FLORAL MICROSTRUCTURE AND GENERIC DELIMITATION IN THE NEW WORLD SENECIONEAE (ASTERACEAE)

by

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INTRODUCTION

This study was undertaken to provide an illustrative analysis of certain microanatomical and micromorphological characters which have been used by previous authors (Robinson and Brettell, 1973; Nordenstam, 1976) in their revisionary studies on the taxonomy of the Compositae, but which have been largely unillustrated in the literature. Five characters were examined and illustrated: (1) configuration and distribution of the stigmatic area on the style branches, (2) stylopodial structure, (3) cellular structure of the carpopodium, (4) configuration of the anther collars, and (5) the form of the exothecial cells. The stability of these characters with age, and over a wide geographical range within one species, was also studied. This study was not a comprehensive analysis of previous authors' taxonomic conclusions, but was intended to provide qualitative photographs of these microcharacters as they occur in the Senecioneae.

LITERATURE REVIEW

Recent authors have studied various microanatomical and micromorphological features associated with the taxonomy of the Compositae. Ovarian crystals (Dormer, 1961), wood anatomy (Carlquist, 1962), and leaf hairs, achene hairs, corolla venation (Drury and Watson, 1965) have all been used in taxonomic studies. King and Robinson (1970) have suggested that gross morphology as a taxonomic tool in the Compositae has reached its full potential, and they suggest that micromorphological and microanatomical characters visible with the compound microscope be used as critical characters for generic determinations.

Those features, according to King and Robinson (1970), that warrant special scrutiny include surface structure of the corolla lobes, cellular structure of the style branches, form and vestiture of the style node, cellular structure of the anther appendage, form of the exothecial cells, structure of the anther collars, pubescence of the corolla, distribution and structure of the setae on the achene, and the cellular structure of the carpopodium.

King and Robinson utilized these characters in their study of the Eupatorieae, and on these characters they proposed many new genera and resurrected others from synonmy. Robinson and Brettell have also used some of these characters in their work on the Senecioneae.

Robinson and Brettell, in their work on the Senecioneae, have treated the Liabum complex as a separate tribe (1973a) and have proposed segregating the "Cacalioid" complex of Mexico and Central America as several distinct genera (1973 g,i,j; 1974a,c). All of their work was based upon the distribution of the microcharacters within these elements.

Unfortunately, few of these characters have ever been adequately illustrated. It was perhaps Koyama (1967) who first noticed and illustrated that a particular type of anther collar was restricted to a certain group of genera. Robinson and Brettell (1973j) provided line drawings of exothecial cells and the cellular structure of the carpopodium. Nordenstam (1976), in conjunction with his work on South African Chrysanthemum, published line drawings of stylopodial structure and photographs of exothecial cells.

Four of the microcharacters studied; 1) configuration and distribution of the stigmatic area on the style branches, 2) cellular structure of the carpopodium, 3) configuration of the anther collars, and 4) form of the exothecial cells, were chosen because of the emphasis given them by Robinson and Brettell (1973 f,g,i,j; 1974a,c) in their treatment of the "Cacalioid" Senecioneae. These authors defined the "Cacalioid" Senecioneae as those species having the "stigmatic area covering the complete inside surface of the style branches," and "anther collars which never have the enlarged or thinner walled basal cells." The "Cacalioid" Senecioneae were segregated out of New World and Asiatic species of Cacalia and

species of Senecio, sects. Fruticosi, Palmatinervii and Terminales. The non-Cacalioid" Senecioneae were defined as those species in which the stigmatic surface is divided into two distinct lines and the anther collars are usually enlarged at the base.

Segregate genera within the "Cacalioid" Senecioneae were established by Robinson and Brettell using the form of the exothecial cells and the cellular structure of the carpopodium.

Stylopodial structure was not used by Robinson and Brettell in their work on the "Cacalioid" Senecioneae but Nordenstam (1976) used it in his work on Chrysanthemum and it was thought worthy of attention in the "Cacalioid" Senecioneae by this author.

Of all the groups treated by various authors utilizing these microcharacters, attention was focused on the "Cacalioid" Senecioneae because they have long been recognized as a taxonomic problem in the Senecioneae, and suitable specimens were already present at Kansas State University for a study by Dr. T. M. Barkley on the Senecioneae of Panama. A large group of Mexican Senecios collected by Dr. E. S. Gibson for his work on Senecio, sect. Palmatinervii, (1969) were also on deposit at Kansas State University. Several non-"Cacalioid" species of Senecio which have been treated by various authors as deserving separate generic status were also examined.

Generic delimitation in the Senecioneae and in particular the delimitation of Cacalia from Senecio have long been obscure. Traditionally, stylar characteristics have been recognized as important in determining tribal and generic relationships. Cassini (1826) was the first to make use of stylar characteristics to separate the Compositae into groups. His works have formed the backbone of all later works. Within the Senecioneae much attention has been given to the shape of the style branch apex as a character to determine generic boundaries and subgeneric groupings. Rydberg (1924a, b) used stylar characteristics as evidence to propose segregate genera out of North American Cacalia. Cabrera (1950) considered stylar characters more important than vegetative characters, and proposed segregating out those species of Senecio "with style-branches triangular at the apex" as two genera, Gynoxys and Pseudogynoxys. "Typical" Senecio is usually considered to have a truncate style branch with a penicillate ring of collecting hairs.

Robinson and Brettell (1973a), in their work on the Senecioneae, have used the anomaloms style of the Liabum complex to segregate this group into a separate tribe. In their work on the "Cacalioid" Senecioneae, these authors dismissed stylar morphology as a key characteristic of the "Cacalioid" Senecioneae, saying "the style tips of the 'Cacalioid' group are blunt in almost all members but the character is neither unique to the group nor totally reliable on

the Asiatic species" (Robinson and Brettell, 1973j). These authors focused their attention on the configuration and distribution of the stigmatic area; so too this study.

The traditional works on the Senecioneae have treated Senecio as a very large genus composed of several semi-distinct sections that none the less compose a natural group. Bentham, in Genera Plantarum (1873b) and his separate publication on the Compositae (1873a), united Cacalia with Senecio. He perceived Senecio as a vast natural group composed of related semi-distinct elements. Hoffman (1890) in Die natürlichen Pflazenfamilien considered Cacalia separate from Senecio, but both genera were conceived very broadly. Greenman (1901) surveyed the North and Central American species of Senecio, followed Hoffman and considered Senecio as a broad concept divisible into several sections.

Rydberg (1924) proposed giving some of the morphologically divergent elements of North American Senecioneae separate generic status. He recognized Psacalium as distinct from Senecio and Cacalia, and suggested that the other species constituting Cacalia would better be placed in Odontotrichum. Rydberg proposed excluding Cacalia from the flora of North America. He argued that the historical type of Cacalia, C. alpina, represented an European entity, and that species formerly placed in Cacalia belonged in segregate genera. Rydberg noted that previous authors had included in the concept of Cacalia several different elements that were not only

distinguishable from one another but also from Senecio if considered separately, but when considered collectively they were no longer separable from Senecio. Hence, he proposed several genera out of the former Cacalia of North and Central America.

Standley (1926), in his Trees and Shrubs of Mexico, followed the traditional lines established by Bentham and by Hoffman, and conceived Senecio as a very broad concept. Cuatrecasas (1955, 1960) following arguments advanced by Rydberg excluded Cacalia from the North American flora. He proposed several new genera or the re-establishment of synonyms for species formerly placed in Cacalia. Pippen (1968) in his treatment of the Mexican "Cacalioid" complex recognized four segregate genera.

Elements in the Senecioneae other than the "Cacalioid" complex have received attention from various authors. Cabrera (1950), as noted above, erected two genera to deal with what he saw as distinctive elements in Senecio. He raised to generic status Senecio, subgenus Psuedogynoxys Greenm. as the genus Psuedogynoxys. This genus includes Senecio confusus and its relatives. Weber (1973) noted that Senecio amplectens and allied species resembled the Asiatic genus Ligularia and transferred them. Holub (1973) transferred Senecio atropurpurea and allies to the resurrected genus Tephroseris. Löve and Löve (1975) suggested placing elements including Senecio aureus in the newly described genus Packera.

An additional problem in "Cacalioid" Senecioneae has been the nomenclatural typification of the name Cacalia. Rydberg (1924), Cuatrecasas (1955, 1960), Pippen (1968), and Robinson and Brettell (1973j) all proposed C. alpina L. as the logical lectotype, thus restricting the name Cacalia to a few European plants. These authors further proposed that the distinctive elements of North America and Asia formerly placed in Cacalia would better be placed in several narrowly circumscribed segregate genera.

Kitamura (1942), Pojarkova (1961), and Vuilleumier and Wood (1969) argued that C. hastata L. was the logical lectotype, primarily by the removal of other Linnean Cacalia species to various genera. Vuilleumier (1969) and Vuilleumier and Wood (1969) treated Cacalia as a genus of North American and Asiatic distribution with at least two distinct groups of elements but overall a "natural" genus.

Philosophical arguments for a broad circumscription of both Senecio and Cacalia have been advanced in the past. Historically, taxonomists working on these genera considered each genus composed of several semi-distinct groups, yet as a whole these semi-distinct elements formed a 'natural' group worthy of recognition. Recent authors have either rejected or accepted the historical treatment depending upon what each author thinks composes a natural group.

MATERIALS AND METHODS

Mature disc florets were removed from herbarium specimens on deposit at Kansas State University (KSC), the Missouri Botanical Garden (MO), Duke University (DUKE), and the United States National Herbarium (US). Abbreviations used are those of Holmgren and Keuken (1974).

Materials were examined using either LM (Light Microscope) techniques or a combination LM and SEM (Scanning Electron Microscope). Locality data for these materials are listed in Table II. Specimens were chosen on their availability. Panamanian material was already on loan to KSU and a supplemental loan was procured from the Missouri Botanical Garden.

All florets were first dissected using Pohl's solution as a softening agent. Material for LM examination only was then directly mounted in Hoyer's solution. Several days elapsed before the material was examined and photographed using a Zeiss photomicroscope II. During this time the Hoyer's solution hardened and cleared the specimens.

Style branches of several species were prepared for sectioning for LM study. Sectioning was done to demonstrate the morphological continuity or discontinuity of the stigmatic area across the breadth of the style branch. Materials prepared for sectioning were first dissected in Pohl's solution, after which they were rinsed with water. The method

outlined by Lersten (1974) was followed, except specimens were not treated with either NaOH or HF, but were placed directly in distilled H_2O. Paraffin was substituted for Tissuemat. Unstained 10μm sections were mounted, and photographed using a Zeiss photomicroscope II.

Materials intended for a combination LM and SEM were mounted in a modified Hoyer's solution after dissection. This solution, locally called Wetter's solution, or a "better wetter", differs from Hoyer's in that the gum arabic was omitted. This medium cleared the specimens for LM, but did not harden and was easily removed from the material. When Wetter's solution was used as the mounting medium, extreme care was taken with the specimens. Any movement of the coverslip resulted in severe mechanical damage to the material. After completion of LM work the coverslips were removed by flooding the slides with water; after several minutes the coverslips floated free without causing any apparent mechanical damage. Before the material was mounted for SEM, it was floated in water-filled petri dishes and several changes of water were made to remove traces of Wetter's solution.

Materials for SEM were then mounted in water on aluminum stubs on double-stick cellophane tape. The stubs were then quick-frozen in liquid nitrogen and freeze-dried using an Edwards vacuum chamber. Specimens were then coated with a gold-palladium alloy using a Kenney vacuum evaporator. Photographs of the specimens were taken using a ETEC Autoscan electron microscope at Kansas State University.

The procedure just outlined permits the same specimen to be used for LM and then SEM, saving dissection time and reducing the amount of material that has to be removed from any one specimen.

Specimens were examined for five different micro-characters. These are: (1) configuration and distribution of the stigmatic area on the style branches, (2) stylopodial structure, (3) cellular structure of the carpopodium, (4) configuration of the anther collars, and (5) the form of the exothecial cells. Only the first four were examined using both LM and SEM. The exothecial cells are an internal tissue and were not examined using SEM.

In the Senecioneae studied the stigmatic area was restricted to the inside surface of the style branches. The stigmatic area becomes receptive to pollen when the two branches of the style have separated from each other, exposing the stigmatic area to the atmosphere. Three different configurations of the stigmatic area were found in the species surveyed.

The most common type of style encountered consisted of the entire inner surface of the style branch being stigmatic. Apparently the stigmatic cells formed a uniform layer of cells across the breadth of the style branches (Figs. 1, 2, 3). In some cases the entire inner surface of the style branch appeared stigmatic but a narrow longitudinal, medial cleft which runs the length of the style branch was noticed.

Figure 1. SEM of the style branch base of Roldana heracleifolia. 130x. Line = 10μ.

Figure 2. SEM of the style branch apex of R. heracleifolia. 130x. Line = 10μ.

Figure 3. LM of the style branch apex of R. heracleifolia. 350x.

Figure 4. SEM of the style branch base of Senecio oerstedianus. 130x. Line = 10μ.

Figure 5. SEM of the style branch apex of S. oerstedianus. 130x. Line = 10μ.

Figure 6. LM of the style branch apex of S. oerstedianus. 236x.

Figure 7. SEM of the style branch base of Pseudogynoxys berlandieri. 130x. Line = 10μ.

Figure 8. SEM of the style branch apex of Pseudogynoxys berlandieri. Line = 10μ.

Figure 9. LM of the style branch apex of Pseudogynoxys berlandieri.

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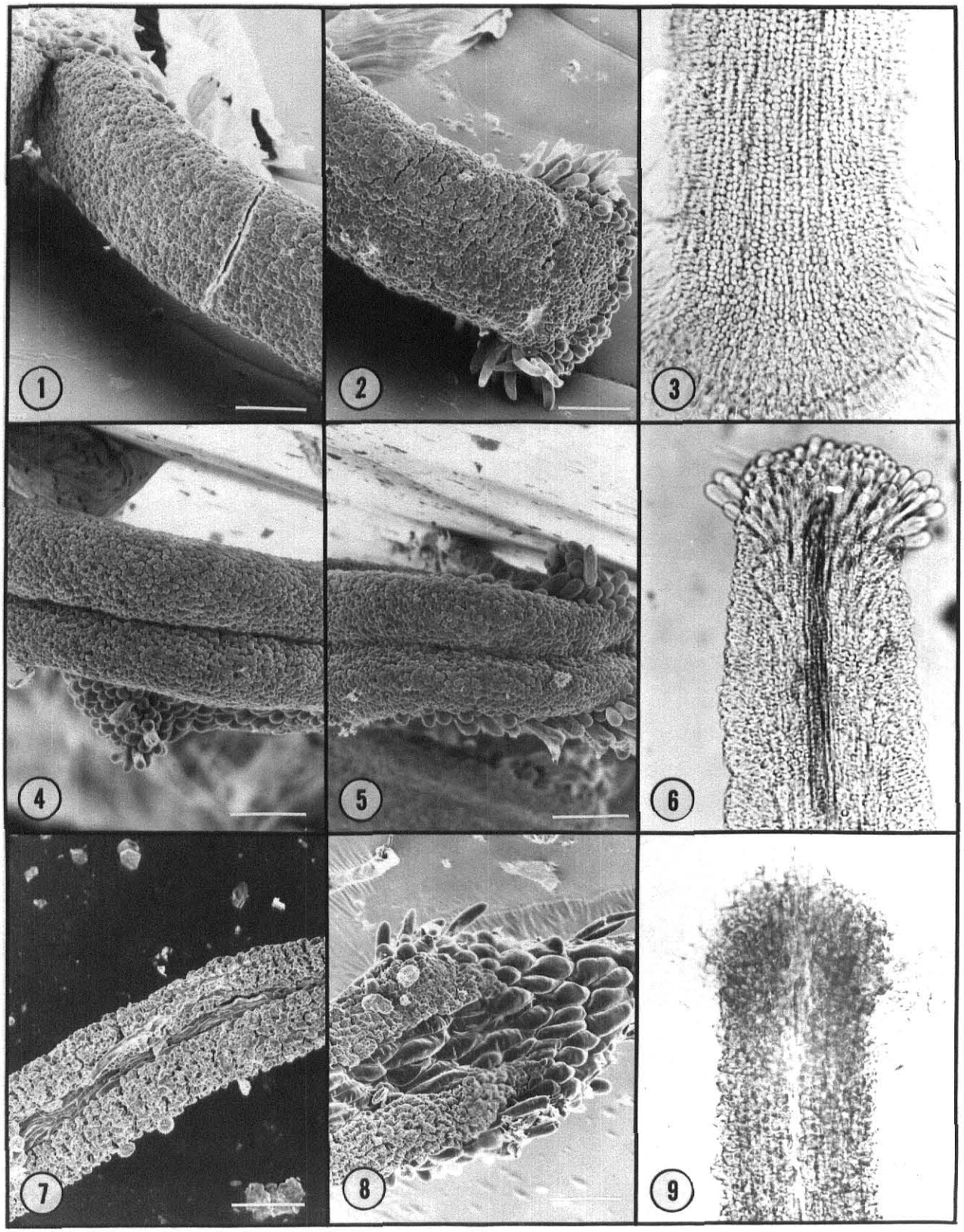
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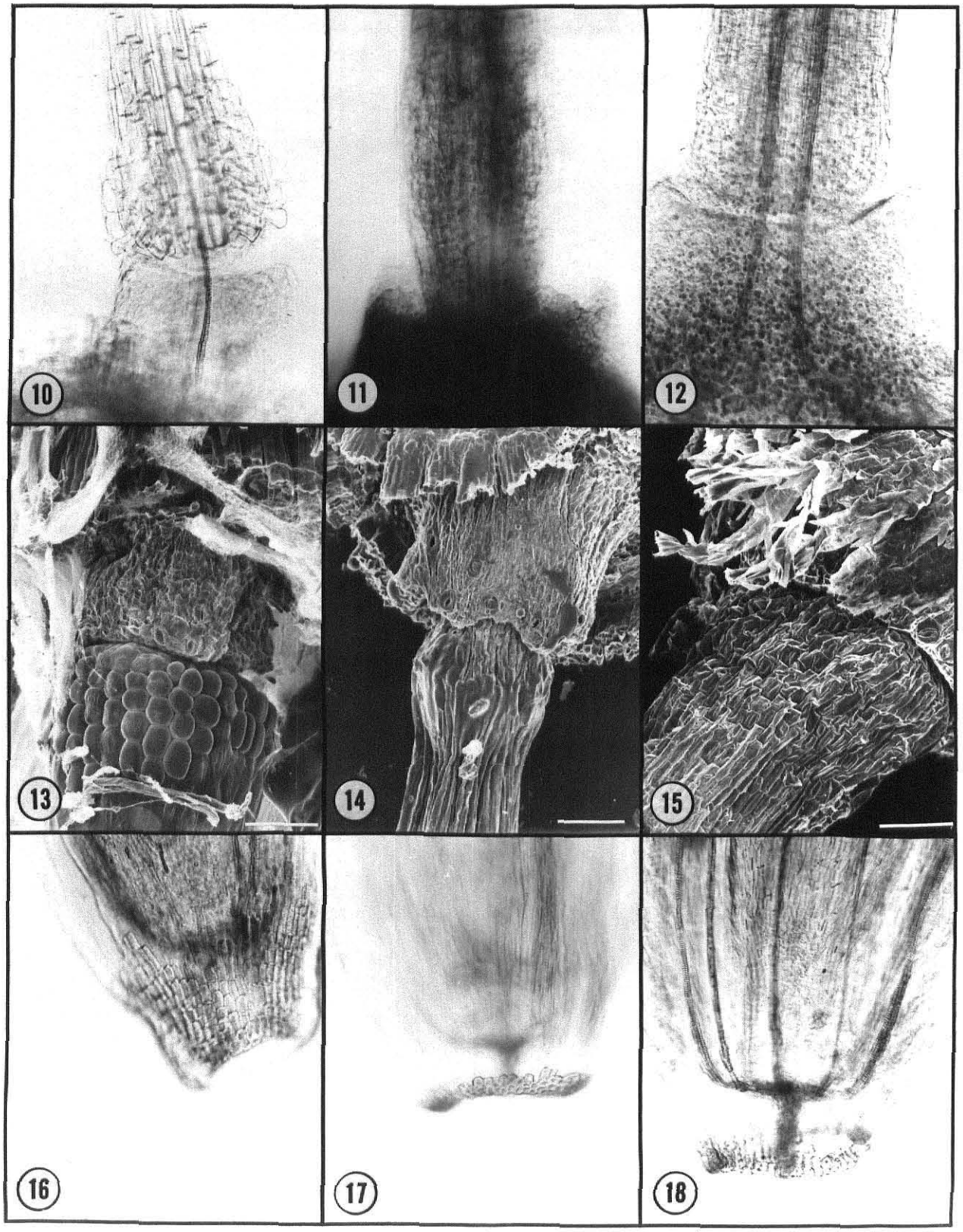
Figures 10, 11, 12. LM of the stylopodium of Roldana angulifolia. 126x.

Figures 13, 14, 15. SEM of the stylopodium of R. angulifolia. 130x. Line = 10μ.

Figure 16. LM of the carpopodium of Psacalium silphiifolium. 236x.

Figure 17. LM of the carpopodium of Senecio oerstedianus. 236x.

Figure 18. LM of the carpopodium of Barkleyanthus salicifolius. 236x.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Apparently there was no morphological distinction between cells of the cleft and the cells of the ridges (Figs. 4, 5, 6). The third type of style was characterized by a stigmatic area that was confined to discrete, marginal ridges or bands by a broad cleft or groove that runs the length of the style branch. In this type of style a morphological distinction between the cells of the groove and the stigmatic cells was noticed (Figs. 7, 8, 9).

Three types of stylopodial structure were found in the species surveyed. A species had either an enlarged style base atop and free from the nectary (Figs. 10, 13), or it had an enlarged style base that was partially immersed in the nectary (Figs. 12, 15), or a tapering carpopodium free from the nectary (Figs. 11, 14).

Of the two types of carpopodium described by Robinson and Brettell (1973j), only one type was found in the species surveyed. This type of carpopodium consisted of thickened quadrate cells (Figs. 16, 17, 18). The squarish to rectangular (quadrate) cells were arranged in one to several rows or series.

The anther collars, the apical end of the filament, which are usually morphologically distinct from the rest of the filament were of two types. The collars were either dilated basally (Figs. 20, 21, 23, 24) or they were of uniform thickness their entire length (Figs. 19, 22).

The exothecial cells line the inside wall of the pollen sacs in the anther. These elongated cells have a

Figure 19. LM of the anther collars of Digitacalia jatrophoides. 158x.

Figure 20. LM of the anther collars of Senecio megaphyllus. 158x.

Figure 21. LM of the anther collars of Senecio cineraria. 158x.

Figure 22. SEM of the anther collars of D. jatrophoides. 130x. Line = 10μ.

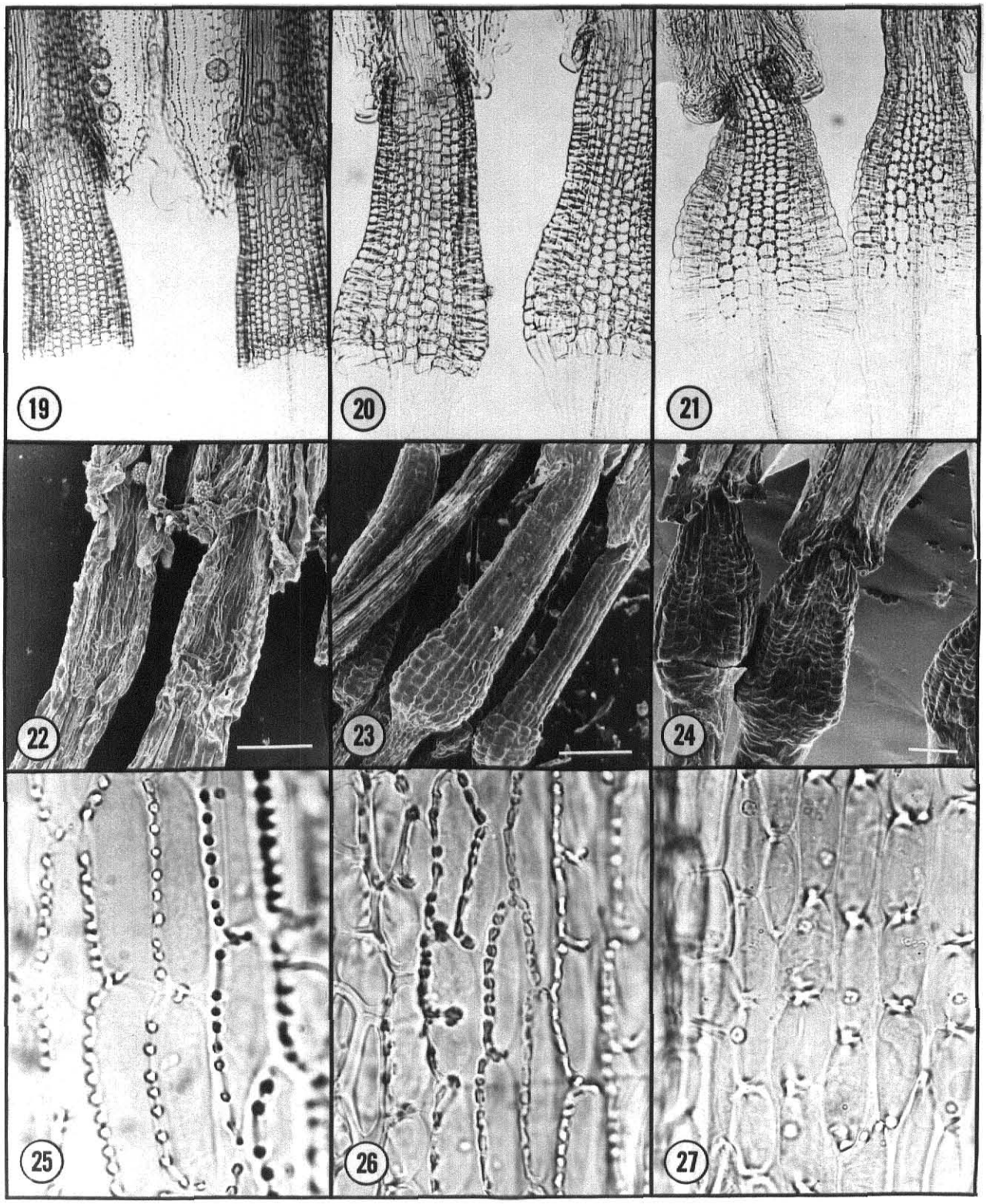
Figure 23. SEM of the anther collars of S. megaphyllus. 130x. Line = 10μ.

Figure 24. SEM of the anther collars of S. cineraria. 130x. Line = 10μ.

Figure 25. LM of the exothecial cells of Telanthophora cobanensis. 800x.

Figure 26. LM of the exothecial cells of Arnoglossum muehlenbergii. 800x.

Figure 27. LM of the exothecial cells of Digitacalia tridactylitis. 800x.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series of moniliform thickenings in their cell walls. When these thickenings are restricted to the transverse or horizontal walls the tissue is said to be polarized (Nordenstam, 1976) (Fig. 27). If the thickenings occurred on the radial walls the tissue is referred to as non-polarized (Nordenstam, 1976) (Figs. 25, 26).

RESULTS

The species surveyed in this study may be divided into several groups. One group, the majority of the species examined in this study, consists of species treated by Robinson and Brettell (1973f,g,i,j; 1974a,c; 1975) in their work on the "Cacalioid" Senecioneae. They considered the "Cacalioid" species properly belonged in ten genera. Species in eight of these genera were surveyed; the genera are Arnoglossum, Barkleyanthus, Digitacalia, Pittocaulon, Psacaliopsis, Psacalium, Roldana, and Telanthophora. Two genera of Robinson and Brettell, Nelsonianthus and Pippenalia were unavailable for examination.

Several species of Senecio which Robinson and Brettell have not transferred to different genera, but which other authors have treated as segregates were also examined. Weber (1973) transferred Senecio amplectens and allied species to Ligularia, based on a close resemblance of these two elements. Cabrera (1950) raised to generic level Senecio subg. Pseudogynoxys as Pseudogynoxys, based on stylar characters. Senecio confusus and allied species were thus transferred to Pseudogynoxys. Both Cautrecasas (1955) and Robinson and Brettell agreed with Cabrera in the establishment of the genus Pseudogynoxys. Löve and Löve (1975) suggested S. aurea and allied species would better be treated as the genus Packera.

Six species of Senecio which have not been trasferred recently to segregate genera were also examined. These were: S. cineraria, S. douglassii, S. megaphyllus, S. oerstedianus, S. parasiticus, S. vulgaris.

For convenience and organizational reasons, the species were treated under the generic names proposed by Robinson and Brettell and the other authors. Treating the genera this way is not meant as an endorsement of the generic concepts outlined by these authors.

The findings are summarized in Table I.

Arnoglossum Raf.

This genus of ten species as recognized by Robinson (1974c) is distributed mainly in the Southeastern United States. Species in this genus were formerly placed in Cacalia sect. Conophora DC., or in Mesadenia Raf. Four species were examined for this study.

1. Arnoglossum atriplicifolium (Linn.) H. Robinson, Phytologia 28:294. 1974.

Cacalia atriplicifolia Linn. Sp. Pl. 835, 1753.

Mesadenia atriplicifolia (Linn). Raf. New Fl. Amer. 4:79. 1836.

Only LM was performed on this species.

The stigmatic area was found to cover entirely the interior of the style branches. No central cleft was present on the style branches. The stylopodium consisted of a slightly

enlarged style base partially immersed in the broad nectary. The carpopodium was composed of one or two rows of thickened quadrate cells. The anther collars were not dilated basally. Exothecial tissue was non-polarized.

2. Arnoglossum muehlenbergii (Sch. Bip.) H. Robinson, Phytologia 28:294. 1974.

Cacalia reniformis Mühl. in Willd. Sp. Pl. 3:1735. 1804. non Cacalia reniformis Lam.

Mesademia reniformis (Muhl.) Raf. New Fl. Amer. 4:79. 1836.

Senecio muehlenbergii Sch. Bip. Flora 28:499. 1845.

Only LM was performed on this species.

The stigmatic area was found to cover completely the interior surface of the style branch. No central cleft was present. A slightly expanded style base free from the nectary was found to compose the stylopodium. Several rows of thickened quadrate cells composed the carpopodium. Elongate anther collars were not dilated basally. Exothecial tissue was non-polarized.

3. Arnoglossum ovatum (Walt) H. Robinson, Phytologia 28:294. 1974.

Cacalia ovata Walt. Fl. Carol. 196. 1788.

Mesadenia elliottii Harper, Torreya 5:184. 1905.

LM, sectioning, and SEM were performed on this species.

The uncleft stigmatic area was found to cover completely the interior of the style branches. Sectioned style branches

showed morphologically identical cells across the breadth of the style branches. A slighly expanded style base partially immersed in the nectary composed the stylopodium. The carpopodium was composed of one-two rows of thickened quadrate cells. Elongate anther collars were not dilated basally. Exothecial tissue was found to be non-polarized.

4. Arnoglossum plantagineum Raf. Fl. Ludov. 65. 1817. Cacalia tuberosa Nutt. Gen. N. Am. Pl. 2:138. 1818. Mesadenia tuberosa (Nutt.) Britton ex Britton and Brown, Fl. N. U.S. 3:474. 1898.

Only LM was used to examine this species.

The uncleft stigmatic area was found to cover completely the interior of the style branches. A slightly expanded style base partially immersed in the nectary was found to constitute the stylopodium. One-two rows of thickened quadrate cells composed the carpopodium. The short anther collars were not dilated basally. Exothecial tissue was non-polarized.

No species of Arnoglossum examined showed any variation in the extent or configuration of the stigmatic area; the uncleft stigmatic area always completely covered the interior of the style branches. Variation in stylopodial structure was observed, individual species had either their style base partially immersed or free from the nectary. Variation in the number of rows of thickened quadrate cells that composed the carpopodium was also observed. Relative lengths of the

anther collars varied, but all were found to be non-dilated basally. Exothecial tissue of all species was non-polarized.

Barkleyanthus H. Robinson and R. D. Brettell.

This monotypic genus found from Arizona to Honduras consists of the species commonly called Senecio salignus.

1. Barkleyanthus salicifolius (H.B.K.) Rob. and Brettell, Phytologia 27:407. 1974.

Cineraria salicifolia H.B.K. Nov. Gen. et Sp., folio ed. 4:148. 1818.

Senecio salignus DC. Prod. 6:430. 1837.

This species was examined using LM and SEM.

The uncleft stigmatic area was found to cover the entire interior of the style branches. The stylopodium was found to consist of an enlarged and thickened style base which was not immersed in the nectary. Several rows of thickened quadrate cells composed the carpopodium. Elongated anther collars were not dilated basally. Exothecial tissue was non-polarized.

Digitacalia Pippen

Digitacalia, as recognized by Robinson and Brettell (1974a), consists of four species. As originally described by Pippen (1968) this genus contained five species, but Robinson and Brettell (1974a) transferred D. heteroidea to Roldana. This genus is distributed in Mexico and Central

America and consists of elements formerly placed in Cacalia. Three species were examined for this study.

1. Digitacalia jatrophoides (H.B.K.) Pippen, Contr. U.S. Nat. Herb. 34:381. 1968.

Cacalia jatrophoides H.B.K. Nov. Gen. et Sp. 4:169. 1820-folio ed 4:132. 1820.

Senecio jatrophoides (H.B.K.) Sch. Bip. Flora 28:498. 1845.

Odontotrichum jatrophoides (H.B.K.) Rydb. Bull. Torrey Bot. Club. 51:419. 1924.

This species was examined using LM and SEM.

The uncleft stigmatic area was found to cover completely the interior of the style branches. The slightly expanded style base was not immersed in the nectary. The carpopodium was composed of several rows of thickened quadrate cells. Relatively short anther collars were not dilated basally. Exothecial tissue was found to be polarized in most anthers, but several of the anthers examined contained cells that were only partially polarized.

2. Digitacalia napeifolia (DC.) Pippen, Contr. U.S. Nat. Herb. 34:382. 1968.

Cacalia napeaefolia DC. Prod. 6:328. 1838.

Senecio napeaefolium (DC.) Schultz Bip. Flora 28:498. 1845.

Odontotrichum napeaefolium (DC.) Rydb. Bull. Torrey Bot. Club 51:418. 1924.

This species was examined using LM and SEM.

The uncleft stigmatic area was found to cover completely the interior of the style branches. The stylopodium was composed of an expanded style base not immersed in the nectary. Several rows of thickened quadrate cells composed the carpopodium. The elongate anther collars were not dilated basally. Exothecial tissue was found to be polarized. No partially polarized cells were observed in the material examined.

3. Digitacalia tridactylitis (Rob. and Greenm.) Pippen, Contr. U.S. Nat. Herb. 34:383. 1968.

Cacalia tridactylitis Rob. and Greenm. Amer. Journ. Sci. III. 50:159. 1895.

Odontotrichum tridactylitis (Rob. and Greenm) Rydb. Bull. Torrey Bot. Club. 51:419. 1924.

LM, sectioning, and SEM were performed on this species.

The uncleft stigmatic area was found to cover completely the entire interior of the style branches. Sections demonstrated that the inner surface of the style branch was composed of morphologically identical cells. The stylopodium consisted of an enlarged style base partially immersed in the nectary. Several rows of thickened quadrate cells composed the carpopodium. The anther collars were not dilated basally. Exothecial tissue was polarized.

Florets of different maturity levels were examined to determine the stability of the microcharacters with age.

All florets removed were from the same specimen but from different capitula. Five maturity levels were examined. These were: (a) corolla lobes tightly appressed to one another, (b) florets at anthesis, (c) florets where anthesis was complete, but the style branches were still appressed to each other, (d) florets in which style branches were fully extended but not recurved, and (e) mature florets with fully recurved style branches.

All five characters studied were found to be stable with age. These characters differed very little in appearance from the youngest to the oldest floret. Any differences noted were no greater than the differences that were found in examining two florets of the same age.

All species of Digitacalia examined were found to have the stigmatic area over the entire interior of the style branches. The stigmatic area was not cut by a cleft, and it appeared to be composed of morphologically identical cells for its entire length. The stylopodium consisted of an enlarged style base which was either partially immersed in the nectary, or free from it. The carpopodium was found to be uniform throughout the genus, consisting of several rows of thickened quadrate cells. Anther collars were variable in their length, but none were dilated basally. Exothecial tissue was polarized in most species, but in D. jatrophoides some of the exothecial cells had thickenings on their radial walls.

Pittocaulon H. Robinson and R. D. Brettell

This genus consists of five species of Mexican distribution. Species of this genus have formerly been placed in Senecio sect Terminales and/or Cineraria. Only one species was available for examination.

1. Pittocaulon bombycophole (Bullock) H. Rob. and R. D. Brettell, Phytologia 26:452. 1973.

Senecio bombycopholis Bullock, Hook. Ic. Pl. 34:t. 3343. 1937.

This species was examined using LM and SEM.

The uncleft stigmatic area was found to cover completely the interior of the style branches. The stylopodium consisted of an enlarged style base placed well above the nectary. Several rows of thickened quadrate cells composed the carpopodium. Elongate anther collars were not dilated basally. Exothecial tissue was non-polarized.

Psacaliopsis H. Robinson and R. D. Brettell

The two species in this genus range from Mexico to Guatemala. One species was formerly placed in Senecio, the other in Cacalia. Only one species was available for study.

1. Psacaliopsis purpusii (Greenm.) H. Rob. and R. D. Brettell, Phytologia 27:408. 1974.

Senecio purpusii Greenm. ex Brandegee, Univ. Calif. Publ. Bot. 3:393. 1909.

This species was examined using LM and SEM.

The uncleft stigmatic area was found to cover completely the interior of the style branches. The enlarged style base was not immersed in the nectary. Several rows of thickened quadrate cells composed the carpopodium. Elongate anther collars were not dilated basally. Exothecial tissue was non-polarized.

Psacalium Cass.

The genus Psacalium, as recognized by Robinson and Brettell (1973), consists of elements formerly placed in Cacalia. Their circumscription of the genus included both Psacalium and Odontotrichum of other authors (Rydberg, 1924; Pippen, 1968). Psacalium is distributed in Mexico and Central America. Three of the thirty-eight species were examined.

1. Psacalium silphiifolium (Rob. and Greenm.) H. Rob. and R. D. Brettell, Phytologia 27:263. 1973.

Cacalia silphiifolia Rob. and Greenm. Amer. Journ. Sci. III. 5:158. 1895.

Odontohichum silphiifolium (Rob. and Greenm.) Rydb. Bull. Torrey Bot. Club 51:416. 1924.

This species was examined using LM and SEM.

The uncleft stigmatic area was found to cover entirely the interior of the style branches. The stylopodium consisted of an enlarged style base which was not immersed in the nectary. The carpopodium was composed of several rows of thickened

quadrate cells. Elongate anther collars were not dilated basally. Exothecial tissue was non-polarized.

2. Psacalium sinuatum (Cerv.) H. Rob. and R. D. Brettell, Phytologia 27:263. 1973.

Cacalia sinuata Cerv. in La Llave and Lex. Nov. Veg. Desc. fac. 1:29. 1824.

Senecio albo-lutescens Sch. Bip. Flora 28:498. 1845.

Senecio calophyllus Hemsl. Biol. Centr. Amer. Bot. 2:237. 1881.

Odontotrichum sinuatum (Cerv.) Rydb. Bull. Torrey Bot. Club 51:415. 1924.

LM, sectioning and SEM were performed on this species.

The stigmatic area was found to be divided into two broad ridges by an area of morphologically distinct cells at the base of the style branch, but the rest of the style branch appeared totally stigmatic. Sectioning only revealed morphologically identical cells across the breadth of the style branch. The enlarged style base was not immersed in the nectary. Three to several rows of thickened quadrate cells composed the carpopodium. Shortish anther collars were not dilated basally. Exothecial tissue was found to be non-polarized.

3. Psacalium tabulare (Hemsl.) Rydb. Bull. Torrey Bot. Club 51:375. 1924.

Senecio tabularis Hemsl. Biol. Centr. Amer. Bot. 2: 248. 1881.

Cacalia tabulare (Hemsl.) A. Gray, Proc. Amer. Acad. 19:52. 1883.

Only LM was performed on this species.

The uncleft stigmatic area was found to cover the complete interior of the style branches. The stylopodium consisted of an enlarged style which was not immersed in the nectary. Several rows of thickened quadrate cells composed the carpopodium. Elongate anther collars were dilated basally. Exothecial tissue was non-polarized.

Some variation in the distribution of the stigmatic area was noticed in the species of Psacalium examined. In both P. silphiifolia and P. tabulare the stigmatic area covered the entire interior surface of the style branches. A small basal portion of non-stigmatic cells was found in P. sinuatum. Stylopodial structure was found constant, consisting of an enlarged style base sitting atop and free from the nectary. A carpopodium of several rows of thickened quadrate cells was common to the three species examined. All species examined in this genus possessed basally non-dilated anther collars. Exothecial tissue was non-polarized in the three species.

Roldana La Llave and Lex.

Roldana contains forty-eight species distributed in Mexico and Central America. The species that compose Roldana were formerly placed in Senecio sect Palmatinervii and sect. Fruticosi. Five species of this genus were examined.

Specimens of Roldana angulifolia were examined to determine the stability of the microcharacters within one population. Specimens of R. schaffneri from nine different locations were examined to determine the stability of the microcharacters over a large geographical range.

1. Roldana angulifolia (DC.) H. Rob. and R. D. Brettell, Phytologia 27:415. 1974.

Senecio angulifolius DC. Prodr. 6:431. 1837.

This species was formerly placed in Senecio sect. Palmatinervii. Three different individuals from one population were examined to determine the stability of the microcharacters within a population.

Specimens were examined using LM and SEM.

All specimens of this species examined were found to have the uncleft stigmatic area completely covering the interior of the style branches. The stylopodial structure was variable; it varied from an enlarged style base free from the nectary (Figs. 10, 13), to an enlarged style base partially immersed in the nectary (Figs. 12, 15), to unenlarged style base tapering into the nectary (Figs. 11, 14). Carpopodial structure was stable throughout the population. It consisted of several rows of thickened quadrate cells. No variation was noted in the anther collars; all were elongate and not dilated basally. Configuration and the extent of the thickenings in the exothecial cells were found to be variable. Some cells were found that had thickenings on both the radial and

the transverse walls, other cells have thickenings only on the radial walls. These differences were noted between different specimens in the population and for cells within the same anther. All exothecial tissue was classified as non-polarized.

2. Roldana chapalensis (S. Wats.) H. Rob. and R. D. Brettell, Phytologia 27:416. 1974.

Senecio chapalensis S. Wats. Proc. Amer. Acad. 25: 155. 1890.

This species was formerly placed in Senecio sect. Palmatinervii. Only LM was used to examine this species.

The uncleft stigmatic area was found to cover the entire interior of the style branch. The stylopodium consisted of a enlarged style base which was not immersed in the nectary. Several rows of small, thickened quadrate cells composed the carpopodium. Shortish anther collars were not dilated basally. Exothecial tissue was non-polarized with occasional cells having thickenings on the transverse walls.

3. Roldana heracleifolia (Hensl.) H. Rob. and R. D. Brettell, Phytologia 27:420. 1974.

Senecio heracleifolius Hemsley, Biol. Centr. Amer. Bot. 2:241. 1881.

This species was formerly placed in Senecio sect. Fruticosi. Both LM and SEM were used to examine this species.

The uncleft stigmatic area was found to cover completely the interior of the style branches. A slightly enlarged style base, not immersed in the nectary, composed the stylopodium. The carpopodium consisted of several rows of thickened quadrate cells. Anther collars were non-dilated basally. Exothecial cells were non-polarized.

4. Roldana heterogama (Hemsl.) H. Rob. and R. D. Brettell, Phytologia 27:420. 1974.

Senecio heterogamus Hemsley, Biol. Centr. Amer. Bot. 2:242. 1881.

This species was formerly placed in Senecio sect. Palmatinervii. LM and SEM were used to examine this species.

The uncleft stigmatic area was found to cover completely the interior of the style branches. The stylopodium consisted of a slightly enlarged style base not immersed in the nectary. Several rows of thickened quadrate cells composed the carpopodium. Elongate anther collars were not dilated basally. Fewer thickenings per exothecial cells characterized this species from other species of Roldana. The exothecial tissue was non-polarized as were other species of Roldana.

5. Roldana schaffneri (Klatt) H. Robinson and R. D. Brettell, Phytologia 27:423. 1974.

Senecio shaffneri Sch. Bip. ex Klatt, Leopoldina 24: 126. 1888.

This species was formerly placed in Senecio sect. Fruticosi. Specimens from nine different populations scattered throughout Mexico and Central America were examined to determine the stability of the microcharacters over a wide geographical range. Five of the specimens were from Mexico, two from Guatemala, and two from Honduras.

LM and SEM were used to examine this species.

All specimens examined were found to have the uncleft stigmatic area completely covering the interior of the style branches. Stylopodial structure was variable with two types being found. One consisted of a tapering style base which was not immersed in the nectary, the other and less common type consisted of an enlarged style base which was not immersed in the nectary. The carpopodium in all specimens examined was composed of several rows of thickened quadrate cells. The length of the anther collars was variable in the material examined, but all were non-dilated basally. The extent and placement of the moniliform thickenings in the walls of the exothecial cells was highly variable. Some specimens examined had exothecial cells with very few thickenings per cell, while other specimens had exothecial cells with walls heavily lined with thickenings. Exothecial cells in some specimens had thickenings on both the radial and transverse walls, while others had thickenings on the radial walls only.

All species of Roldana examined had the uncleft stigmatic area completely covering the interior of the style branches. The

structure of the stylopodium was found to be variable both within one population and over a large geographical range. The carpopodium in all species examined consisted of several rows of thickened quadrate cells. All anther collars examined were non-dilated basally. Variation in extent and placement of the moniliform thickenings of the exothecial cells was found both within one population and over a wide geographical range of one species.

Telanthophora H. Robinson and R. D. Brettell

This genus of fourteen species ranges through Mexico and Central America. Species in this genus were formerly placed in Senecio sect. Terminales. Four species of Telanthophora were examined.

1. Telanthophora arborescens (Steetz), H. Rob. and R. D. Brettell, Phytologia 27:426. 1974.

Senecio arborescens Steetz in Seem. Bot. Voy. Herald, 162t.31. 1854.

LM, sectioning and SEM were performed on this species.

The stigmatic area covered the entire interior surface of the style branches but was divided into two broad ridges by a cleft which runs the length of the style branch. The cells of the cleft appeared morphologically identical with those of the stigmatic area proper. This apparent similarity was further borne out by the sections. A slightly expanded style base not immersed in the nectary composed the stylopodium. The carpopodium consisted of several rows of thickened quadrate

cells. Elongate anther collars were not dilated basally. Exothecial tissue was found to be non-polarized.

2. Telanthophora cobanensis (Coulter) H. Rob. and R. D. Brettell, Phytologia 27:427. 1974.

Senecio cobanensis Coulter, Bot. Gaz. 16:101. 1891.

This species was examined using LM and SEM.

The style branches of this species showed some variation in configuration of the stigmatic area. Several styles had a cleft which separated the stigmatic area into two broad ridges present on the basal portion of the style branch. Apparently the cells of the cleft are morphologically distinct from the stigmatic cells. Apically on these style branches, the stigmatic area was fused into a continuous unit. One style had a triangular area of non-stigmatic cells present at the base of the branch, but was otherwise totally stigmatic across the breadth of the style branch. The stylopodium consisted of a slightly enlarged style base not immersed in the nectary. Several rows of thickened quadrate cells composed the carpopodium. Anther collars were not dilated basally. Exothecial tissue was non-polarized.

3. Telanthophora grandifolius (Less.) H. Robinson and R. D. Brettell, Phytologia 27:427. 1974.

Senecio grandifolius Less. Linnaea 5:162. 1830.

Only LM was performed on this species.

The uncleft stigmatic area was found to cover completely the interior of the style branches. The stylopodium

consisted of a slightly enlarged style base not immersed in the nectary. Several rows of thickened quadrate cells composed the carpopodium. Elongate anther collars were not dilated basally. Exothecial tissue was found to be non-polarized.

4. Telanthophora standleyi (Greenm.) H. Rob. and R. D. Brettell, Phytologia 27:428. 1974.

Senecio standleyi Greenm. in Standley Contr. U.S. Nat. Herb. 2(6):286. 1907.

Only LM was used to examine this species.

The uncleft stigmatic area was found to cover the entire interior of the style branches. A slightly expanded style base not immersed in the nectary composed the stylopodium. Several rows of thickened quadrate cells composed the carpopodium. Anther collars were not dilated basally. Exothecial tissue was found to be non-polarized, but with an occasional cell with thickenings on both the radial and transverse walls.

Species in Telanthophora showed some variation in the configuration of the stigmatic area. In two species the uncleft stigmatic area was found to cover completely the interior of the style branches. The stigmatic area in the other two species was variously divided by an area of non-stigmatic cells. Stylopodial structure showed little variation, it always consisted of a slightly expanded style base not immersed in the nectary. All species had a carpopodium of

several rows of thickened quadrate cells. Anther collars of all species were non-dilated basally. Exothecial tissue was found to be non-polarized with one or two cells occasionally having thickenings on the transverse walls.

Ligularia

Only one species of this genus was examined. Weber (1973) suggested S. amplectens and allies resembled the Asiatic Ligularias enough to warrant their transfer to that genus. These species were formerly placed in Senecio sect. Amplectentes.

1. Ligularia amplectens (A. Gray) W. A. Weber, Southw. Nat. 18:321. 1973.

Senecio amplectens A. Gray, Am. Jour. Sci. II. 33: 240. 1862.

This species was examined using LM and SEM.

The stigmatic area was found to be separated into two broad bands at the base of the style branch by an area of non-stigmatic cells. These cells were morphologically distinct from those of the stigmatic area. Apically this area of non-stigmatic cells graded into cells that were morphologically identical with stigmatic cells but possessed a different orientation. These cells were aligned parallel to the longitudinal axis of the style branch. Stigmatic cells were aligned perpendicular to the longitudinal axis. The stylopodium consisted of an enlarged style base not immersed

in the nectary. One or two rows of thickened quadrate cells composed the carpopodium. Elongate anther collars were dilated basally. Exothecial tissue was non-polarized.

Packera

Löve and Löve (1975) suggested that Senecio aureus and allies should be segregated from Senecio and they erected the genus Packera to accomodate those species.

1. Packera aurea (Linn.) Löve and Löve, Bot. Notiser 128:520. 1975.

Senecio aureus Linn. Sp. Pl. 2:870. 1753.

LM and SEM were used to examine this species. Material for SEM collapsed during freeze-drying.

The stigmatic area was found to cover completely the interior of the style branch, but it was divided into two broad ridges by a longitudinal cleft which ran the length of the style branch. A slightly enlarged style base, not immersed in the nectary, composed the stylopodium. Several rows of thickened quadrate cells composed the carpopodium. Elongate anther collars were dilated basally. Exothecial tissue was non-polarized with some cells having thickenings on the transverse walls too.

Pseudogynoxys (Greenm.) Cabrera

Cabrera (1950) suggested that the species in Senecio sect. Pseudogynoxys be elevated to the genus Pseudogynoxys. Among these species was what is commonly called S. confusus

Britten. Later authors (Williams, 1975) placed S. confusus in synonym under S. chenopodioides HBK. Cabrera's nomenclature is followed here.

1. Pseudogynoxys berlandieri (DC.) Cabrera, Brittonia 7:56. 1950.

Gynoxys berlandieri DC. Prod. 6:326. 1837.

Senecio confusus Britten, Jour. Bot. 36:260. 1898.

(Gynoys berlandieri DC., basionym).

LM, sectioning and SEM were performed on this species.

The stigmatic area consisted of marginal ridges on the interior of the style branches. The longitudinally aligned cells in the middle of the style branch differed morphologically from those of the stigmatic area. This morphological difference was also apparent in the sections. The stylopodium consisted of a slightly enlarged style base which was not immersed in the nectary. Several rows of thickened quadrate cells composed the carpopodium. Elongate anther collars were dilated basally. Exothecial tissue was non-polarized.

Senecio L.

This huge genus of world wide distribution is readily divisible into semi-distinct groups, and several of the groups have been treated as segregate genera by various authors, as is done in this paper. Six species of Senecio which have not been treated in segregate genera were examined.

1. Senecio cineraria DC.

This species is cultivated as "Dusty miller". It is placed in Senecio sect. Incani.

This species was examined using LM and SEM.

The stigmatic area was found to be separated into two ridges by a cleft that ran the entire length of the style branch. The cells of the cleft appeared morphologically identical with those of the stigmatic area, so the style branch was totally stigmatic within. The stylopodium consisted of a slightly enlarged style base not immersed in the nectary. A single row of thickened quadrate cells composed the carpopodium. The anther collars were found to be composed of a dilated upper section of thickened cells and a lower portion of non-thickened cells. This type of anther collar was unique among all the species examined. Exothecial tissue was non-polarized with occasional cells having thickenings on the transverse walls.

2. Senecio douglasii DC. Prod. 6:429. 1837.

This species belongs in sect. Suffruticosi.

LM and SEM were used to examine this species.

The stigmatic area in this species was found to be divided into two broad ridges by a longitudinal cleft. Cells within the cleft appeared morphologically identical to the cells of the stigmatic area. At the apex of the style branch there was a triangular region of non-stigmatic cells. These cells were morphologically distinct from those of the stigmatic area. The stylopodium consisted of an enlarged style base

which is not immersed in the nectary. Elongate anther collars were dilated basally. Exothecial tissue was found to be non-polarized.

3. Senecio megaphyllus Greenm. Publ. Field Columbian Mus. Bot. 2:284. 1907.

This species is placed in Senecio sect. Multinervii.

This species was examined using LM and SEM. The materials of this species seemed to be prone to collapse during freeze-drying.

The stigmatic area was confined to two broad marginal ridges on the interior of the style branches. A longitudinal cleft composed of cells which are morphologically distinct from those of the stigmatic area separated the two ridges. The stylopodium consisted of an enlarged style base not immersed in the nectary. Several rows of thickened quadrate cells composed the carpopodium. Elongate anther collars were dilated basally. Exothecial tissue was found to be non-polarized.

4. Senecio oerstedianus Benth. ex Oersted, Vid. Medal. Kjoeb. 109. 1852.

LM, sectioning and SEM were performed on this species.

The stigmatic area was found to be divided into two broad ridges by a longitudinal cleft. The cells of the cleft appeared morphologically identical with the cells of the stigmatic area. Their morphological similarity was confirmed by the sections. An expanded style base not immersed in the nectary composed the stylopodium. Two or three rows of thickened quadrate cells composed the carpopodium. Elongate anther

collars were dilated basally. Exothecial cells were found to be non-polarized.

5. Senecio parasiticus Schultz Bip. ex Hemsley, Biol. Centr. Amer. Bot. 2:244. 1881.

This species belongs in Senecio sect. Streptothamni.

LM and SEM were used to examine this species.

The stigmatic area was confined to two ridges on the margins of the style branch interior. The cleft between the two ridges was composed of cells that are morphologically distinct from those of the stigmatic area. Stylopodial structure consisted of a slightly expanded style base not immersed in the nectary. Several rows of thickened quadrate cells composed the carpopodium. Exothecial tissue was non-polarized.

6. Senecio vulgaris Linn. Sp. Pl. 2:867. 1753.

This species is placed in Senecio sect. Annui.

LM and SEM were used to examine this species.

The stigmatic area was found to be divided into two broad ridges by a longitudinal cleft. The cells which composed the cleft were morphologically distinct from the cells of the stigmatic area. The stylopodium consisted of an expanded style base not immersed in the nectary. A single row of thickened quadrate cells composed the carpopodium. Elongate anther collars are slightly dilated basally. Exothecial tissue was found to be non-polarized.

Great variation in the extent and configuration of the stigmatic area was found in the species of Senecio examined. It

varied from completely covering the interior of the style branch, to being confined to two broad ridges on the margins of the style branches. Stylopodial structure was found to be less variable than that of stigmatic area. The stylopodium consisted of an enlarged style base which was not immersed in the nectary. The carpopodium varied from a single row of thickened quadrate cells to several rows of thickened cells. Anther collars in the species of Senecio examined were dilated basally. Exothecial tissue was non-polarized with occasional cells having thickenings on their transverse walls also.

TABLE I

Species	Stigmatic * area	Stylopodium	Carpopodium	Anther Collars	Exothecial Tissue
CACALIOID					
Arnoglossum					
atriplicifolia	Entire	immersed	2-rows	Non-dilated	Non-polarized
muehlenbergii	Entire	free	3+ rows	Non-dilated	Non-polarized
ovatum	Entire	immersed	2-rows	Non-dilated	Non-polarized
plantagineum	Entire	immersed	2-rows	Non-dilated	Non-polarized
Barkleyanthus					
salicifolius	Entire	free	3+	Non-dilated	Non-polarized
Digiticalia					
jatrophoides	Entire	free	3+	Non-dilated	± polarized
napeifolia	Entire	free	3+	Non-dilated	Polarized
tridactylitis	Entire	immersed	3+	Non-dilated	Polarized
Pittocaulon					
bombycophole	Entire	free	3+	Non-dilated	Non-polarized
Psacaliopsis					
purpusii	Entire	free	3+	Non-dilated	Non-polarized
Psacalium					
silphiifolium	Entire	free	3+	Non-dilated	Non-polarized
sinuatum	Cleft	free	3+	Non-dilated	Non-polarized
tabulare	Entire	free	3+	Non-dilated	Non-polarized
Roldana					
angulifolia	Entire	± free	3+	Non-dilated	± non-polarized
chapalensis	Entire	free	3+	Non-dilated	± non-polarized
heracleifolia	Entire	free	3+	Non-dilated	Non-polarized
heterogamus	Entire	free	3+	Non-dilated	Non-polarized
schaffneri	Entire	free	3+	Non-dilated	± non-polarized

Species	Stigmatic * area	Stylopodium	Carpopodium	Anther Collars	Exothecial tissue
Telanthophora					
arborescens	Cleft	free	3+	Non-dilated	Non-polarized
cobanensis	Divided-basally	free	3+	Non-dilated	Non-polarized
grandifolius	Entire	free	3+	Non-dilated	Non-polarized
standleyi	Entire	free	3+	Non-dilated	± non-polarized
SENECIONOID					
Ligularia amplectens	Divided-basally	free	1-2	Dilated	Non-polarized
Packera					
aurea	Cleft	free	3+	Dilated	Non-polarized
Pseudogynoxys					
berlandieri	Divided	free	3+	Dilated	Non-polarized
Senecio					
cineraria	Cleft	free	1	Dilated	± non-polarized
douglasii	Cleft-divided apically	free		Dilated	Non-polarized
megaphyllus	Divided	free	3+	Dilated	Non-polarized
oerstedianus	Cleft-divided apically	free	2-3	Dilated	Non-polarized
parasiticus	Divided	free	3+	Dilated	Non-polarized
vulgaris	Divided	free	1	Dilated	Non-polarized

*Explanation of terminology for stigmatic area distribution.

Entire - undivided stigmatic area completely covers entire interior of the style branches.

Cleft - stigmatic area divided by a longitudinal cleft but whole interior of the style branch appears stigmatic.

Divided - stigmatic area divided into two broad bands on the margins of the style branches by a longitudinal cleft which is presumedly non-stigmatic or at least morphologically distinct from the marginal bands.

DISCUSSION

King and Robinson (1970) suggested "that syantherology, like bryology, is most properly a study for the compound microscope," yet many of the characters they proposed as significant can just as readily be observed with SEM. Although SEM preparation is somewhat more complicated, the results are more easily interpreted than those achieved with LM when studying cryptic features such as the cleft in certain style branches. Some of the more fragile characters such as the stylopodium, tended to fall apart during SEM preparation unless young specimens were used, but good results can still be achieved. SEM results were better if materials were first prepared for LM using Wetter's solution as the mounting medium. Apparently Wetter's solution hardens the specimen so it does not collapse during SEM preparation.

From the table of results it is apparent that the only "Cacalioid" character that does not show some transition into the other Senecioneae is that of the anther collars. Basally non-dilated anther collars were restricted to the "Cacalioid" Senecioneae, with basally dilated anther collars being restricted to the other Senecioneae examined.

Since the historical treatments of the Senecioneae have placed much emphasis on stylar characteristics, it is interesting to note that the distribution and configuration

of stigmatic area in the "Cacalioid" Senecioneae show transitions into the various configurations found in the other Senecioneae examined.

An uncleft stigmatic area was found to cover completely the interior of the style branches in all species examined of the "Cacalioid" genera Arnoglossum, Barkleyanthus, Digitacalia, Pittocanlon, Psacaliopsis and Roldana. As can be seen from the table, none of the non-"Cacalioid" Senecioneae examined had this type of stigmatic distribution. Some species of Psacalium and Telanthophora also had the uncleft type of configuration, but other species in these genera had differing configurations.

The stigmatic area in the non-"Cacaliod" genus Packera and Senecio cineraria, and in the "Cacalioid" species, Psacalium sinuata and Telanthophora arborescens completely covered the interior of the style branch but was divided into ridges by a longitudinal cleft. The cells within this cleft appeared morphologically identical to those on the ridges. Apparently the whole interior of the style branch was stigmatic.

The non-Cacalioid Senecio douglassii and S. oerstedianus had stigmatic areas that were divided by a longitudinal cleft of cells that morphologically resembled the cells of the ridges. At the tip of the style branches in these two species there was a triangular area of cells that differed morphologically from the cells of the ridges, presumably these cells were non-stigmatic. These two species were the only ones with this type of stigmatic distribution.

The "Cacalioid" species, Telanthophora cobanensis, and the non-"Cacalioid" Ligularia amplectens both had a basal area on the interior of the style branch that differed morphologically from the rest of the style branch interior. Except for the basal portion of non-stigmatic cells, the rest of the style branch interior appeared stigmatic.

A stigmatic area divided into two broad marginal ridges by a longitudinal cleft composed of cells morphologically distinct from those of the ridge was found only in the non-"Cacalioid" species, Pseudogynoxys berlandieri, Senecio megaphyllus, S. parasiticus, and S. vulgaris.

As can be seen from the table, the stylopodium and carpopodium structures showed no alignment along "Cacalioid" or non-"Cacalioid" generic lines, except that a carpopodium composed of only one row of quadrate cells was found only in two species of non-"Cacalioid" Senecioneae, Senecio cineraria and S. vulgaris. Stylopodial structure was variable not only between "Cacalioid" and non-"Cacalioid" but also between members of the same population and between members of the same species distributed over a large geographical range.

Placement of moniliform thickenings in the exothecial cell walls was not a character that could be used to separate "Cacalioid" from non-"Cacalioid" genera. Of all the genera surveyed, only Digitacalia had exothecial cells which were polarized. The polarization of exothecial cells in one species of Digitacalia, D. jatrophoides, was not always

complete. Some of the exothecial cells in this genus had thickenings not only on their transverse walls (polarized) but also had thickenings on the radial walls (non-polarized).

These results suggest that the microcharacters are in themselves insufficiently consistent to form a basis for generic segregation. Furthermore, the variation observed in these microcharacters is similar to the variations observed in gross morphology and thereby do little to refine the traditional and conservative broad circumscriptions of Senecio and Cacalia. Although non-dilated anther collars are re-restricted to "Cacalioid" Senecioneae examined, further examination of other species of Senecio and other Senecioneae genera may prove or disprove the uniqueness of this character. Variation in the configuration of the anther collars in Senecio existed; the anther collars of S. cinenaria being different from all others observed in Senecio. The morphological intergradation of the configuration of stigmatic area between the "Cacalioid" genera and the various non-"Cacalioid" genera should become better documented with examination of further species of Senecio and Senecioneae.

At present it would be better to use the microcharacters to help establish sub-generic groups within the genera Cacalia and Senecio. The polarization of exothecial cells characterizes species segregated in Digitacalia from other species in Cacalia. The uncleft type of stigmatic area characterizes the species of Senecio, segregated in

various "Cacalioid" genera by Robinson and Brettell, from other species of Senecio.

The five microcharacters examined do not warrant the emphasis placed on them by recent authors because (1) some of them are not stable within one population, (2) some of them are not stable within one species over a wide geographical range, (3) transitional forms are present that fade into other genera, (4) they are no less variable than features of gross morphology which have served taxonomy so well for so long.

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TABLE II

Taxon	Locality and Voucher
Arnoglossum atriplicifolia (Linn) H. Rob.	Kansas: Douglas Co., 1 mi. N. Lone Star. McGregor 103 (KSC).
	Missouri: Atchison Co., Shaded road, on US #136 at E edge of Rock Point. Henderson and Law 66-876 (KSC).
Arnoglossum muehlenbergii	Iowa: Allamakee Co. In upper Iowa Valley near Winneschiek Co. border. Tolstead s.n. (KSC).
	Missouri: Eagle Rock, Common on river bank. Bush 57 (KSC).
Arnoglossum ovatum (Walt.) H. Rob.	Georgia: Clearing on edge of swamp near Smithville, Curtiss 6884 (KSC).
	Texas: San Augustine Co., Sandy swamps, San Augustine. Palmer 10652 (MO).
Arnoglossum plantagineum Raf.	Illinois: Cook Co., Norwood Park (Chicago). Benke 6074 (KSC).
	Missouri: Prairie near Buckner. Bush 381 (KSC).
	Missouri: Eagle Rock. Bush 59 (KSC).
Barkleyanthus salicifolius (H.B.K.) H. Rob. and R. D. Brettell	Mexico: Along highway between Chilpancingo and Acapulco. Nelson and Nelson 5182 (KSC).
Digitacalia jatrophoides (H.B.K.) Pippen	Mexico: Guanajuato. Hills near Acambaro. Pringle 4262 (MO).
	Mexico: Oaxaca, Las Sedas. Smith 388 (MO).
Digitacalia napeifolia (D.C.) Pippen	Mexico: Oaxaca. Pringle 4478 (MO).

Taxon	Locality and Voucher
Digitacalia tridactylitis (Rob. & Greenman) Pippen	Mexico: Morelos, Barrancas near Cuernavaca. Pringle 6164 (MO).
	Mexico: Oaxaca, Sierra de San Filipe. Smith 380 (MO).
	Mexico: Morelos, Slopes of canyon above Cuernavaca. Pringle 9877 (MO).
Ligularia amplectens (A. Gray) Weber	Coloarado: Gunnison Co., Head of Crystal Canyon. Schofield Pass in Schofield Park, on road north from Gothic. Barkley and Robinson 229 (KSC).
	Colorado: San Juan Co., Red Mountain Pass. 14 m. S. of Ouray. Russell 61-115. (KSC).
	New Mexico: Colfax Co., Baldy Mo. 1 m. W. of Cooper Park. Hartman 2273 (KSC).
Packera aurea (Linn.) Löve and Löve	Arkansas: Garland Co., Low areas on Hickory Nut Mount. Crystal Springs. Demaree 55096 (KSC).
	New York: Westchester Co., Yard of A. Cronquist. 29 Dunderave Road, White Plains. Barkley s.n. (KSC).
Pittocaulon bombycophole (Bullock) H. Rob. and R. D. Brettell	Mexico: Temascaetepec Pungaracho. Hinton 5898 (MO).
Psacaliopsis purpusii (Greenm.) H. Rob. and R. D. Brettell	Mexico: Cerro del Gavèlar Puebla. Purpus 3843 (MO).
Psacalium silphiifolium (Rob. & Greenm.) H. Rob. and R. D. Brettell	Mexico: Oaxaca, Crest of the Sierra San Felipe, 14 mi. NE of Tlacolula. Cronquist and Sousa 10430 (KSC).

Taxon	Locality and Voucher
Psacalium sinuatam (Cerv.) H. Rob. & R. D. Brettell	Mexico: Michoacan, NE slope of savanna 6 or 7 miles E of Morelia. Cronquist 10305 (KSC).
	Mexico: Jalisico, Pastured plateau 19 miles NE of Zapotlanejo, road to Tepatitlan. Dieterle 3560 (MO).
	Mexico: Michoacan, Trans-Mexican volcanic belt ca 7.5 km. SW of Jacona. Cronquist and Becker 11201 (MO).
Psacalium tabulare (Hemsl.) Rydlb.	Mexico: Vera Cruz, E. slope of mts. between Tehuacan and Acultzingo 4 miles W of Acultzingo. Cronquist and Sousa 10350 (KSC).
Pseudogynoxys berlandieri (DC.) Cabrera	El Salvador: Dept. de Santa Ana, Lower slopes of the Volcan Monte Cristo. Winding road ca 8 km. NE of Metapan. Wilbur, Almeda and Luteyn 16351 (Duke).
	Guatemala: Dept. of Baja Verapaz, Guat. Hwy. #17 ca. 24 miles N of turn-off to El Progresso. Almeda and Luteyn 1804 (Duke).
	Panama: Cocle, Road to El cope from InterAmerican Hwy. Burch, Oliver, and Robertson 1369 (MO).
Roldana angulifolia (DC.) H. Rob. and R. D. Brettell	Mexico: Mexico, Mt Iztaccihuatl, 1 1/2 miles E of San Rafael, Gibson 1005 (KSC).
	Mexico: Mexico, Mt Iztaccihuatl, 1 1/2 miles E of San Rafael, Gibson 1004 (KSC).
	Mexico: Mexico, Mt. Iztaccihuatl, 1 1/2 miles E of San Rafael. Gibson 1003 (KSC).
	Mexico: Michoacan, 35 road miles E of the aquaduct in Morelia. Gibson 1023 (KSC).

Taxon	Locality and Voucher
	Mexico: Mexico, Parque Nacional Desierto de Leones. 4 km. off hwy 15. Gibson 1016 (KSC).
	Mexico: Puebla, Mt. Popocatepetl. Gibson 1002 (KSC).
Roldana chapalensis (S. Wats.) H. Rob. & R. D. Brettell	Mexico: Michoacan, 21 miles W of Ciudad Hidalgo, 4 1/2 miles E of Morelia. Gibson 1021 (KSC).
	Mexico: Michoacan, 21 road miles W of Ciudad Hidalgo. Gibson 1019 (KSC).
	Mexico: Jalisco, Mountains ca. 31 road miles of Ayatla, ca. 70 miles NW of Autlan. Cronquist 9797 (KSC).
Roldana heracleifolia (Hemsl.) H. Rob. and R. D. Brettell	Mexico: Michoacan, 12 miles E of Morelia. Cronquist 9724 (KSC).
	Mexico: Michoacan, Tree-Opuntia savanna 6 or 7 miles E of Morelia. Cronquist 10304 (KSC).
	Mexico: Jalisco, Small stream 18 miles SE of Encarnacion de Diaz and 9 miles NW of Lagos de Moreno. Cronquist 10528 (KSC).
Roldana heterogama (Hemsl.) H. Rob. & R. D. Brettell	Costa Rica: San Jose, Cerro de las Vueltas. Standley and Valerio 43590 (US).
	Costa Rica: Cartago, Ca. 19-20 km NW of Cerro Asuncion (Cero de la Muerte) on CR #2 19.6 km beyond El Empalne. Almeda and Flowers 2091 (DUKE).
Roldana schaffneri (Klatt) H. Rob. & R. D. Brettell	Mexico: Vera Cruz, Huacapan NW de Sta Ana Atzacan 51-B-2. Rosas 264 (MO).
	Mexico: Vera Cruz, Arizaba Purpus 1172 (MO).
	Mexico: Vera Cruz, Mt. Pasitas Matuda 0739 (MO).

Taxon	Locality and Voucher
	Mexico: Vera Cruz, Mt. Pasitas Matuda 0734 (MO).
	Mexico: Vera Cruz, Hills about Jalapa. Pringle 8082 (MO).
	Guatemala: Dept. Quezaltenango, Above Santa Maria de Jesus. Standley 67201 (MO).
	Guatemala: Dept. El Progresso, Hill N. of Finia Piamonte, between Finea Piamonte and summit Volican Santa Luisa. Steyermark 43601 (MO).
	Honduras: Dept. Intebuca, Los Banos, La Esperanza town. Molina and Molina 25534 (MO).
	Honduras: Ocotepeque, Along Yoroconte river between El Moral and Sinuapa. Molina 24189 (MO).
Telanthpohora arborescens (Steetz) H. Rob. and R. D. Brettell	Panama: Chiriqui, Vicinity of Methodist camp near Nueva Swissa Croat 13502 (DUKE).
	Panama: Chiriqui, Rio Chiriqui Viejo valley, between El Volcan and Cerro Punta. White 7 (US).
Telanthophora cobanensis (Coulter) H. Rob. & R. D. Brettell	Mexico: Mt. Ovando, Esquintla Chis. Matuda 16257 (MO).
	Honduras: Intibuca, Mixed forest along Hiuse river, 9 kms. E of La Esperanza. Molina and Molina 25563 (MO).
	Guatemala: Alta Verapaz. Tuerckheim II. 1656 (MO).
Telanthophora grandifolius (Less.) H. Rob. & R. D. Brettell	Mexico: Puebla, N. slope, 2 or 3 miles E of Xicotepeode Juarez. Cronquist 9630 (KSC).

Taxon	Locality and Voucher
Telanthophora standleyi (Greenm.) H. Rob. and R. D. Brettell	Mexico: Jalisco, Headwaters of Rio Masconta [20-25 km., airline, SE of Talpa de Allende]. McVaugh 23443 (MO).
Senecio cineraria DC.	California: San Joaquin Co., Cultivated in Escalon. Barkley and Burroughs 299 (KSC).
Senecio douglasii DC. var. douglasii	Mexico: Baja, Arroyo in mounts. 14 miles E of Ojos Negros along road to Laguna Hanson. Wiggins 16696 (KSC).
	California: San Luis Okispo Co. On a flat rocky short grassland 34 miles E of Jct. US 101 and C. 166. Ediger 529 (KSC).
	California: Santa Barbara Co., State hwy. near Orcutt. Abrams 7648 (KSC).
Seneció megaphyllus Greenm.	Costa Rica: Volcan Coas. Greenman and Greenman 5396 (DUKE).
	Costa Rica: Steep wet slopes below La Palma. Rev Clara (upper Rio La Hondura) along the trail to Guapiles. Burger 3953 (DUKE).
	Costa Rica: Cartago, Hwy. 224 on property of ICE hydroelectric plant. ca. 11.6-2.0 km. E. of church in Orosi, beyond the town of Tapanti. Almeda, Flowers and Wyatt 2182 (DUKE).
Senecio oerstedianus Benth. ex Oersted.	Costa Rica: Cartago, Cloud forest area Cordillera Tulamanca, mount. of Cerro La Muerte. Molina, Burger, and Wallenta 18329 (DUKE).
	Costa Rica: Cartago, Pasture lands on Hwy 8 towards Volean Irazii 28-30 km. N of San José. Luteyn 677 (DUKE).

Taxon	Locality and Voucher
	Costa Rica: Cartago, Pasture ca 1 km. of the Rio Birris at elev. of ca. 2850 m. ca. 9 km. NE of Cartago in a straight line. Wilbur 14300 (DUKE).
	Costa Rica: Cartago, Upper slopes of Volcan Irazu. Wilbur and Teeri 13731 (DUKE).
	Costa Rica: Cartago. Wooded slopes along the Carretera Interamericana et ca. km. 97 at elev. 3100 m. in the vicinity of the Restaurante La Georgina. Wilbur and Stone 10075 (DUKE).
	Panama: Chiriqui, Peak, Volcan de Chiriqui, Bouguele district. Terry 1314 (MO).
Senecio parasitius Sch. Bip. ex Hemsley.	Panama: Bocas del Toro - Chiriqui Border, Elfen forst at divide on Chiriquiicito-Caldera trail. Kirkbride and Duke 977 (MO).
	Guatemala: Sololá, Cut over forest between Maria Tecun and Los Encuentros. Molina and Molina 24982 (DUKE).
Senecio vulgaris Linn.	California: Santa Barbara Co., Ca. 3 mi. S of Santa Maria, Rte. 101 frontage road. Reeves and Pinkava 11790.
	New Mexico: Collected at Santa Fe. Heller 3657 (KSC).

FLORAL MICROSTRUCTURE AND GENERIC DELIMITATION IN THE NEW WORLD SENECIONEAE (ASTERACEAE)

by

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ABSTRACT

Recent systematic investigations have placed great reliance on micromorphological floral features in generic delimitation in the Senecioneae. Thirty-one species of New World "Cacalioid" and "Senecionoid" Senecioneae were examined for five micromorphological characters: (1) configuration and distribution of the stigmatic area on the style, (2) stylopodial structure, (3) cellular structure of the carpopodium, (4) configuration of the anther collar, and (5) form of the exothecial cells in the anther. LM and/or SEM photographs were made for each character for each species. Studies were made on the stability of each of these characters with age and with geographical range. Variation was found to exist with both age and range, and sometimes within florets of the same capitulum. Differences were found to exist in the morphology of these five microcharacters between the "Cacalioid" and "Senecionoid" genera, however these microcharacters were no more consistent than the traditional characters employed in generic delimitation.