringle 2777 (LL); Saltillo, Cañon de S. Lorenzo, P. Lyonnet 3488 (LL); 11 kilo. NE of Jimulco, L. R. Stanford, K. L. Retherford and R. D. Northcraft 43 (LL); 10 mi. north of camp at La Noria, Sierra del Pino, I. M. Johnston and C. H. Muller 553 (LL); 12 mi. west of Hacienda de la Encantada, Cañon de Milagro, east side of the Sierra de los Guajes, R. M. Stewart 1711 (LL).

Nuevo Leon: Hacienda Pablilla, Galeana, M. Taylor 139 (LL).

Cheilanthes tomentosa

UNITED STATES. Alabama: Chilton Co., ledges near Coosa River and between Mitchell Dam and Knight's Ferry, R. M. Harper 3576 (US); Cullmin Co., Mobile, C. Mohr s. n. (US).

Arizona: Santa Rita Mts., C. G. Pringle 239 (US); Bodoquivari Mts., L. N. Goodding s. n. (US).

Arkansas: Montgomery Co., D. Demaree 41757 (US).

Georgia: Lincoln Co., 4 mi. SW of Lincolnton, Graves Mt., R. L. Wilbur and G. L. Webster 2801 (US); near summit of Graves Mt., D. S. Correll and E. T. Wherry 11051 (US).

New Mexico: Organ Mts., E. T. W. s. n. (US).

North Carolina: Rutherford Co., rock ridge NW of Chimney Rock Village, E. Wherry s. n. (US).

Oklahoma: Johnston Co., 1 mi. east of Troy, D. S. Correll and H. B. Correll 25019 (LL); Comanche Co., Cache, E. J. Palmer 12588 (US).

South Carolina: Greenville Co., south side of Paris Mt., R. T. Clausen and H. Trapido 3658 (US).

Tennessee: Chilharvee Mts., A. Gattinger s. n. (US); Monroe Co., cliffs of Tellico River, A. N. Leeds s. n. (US).

Texas: Bandera Co., head of Sabinal Canyon, D. S. Correll and H. B. Correll 12824 (LL); Brewster Co., Chisos Mts., Green Gulch, D. S. Correll 13667A (LL); Emory Peak, in basin above Laguna, C. L. Lundell 14616 (LL); Big Bend National Park, Chisos Mts., Pine Canyon, D. S. Correll and D. C. Wasshausen 27872 (LL); Chisos Mts., Mt. Emory, in basin, D. S. Correll 13648 (LL); Chisos Mts., Cat-tail Falls, D. S. Correll and B. H. Warnock 14986 (US); Burnet Co., Inks Lake State Park,

C. L. Lundell 13492 (LL); rock crevices on Granite Mt. near Marble Falls, D. S. Correll 13419 (LL); granite rocks near Granite Mt., D. S. Correll and H. B. Correll 12736 (LL); Cherokee Co., just beyond Jim Hogg State Park, D. S. Correll and H. B. Correll 27191 (LL); Edwards Co., on bluffs along Pulliam Creek, near Real Co., D. S. Correll 15195 (LL); 12 mi. NW of Barksdale, "Blue Hole" on Cedar Creek, D. S. Correll 13452 (LL); Gillespie Co., 3 mi. north of Fredericksburg, Bare Face Rock, D. S. Correll 15235 (LL); Jeff Davis Co., 6 mi. SE of Fort Davis, tributary of the Musquiz Canyon, D. S. Correll 13502 (LL); Davis Mts., Madera Canyon, near Mt. Livermeor, E. J. Palmer 34289 (US); Davis Mts. upper slopes of Sawtooth Mt., D. S. Correll 15011 (LL); Llano Co., NE of Baby Head, Wilbern's Glen, D. S. Correll and H. B. Correll 12700 (LL); Palo Pinto Co., 5 mi. north of Santo, R. McVaugh 8355 (LL); Tyler Co., Angelina National Forest, east of Rockland, D. S. Correll 13309 (LL); Walker Co., Huntsville, H. B. Parks s. n. (LL).

Virginia: Natural Bridge Station, B. Long and E. B. Bartram s. n. (US).

West Virginia: 4 mi. SE of Charlestown, E. T. Wherry s. n. (US).

MEXICO. Chihuahua: Cuiteco, I. W. Knobloch 953 (MSC); 30 mi. south of Creel at Divisadero, I. W. Knobloch 847 (MSC); Moharachic, I. W. Knobloch 5972 (MSC).

Nuevo Leon: Monterrey, J. Sanchez VIII-48 (US); La Trinidad, Municipio De Montemorelos, C. H. Muller 2859 (LL); between Las Ajuntas and Potrero Redondo, Municipio Villa Santiago, C. H. Muller 2701 (LL); near Monterrey, ledges of Sierra Madri, C. G. Pringle 2603 (LL).

Sonora: Bavispe River, C. V. Hartman 360 (US).

Tamaulipas: San Jose, above La Vegonia, H. H. Bartlett 10050 (US).

Specimens examined - Table I. Spore diameter

Specimens previously listed under frond measurements are referred to only by collector and collection number.

Cheilanthes tomentosa

UNITED STATES. Alabama: Alabama Co., Blount Springs, I. W. Knobloch 2048 (MSC).

Arkansas: D. Moore s. l., s. n., accession no. 64-16 (MSC).

New Mexico: Carlsbad Caverns National Park, Guadalupe Mts., E. Castetter s. n., accession no. 63-60 (MSC).

Virginia: Ironto, I. W. Knobloch 1953 (MSC).

MEXICO. I. W. Knobloch 847 (MSC).

Cheilanthes eatonii

MEXICO. D. S. Correll and I. M. Johnston 21625 (MSC); D. S. Correll 23291 (MSC).

Chihuahua: Picacho de San Jose, R. M. Stewart 1112, I. W. Knobloch's accession no. 63-49B (MSC); in canyon SE of Hidalgo de Parral, I. W. Knobloch 752 (MSC).

Cheilanthes eatonii f. castanea

UNITED STATES. New Mexico: Carlsbad Caverns National Park, J. K. Baker s. n., accession no. 64-21 (MSC).

Oklahoma: Caddo Co., Caddo Canyons near Hinton, G. Goodman s. n., accession no. 63-49D (MSC).

Texas: Davis Mts., B. H. Warnock s. n., accession nos. 63-28 and 63-30 (MSC).

MEXICO. Lefebure 1161, accession no. 63-52 (MSC).

Specimens examined - Table II. Rhizome Scale Measurements

Cheilanthes tomentosa

UNITED STATES. Texas: Llano Co., Turkey Peak, D. S. Correll and H. B. Correll 12771 (LL); Gillespie Co., Bear Mt., H. B. Parks s. n. (LL); D. S. Correll and B. H. Warnock 14986 (LL); C. L. Lundell 14616 (LL); D. S. Correll and H. B. Correll 12700 (LL); C. H. Muller 2701 (LL).

Cheilanthes eatonii

MEXICO. Coahuila: San Jose, base of Sierra de las Cruces, I. M. Johnston and C. H. Muller 980 (LL).

C. L. Lundell 13212 (LL); D. S. Correll 13647, 13768, and 13739 (LL); C. H. Muller 162 (LL); H. B. Parks s. n. (LL); C. L. Hitchcock 4314 (LL).

Cheilanthes eatonii f. castanea

UNITED STATES. Texas: Brewster Co., north slope of Mt. Emory, Chisos Mts., D. S. Correll 13678 (LL).

MEXICO. Sierra de la Madera, Cañon del Agua, Cuatro Ciengas Municipiade, C. H. Muller 3252B (LL).

D. S. Correll 13642, 13682, 13748, and 13663 (LL); C. L. Lundell and A. A. Lundell 14253 (LL); C. G. Pringle 2777 (LL).

Specimens examined - Table IV. Measurements of Epidermal
Cells and Stomata

Cheilanthes tomentosa

MEXICO. Nuevo Leon: Cañon de San Francisco, I. W. Knobloch 1966 (MSC).

I. W. Knobloch 2048, and 847 (MSC); D. Moore s. n., accession no. 61-16 (MSC); E. Castetter s. n., accession no. 63-60 (MSC).

Cheilanthes eatonii

MEXICO. Chihuahua: El Kilo Mt., south of Juarez, I. W. Knobloch 2062 (MSC).

D. S. Correll and I. M. Johnston 21625 (MSC); R. M. Stewart 1112 I. W. Knobloch's accession no. 63-49B (MSC); I. W. Knobloch 752 (MSC); D. S. Correll 23291 (MSC).

Cheilanthes eatonii f. castanea

Lefebure 1161 (MSC); B. H. Warnock s. n., accession nos. 63-28 and 63-30 (MSC); G. Goodman s. n., accession no. 64-21 (MSC); J. K. Baker s. n., accession no. 63-49B (MSC).

Specimens examined - Table V. Larger Scale Measurements

Cheilanthes eatonii

D. S. Correll 23291 and 13739 (LL); T. Soderstrom 916 (LL); R. M. Stewart 1112 (MSC).

Cheilanthes eatonii f. castanea

B. H. Warnock 20891 (LL); D. S. Correll 13718A, 13682, and 23285 (LL).

Cheilanthes tomentosa

C. L. Lundell 14616 (LL); D. S. Correll and Wasshausen 27872 (LL); R. McVaugh 8355 (LL); C. H. Muller 2701 (LL).

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