

COMPARATIVE LEAF ANATOMY OF SOLIDAGO AND SEGREGATE GENERA BRACHYCHAETA,
BRINTONIA, CHRYSOMA, OLIGONEURON, AND PETRADORIA, (COMPOSITAE)

by

613-8302

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B.S., University of North Carolina at Chapel Hill, 1966

A MASTER'S THESIS

submitted in partial fulfillment of the

requirements for the degree

MASTER OF SCIENCE

Division of Biology

KANSAS STATE UNIVERSITY

Manhattan, Kansas

1973

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ACKNOWLEDGEMENTS

I would like to express my appreciation to all those who have helped me to prepare this thesis. I am particularly indebted to Dr. Loran C. Anderson, my major advisor, who suggested this problem and shared his knowledge of the goldenrod complex as well as his large personal collection of specimens and slides and who helped prepare the photographs for this paper.

Deserving special mention are Dr. T. M. Barkley and Dr. Jerry S. Weis for reading the manuscript and offering many invaluable suggestions. Miss Kathleen Smiley helped prepare some of the slides; Dr. Gary Morton provided specimens, read my manuscript, and made many helpful comments.

I would also like to thank the Kansas State University Herbarium and Farrell Library for their help in locating valuable materials.

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INTRODUCTION

The genus Solidago (tribe Astereae of the Compositae) consists of about 125 species. It is predominantly a North American genus, however a few species occur in South America and the Old World. Solidago, like many other Composites is a complex genus, due in part to extensive interspecific hybridization; however, apomixis is not known to be present.

The taxonomic status of the group under study has been variously interpreted by different authors. There are two general schools of thought: one interpretation places all the generic taxa Brachychaeta, Brintonia, Chrysoma, Euthamia, Oligoneuron, and Petradoria within the genus Solidago, based largely upon differences in floral morphology. The other interpretation segregates some or all of these genera, considering the differences in habit and vegetative morphology as important as those of floral morphology. Recently authors have considered cytological and anatomical studies as well. During the past century the generic taxa have been transferred in and out of Solidago by various authors to conform to their interpretation and philosophy of the group.

The present study was initiated to ascertain if any internal anatomic structures were consistent, particularly in the leaves. Stability of internal structures is generally conceded to be greater than that of superficial morphological features, which are more apt to reflect environmental differences. Therefore, anatomic features such as the vascular bundles, secretory canals and cavities, nonphotosynthetic storage parenchyma, and the bundle sheath extensions might be particularly useful to more accurately define the relationships of the several entities here considered.

HISTORY OF THE GROUP

The name Solidago was used by Linneaus in *Species Plantarum* (1753). Nuttall applied the name Euthamia as a subgenus of Solidago for a group of allied plants in 1818 when he published Genera of North American Plants. In 1840 he suggested that Euthamia and Chrysoma were both distinct genera from Solidago. Torrey and Gray (1842) transferred Euthamia back to Solidago. In 1876 Bentham and Hooker recognized Euthamia and Chrysoma as sections of Solidago, and they recognized Brachychaeta as a separate genus. Gray (1882) listed three sections of Solidago: Virgaurea (section Solidago according to current rules of nomenclature), Euthamia and Chrysoma, then in his 1884 *Flora*, Gray applied generic rank to Brachychaeta and retained his earlier idea of Virgaurea, Euthamia, and Chrysoma as sections of Solidago.

Greene (1894) treated Euthamia as a separate genus, and stated that N. L. Britton arrived at the same conclusion independently. Greene believed that Chrysoma and Brachychaeta were also distinct genera. In 1895, Greene placed Solidago pauciflosculosa in the genus Chrysoma, and placed Chrysoma pumila (considered a Solidago by some) in the new genus Petradoria. He established the new genus Brintonia to accomodate the plant known as Solidago discoidea.

Francis E. Lloyd (1901), in reporting the first major anatomical work done on Chrysoma, suggested that Chrysoma be considered a distinct genus. Britton (1907) recognized the genera Solidago, Euthamia, and Brachychaeta. In the seventh edition of *Gray's Manual* by Robinson and Fernald (1908), Brachychaeta and Solidago were assigned generic rank, but Euthamia and Virgaurea were retained as sections of Solidago. Small in his 1913 *Flora of the Southeastern United States* listed as separate genera Brintonia,

Brachychaeta, Chrysoma, Euthamia, Solidago, and the new genus Oligoneuron. Taylor (1915) followed Small in separating Euthamia from Solidago. B. F. Bush (1918) studied Euthamia in Missouri and concluded that Euthamia was distinct from Solidago, but he followed Fernald and left the plants in Solidago. Friesner (1933), Harris (1943), and Rosendahl and Cronquist (1945) also concurred with Fernald and left Euthamia in Solidago. Small in his 1933 edition retained all the genera found in his 1913 treatment. L. H. Shinnars worked with the Texas Euthamias in 1951, and recognized them as separate from Solidago. Cronquist in Gleason (1952) treated the group (Brachychaeta, Euthamia, Oligoneuron, and Virgaurea) as one genus Solidago. In some of his early work J. R. Beaudry, with D. L. Chabot (1959) recognized that the members of the section Euthamia had the same chromosome number as the Solidagos; but he stated that there might be other factors which would justify their separation. In Euthamia the base chromosome number of $X = 9$ is also the same as in most of the other *Astereae*.

B. M. Kapoor and Beaudry (1966) did an extensive karyological study in the group. Although chromosomal structure showed no marked distinctions among the various members of the goldenrod complex; the authors summarized morphological characters and concluded that the taxa were generically distinct from Solidago in varying degrees. They said that Oligoneuron was the weakest genus differing from Solidago only in habit. Euthamia has one more distinctive character and Petradoria, two more distinctive characters. Brachychaeta and Brintonia have the Solidago habit; but Brachychaeta has two, and Brintonia, three other characters that are distinctive from Solidago. They suggested that biologists might consider the group as one genus (Solidago) or as several, depending upon their personal concept of

the genus. They chose to consider the segregate taxa as distinct genera. Correll and Johnston (1970), following Shinnars (1951), also chose to segregate Euthamia from Solidago. Sieren (1970) in an unpublished doctoral dissertation made a study of the euthamoid goldenrods and concluded that Euthamia is a distinct genus.

Only limited anatomical data are available on the Solidago complex. Whitaker (1918), reported that stems of Euthamia graminifolia were divided into 5 parts between the rays; whereas Solidagos that she studied were roughly divided into 6 segments. Phillips (1963) in her anatomical studies of Chrysoma concurred with Lloyd's 1901 report that Chrysoma was distinct from Solidago. Anderson (1963) did an extensive study on the anatomy, cytology and taxonomy of Petradoria, and concluded that Petradoria should be a separate genus. He maintained that Petradoria is more closely allied to Haplopappus than to Solidago.

MATERIALS AND METHODS

Observations were made on sectioned materials prepared according to the general techniques of Sass (1958). Fresh materials from the field or greenhouse were fixed in formalin-propionic-alcohol. Dried materials were first treated in 2.5% aqueous NaOH to restore cell shape and size, then dehydrated and processed in the same manner as the fixed materials. Leaves were dehydrated in a graded tertiary butyl alcohol series, infiltrated, embedded in Paraplast, and sectioned at 12 μ . The staining schedule included mordanting with tannic acid followed by ferric chloride (Sass, 1958), and staining in Saffranin (1% in absolute alcohol) overnight. Slides were then counterstained with fast green, followed by orange green, passed to xylene and mounted in Permount. Whole leaves were cleared and stained in basic fuchsin according to Fuchs' technique (1963).

Fixed materials were graciously provided by Loran C. Anderson, James A. Pringle, Russell B. Miller, and Arnold van der Valk. Voucher specimens are located in the Kansas State University Herbarium unless otherwise stated. In the tables collections of Anderson and Creech are labeled A and C respectively.

Table I represents a compilation of all species studied and collection data. Observations were made on selected specimens representative of the groups under study.

Table 1. Source of Material

BRACHYCHAETA Britt.

Brachychaeta sphacelata (Raf.) Britt.IN: Monroe Co.: Potzger 2165.(Solidago sphacelata Raf.)

BRINTONIA Greene

Brintonia discoidea (Ell.) GreeneAL: Mohr in 1878.(Solidago discoidea (Ell.) T. & G.)

CHRYSOMA Nutt.

Chrysoma pauciflosculosa (Michx.) GreeneFL: Washington Co.: A. 3485;(Solidago pauciflosculosa Michx.)Bay Co.: A. 3487. AL:Baldwin Co.: A. 3488.EUTHAMIA Nutt. ex Cass.Euthamia galetorum Greene

NOVA SCOTIA: Yarmouth Co.:

(Solidago galetorum (Greene) Friesner)Fernald & Long 22732 (US);Queens Co.: Weatherby 7096 (US)Euthamia graminifolia (L.) Nutt.MI: Clinton Co.: A. 2153, A. 2175.(Solidago graminifolia (L.) Salisb.)MD: Montgomery Co.: A. 3507.Euthamia gymnospermoides GreeneKS: Reno Co.: A. 3440.(Solidago gymnospermoides (Greene) Fern.)Euthamia hirtepes (Fern.) Sieren ined.NC: Dare Co.: A. 3498.(X Solidago hirtepes Fern.)Euthamia leptcephala (T. & G.) GreeneTX: Brazos Co.: A. 3180.(Solidago leptcephala T. & G.)FL: Pasco Co.: A. 3472.Euthamia occidentalis Nutt.CO: Fremont Co.: A. 2786.(Solidago occidentalis (Nutt.) T. & G.)UT: Emory Co.: A. 2879.

Table 1 (continued).

| | |
|---|--|
| <u>Euthamia pulverulenta</u> Greene | TX: Brazos Co.: <u>A. 3181.</u> |
| (<u>Solidago texensis</u> (Friesner) | |
| <u>Euthamia remota</u> Greene | IN: Lake Co.: <u>Deam 1392</u> (US). |
| (<u>Solidago graminifolia</u> var. <u>remota</u> | |
| (Greene) S. K. Harris) | |
| <u>Euthamia tenuifolia</u> (Pursh) Nutt. | GA: Washington Co.: <u>A. 3451.</u> |
| (<u>Solidago tenuifolia</u> Pursh) | FL: Pasco Co.: <u>A. 3476.</u> |
| SOLIDAGO | |
| <u>Solidago alpestris</u> Waldst. & Kit. | POLAND: <u>Lilpop</u> (US). |
| <u>Solidago bigelovii</u> Gray | NM: Sierra Co.: <u>A. 3046.</u> |
| <u>Solidago caesia</u> L. | MI: Clinton Co.: <u>A. 2176.</u> |
| | IL: Effingham Co.: <u>A. 3503.</u> |
| <u>Solidago californica</u> Nutt. | CA: Plumas Co.: <u>Balls & Everett</u> |
| | <u>18128</u> (RSA). |
| <u>Solidago canadensis</u> L. | MI: Clinton Co.: <u>A. 2174.</u> |
| | KS: Riley Co.: <u>C. 527</u> , <u>C. 536.</u> |
| <u>Solidago flexicaulis</u> L. | MI: Clinton Co.: <u>A. 2156.</u> |
| <u>Solidago gigantea</u> Ait. | NC: Pasquotank Co.: <u>A. 3494.</u> |
| <u>Solidago hispida</u> | MI: Crawford Co.: <u>A. 2189.</u> |
| <u>Solidago juncea</u> Ait. | MI: Crawford Co.: <u>A. 2194.</u> |
| <u>Solidago macrophylla</u> Pursh | CANADA: Ontario: <u>Pringle 1276</u> (EAM). |
| <u>Solidago missouriensis</u> Nutt. var. | KS: Barton Co.: <u>A. 2580</u> ; Riley Co.: |
| <u>fasciculata</u> Holtz | <u>C. 525</u> , <u>C. 528</u> , <u>C. 529.</u> |
| <u>Solidago mollis</u> Bartl. | CO: Pueblo Co.: <u>A. 2796.</u> |

Table 1 (continued).

| | |
|--|---|
| <u>Solidago multiradiata</u> Ait. | CA: Inyo Co.: <u>A. 3393</u> . CO: Grand Co.: <u>A. 2646</u> . |
| <u>Solidago nemoralis</u> Ait. | MI: Crawford Co.: <u>A. 2188</u> . |
| <u>Solidago odora</u> Ait. | NC: Dare Co.: <u>A. 3496</u> , <u>A. 3499</u> . |
| <u>Solidago petiolaris</u> Ait. | KS: Riley Co.: <u>A. 2164</u> . |
| <u>Solidago petiolaris</u> Ait. var. <u>Wardii</u> (Britt.) Fern. | TX: Roberts Co.: <u>A. 2990</u> . |
| <u>Solidago pseudoyadkinensis</u> G. Morton ined. | NC: Martin Co.: <u>A. 3502</u> ; Beaufort Co.: <u>A. 3501</u> . |
| <u>Solidago radula</u> Nutt. | TX: Fayette Co.: <u>A. 3169</u> . |
| <u>Solidago rugosa</u> Ait. | MI: Crawford Co.: <u>A. 2192</u> . |
| <u>Solidago sempervirens</u> L. | NJ: Atlantic Co.: <u>Miller 7101</u> , <u>7102</u> . VA: Accomack Co.: <u>Miller 7103</u> . NC: Dare Co.: <u>A. 3497</u> ; <u>van der</u> <u>Valk 7101</u> , <u>7102</u> . |
| <u>Solidago simplex</u> HBK. | MEXICO: Hidalgo: <u>Beaman 2736</u> (US). |
| <u>Solidago sparsiflora</u> Gray | WY: Johnson Co.: <u>A. 2710</u> . |
| <u>Solidago spathulata</u> DC | NM: Taos Co.: <u>A. 2480</u> . |
| <u>Solidago spithmaea</u> M.A. Curtis | NC: Mitchell Co.: <u>Morton 3865</u> . |
| <u>Solidago stricta</u> Ait. | GA: Tatnall Co.: <u>A. 3457</u> . |
| <u>Solidago tortifolia</u> Ell. | FL: Duval Co.: <u>Curtis 6051</u> . |
| <u>Solidago affin. vaseyi</u> Heller | GA: Chattahoochee Co.: <u>A. 3100</u> . |
| <u>Solidago virgaurea</u> L. | OKINAWA: <u>Takamine 2239</u> (US). OKINAWA: <u>Amano 6852</u> (US). |

Table 1 (continued).

OLIGONEURON Small

Solidago houghtonii T. & G.MI: Cheboygan Co.: Pringle 1221

(apparently the combination of this
species as an Oligoneuron has not
been made; nonetheless it belongs
with this grouping of species)

(HAM).

Oligoneuron nitidum (T. & G.) SmallTX: Angelina Co.: Lundell 14047 (US).(Solidago nitida T. & G.)Oligoneuron ohioense (Riddell). G. N. JonesCANADA: Ontario: Pringle 1298 (HAM).(Solidago ohioensis Riddell)Oligoneuron riddellii (Frank) Rydb.CANADA: Ontario: Pringle 1259 (HAM).(Solidago riddellii Frank)Oligoneuron rigidum (L.) SmallKS: Riley Co.: C. 533, C. 535.(Solidago rigida L.)WY: Johnson Co.: A. 2709.

RESULTS

The names Brachychaeta, Brintonia, Chrysoma, Euthamia, Oligoneuron, Petradoria, and Solidago will be used for convenience of presentation, however no particular taxonomic status is implied. The major features of leaf anatomy are recorded in Table II. Leaf anatomy of Chrysoma has been reported by Lloyd (1901) and Phillips (1963). My observations generally confirm their interpretations; therefore only minimal reference will be made to Chrysoma anatomy. Minimal reference will be made to Petradoria, keeping in mind the anatomical study of Anderson (1963).

The epidermis of all collections examined consisted of one cell layer. Cuticle was present in all of the genera, but varied in thickness and relief among the genera. Euthamias had thinner cuticles 2.0 - 5.0 μ (usually 2.3), than the other taxa; and Oligoneurons were thicker at 7.0 - 16.0 μ . The thickest cuticles were found in the basal rosettes of Oligoneurons at 9.0 - 16.0 μ . The cuticle of Chrysoma was 2.3 μ , Brachychaeta, 2.2 μ ; and Brintonia, 2.0 μ . Solidagos ranged from 2.0 - 13.5 μ . Cuticular relief was found in some species as rounded to peaked ridges. There was no definite pattern of the ridges, except a tendency to be parallel to the midvein and major lateral veins. Stomata were found on both the abaxial and adaxial surfaces of the leaves. Stomates were always anomocytic (ranunculaceous) as described by Esau (1953) and oblong in paradermal sections. They were usually frequent over both leaf surfaces, except in Brintonia discoidea, Solidago canadensis, S. flexicaulis, S. gigantea, Oligoneuron riddellii, S. rugosa, and S. virgaurea where they more often occurred on the abaxial side close to the midveins. In Euthamias stomates were usually parallel to the midvein, but this may be explained by the relative narrowness of the leaves. Stomates in

the Solidagos, Oligoneurons, Brachychatea, and Brintonia sometimes were parallel to the midrib, but frequently were located at angles to the midrib. Substomatal chambers (Cutter, 1971), were largest in Oligoneuron, especially under the abaxial surface. The average width of the chambers was 50 - 90 μ and depth ranged from 50 - 80 μ . In O. ohioense, the chambers were much larger (width up to 140 μ and depth up to 100 μ . Those of Brachychatea, Brintonia, and Solidago were smaller, and those of Euthamia were usually smallest (11.0 to 34.0 μ wide and 9.0 to 22.0 μ deep). The mesophyll of the Euthamias was very tightly packed whereas the palisade and spongy tissue in the other taxa were more spread apart by air spaces and large substomatal chambers. In Oligoneurons several stomata frequently led into an enlarged, common substomatal chamber. In Euthamia the smaller chambers and tightly packed mesophyll gave the appearance of a compact, thicker leaf than those of the other taxa observed.

In Euthamia the epidermal surface was dotted with round pits, often referred to as pellucid punctations. One glandular trichome was usually located at the bottom of these pits; however, two or three were rarely seen. The pits were generally 4 - 9, (usually 6) cells in circumference at the top of the pits, which were level or slightly elevated at the leaf surface. When viewed in transection the cells lining the pits decreased in size toward the bottom of the pit. The pits were frequently associated with the vascular bundles, but were found over the entire laminar surface. They varied in depth, with E. occidentalis having the deepest pits (18.0 - 45.0 μ) to E. graminifolia with the shallowest (16.0 to 27.0 μ). Trichomes in pits were also observed in all of the Oligoneurons except O. rigidum. These leaves were densely covered with nonglandular hairs. Some Solidago species: S. canadensis, S. bigelovii, S. caesia, and S. multiradiata had

no pitting, and others such as S. californica, S. flexicaulis, S. gigantea, S. hispida, S. macrophylla, S. missouriensis, S. juncea, and S. decumbens, had frequent pitting often associated with the vascular bundles similar to those described for Euthamia. These pits do not resemble the epidermal grooves, (or termed sulci by Lloyd, 1901) of Chrysoma, which exactly follow the venation of the leaf and also contain trichomes.

Uniseriate trichomes were of two distinct types, nonglandular and glandular. The nonglandular trichomes were found in all the taxa studied. They consisted of a unicellular or bicellular base, followed by one to several elongated cells, capped by a simple pointed cell. These trichomes were found along the leaf margins, over the lamina, and frequently in association with the major vascular bundles. They were not significantly different qualitatively in any of the taxa observed; however quantitative differences were apparent.

The second type observed, the glandular trichome, is found in most of the species studied. The hair consists of a uniseriate pedestal, 2 to 7 cells in height, capped by an enlarged, elongated whip-like cell. Solerader (1908) described this type of hair as a whip or lash cell. Sieren (1970) reported Euthamia hairs consisted of pedestals, 4 to 7 cells in height, which were usually broader than long. In Solidago and Oligoneuron, the pedestals were 2 to 4 cells (usually 3) in height and longer than broad. The length of the whip-like cell was variable in each taxon.

The biseriate glandular collectors reported in the leaves of Euthamia were not seen by this author. However, biseriate glandular trichomes rarely were found in both Euthamia and Solidago. The biseriate glandular trichomes of Chrysoma were distinctive in the presence of crystals in the top cells of the hair reported to be calcium oxalate by Lloyd (1901). Another dis-

tion of the Chrysoma trichomes was their consistent location, the bottom of the epidermal grooves.

The venation in the taxa studied was variable, but no differences among Euthamia, Solidago, Brachychaeta, Brintonia, or Oligoneuron were observed. The leaves of Euthamia were linear to linear-lanceolate and varied from leaves in the other taxa in size and shape. The areoles of Euthamia were more oblong than the other taxa.

The mesophyll structure (cf. Table II) was isolateral in Euthamia, except E. graminifolia was bifacial and collections of E. occidentalis were isolateral or bifacial. Oligoneurons were bifacial to isolateral; Brachychaeta sphacelata and Brintonia discoidea were both bifacial. Solidagos were bifacial or less frequently isolateral.

Secretory canals or ducts were characteristic of all the taxa studied. These ducts described in Esau (1953) are characteristic of all the Compositae. These schizogenous canals were distinguishable by their lining of secretory epithelial cells and the consistent location, the abaxial side of major vascular bundles as in S. missouriensis (Table II). The canals ran continuously along the veins and were seldom interrupted by cell walls. They then resumed on the other side of the wall as a new canal. These abaxial canals were also observed in Chrysoma, which were reported by Phillips (1963) as lacunar spaces, and in Petradoria (Anderson, 1963).

Secretory cavities, characteristic of some of the taxa, were easily identified in paradermal sections, but could also be determined from successive transections. In Euthamia the cavities were always between vascular bundles, except in E. occidentalis, which had no cavities. No cavities have been observed in Oligoneuron, Brachychaeta, or Brintonia. Cavities were absent in the majority of Solidago species, and in the species which did have

Symbols used in Table 2 and Table 3

| | |
|-----|-------------------------------------|
| B | bifacial |
| I | isolateral |
| M | midvein |
| L | primary lateral veins |
| V | minor vascular bundles |
| ab | abaxial |
| ad | adaxial |
| bv | between veins |
| col | collenchyma |
| fib | fibers |
| 0 | absent |
| - | seldom present |
| + | present |
| ++ | abundant |
| ± | present or absent to varying degree |

Table 2. Selected Features in Leaf Anatomy of Certain Goldenrods

| Species and Collection | Mesophyll | Secretory Canals | Secretory Cavities | Sheath Extensions | Storage Parenchyma | Midvein |
|---|-----------|---------------------|-----------------------|----------------------|-----------------------|-----------------|
| EUTHAMIA | | | | | | |
| <u>E. galetorum</u> Greene | | | | | | |
| <u>Fernald & Long 22732;</u> <u>Weatherby 7096</u> | +I | ab,M,L,V | bv | 0 | + | col++,fib ab,ad |
| <u>E. graminifolia</u> (L.) Nutt. | | | | | | |
| A. 2175; A. 3507 | -B | ab,M,L | bv | - | -- | col--,fib ab,ad |
| A. 2153 | | | | | + | col+,fib 0 |
| <u>E. gymnospermoides</u> Greene | | | | | | |
| A. 3440 | I | ab,M,L | bv | 0 | ++ | col-,fib ab,ad |
| <u>E. hirtepes</u> (Fern.) Sieren | | | | | | |
| in ed. | | | | | | |
| A. 3498 | I | ab,M,L | bv | 0 | ++ | col-,fib ab,ad |
| <u>E. leptcephala</u> (T & G.) | | | | | | |
| Greene | | | | | | |
| A. 3180; C. 3125; <u>Palmer 6639</u> | +I | ab,M | bv | 0 | ++ | col-,fib ab,ad |
| A. 3472 | I | ab,M,L | bv | 0 | + | col+,fib ab,ad |
| <u>E. occidentalis</u> Nutt. | | | | | | |
| A. 2735 | +B | ab,M,L | 0 | - | - | col-,fib 0 |
| A. 2879 | +I | ab,M,L | 0 | - | ++ | col-,fib ad,m |

Table 2 (continued).

| Species and Collection | Mesophyll | Secretory Canals | Secretory Cavities | Sheath Extensions | Storage Parenchyma | Midvein |
|--|-----------|---------------------|-----------------------|----------------------|-----------------------|-----------------|
| <u>E. pulverulenta</u> Greene | | | | | | |
| <u>A. 3181</u> | +I | ab,M,L | bv | 0 | ++ | col-,fib ab,ad |
| <u>E. remota</u> Greene | | | | | | |
| <u>Deam 1392</u> | I | ab,M,V | bv | 0 | + | col-,fib ab,ad |
| <u>E. tenuifolia</u> (Pursh) Nutt. | | | | | | |
| <u>A. 3451; A. 3476</u> | +I | ab,M,L | bv | - | ++ | col-,fib ab,ad |
| OLIGONEURON | | | | | | |
| <u>S. houghtonii</u> (T. & G.) | | | | | | |
| <u>Pringle 1221</u> (HAM) | +I | ab,M,L,V | 0 | + | 0 | col--,fib ab,ad |
| <u>O. nitidum</u> (T. & G.) Small | | | | | | |
| <u>Lundell 14047</u> | I | ab,M,L | 0 | + | 0 | col++,fib ab,ad |
| <u>O. ohioense</u> (Riddell) G.N. Jones | | | | | | |
| <u>Pringle 1298</u> | +B | ab,M,L | 0 | + | - | col++,fib ab,ad |
| <u>O. riddellii</u> (Frank) Rydb. | | | | | | |
| <u>Pringle 1250</u> | +B | ab,M,L | 0 | + | - | col++,fib ab,ad |
| <u>O. rigidum</u> L. | | | | | | |
| <u>C. 533; A. 2709</u> | +I | ab,M,L | 0 | + | - | col++,fib ab,ad |
| <u>C. 535</u> | +B | ab,M,L | 0 | + | - | col++,fib ab,ad |

Table 2 (continued).

| Species and Collection | Mesophyll | Secretory Canals | Secretory Cavities | Sheath Extensions | Storage Parenchyma | Midvein |
|------------------------------------|-----------|---------------------|-----------------------|----------------------|-----------------------|-----------------|
| SOLIDAGO | | | | | | |
| <u>S. alpestris</u> Waldst. & Kit. | | | | | | |
| <u>Lilpop</u> | +B | ab,M,L | 0 | ++ | - | col+,fib 0 |
| <u>S. bigelovii</u> Gray | | | | | | |
| <u>A. 3046</u> | I | ab,J,L | 0 | + | + | col++,fib 0 |
| <u>S. caesia</u> L. | | | | | | |
| <u>A. 2176; A. 3508</u> | B | ab,M,L | 0 | + | - | col++,fib ad |
| <u>S. californica</u> Nutt. | | | | | | |
| <u>Balls & Everett 18128</u> | B | ab,M,L | ad V | + | - | col++,fib ad |
| <u>S. canadensis</u> L. | | | | | | |
| <u>A. 2174; C. 527; C. 536</u> | +B | ab,M,L | ad V | ++ | + | col++,fib ab,ad |
| <u>S. flexicaulis</u> L. | | | | | | |
| <u>A. 2156</u> | +B | ab,M,L | 0 | + | 0 | col++,fib 0 |
| <u>S. gigantea</u> Ait. | | | | | | |
| <u>A. 3494</u> | +B | ab,M,L | ad V | + | + | col++,fib 0 |
| <u>S. hispida</u> Muhl. | | | | | | |
| <u>A. 2189</u> | B | ab,M,L | 0 | + | + | col++,fib 0 |
| <u>S. juncea</u> Ait. | | | | | | |
| <u>A. 2194</u> | +I | ab,M,L | ad | - | + | col-,fib 0 |
| <u>S. macrophylla</u> Pursh | | | | | | |
| <u>Pringle 1276</u> | -B | ab,J,L,V | 0 | + | 0 | col++,fib 0 |

Table 2 (continued).

| Species and Collection | Mesophyll | Secretory Canals | Secretory Cavities | Sheath Extensions | Storage Parenchyma | Midvein |
|---|-----------|---------------------|-----------------------|----------------------|-----------------------|-----------------|
| <u>S. missouriensis</u> Nutt. | | | | | | |
| var. <u>fasciculata</u> Holtz. | | | | | | |
| A. 2580 | I | ab,M,L,V | ad V | + | - | col-,fib ab,ad |
| C. 525; C. 528; C. 529 | I | ab,M,L,V | ad V | + | - | col+,fib ab,ad |
| <u>S. mollis</u> Bartl. | | | | | | |
| A. 2796 | +I | ab,M,L | ad V | + | - | col++,fib ab,ad |
| <u>S. multiradiata</u> Ait. | | | | | | |
| A. 2646; A. 3393 | B | ab,M,L | 0 | - | 0 | col-,fib 0 |
| <u>S. nemoralis</u> Ait. | | | | | | |
| A. 2188 | +I | ab,M,L | 0 | + | 0 | col++,fib 0 |
| <u>S. odora</u> Ait. | | | | | | |
| A. 3496; A. 3499 | +B | ab,M | ad | + | 0 | col++,fib ab,ad |
| <u>S. petiolaris</u> Ait. | | | | | | |
| A. 2614 | B | ab,M,L,V | 0 | + | 0 | col++,fib ab,ad |
| <u>S. petiolaris</u> var. <u>Wardii</u> | | | | | | |
| A. 2990 | +B | ab,M,L,V | 0 | + | 0 | col++,fib ab,ad |
| <u>S. pseudoyadkinesis</u> | | | | | | |
| G. Morton ined. | | | | | | |
| A. 3501; A. 3502 | I | ab,M,L,V | 0 | + | 0 | col++,fib 0 |

Table 2 (continued).

| Species and Collection | Mesophyll | Secretory Canals | Secretory Cavities | Sheath Extensions | Storage Parenchyma | Midvein |
|-----------------------------------|-----------|---------------------|-----------------------|----------------------|-----------------------|-----------------|
| <u>S. radula</u> Nutt. | | | | | | |
| <u>A. 3169</u> | I | ab,M,L | ad V | + | 0 | col++,fib ab,ad |
| <u>S. rugosa</u> Ait. | | | | | | |
| <u>A. 2192</u> | B | ab,M,L,V | ad V | + | 0 | col++,fib ad |
| <u>S. sempervirens</u> L. | | | | | | |
| <u>Miller 7101; 7102; 7103; I</u> | | ab,M,L,V | ad bv | + | + | col+,fib ab,ad |
| <u>Van der Valk 7101; 7102;</u> | | | | | | |
| <u>A. 3497</u> | | | | | | |
| <u>S. simplex</u> HBK. | | | | | | |
| <u>Beaman 2736</u> | B | ab,M,L | ad V | + | 0 | col+,fib 0 |
| <u>S. sparisflora</u> Gray | | | | | | |
| <u>A. 2701</u> | I | ab,M,L,V | ad V | + | + | col++,fib ad |
| <u>S. spathulata</u> DC | | | | | | |
| <u>A. 2480</u> | I | ab,M,L | ad | ++ | - | col++,fib 0 |
| <u>S. spithmaea</u> M.A. Curtis | | | | | | |
| <u>Morton 3865</u> | B | ab,M,L | 0 | + | 0 | col-,fib 0 |
| <u>S. stricta</u> Ait. | | | | | | |
| <u>A. 3457</u> | +B | ab,M,L,V | ad V | + | 0 | col-,fib ad |
| <u>S. tortifolia</u> Ell. | | | | | | |
| <u>Curtis 6051</u> | I | ab,M,L,V | ad V | + | + | col++,fib ad |
| <u>S. affin. vaseyi</u> Heller | | | | | | |
| <u>A. 3100</u> | B | ab,M,L,V | ad V | + | 0 | col++,fib 0 |

Table 2 (continued).

| Species and Collection | Mesophyll | Secretory Canals | Secretory Cavities | Sheath Extensions | Storage Parenchyma | Midvein |
|------------------------------------|-----------|---------------------|-----------------------|----------------------|-----------------------|----------------|
| <u>S. virgaurea</u> L. | | | | | | |
| <u>Takamine 2239</u> | B | ab,M,L,V | 0 | + | 0 | col+,fib 0 |
| <u>Amano 6852</u> | +B | ab,M,L,V | 0 | + | 0 | col-,fib 0 |
| BRACHYCHAETA | | | | | | |
| <u>B. sphacelata</u> (Raf.) Britt. | | | | | | |
| <u>Potzger 2165</u> | B | ab,M | 0 | + | 0 | col+,fib 0 |
| BRINTONIA | | | | | | |
| <u>B. discoidea</u> (Ell.) T. & G. | | | | | | |
| <u>Mohr</u> in 1878 | +B | ab,M,L | 0 | + | 0 | col+,fib 0 |
| CHRYSONIA | | | | | | |
| <u>C. pauciflosculosa</u> (Michx.) | | | | | | |
| Green | | | | | | |
| <u>A. 3485; A. 3487; A. 3488</u> | I | ab,M,L,V | 0 | 0 | 0 | col0,fib ab,ad |

cavities they were distinct topographically. The cavities observed in Solidago were always in the adaxial side of the mesophyll, and occurred between or adjacent to the vascular bundles. An exception was S. odora, which contained exceptionally large cavities located in the middle of the mesophyll between veins, such as the positioning of those found in Euthamia. Holm (1913) mistakenly reported these as resin ducts.

Bundle sheaths enclosed the vascular bundles of all species observed, but bundle sheath extensions were not present in Euthamia. Occasionally a major lateral vein appeared to have a bundle sheath extension on the abaxial side, but it was always with the presence of a secretory canal and its accompanying cells. Examples of this were seen in E. graminifolia, E. occidentalis, and E. tenuifolia. Oligoneuron always had bundle sheath extensions. In many Oligoneurons, the narrowness of the leaf compared to its relative size, caused crowding of the vascular bundles. Collenchyma was present beneath the epidermis, especially in the Oligoneuron and Solidago collections. The collenchyma, bundles, canals, and associated cells comprised the veins. This may explain the externally distinct veins in these species. In Euthamia, however, collenchyma is rare to absent. Bundle sheath extensions were observed in all the Solidagos. Wylie (1952) in a study of the bundle sheath extensions, observed that they are most frequent in "northern deciduous leaves, which as a group, have the thinnest blades, the least mechanical tissue, and the thinnest cuticle."

If vascular bundles in S. sempervirens contained equal or greater amounts of phloem than xylem, then bundle sheath extensions were present. Where xylem was present in the minor veins, bundle sheath extensions were absent or extended only to the adaxial surface. Secretory cavities were not associated only with adaxial bundle sheath extensions. Canals frequently

occurred if the sheaths extended both abaxially and adaxially. Holm (1913) noted in S. odora that the "thin, lateral veins lack water- storage-[t]issue, but are surrounded by green parenchyma sheaths." This observation was confirmed in the collections of S. odora which I studied.

In Euthamia storage parenchyma was generally abundant (Table I), except in some collections of E. occidentalis it was infrequent; whereas, in Oligoneuron storage parenchyma was infrequent or absent. In Solidago, storage tissue was absent in about half the collections studied; there was no storage parenchyma in Brintonia. Storage parenchyma was observed in Brachychaeta.

Fibers were found abaxially and adaxially to the vascular bundles in both Euthamia and Oligoneuron, but they are not as massive as the sclerenchyma enveloping the vascular bundles in Petradoria (Anderson, 1963). Exceptions were E. occidentalis and Brachychaeta, which had fibers capping only the xylem, and Brintonia which had no fibers. In Solidago 15 species had no fibers; 10 others had fibers on both abaxial and adaxial sides; and in 6 species fibers were present on only the adaxial side of the vascular bundles.

DISCUSSION AND CONCLUSION

It is apparent that the internal characteristics of Euthamia such as the cavities, bundle sheath extensions, nonphotosynthetic storage parenchyma and midvein collenchyma are consistently different (cf. Table III) from the other taxa and may represent the basis of the segregation of Euthamia from Solidago and the other taxa. All the taxa studied have secretory canals, but only Euthamia and some Solidago species have secretory cavities. The secretory cavities of Solidago differ from those of Euthamia topographically, being present only the adaxial side of the mesophyll between or adjacent to the vascular bundles. Storage parenchyma was abundant in Euthamia, present in about half the Solidago and Brachychaeta, and was absent in the Oligoneurons and Brintonia. Substomatal chambers were very large in Oligoneuron, intermediate in the other taxa, except Euthamia where they were minute. Sulci were present only in Chrysoma. Midvein collenchyma was present in all the taxa except Chrysoma and Euthamia where it was rarely present. Massive sclerenchyma fibers surrounded the vascular bundles in Petradoria. Fewer fibers were present in the other taxa except Brachychaeta and Brintonia had no fibers. The mesophyll in Brachychaeta and Brintonia and Oligoneuron was mostly bifacial. Solidago was bifacial or isolateral and Chrysoma, Petradoria and Euthamia were isolateral. Bundle sheath extensions were present only in Brachychaeta, Brintonia, Oligoneuron and Solidago.

Based on internal structure, external morphology and habit, I have concluded that Euthamia represents a distinct genus. Internal leaf anatomy of Brachychaeta and Brintonia more closely resembles Solidago than any other taxa. Chrysoma (Lloyd, 1901; Phillips, 1963) has been recognized by many biologists as a distinct genus. Petradoria (Anderson, 1963) has been shown to be distinct. I concur with these opinions that Chrysoma and Petradoria

should not be included in the Solidago complex due to the distinct differences in internal anatomy, as well as, habit and external morphology.

Table 3. Summary of Results

| Group | Secretory Cavities | Secretory Canals | Storage Parenchyma | Substomatal Chambers | Sulci | Midvein Collenchyma | Fibers | Mesophyll | Bundle Sheath Extensions |
|---------------------|-----------------------|---------------------|-----------------------|-------------------------|-------|------------------------|--------|-----------|-----------------------------|
| <u>Brachychaeta</u> | 0 | + | + | + | 0 | + | 0 | B | + |
| <u>Brintonia</u> | 0 | + | 0 | + | 0 | + | 0 | B | + |
| <u>Chrysoma</u> | 0 | + | 0 | + | ++ | 0 | + | I | 0 |
| <u>Euthamia</u> | ++ | + | ++ | 0 | 0 | 0 | + | I | 0 |
| <u>Oligoneuron</u> | 0 | + | 0 | ++ | 0 | ++ | + | +B | + |
| <u>Petradoria</u> | 0 | + | 0 | + | 0 | + | ++ | I | 0 |
| <u>Solidago</u> | + | + | + | + | 0 | + | + | B or I | + |

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Figs. 1-3. Leaf transections of Euthamia; adaxial surfaces toward top of page. All, X 100.

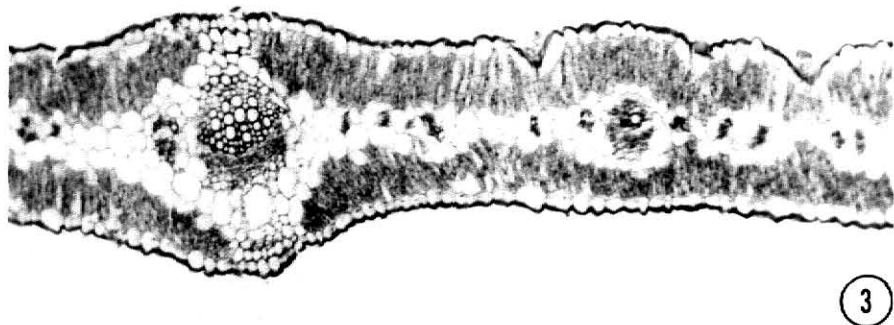
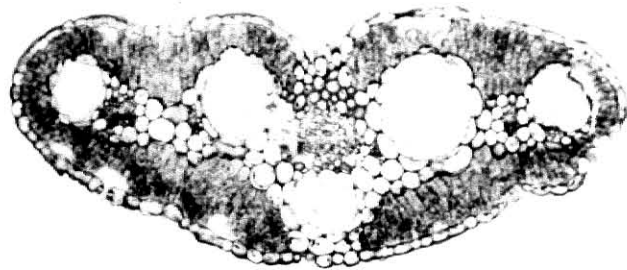
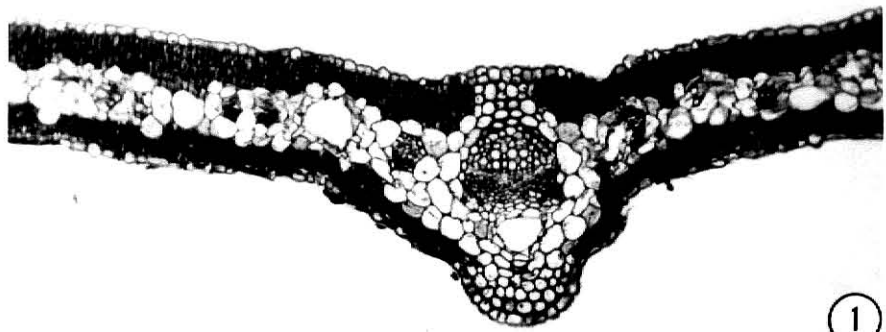
Fig. 1. Midvein and portion of blade of E. leptcephala (Anderson 3180) showing secretory canal with midvein, secretory cavity in mesophyll to the left, and extensive storage parenchyma between the isolateral palisade layers. Bundle sheath extensions absent on smaller veins.

Fig. 2. Whole leaf of E. tenuifolia (Anderson 3476) showing trichomes in adaxial groove of midvein, secretory canal associated abaxially with midvein, and four large secretory cavities located between veins rather than with them.

Fig. 3. Lateral vein and portion of blade of E. occidentalis (Anderson 2879) showing short glandular trichomes on adaxial epidermis and extensive storage parenchyma but secretory cavities are absent.

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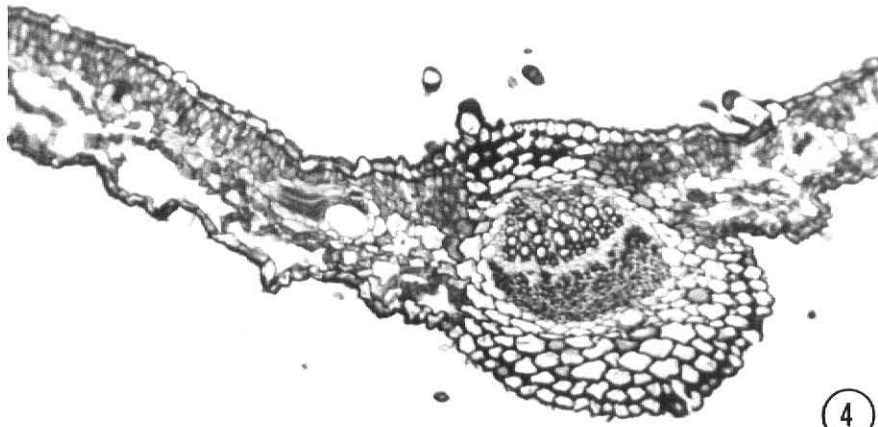


Figs. 4-6. Leaf transections of Brintonia and Oligoneuron; adaxial surfaces toward top of page. All, X 100.

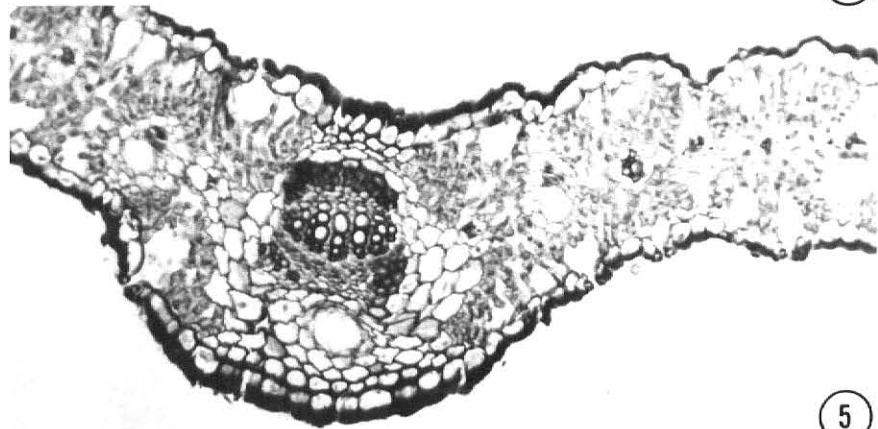
Fig. 4. Midvein and adjacent blade of B. discoidea (Mohr in 1878) showing bifacial mesophyll.

Fig. 5. Midvein and adjacent blade of O. nitidum (Lundell 14047) showing heavy cuticle, large substomatal chambers, secretory canals, and + isolateral mesophyll.

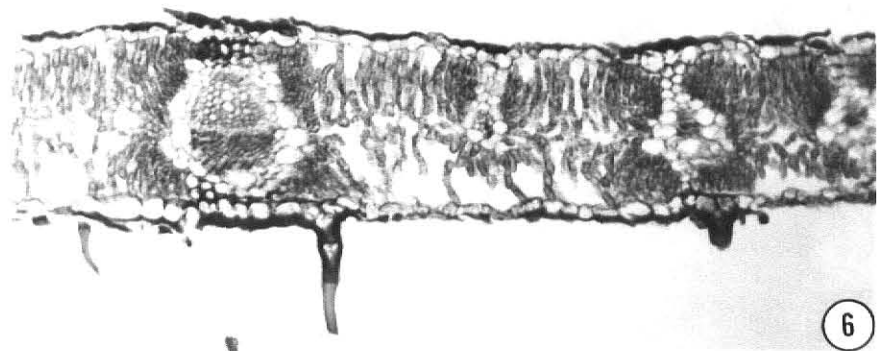
Fig. 6. Lateral vein of O. rigidum (Anderson 2709) showing nonglandular trichomes, heavy cuticle, + isolateral mesophyll, and bundle sheath extensions.



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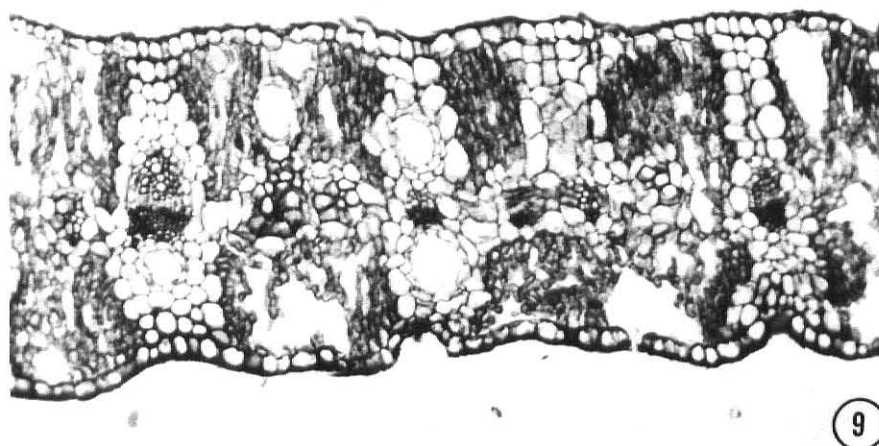
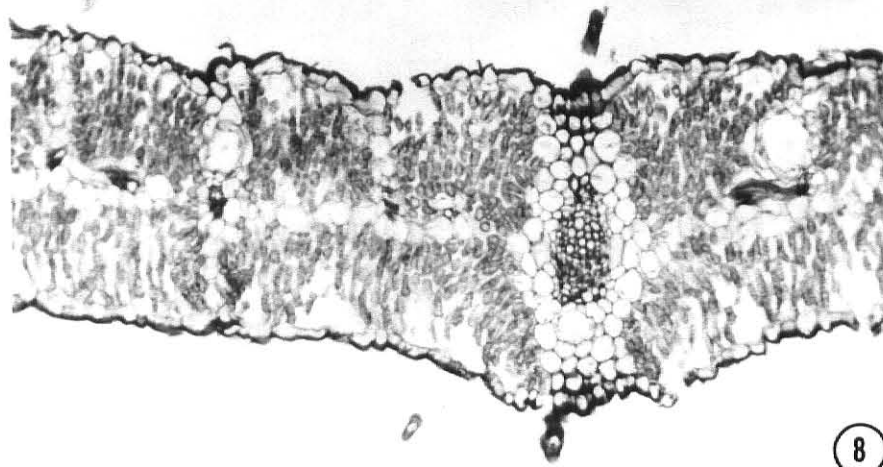
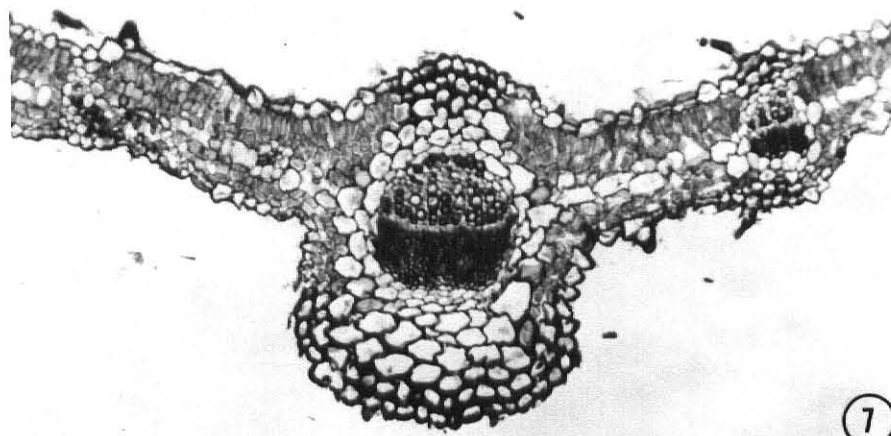
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Figs. 7-9. Leaf transections of Brachychaeta and Solidago; adaxial surface toward top of page. Note relative thicknesses of leaves. Brachychaeta is a woodland species and the two Solidagos grow in more open areas. All, X 100.

Fig. 7. Midvein of B. sphacelata (Potzger 2165) showing nonglandular trichomes and + bifacial mesophyll.

Fig. 8. Lateral vein and blade of S. mollis (Anderson 2796) showing trichomes, adaxial secretory cavities on smaller veins, and abaxial secretory canal on largest vein.

Fig. 9. Portion of leaf blade of S. sempervirens (Miller 7101) with several adaxial secretory cavities and abaxial secretory canals. Secretory apparatus always associated with the massive bundle sheath extensions.

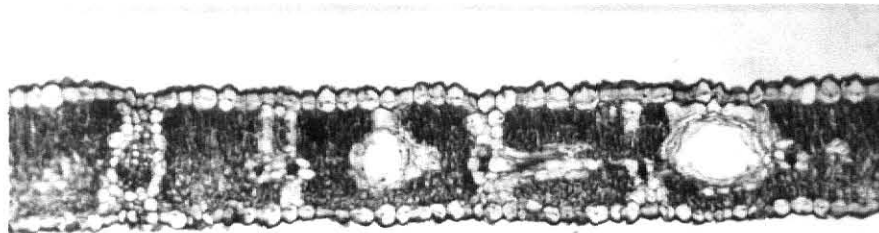


Figs. 10-12. Leaf sections of Solidago odora (Anderson 3499).

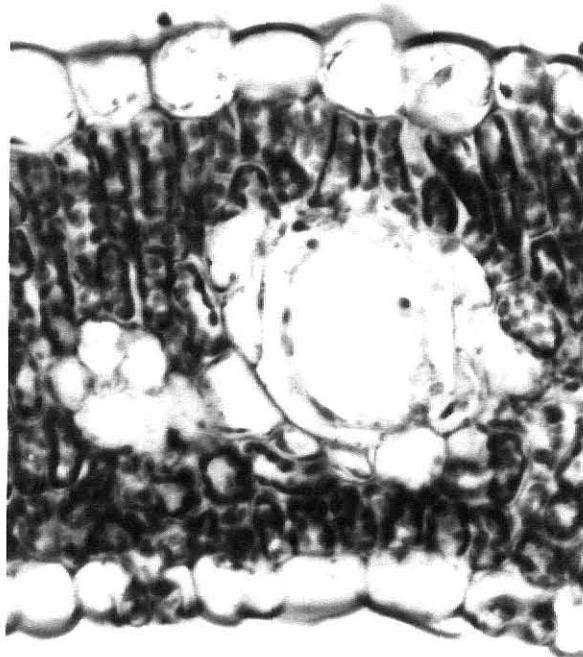
Fig. 10. Transection of blade showing compact mesophyll, large secretory cavities, and numerous bundle sheath extensions. X 100.

Fig. 11. Transection of secretory cavity. Note lysoschizogenous nature of cavity; cavities of all other taxa in which they are found are smaller and apparently only schizogenous. X 458.

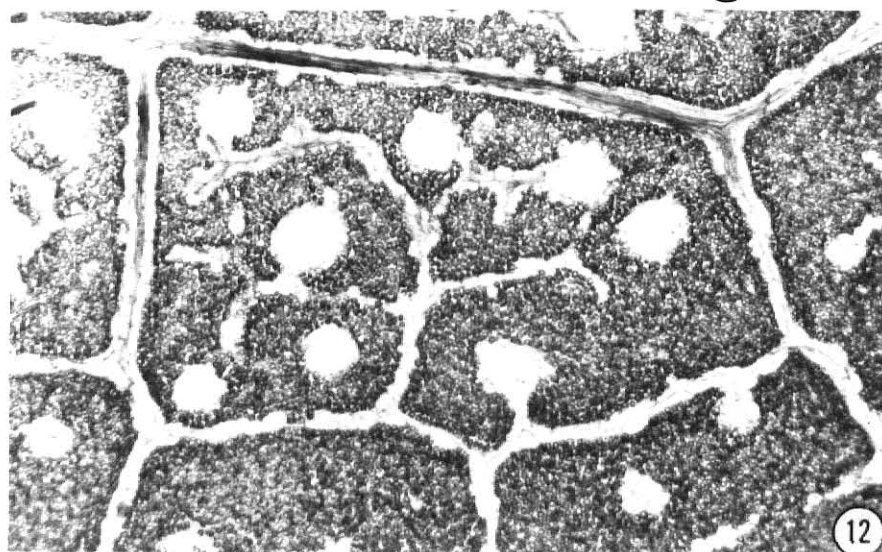
Fig. 12. Paradermal section showing vascular bundle along top of picture and interconnecting network of bundle sheath extensions. Secretory cavities primarily associated with bundle sheath extensions rather than in mesophyll as in Euthamia. X 77.



10



11



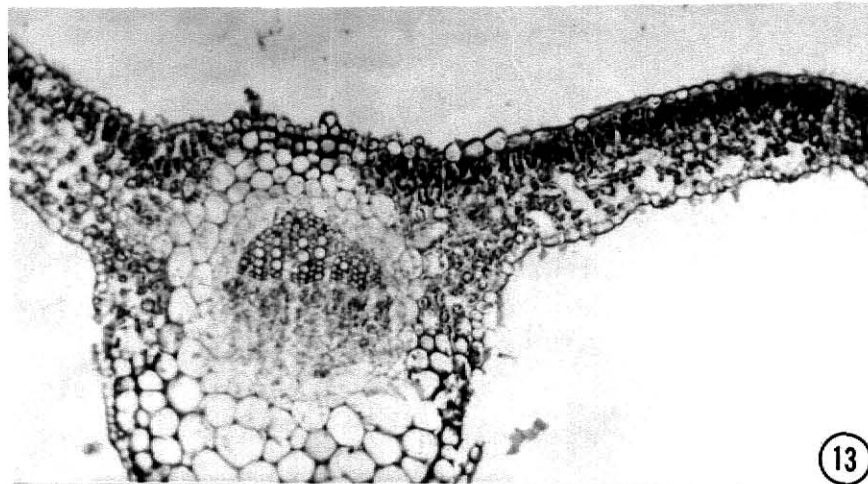
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Figs. 13-15. Leaf transections of Solidago; adaxial surface toward top of page. All X 100.

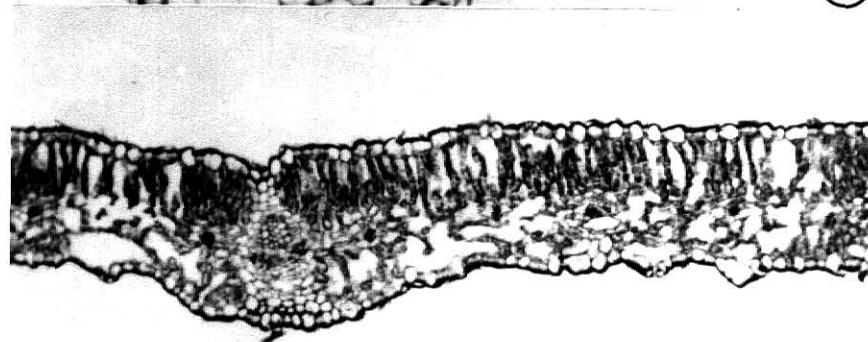
Fig. 13. Midvein and adjacent blade of S. macrophylla (Pringle 1276) showing bifacial mesophyll and no secretory apparatus.

Fig. 14. Lateral vein and portion of blade of S. multiradiata (Anderson 3393) with bifacial mesophyll.

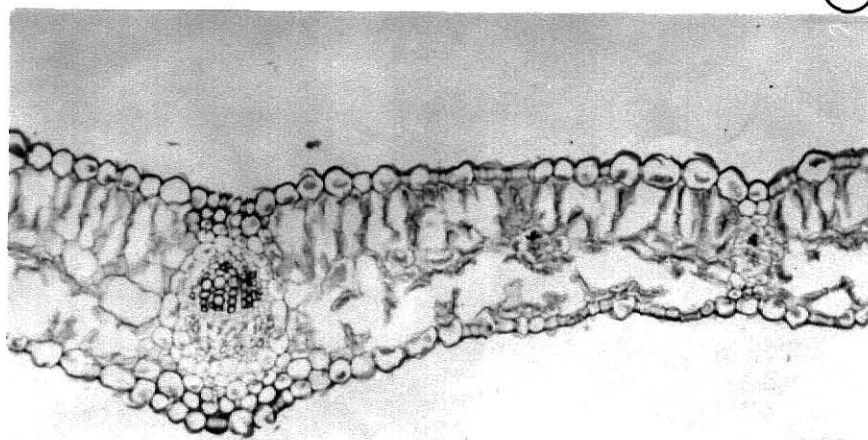
Fig. 15. Lateral vein and portion of blade of S. spithmaea (Morton 3865), a close relative of S. multiradiata, showing bifacial mesophyll.



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14



15

COMPARATIVE LEAF ANATOMY OF SOLIDAGO AND SEGREGATE GENERA BRACHYCHAETA,
BRINTONIA, CHRYSOMA, OLIGONEURON, AND PETRADORIA (COMPOSITAE)

by

JESSICA BUCHANAN CREECH

B.S., University of North Carolina at Chapel Hill, 1966

AN ABSTRACT OF A MASTER'S THESIS

submitted in partial fulfillment of the

requirements for the degree

MASTER OF SCIENCE

Division of Biology

KANSAS STATE UNIVERSITY

Manhattan, Kansas

1973

ABSTRACT

The genus Solidago (Compositae) has been variously treated by different authors to include any or all the following taxa: Brachychaeta, Brintonia, Chrysoma, Euthamia, Oligoneuron, and Petradoria. The internal anatomy is considered to be more stable than superficial morphological features and is used to elucidate the relationships of the taxa considered. Internal leaf characteristics, such as amount and distribution of secretory canals, secretory cavities, nonphotosynthetic storage parenchyma, bundle sheath extensions, substomatal chambers, extraxylary fibers, and midvein collenchyma provide evidence that some of the entities should be recognized as distinct genera, separate from Solidago. Chrysoma, Petradoria and Euthamia are definitely distinct from Solidago. Oligoneuron is not distinct enough to refer to it as a separate genus at this time. Further work may elucidate this question. Brachychaeta and Brintonia seem best retained in Solidago.