

A Study of the Genus *Schistocarpa*  
(Heliantheae: Asteraceae)

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## ABSTRACT

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# A Study of the Genus *Schistocarpha* (Heliantheae: Asteraceae)

*Harold Robinson*

## Introduction

The Neotropical genus *Schistocarpha* is a member of the tribe Heliantheae and is notable in the tribe, along with the genus *Neurolaena*, for having a pappus of many capillary bristles. The genus is widely distributed from Central Mexico southward through Central America into the northern Andes from Venezuela and Colombia to Bolivia. The present study was derived partly from the common occurrence of specimens misidentified as "*Eupatorium*," and interest was augmented during efforts to purify the concept of the tribe Senecioneae (Robinson & Brettell, 1973). Additional isolated problems have been studied (Robinson 1974, 1975), but the lack of a concerted effort has resulted in some errors. The existing partial treatment by Rydberg (1927) has proven less satisfactory than once believed, and important new information has accumulated since 1975. The present effort attempts to make necessary corrections and to survey the anatomy and relationships of the genus, while providing a preliminary treatment of the species.

The genus came to the attention of taxonomists late, considering that one of the species is very widely distributed in the Neotropical region. The first recognized species was described with the genus as *Schistocarpha bicolor* Lessing (1831), based on Mexican material. The genus was placed with *Neurolaena* in the subtribe Anthemideae in the extremely broad tribal concept Senecionoideae of

Lessing. Lessing mentioned that the pappus of *Schistocarpha* was uniseriate rather than biseriate as in "*Neurochlaena* R. Br.," a reflection of the greater number of series that is found in the later genus. Candolle (1836) placed *Schistocarpha bicolor* in the synonymy of *Perymenium discolor*, apparently without seeing material. The most widely distributed species of the genus did not enter the literature until 1850, when it was described as *Neilreichia eupatorioides* by Fenzl.

In the Bentham and Hooker system (1873), tribes of the Compositae were resegmented and many tribes of Cassini were restored. The tribe Senecioneae, however, was allowed to retain various mostly epaleaceous groups having a capillary pappus, while the tribe Helenieae was established for many similar genera that lacked a capillary pappus. On the basis of the pappus, *Schistocarpha* and *Neuroleana* remained in the Senecioneae in the subtribe "Liabae." The tribal disposition was followed by Hoffmann (1894), where the genera were placed in the subtribe Senecioninae. Most workers since Bentham and Hooker have accepted the placement of *Schistocarpha* in the Senecioneae.

An early exception to the Bentham and Hooker placement was by Rydberg (1927), who in a highly individual treatment placed *Neurolaena* and *Schistocarpha* together in a separate tribe, *Neurolaeneae*. He separated the two genera as follows:

Heads radiate, but the ligules in some species very inconspicuous; paleae of the receptacle lacerate, often 3-cleft; leaves opposite ..... 1. *Schistocarpha*  
Heads discoid or rarely radiate; paleae of the receptacle narrow, 1-nerved; leaves alternate. .... 2. *Neurolaena*

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Rydberg also presented a treatment of the 10 species of *Schistocarpha* then recognized from Mexico and Central America.

After Rydberg, nothing was done with the genera until Robinson and Brettell in 1973 transferred *Schistocarpha* and *Neurolaena* along with *Alepidocline* Blake from the Senecioneae to the Heliantheae on the basis of characters of the corolla hairs, the paleaceous receptacle, anther structure, and nectary shape. At that time, the genera were regarded as possibly closest to the subtribe Galinsoginae of the Heliantheae, but basic differences, especially in the achene striation, were noted between *Schistocarpha* and *Neurolaena*. More recently, Turner (1976) has placed the genus *Alepidocline* in the synonymy of *Sabazia*, which is placed in the Galinsoginae. Stuessy (1978), in contrast, has placed *Schistocarpha* and *Neurolaena* together in a separate subtribe Neurolaeninae in the Heliantheae.

### Relationships

Robinson and Brettell (1973) have listed a number of differences between *Schistocarpha* and *Neurolaena* which indicate that the two are not each other's closest relatives. Nevertheless, the two genera could have both been encompassed in the then prevailing broad concept of the subtribe Galinsoginae. The narrower subtribal interpretation by Stuessy (1973), however, places the two genera together in the segregate subtribe Neurolaeninae, a concept that seems to emphasize historical considerations and pappus structure. Such a use of the pappus seems untenable in view of the similar structure in *Bebbia*, *Oteiza*, *Tridax*, and some species of *Sabazia* and *Selloa*, which are members of the Galinsoginae. A more accurate placement of *Schistocarpha* and *Neurolaena* has required a completely new study of the problem.

The two subtribes under consideration, Galinsoginae and Neurolaeninae, share the more obvious characters of usually imbricated, nonherbaceous involucre bracts and prismatic achenes with a radially symmetrical pappus. As recognized here, the two subtribes share the additional features of rays usually with three distinct apical teeth and the corollas containing secretory ducts, usually filled with yellowish resin. The secretory ducts in the

style are almost always internal or lateral to the veins. The style branches each have two stigmatic lines.

A search for differences has emphasized *Neurolaena* and *Galinsoga* as representatives of their respective subtribes. Three significant characters have been found that correlate closely through the whole series of related genera.

ACHENE WALL.—The lack of clear striations in the carbonized achene wall of *Neurolaena* was first noted by Robinson and Brettell (1973). A similar lack has been seen now in *Brasilia* Barroso, *Calea* L., *Staurochlamys* Baker, and *Tyleropappus* Greenm. In contrast, *Galinsoga* Ruiz & Pavon has striations in the walls between the veins, a character shared by *Alloispermum* Willd., *Aphanactis* Wedd., *Bebbia* Greene, *Cuchumatanea* Seiden-schnur & Beaman, *Cymophora* B. L. Robins., *Jaegeria* H.B.K., *Oteiza* La Llave, *Sabazia*, Cass., *Selloa* H.B.K., *Tetragonotheca* L., and *Tridax* L.

CARPOPODIUM.—In *Neurolaena* and *Galinsoga* and all associated genera, the base of the prismatic achene is asymmetrical, apparently reflecting the basically conical receptacle to which they are attached. The outer side, consisting of distinctly sclerified cells, extends downward and curves inward. The inner side consists of radially arranged cells, usually forming a cushion. In *Neurolaena* and associated genera, the cells of the inner cushion are firm in texture. In *Galinsoga* and the related series, the inner cushion consists of thin-walled cells that collapse to leave the outer side of the carpodium as an isolated, sclerified plate.

SECRETORY DUCTS.—Ducts can be seen in *Neurolaena* most clearly in *N. intermedia* and *N. macrophylla* Greenm., both of which have yellowish resin present. In these species the ducts are broad and single along the inner surface of the veins in the throat of the disk corolla. At the sinus, the ducts split and diverge with the veins along the margins of the corolla lobes. The ducts have the same positions in *Calea*, *Staurochlamys*, and related genera. In the *Galinsoga* series, the ducts of the disk corolla throat are narrower and usually paired, with one along each side of the vein. The ducts pass into the lobes usually on the inside of the veins and they are often widely separated from the margin. In some genera with reduced amounts of resin, such as *Aphanactis* and *Cuchumatanea*, only a single duct may occur per vein, but the duct

is narrow and is lateral to the vein, and ducts from adjacent lobes do not normally join at the sinus.

These three characters are found in a consistent pattern that can be used as a basis for subtribal distinction. Additional correlated characters are the nonpapillose inner surfaces of the corolla lobes and the trend for elongate lobes in the *Neurolaena* series, versus the slightly to strongly papillose inner surfaces and short lobes in the *Galinsoga* series. The *Neurolaena* series is here recognized as the subtribe Neurolaeninae, while the *Galinsoga* series is recognized as the Galinsoginae.

When compared with the revised subtribal concepts, the genus *Schistocarpha* shows all the characters of the Galinsoginae and obviously is not closely related to *Neurolaena*. The closest relative of *Schistocarpha* seems to be the genus *Oteiza* La Llave (1832). One of the species of the latter, *O. raucophila* (J. D. Smith) Fay, recently was unnecessarily redescribed as *S. steyermarkii* H. Robins. because it had a habit and involucre bract form identical to that in *Schistocarpha*. *Oteiza* shares even the distinctive four secretory ducts of the style seen in *Schistocarpha*. *Oteiza* has been placed in the synonymy of *Perymenium* by most treatments, but recently it has been reestablished for two species by Fay (1975, 1976). The strong resemblance of *Oteiza raucophila* to *Schistocarpha* might suggest a broadened concept for the latter genus, which has priority by one year, but the type-species of *Oteiza*, *O. acuminata* La Llave, does not share the aspect and would seem an unwise addition. Also, both species of *Oteiza* do differ from *Schistocarpha* by having nonlacerate paleae, having glabrous lobes of the disk corollas, having extremely deciduous pappus setae more fragile than any in *Schistocarpha*, and by lacking resin in the lower parts of the secretory ducts in the disk corollas and styles. Thus, the species of *Oteiza* seem clearly outside of *Schistocarpha* and more closely related to each other, but differences between the two species are greater than any seen within the larger genus *Schistocarpha*.

### Reliability of Characters

A number of characters appear in species of *Schistocarpha* that vary in reliability. A few are worth special note.

Density of pubescence on leaves and stems has

been used to distinguish some species but has been regarded in this study as too unreliable to be used without other supporting evidence. Two species previously distinguished only by pubescence are reduced to synonymy: *S. velutina* under *S. bicolor* and *S. kellermanii* under *S. platyphylla*.

Distinctive broadly winged petioles are highly developed in *S. bicolor* but are not present in all specimens. The narrow-winged forms scarcely can be distinguished from the slightly winged condition present in all petiolate members of the Asteraceae.

Presence of stipitate glands on the pedicels and involucre was used by Rydberg (1927) to distinguish *S. paniculata* and *S. pedicellata* from other prominently rayed species. Only in *S. pedicellata* do glands appear to be a consistent feature. In *S. paniculata*, the glands are consistent in any one plant but plants from the same area that are distinguishable by no other feature lack glands. A smaller form of gland that is easily overlooked has been seen on some South American specimens of *S. eupatorioides* and on one specimen of *S. sinforosii*.

Completely elimbate rays occur in some specimens of *S. eupatorioides* and *S. platyphylla*, but small limbs are common in both species. The two species represent two basically different groups in the genus, indicating a parallel development. All of the *S. platyphylla* group except *S. sinforosii* are characterized by limbs less than 6 mm long. Reduced limbs also are characteristic of *S. margaritensis*, *S. croatii*, and *S. matudae*, which shows that a tendency toward limb reduction exists throughout the genus.

The pappus of all species of *Schistocarpha* is deciduous, with a slight variation in degree. It is most persistent in *S. eupatorioides*, where it remains on most mature achenes. Some species of the *S. platyphylla* group have a more fragile pappus, with mature achenes often retaining no setae. No species of *Schistocarpha* has a pappus as persistent as that of *Neurolaena* nor as fragile as that of *Oteiza*.

The paleae of the receptacle are characteristically lacerate in the genus. In the *S. eupatorioides* and *S. paniculata* groups and in *S. bicolor*, a generally trilobed condition is obvious, with a long, narrow central lobe often projecting above the flowers in the immature heads. Members of the

*S. platyphylla*–*S. liebmannii* group and other members of the *S. bicolor* group, such as *S. seleri* and *S. longiligula*, have a characteristically unequal laceration that usually lacks the well-defined narrow central lobe.

The disk corollas of *Schistocarpha* often have a secretory duct running up the center of each lobe, in addition to those along the veins. The expression of the character is variable, but even when a duct is not evident there is sometimes a partial row of hairs in the area. The only species that seem to characteristically lack the duct are *S. eupatorioides* and the closely related *S. margaritensis*. Other species in which the duct is weak or not observed, such as *S. longiligula*, *S. pedicellata*, and *S. pseudoseleri*, are represented by too few specimens for the character to be known reliably.

The form of the hairs on the corolla proves to be one of the two most valuable characters in the genus. Slender hairs with elongate cells (Figure 1) are characteristic on the disk corolla lobes of *S. eupatorioides* and *S. margaritensis*. Thicker hairs with mostly 3–6 cells (Figures 2, 3) are characteristic of *S. croatii*, *S. paniculata*, *S. wilburii*, and *S. longiligula*. Shorter hairs with mostly 2–3 cells (Figures 5, 6) are found in most species of the *S. bicolor* and *S. platyphylla* groups. The evenly distributed hairs on the throat and lobes of the disk corolla are a distinctive feature of *S. hondurensis*. On the ray corollas, the lax pilosity on the tubes in *S. eupatorioides* is distinctive of the species and markedly different from the densely hispidulous condition in *S. croatii*, *S. paniculata*, and *S. wilburii*. There is considerable variation in pubescence density on the ray tubes of some other species, such as *S. liebmannii* and *S. seleri*.

The most useful character in *Schistocarpha* is the number of rays in the head. The *S. eupatorioides* and *S. paniculata* groups each have over 20 rays per head, while the remaining species all have fewer. Of the remaining species, only *S. pedicellata* comes close to the higher number, with some heads having about 18 rays. The basic subdivision is accentuated by the evident multiseriate condition associated with the greater number of rays. A further subdivision involves the *S. platyphylla* group, with 8–10 or rarely 12 rays, and the *S. pedicellata* and *S. bicolor* groups, with 12–18 rays in the head. This correlates with the number of involucre bracts, the former group having 16–20 and the

latter groups 20–30. The seeming overlap of number is no obstacle to the delimitation of the groups, since numerous heads are available on specimens and estimates based on counts of exposed halves are adequate. The primary need for caution derives from the deciduous nature of the rays, and for this reason younger heads serve best.

### Patterns in the Genus

On even superficial examination, the basic uniformity of *Schistocarpha* as defined in this paper is most obvious. Previous taxonomic treatments of the genus have been unsatisfactory because they utilized certain obvious but often unreliable characters. All species have been subject to misidentification. Geographic patterns have not been evident previously for the foregoing reasons, but in the present study distribution has proven a valuable guide to the understanding of species and groups of species. This has been aided by the fact that most closely related species occur in adjacent areas, but they rarely overlap in distribution. The combination of distribution, number of ray and disk flowers in the head, number of involucre bracts, and form of hairs on the corollas has led to the recognition of the following five groups.

1. The *eupatorioides* group, including *S. eupatorioides* and *S. margaritensis*. The group is Andean, with one species having extended its distribution throughout the entire range of the genus. The heads contain 25–30 involucre bracts and 22–70 rays in 2–3 series. Tubes of the rays are laxly pilosulous, and the lobes of the disk corollas have slender hairs.

2. The *paniculata* group, including *S. croatii*, *S. paniculata*, and *S. wilburii*. The group is restricted to Costa Rica and western Panama. The heads contain 20–40 involucre bracts and 20–60 rays in 2–3 series. Tubes of the rays are densely hispidulous and the lobes of the disk corolla have stout, tapering 3–6-celled hairs.

3. The *pedicellata* group, including *S. pedicellata*. The group is restricted to the eastern escarpment in central Mexico. The plants consistently bear numerous glandular hairs. The heads have 30–40 externally reddish involucre bracts and 15–18 rays in 1 series. Tubes of the rays are minutely hispidulous, and the lobes of the disk corollas have mostly 1- or 2-celled hairs.

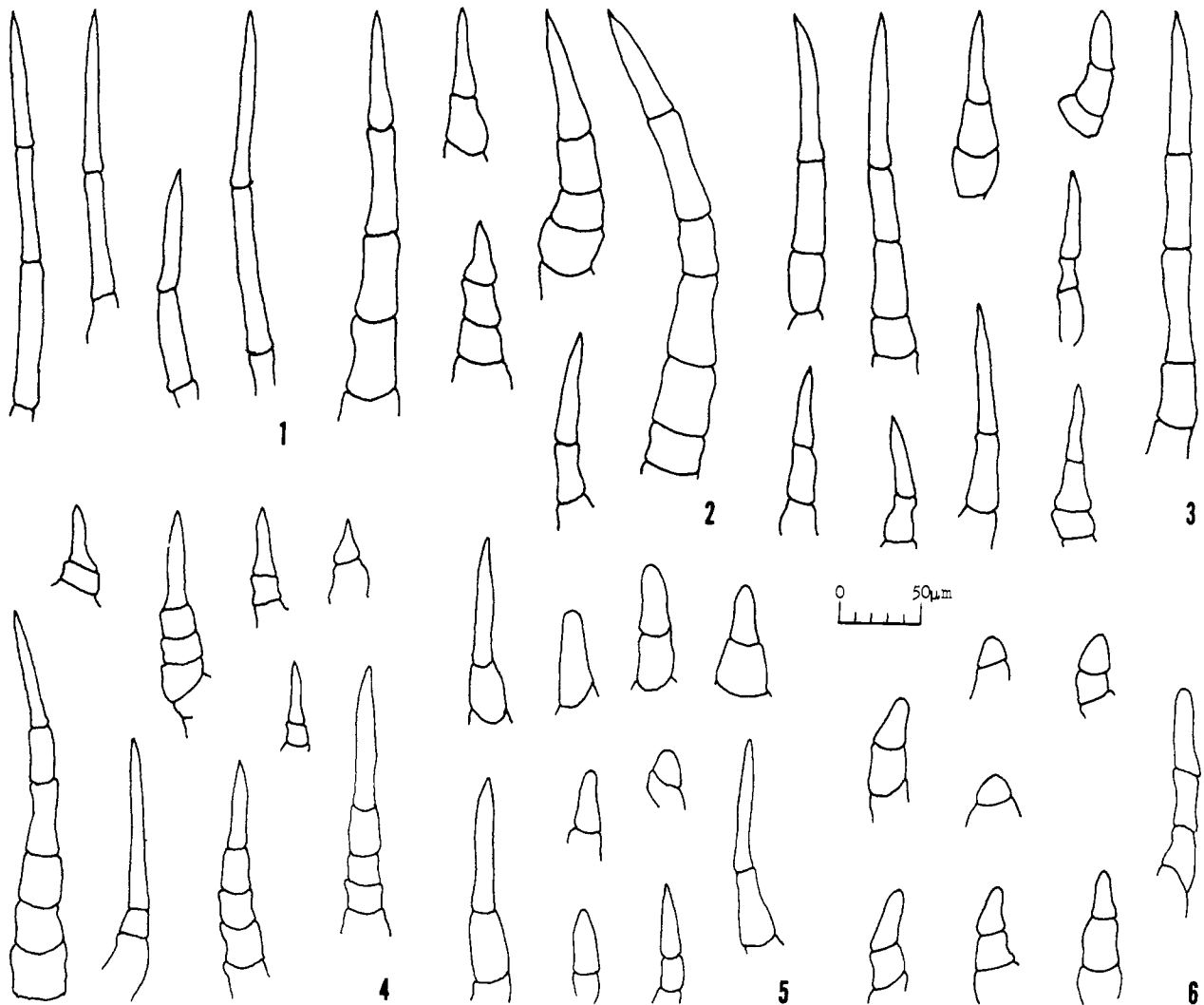


4. The *bicolor* group, including *S. bicolor*, *S. longiligula*, *S. matudae*, and *S. seleri*. The group is restricted to the eastern or northern ranges or escarpments in Mexico and Guatemala, with the exception of *S. matudae* on Mt. Ovando in Chiapas. The heads contain 20–25 involucre bracts and 12–15 rays in 1 series. Tubes of the rays are sparsely to densely hispidulous, and the lobes of the disk corollas have short 1-3-celled hairs, except for longer 3-5-celled hairs in *S. longiligula*.

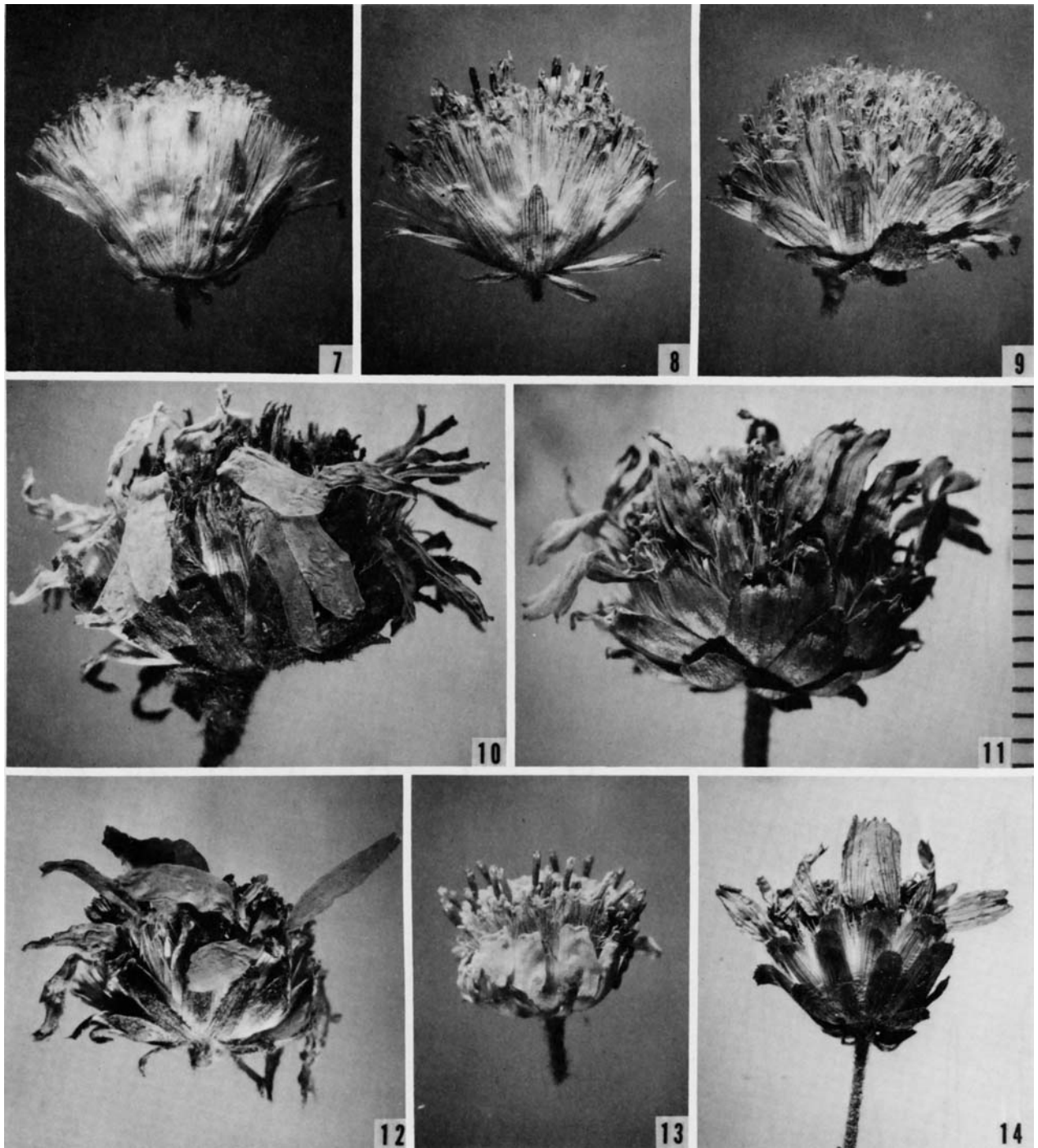
5. The *platyphylla* group, including *S. chiapensis*, *S. hondurensis*, *S. liebmannii*, *S. platyphylla*,

*S. pseudoseleri*, and *S. sinforosii*. The group is concentrated in southern Guatemala and adjacent El Salvador and Honduras, with *S. liebmannii* on the eastern escarpment in central Mexico and *S. sinforosii* in the northern Andes in South America. The heads contain 16–20 involucre bracts and 8–12 rays in 1 series. Tubes of the rays are glabrous to hirtellous or hispidulous and the disk corollas have short, 1-3-celled hairs on the lobes. All species except *S. sinforosii* have limbs of the rays less than 6 mm long.

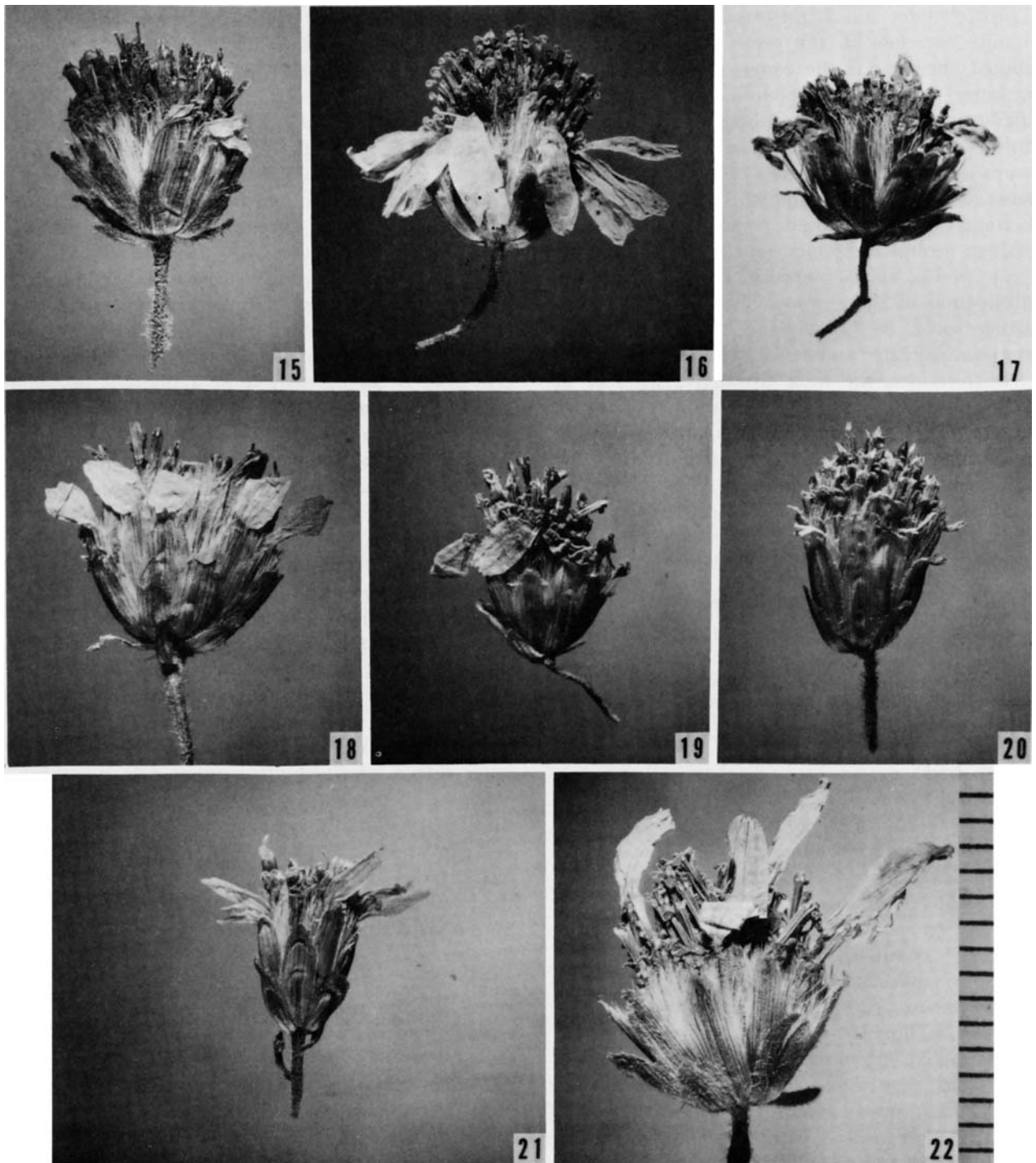
An overall pattern can be seen in distribution.



FIGURES 1-6.—Hairs of disk corolla lobes: 1, *Schistocarpha eupatorioides*; 2, *S. paniculata*; 3, *S. longiligula*; 4, *S. sinforosii*; 5, *S. pedicellata*; 6, *S. seleri*.



FIGURES 7-14.—Heads of *Schistocarpa* (scale in mm): 7, *S. eupatorioides*, Asplund 8859; 8, *S. margaritensis*, Pennell 8694; 9, *S. croatii*, Davidson 337; 10, *S. paniculata*, Wilbur 14341; 11, *S. wilburii*, Wilbur & Almeda 16097; 12, *S. pedicellata*, Pringle 6134; 13, *S. bicolor*, King 4144; 14, *S. longiligula*, Lundell & Contreras 21164.



FIGURES 15-22.—Heads of *Schistocarpa* (scale in mm): 15, *S. matudae*, Matuda 0709; 16, *S. seleri*, Breedlove 9313; 17, *S. chiapensis*, Matuda 2018; 18, *S. hondurensis*, Molina 7729; 19, *S. liebmannii*, Purpus 7763; 20, *S. platyphylla*, Skutch 189; 21, *S. pseudoseleri*, Williams 26256; 22, *S. sinforosii*, Archer 1513.

The pattern initially is obscured by the ranges of *S. eupatorioides* and *S. sinforosii*, which represent opposite extremes in the genus. The first is distributed throughout the range of the genus and the latter is found in Colombia and Peru. Both distributions are interpreted here as secondary extensions from the evident places of origin of the groups to which the species are related. When places of origin are considered, the following simple trend can be recognized in the genus. The more northern groups of species have a smaller number of rays (8–18), and *S. sinforosii* is seen as a recent introduction of these groups into South America. Farther south in Costa Rica, the *S. paniculata* group has a greater number of rays (20–60). Finally, *S. eupatorioides*, the most distinctive member of the genus with up to 70 rays, would seem to be at the extreme of the progression, with origins in South America, where it has most of its variation and where its only close relative, *S. margaritensis*, occurs in Colombia. The wide occurrence of *S. eupatorioides* is regarded as a range expansion from a South American point of origin.

### *Schistocarpha* Lessing

*Schistocarpha* Less., *Linnaea*, 6:409, 1831. [Type: *S. bicolor* Less.]

*Neilreichia* Fenzl, *Denkschrift. der Kaiserlich. Akad. der Wissenschaft.*, 1:258, 1850. [Type: *N. eupatorioides* Fenzl.]

*Zyconia* O. Kuntze, *Rev. Gen. Pl.*, 1:373, 1891. [Type: *Z. oppositifolia* O. Kuntze.]

Large herbs or subshrubs to 4 m tall, sparsely branching. Stems subterete, striated, pith solid; internodes 7–20 cm long. Leaves opposite, sometimes alternate above, long-petiolate with wing on at least distal half; lamina chartaceous, ovate to broadly subdeltoid, base abruptly acuminate and decurrent on petiole, trinervate from near base, apex short-acuminate, surfaces usually scabrid to velutinous. Inflorescence corymbose-paniculate or with corymbose branches, pedicels mostly 2–20 mm long. Heads broadly campanulate, ca. 6–10 mm high; involucre subimbricate, 16–40 unequal bracts in 2–4 series, mostly chartaceous to coriaceous, with 6–8 striations, mostly greenish to yellowish brown; receptacle short-conical; paleae scarious, rather deciduous, trifold to irregularly lacinate, enclosing

outer half of achene. Rays 8–70 in 1–3 series, pistillate, usually white, with tube about as long as pappus, limb sometimes lacking, when fully developed being papillose above and with 3 small distinct teeth at tip; disk flowers 5–75, hermaphroditic, yellow; basal tube slender, glabrous to densely pilosulous or hispidulous; throat cylindrical; lobes 5, triangular, slightly longer than wide, with slightly papillose inner surface, outer surface with numerous stiff hairs; secretory ducts with yellowish resin, paired along veins of tube and throat, extending to base of corolla; anther collar cylindrical, lacking more crowded cells in lower part; thecae acute at base, usually not reaching level of base of collar, exothecium pale to greenish, endothecial cells shortly oblong with 1 or 2 nodular thickenings on transverse walls; appendage ovate, concave abaxially, with radially oriented marginal cells, without glands; style partially immersed in nectary, with distinct basal node sclerified in lower half at maturity, shaft with 2 veins and with 4 collateral secretory ducts, ducts of branches inside of veins, resin prominent; branches with 2 stigmatic lines; appendage small, short-acute; achenes of ray and disk flowers alike, prismatic to terete, shortly obovate, 1–2 mm long, with carbonized, minutely punctate walls interrupted by numerous broad striations; cells of seed coat irregular with undulating to angular walls, with transverse linear thickenings across inner surface; carpopodium bilateral, outer side a sclerified plate, inner side a cushion of clustered thin-walled cells; pappus born on distinct callus, radially symmetrical, with 25–35 slender capillary setae 2.5–5.5 mm long, mostly in 1 series, rather deciduous, tips not or slightly broadened, apical cells sharply acute. Pollen grains ca. 27  $\mu\text{m}$  in diameter, sharply spinose. Chromosome number  $n=8$ .

The most useful distinguishing characters of the genus are the trifold or lacinate paleae of the receptacle and the pappus of 25–35 slender capillary setae.

In the following treatment of the species, the most common species are provided with only general distribution data and citations of only particularly significant collections.

### Key to the Species of *Schistocarpha*

1. Heads with more than 20 ray flowers in 2 or 3 series.
2. Tubes of ray flowers densely hispidulous with short hairs; rays white; lobes of disk yellow; lobes of disk corollas with slender, cylindrical hairs 10–15  $\mu\text{m}$  wide.

3. Heads with 25–30 rays, with limbs mostly near 3 mm long; disk flowers 25–40; pedicels mostly 10–20 mm long (Colombia) .....*S. margaritensis*
3. Heads with 40–70 rays, with limbs usually less than 1 mm long and often totally lacking; disk flowers 5–15; pedicels mostly 2–10 mm long (Mexico, Central America, South America) .....*S. eupatorioides*
2. Tubes of ray flowers densely hispidulous with short hairs; rays white; lobes of disk corollas with stout, tapering hairs usually 30–40  $\mu$ m wide at base.
  4. Heads with 40–60 rays, with limbs ca. 2 mm long (Panama) .....*S. croatii*
  4. Heads with 20–30 rays, with limbs 5–10 mm long.
    5. Involucral bracts not strongly convex at maturity; central awn of paleae slender and chartaceous (central Costa Rica) .....*S. paniculata*
    5. Involucral bracts strongly convex and coriaceous at maturity, with prominent recurved tips; central awn of paleae broad and indurated (southern Costa Rica) .....*S. wilburii*
1. Heads with fewer than 20 ray flowers in 1 series.
  6. Heads with 12–18 rays, with 20–40 involucral bracts.
    7. Stems, pedicels, and involucral bracts with gland-tipped hairs; heads 7–9 mm high with reddish or reddish-tinged outer surfaces of involucral bracts; limb of rays 8–12 long (Veracruz) .....*S. pedicellata*
    7. Plants without gland-tipped hairs; heads 6–7 mm high; outer surfaces of involucral bracts greenish to brownish; limb of rays 1.5–7.0 mm long.
      8. Rays with limb 1.5–2.0 mm long (southern Chiapas) .....*S. matudae*
      8. Rays with limb 4–7 mm long.
        9. Petioles winged in at least upper half, with wing often broad to the base and continuous across the node; paleae with slender central awn; outer surface of involucral bracts pilose with few to many hairs (Hidalgo, Puebla, San Luis Potosí, Veracruz) .....*S. bicolor*
        9. Petioles winged only in distal third; paleae usually without slender central awn; involucral bracts glabrous on outer surface or sparsely puberulous near tips.
          10. Stems hirsute; lobes of disk corollas with mostly 3- to 5-celled hairs (central Guatemala) .....*S. longiligula*
          10. Stems glabrous to sparsely hirtellous; lobes of disk corollas with mostly 1- or 2-celled hairs (northern Chiapas) .....*S. seleri*
    6. Heads with mostly 8–10 rays, rarely 12, with 16–20 involucral bracts.
      11. Rays with limbs mostly 6–11 mm long (Colombia, Peru) .....*S. sinforosii*
      11. Rays with limbs less than 6 mm long (Mexico, Central America).
        12. Rays with limbs narrowly vestigial or lacking, less than 2 mm long (southern Guatemala, El Salvador, Chiapas, Oaxaca) .....*S. platyphylla*
        12. Rays with limbs 2–5 mm long, broad in shorter forms.
          13. Stems sparsely to densely hirsute.
            14. Heads with 8–10 disk flowers; disk corollas with hairs denser on lobes than on throat (western Guatemala) .....*S. pseudoseleri*
            14. Heads with ca. 20 disk flowers; disk corollas with hairs equally dense on throat and lobes (Honduras, Nicaragua, El Salvador) .....*S. hondurensis*
          13. Stems glabrous to slightly puberulous.
            15. Heads with ca. 12 disk flowers; leaf blades glabrous above, distinctly paler below (Veracruz) .....*S. liebmanni*
            15. Heads with ca. 25 disk flowers; leaf blades pilose above with stiff hairs, not distinctly paler below (southern Chiapas) .....*S. chiapensis*

### The *eupatorioides* group

#### 1. *Schistocarpha eupatorioides* (Fenzl) O. Kuntze

FIGURES 1, 7

*Schistocarpha eupatorioides* (Fenzl) O. Kuntze, Rev. Gen. Pl., 3 (2): 170, 1898.

*Neilreichia eupatorioides* Fenzl, Denkschrift. der Kaiserlich.

Akad. der Wissenschaft., 1:258, 1850. [Type: near Cuchero, Peru. *Poeppig 74*, holotype W?, not seen.]

*Neurolaena (Schistocarpha) lindeni* Sch.-Bip. ex A. Gray, Proc. Amer. Acad., 5:185, 1861. [Nomen nudum.]

*Schistocarpha lindeni* J. Donn. Smith, Enum. Pl. Guat., 1:24, 1881. [Nomen nudum.]

*Zyconia oppositifolia* O. Kuntze, Rev. Gen. Pl., 1:373, 1891.

[Type: La Guayra, Venezuela. *O. Kuntze s.n.*, holotype NY.]

*Schistocarpha hoffmanii* O. Kuntze, Rev. Gen. Pl., 3 (2):170, 1898. [Type: Río Juntas, Bolivia. 2600 m. O. Kuntze s.n., holotype and isotype NY.]

*Schistocarpha oppositifolia* (O. Kuntze) Rydb., North American Flora, 34 (4):306, 1927.

Stems usually brownish yellow to castaneous, densely puberulous to pilose, somewhat glabrescent. Petioles 1–5 cm long, winged only in distal half; lamina ovate to broadly ovate, mostly 10–20 cm long and 6–17 cm wide, margin closely to remotely serrate. Inflorescence thyrsoïd to pyramidally paniculate with densely corymbose branches; pedicels mostly 2–10 mm long, puberulous to pilosulous, sometimes with intermixed minute stipitate glandular hairs. Heads (Figure 7) ca. 8 mm high; involucre bracts 25–30 in 3–4 series oblong to linear-lanceolate, 1.5–6.0 mm long, 1.0–1.5 mm wide, apices mostly rounded with minute fringe of hairs, outer surface glabrous; paleae trifid with filiform central awn, 5–6 mm long. Rays 40–70 in 3–4 series, yellow to greenish yellow; tube 4–5 mm long, usually sparsely pilosulous; limbs 1 mm or less long, sometimes lacking. Disk flowers 5–11, rarely to 18; corollas 5.0–6.0 mm long; tube 2.5–3.0 mm long, glabrous or with a few hairs at apex; lobes with slender cylindrical hairs on outer surface (Figure 1); resin ducts not present in middle of lobes; anther thecae 1.3–1.5 mm long. Achenes 1.3–1.5 mm long; pappus setae ca. 30, 4–5 mm long, moderately deciduous, not broadened above.

The species is common throughout the range of the genus, extending farther north in Mexico and farther south in South America than any other species of the genus. Numerous specimens have been seen from Mexico, from every country of Central America except El Salvador, and from Colombia, Venezuela, Ecuador, Peru, and Bolivia in South America.

Fenzl originally cited an additional specimen from Rio de Janeiro, but the species does not seem to occur naturally in Brazil. There is an amazing uniformity of structure throughout the range of the species. Two slight exceptions involve the glabrous tubes of the disk corollas, which seem to be most common in Central American specimens, and minute glandular hairs, which occur in some specimens from the Andes. Fenzl reported 11–17 disk flowers in the head. A brief survey has shown usually 5–10, with 11 seen twice and 18 one time. I find no basis for higher numbers often cited.

## 2. *Schistocarpha margaritensis* Cuatrecasas

FIGURE 8

*Schistocarpha margaritensis* Cuatr., Rev. Acad. Colomb. Cienc., 9:244, 1954. [Type: Pichindé, El Valle, Colombia. Cuatrecasas 18566, holotype F, not seen, isotype US.]

Stems dark greenish brown, stiffly short-hirsute. Petioles mostly 3–8 cm long, winged in distal half; lamina ovate, 6–18 cm long and 4–11 cm wide, margin closely serrulate. Inflorescence corymbose-paniculate; pedicels mostly 10–20 mm long, pilosulous with nonglandular hairs. Heads (Figure 8) ca. 8 mm high; involucre bracts ca. 25 in 3–4 series, oblong to linear-lanceolate, 1.5–6.0 mm long, 1.0–1.5 mm wide, apices mostly rounded with minute fringe of hairs, outer surface glabrous; paleae trifid with filiform central awn, 5–6 mm long. Rays ca. 25–30 in 2 or 3 series, yellow; tube 4.5–5.0 mm long, densely pilosulous with fine hairs above; limbs mostly near 3 mm long. Disk flowers 25–40; corollas 4.5–5.0 mm long; tube ca. 2 mm long, with a few small hairs at apex; lobes with slender cylindrical hairs on outer surface; resin ducts not present in middle of lobes; anther thecae ca. 1.3 mm long. Achenes ca. 1.5 mm long; pappus setae ca. 30–35, ca. 4 mm long, moderately deciduous, not or scarcely broadened below tips.

ADDITIONAL SPECIMEN SEEN.—COLOMBIA. CALDAS: Río Quindo above Armenia, 1300–1500 m. Pennell, Killip & Hazen 8694 (US).

The species is closely related to *S. eupatorioides* but is more than just an extreme form of that species. The corymbose inflorescence with longer pedicels differs from the more thyrsoïd form with densely corymbose branches in *S. eupatorioides*. The smaller number of ray flowers with longer limbs and the larger number of disk flowers provide additional significant distinctions.

### The *paniculata* group

## 3. *Schistocarpha croatii* Robinson

FIGURE 9

*Schistocarpha croatii* H. Robinson, Phytologia, 29:339, 1975. [Type: Chiriqui, Panama. Croat 26411, holotype MO.]

Stems brownish to reddish, pilose with coarse hairs. Petioles 1–4 cm long, winged only in distal

third; lamina ovate, 6–10 cm long and 2.5–5.0 cm wide, margin coarsely serrate. Inflorescence corymbose-paniculate pedicels 3–10 mm long, densely pilosulous. Heads (Figure 9) ca. 8 mm high; involucre bracts 20–30 in ca. 3 series, oblong to linear-lanceolate, 2–5 cm long, 1.0–2.3 mm wide, apices mostly obtuse with a minutely toothed edge, outer bracts sparsely pilose on outer surface; paleae trifold with filiform central awn, 4–5 mm long. Rays 40–60 in 2 or 3 series, white; tube 2.5–3.0 mm long, densely hispidulous; limb 2.0–2.5 mm long. Disk flowers 30–70; corollas ca. 5 mm long; tube 1.5–2.0 mm long, densely hispidulous; lobes with stout tapering hairs having 3–6 cells; resin ducts not seen in middle of lobes; anther thecae ca. 1.3 mm long. Achenes ca. 1.5 mm long; pappus setae 30–35, mostly 4.0–4.5 mm long, moderately deciduous, slightly broadened below tips.

The species is apparently endemic to the Chiriquí region of Panama.

ADDITIONAL SPECIMEN SEEN.—PANAMA. CHIRIQUÍ: Bajo Chorro, Boquete. *Davidson 337* (US).

Most of the distinctions of the species from *S. eupatorioides* given with the original description prove unreliable. However, the species is thoroughly distinct in the densely hispid tubes of the ray and disk corollas, the color and size of the rays, the larger number of disk flowers, and the coarse hairs on the lobes of the disk corollas. Closest relation is actually to *S. paniculata* of Costa Rica, though the latter differs clearly by the smaller number of rays with larger limbs.

#### 4. *Schistocarpha paniculata* Klatt

FIGURES 2, 10

*Schistocarpha paniculata* Klatt, Bull. Soc. Roy. Bot. Belg., 31:210, 1892. [Type: Volcán Irazú, Costa Rica. *Pittier 866*, GH, not seen.]

Stems brownish to reddish, pilose with coarse hairs, with or without long-stalked capitate glands. Petioles 2–8 cm long, winged only in distal third; lamina ovate to subdeltoïd, 6–16 cm long and 3–13 cm wide, margin closely serrate. Inflorescence corymbose-paniculate; pedicels 1–4 cm long, densely pilose, with or without stipitate glands. Heads (Figure 10) ca. 1.0–1.3 mm high; involucre bracts 35–40 in ca. 4 series, oblong to lanceolate, 3–6 mm long, mostly 1.5–2.3 mm wide, apices obtuse to

acute, often with densely fringed margin, outer surface with few to many hairs or stipitate glands; paleae trifold, scarious, 5–6 mm long, awn linear with filiform tip. Rays 20–25 in ca. 2 series, white; tube 5–6 mm long, densely hispidulous; limb 5–10 mm long. Disk flowers 40–70; corollas 6–7 mm long; tube ca. 3 mm long, densely hispidulous; lobes with stout tapering hairs having 3–5 cells (Figure 2), resin ducts often present in middle of lobes; anther thecae ca. 1.7 mm long. Achenes ca. 1.8 mm long; pappus setae 30–35, mostly 4.5–5.5 mm long, moderately deciduous, slightly broadened below tips.

The species is restricted to central Costa Rica.

ADDITIONAL SPECIMENS SEEN. — COSTA RICA. CARTAGO: Southern slopes of Volcán Turrialba, ca. 6 kms generally NE of San Rafael de Irazú, ca. 8600 ft. *King 6826* (US); southern slopes of Volcán Turriabla, ca. 12 km generally NE of San Rafael de Irazú, ca. 8500 ft. *King 6837* (US); region of La Esperanza, southern slope of Volcán de Irazú. *Standley 35354* (US); Laguna del Reventado, Volcán Irazú, 2300 m. *Pittier 14089* (US); between Hacienda Central and Finca Quemado, about 2800 m. *Wilbur 14341* (DUKE, US). HEREDIA: Vara Blanca de Sarapiquí, north slope of Central Cordillera, between Poás and Barba volcanoes, 1680 m. *Skutch 3399* (US); El Roble, *Stork 2003* (US); Volcán Barba above Hacienda Sacramento, about 8700 ft. *Wilbur & Almeda 17042* (DUKE, US). SAN JOSÉ: Route 216, ca. 2–3 kms S of Cascajal, ca. 5000 ft. *King 6785* (US); Las Nubes, about 1500–1900 m. *Standley 38341, 38759* (US); Bords de río Parrita à Santa Rosa de Copey, 1800 m. *Tonduz 12194* (US).

Stipitate glands are present on the stems, pedicels, and involucre bracts of some plants of *S. paniculata*, and Rydberg (1927) distinguishes the species on that basis. However, most specimens seen from the area completely lack the glands, though they differ in no other character.

The name *S. paniculata* has suffered from some confusing misapplications. One specimen from Costa Rica (*Pittier 14089*) bears an annotation by B. L. Robinson of some interest: "This is the Costa Rican plant which Klatt described as *S. paniculata* in Bull. Soc. Bot. Belg. xxx pt. 1. Klatt later republished the same description and cited a Pringle plant as though it were the type, though it was very different." Rydberg (1927) pointed out that one of the syntypes in the original paper, *Pittier 3138* of Costa Rica, was actually *S. oppositifolia* (= *S. eupatorioides*). The situation is confused still further by the fact that one other Klatt syntype, *Pittier 3411* from southern Costa Rica, is actually *S. wilburii*, described below as a new species.

5. *Schistocarpha wilburii*, new species

FIGURE 11

A *S. paniculata* cui affinis bracteis involucris convexioribus in apice valdius deformibus et paleis valdius induratis in apice parum latoribus differt.

Stems brownish to reddish, pilose with coarse hairs. Petioles 2–5 cm long, winged only in distal third; lamina ovate to subdeltoid, 6–15 cm long and 3–11 cm wide, margin closely serrate. Inflorescence corymbose-paniculate; pedicels 5–27 mm long, densely pilose. Heads (Figure 11) ca. 1 cm high; involucral bracts 35–40 in ca. 4 series, mostly oblong, 2.5–7.0 mm long, mostly 1.5–2.5 mm wide, becoming convex and coriaceous below, usually with constriction near tip, tips of inner bracts acute and densely fringed, tips of other bracts oblong and blunt, darkened and often recurved, outer surface of bracts sparsely pilose; paleae trifid, indurated to coriaceous, 5–6 mm long, linear awns with lanceolate tips. Rays 20–25 in ca. 2 series, white; tube 4.0–4.5 mm long, densely hispidulous; limb 5–8 mm long. Disk flowers ca. 60–90; corollas 5.0–6.5 mm long; tube 2–3 mm long, densely hispidulous; lobes with stout tapering hairs having 3–6 cells; resin ducts often present in middle of lobes; anther thecae ca. 1.7 mm long. Achenes ca. 1.8 mm long; pappus setae 30–35, mostly 4–5 mm long, moderately deciduous, slightly broadened below tips.

TYPE.—COSTA RICA. SAN JOSÉ: About 14 km SE of La Asunción of the Cerro de la Muerte on the Interamerican Highway at an elevation of about 8500 ft, shrub 2.5 m tall. Rays white; disk yellow. 8 Jan 1972. *Wilbur, Almeda & Luteyn 16097* (holotype DUKE; isotype US).

PARATYPES.—COSTA RICA. SAN JOSÉ: Vallée du Général. clairieres, 600 m. Jan 1891. *Pittier 3411* (US); cutover montane cloud forest area, Cordillera de Talamanca, about 20 km N of San Isidro de General along Pan American Highway, alt. 2800 m. 29 Jan 1965. *Williams, Molina, Williams & Gibson 28506* (US).

The species is apparently restricted to the Valle del General area of southern Costa Rica. The species is closely related to *S. paniculata*, but the involucral bracts of well-developed heads present a

markedly different appearance. Both the involucral bracts and the paleae seem to share the general effects of a more indurated texture and broader tips.

The *pedicellata* group6. *Schistocarpha pedicellata* Klatt

FIGURES 5, 12

*Schistocarpha pedicellata* Klatt, Leopoldina, 23:146, 1887.

[Type: Dos Puentes, Veracruz, Mexico. *Liebmann 488*, holotype C not seen, photo and fragment. US.]

*Neurolaena pedicellata* Schultz-Bip. ex Klatt, Leopoldina, 23:147, 1887. [Nomen nudum in synonymy.]

Stems reddish to reddish tinged, densely hirsute, with many intermixed gland-tipped hairs. Petioles 1–5 cm long, winged in distal half; lamina ovate, 6–15 cm long, 3–10 cm wide, margins closely to remotely serrate. Inflorescence laxly to densely corymbose-paniculate; pedicels 4–35 mm long, densely hirsute, with many gland-tipped hairs. Heads (Figure 12) 7–9 mm high; involucral bracts 30–40 in 2 or 3 series, reddish or reddish tinged, oblong-lanceolate to lanceolate, 3–6 mm long, 1.0–1.5 mm wide, tips short-acute, tips of inner bracts densely fringed with pale hairs, margins and outer surface with few to many gland-tipped hairs; paleae usually trifid with a slender central awn, 4–5 mm long. Rays 15–18 in one series, white?; tube 3–4 mm long, minutely hispidulous above; limb 8–12 mm long. Disk flowers 40–75; corollas 4.5–6.0 mm long; tube 1.8–2.5 mm long, minutely hispidulous above; outer surface of lobes with numerous sometimes narrow 1- or 2-celled hairs (Figure 5); without resin ducts in middle of lobes; anther thecae 1.5–1.9 mm long. Achenes 1.3–1.7 mm long; pappus setae ca. 35, mostly 3.5–4.5 mm long, easily deciduous, slightly broadened below the sharp tips.

The species is restricted to the Orizaba region of Mexico.

ADDITIONAL SPECIMENS SEEN.—MEXICO. VERACRUZ: Eastern slope, Mt. Orizaba, 8000–7500 ft. *Nelson 315* (US); hills above Orizaba, 4500 ft. *Pringle 6134* (US).

*Schistocarpha pedicellata* is distinctive within the Mexican-Guatemalan complexes by the generally reddish color and the larger heads. The species is the only one in the genus that seems to consistently



bear gland-tipped hairs on the stems, pedicels, and involucre.

### The *bicolor* group

#### 7. *Schistocarpha bicolor* Lessing

FIGURE 13

*Schistocarpha bicolor* Less., *Linnaea*, 6:409, 1831. [Type: Mexico. *Schiede & Deppe*, holotype HAL, not seen; isotype BM?, not seen.]

*Schistocarpha velutina* Rydb., *North American Flora*, 34(4): 304, 1927. [Type: Mirador, Veracruz, Mexico. *Liebmann 490*, holotype GH, not seen.]

Stems greenish yellow to dark brownish, sparsely to densely hirsute. Petioles 2–9 cm long, winged in at least distal half, often broadly winged to base with fused nodal disk; lamina ovate to subdeltoid, 6–21 cm long and 3–16 cm wide, margins closely short-serrate. Inflorescence of numerous corymbose panicles on ends of branches; pedicels 2–25 mm long, densely pilosulous. Heads (Figure 13) 6–7 mm high; involucre bracts 20–25 in ca. 3 series, oblong to oblong-lanceolate, 2–4 mm long, mostly 1.0–1.3 mm wide, tips rounded to acute, fringed with minute hairs, outer surface pilose with few to many hairs; paleae trifid with slender central awn, 3–4 mm long. Rays 12–15 in one series, white; tube 3–4 mm long, hirtellous to minutely pilosulous; limb ca. 5 mm long. Disk flowers mostly 35–75; corollas 4–5 mm long; tube 1.5–2.0 mm long, rather sparsely hispidulous above; outer surface of lobes with numerous 2- or 3-celled hairs; with or without resin ducts in middle of lobes; anther thecae 1.3–1.5 mm long. Achenes 1.1–1.5 mm long; pappus setae ca. 30, mostly 3.0–3.5 mm long, somewhat deciduous, slightly broadened below the sharp tips.

The species is restricted to the eastern escarpment area of Mexico in the states of Veracruz, Puebla, Hidalgo, and San Luis Potosí.

The species is notable for the unique, broad wing that often extends to the base of the petiole and onto the node. Unfortunately the wing is not so extensive in all specimens, but it always extends at least half the length of the petiole. *Schistocarpha bicolor* is the only member of the Mexican-Guatemalan series that characteristically bears a long

slender awn on the paleae. The awn is most noticeable projecting above the unopened disk flowers in the young heads.

#### 8. *Schistocarpha longiligula* Rydberg

FIGURES 3, 4

*Schistocarpha longiligula* Rydb., *North American Flora*, 34(4):305, 1927. [Type: San Miguel, El Quinché, Guatemala. *Heyde & Lux 3383*, holotype GH, not seen; isotype US.]

Stems pale brownish to reddish brown, hirsute. Petioles 2–5 cm long, winged only in distal third; lamina ovate to subdeltoid, 6–20 cm long, 3–15 cm wide, margins closely serrate. Inflorescence broadly corymbose-paniculate; pedicels 5–20 mm long, densely pilosulous. Heads (Figure 14) 6–7 mm high; involucre bracts 20–25 in ca. 3 series, mostly oblong, 1.5–5.0 mm long, 1.0–1.5 mm wide, tips rounded to obtuse with fringe of minute hairs, outer surface sparsely puberulous distally, usually glabrescent; paleae irregularly lacerate, ca. 3.5 mm long. Rays ca. 12 in one series, white; tube 3–4 mm long, densely hispidulous; limb 4–7 mm long. Disk flowers ca. 25–30; corollas 4–5 mm long; tube ca. 1.5 mm long, sparsely to densely hispidulous; outer surface of lobes with sharp, mostly 3- or 4-celled hairs (Figure 3); resin ducts usually not present in middle of lobes; anther thecae 1.3–1.5 mm long. Achenes 1.3–1.6 mm long; pappus setae 35–40, mostly ca. 3.8 mm long, moderately persistent, slightly broadened below the sharp tips.

The species is restricted to central Guatemala.

ADDITIONAL SPECIMENS SEEN.—GUATEMALA. ALTA VERAPAZ: Along the road to San Pedro Carcha, ca. 3 kms generally ENE of Cobán, ca. 4200 ft. *King 7326* (US); Cobán, 4300 ft. *Türckheim 1151* (US), 1350 m. *Türckheim 111662* (US). 1600 m. *Türckheim II 2131* (US). BAJA VERAPAZ: Miño Perdido. *Lundell & Contreras 21164* (UTD).

Rydberg distinguished the species from *S. seleri* by longer rays and more linear involucre bracts. More recent collections show the same range of variation for the rays of both species. The type of *S. longiligula* does have somewhat more pointed involucre bracts, but material from Alta Verapaz and Baja Verapaz cannot be distinguished on this basis from *S. seleri*. Pubescence of the stem and the longer, more septate hairs of the disk corolla lobes serve to distinguish *S. longiligula*, and also the pappus setae seem somewhat more persistent.

### 9. *Schistocarpha matudae*, new species

FIGURE 15

A *S. bicolor* cui affinis differt limbis radiorum brevioribus et paleis receptaculorum irregulariter laceratis.

Stems brownish, coarsely and stiffly hirsute. Petioles 1–5 cm long, wing mostly restricted to distal half; lamina ovate, 6–15 cm long, 3.0–9.5 cm wide, margins closely and sharply serrate. Inflorescence a broad corymbose panicle; pedicels 1–10 mm long, densely hirtellous. Heads (Figure 15) 6–7 mm high; involucre bracts 20–23 in 2 or 3 series, oblong to oblong-lanceolate, 2–5 mm long, 1.0–1.3 mm wide, obtuse to narrowly acute, tips of inner bracts with dense fringe of hairs, outer surface pilose; paleae irregularly lacerate, 2.0–2.5 mm long. Rays 12–15 in one series, white; tube 2.3–3.0 mm long, densely hispidulous; limb 1.5–2.0 mm long. Disk flowers 30–40; corollas ca. 4.0–4.5 mm long; tube ca. 2 mm long, densely hispidulous; outer surface of lobes with numerous small 1-3-celled hairs; resin ducts usually present in middle of lobes; anther thecae ca. 1.5 mm long. Achenes 1.5 mm long; pappus setae ca. 30, mostly 3–4 mm long, easily deciduous, slightly broadened below the sharp tips.

TYPE.—MEXICO, CHIAPAS: Mt. Ovando, 20 Dec 1936. *Matuda 709* (holotype US).

The pubescence and form of the involucre bracts and the number of ray and disk flowers indicate that the new species is most closely related to *S. bicolor* of the escarpment areas of Veracruz and Hidalgo. The geographic disjunction, the reduced limbs of the rays, and the lack of a central awn on the paleae provide ample basis for distinction.

### 10. *Schistocarpha seleri* Rydberg

FIGURES 6, 16

*Schistocarpha seleri* Rydberg, North American Flora, 34(4): 305, 1927. [Type: zw. San Martin und Ococingo, Chiapas, Mexico. *Seler 2191*, holotype NY; isotype US.]

Stems yellowish brown, sparsely hirtellous above, glabrous or glabrescent below. Petioles 2–4 cm long, winged only in distal third; lamina ovate, 6–15 cm long and 3–8 cm wide, margins closely and sharply serrate. Inflorescence broadly densely corymbose-paniculate; pedicels 4–20 mm long, densely pilosulous. Heads (Figure 16) 6–7 mm high; involucre

bracts 20–24 in 2 or 3 series, oblong, 1.5–4.0 mm long, 1.0–1.3 mm wide, tips rounded to obtuse with fringe of minute hairs, outer surface glabrous or nearly glabrous; paleae irregularly lacerate or sometimes with longer central awn, 3–4 mm long. Rays 12–15 in one series, white; tube 2.5–3.0 mm long, sparsely to densely hispidulous; limb mostly 4–7 mm long. Disk flowers ca. 25–35; corollas 4–5 mm long; tube 1.3–2.0 mm long, sparsely to densely hispidulous; outer surface of lobes with small mostly 1- or 2-celled hairs (Figure 6); resin ducts present in middle of lobes; anther thecae 1.3–1.5 mm long. Achenes 1.5 mm long; pappus setae ca. 27–30, mostly 3–4 mm long, easily deciduous, broadened below the sharp tips.

The species is restricted to the northeastern escarpment area in Chiapas.

ADDITIONAL SPECIMENS SEEN.—MEXICO, CHIAPAS: The Sukleh of Hohoch'en in the Paraje of Shishintonil. Municipio of Tenejapa, 7600 ft. *Breedlove 9313* (US); Paraje Balum K'anal, Municipio of Tenejapa, 8400 ft. *Ton 806* (US).

In number of involucre bracts and flowers the species seems closest to *S. bicolor*, which occurs in the escarpment area farther west in Veracruz. *Schistocarpha seleri* differs by the very restricted wing on the petioles, the more sharply serrate leaves, the glabrous outer surfaces and shorter tips of the involucre bracts, and the usually irregularly lacerate paleae.

### The *platyphylla* group

#### 11. *Schistocarpha chiapensis*, new species

FIGURE 17

A *S. pseudoseleri* cui affinis differt caulibus puberulis floribus radii 10 et floribus disci ca. 25.

Stems reddish brown, minutely puberulous to glabrous. Petioles to over 5 cm long, winged in distal half; lamina ovate, 6–21 cm long, 3–14 cm wide, margins closely short-serrate. Inflorescence broadly corymbose-paniculate; pedicels 4–15 mm long, rather densely puberulous to pilosulous. Heads (Figure 17) 6–7 mm high; involucre bracts 16–20 in ca. 3 series, oblong to oblong-lanceolate, 1.5–4.5 mm long, 1.0–1.5 mm wide, obtuse to acute, inner bracts densely fringed with hairs, outer surface sparsely minutely puberulous; paleae irregularly lacerate, 3.0–3.5 mm long. Rays 10 in one series, white; tube

3.0–3.5 mm long, densely hispidulous; limb 4–5 mm long. Disk flowers ca. 25; corollas 4.5–5.0 mm long; tube ca. 1.8 mm long, densely hispidulous; outer surface of lobes with numerous short 2- or 3-celled hairs; resin ducts present in middle of lobes; anther thecae ca. 1.3 mm long. Achenes 1.5 mm long; pappus setae ca. 30, mostly 3–4 mm long, easily deciduous, slightly broadened below the sharp tips.

TYPE.—MEXICO. CHIAPAS: Sta. Rita, Mapastepec. Jan 1938. *Matuda 2018* (holotype US).

The species is closely related to *S. pseudoseleri*, and the two occur in closely adjacent regions on different sides of the Mexican-Guatemalan border. Since only one specimen of each species is known, the value of some characters remains in doubt. The leaves of the type of *S. chiapensis* are larger than those seen in the type of *S. pseudoseleri*, the pedicels are generally longer, and the disk corollas differ by having resin ducts in the middle of the lobes, but these characters are probably subject to variation. Experience with related species such as *S. platyphylla*, however, would indicate that the differences in stem pubescence, number of ray flowers, and especially the number of disk flowers, are not so variable. The available stem segment completely lacks any of the coarser hairs found in related species. The outer surfaces of the involucre bracts are minutely puberulous, while those of both *S. platyphylla* and *S. pseudoseleri* are puberulous only near the tips or are glabrous.

## 12. *Schistocarpha hondurensis* Standley & Williams

FIGURE 18

*Schistocarpha hondurensis* Standley & L. O. Williams, Ceiba, 3:65, 1952. [Type: San Juancito, Francisco Morazan, Honduras. *Williams & Molina 13780*, holotype EAP, not seen; isotype US.]

Stems brownish, sparsely to densely hirsute. Petioles 2–7 cm long, winged only in distal half or third; lamina ovate to broadly ovate, 6–24 cm long, 3–17 cm wide, margin closely serrate. Inflorescence broadly corymbose-paniculate; pedicels 2–15 mm long, densely pilosulous. Heads (Figure 18) ca. 8 mm high; involucre bracts 16–20 in ca. 3 series, mostly oblong, 1.5–4.5 mm long, 1.0–1.8 mm wide, tips obtuse to short-acute with dense fringe of minute hairs, outer surface sparsely puberulous,

glabrescent; paleae irregularly lacerate, ca. 4 mm long. Rays 8 in one series, white; tube 2–4 mm long, densely minutely hispidulous; limb 2–5 mm long. Disk flowers ca. 20; corollas ca. 5 mm long; tube ca. 1.5 mm long, scabrid above with few to many short hairs; outer surface of throat and lobes evenly scabrid with numerous short mostly 2-celled hairs; resin ducts usually present in middle of lobes; anther thecae ca. 1.7 mm long. Achenes 1.5–1.7 mm long; pappus setae ca. 30, mostly 2.5–3.5 mm long, easily deciduous, slightly broadened below apex and tapered to a sharp tip.

The species occurs in El Salvador, Honduras, and Nicaragua.

ADDITIONAL SPECIMENS SEEN. — EL SALVADOR. CHALATENANGO: East slope of Los Esesmiles. *Tucker 1005* (US), SAN VICENTE: Volcán de San Vicente, 1200–1500 m. *Standley 21523* (US). HONDURAS. COMAYAGUA: 10 kms W of Siguatepeque, 1200 m. *Molina 26023* (US). CORTÉS: entre Buenos Aires y Bañaderos, Montaña San Idalfonso, 1500 m. *Molina 11595* (US), FRANCISCO MORAZÁN: La Vuelta del Caite NE de San Juancito, Montaña La Tigra, 2300 m. *Molina 7729* (US); Montaña La Tigra, SW de San Juancito, 2000 m. *Molina 8818a* (US); western slopes of Peña Blanca, San Juancito Mountains, 1800–2100 m. *Morton 7493* (US); San Juancito, 2000 m. *Williams & Molina 13780* (US). SANTA BARBARA: 10 kms W de Lago Yojoa, Cerro Santa Barbara, 1500–2000 m. *Clewell & Hazlett 3896* (US). NICARAGUA. MATAGALPA: Between El Triunfo and Fuente Pura, NE above Santa María de Ostuma, 1800 m. *Molina 20387* (US).

The original description compared the species with *S. seleri*, but the characters mentioned proved unreliable and the species has been reduced to synonymy (Robinson, 1974). On reexamination, the species proves thoroughly distinct by the lower number of rays in the head and by the unique, uniformly scabrid surface of the disk corollas.

## 13. *Schistocarpha liebmannii* Klatt

FIGURE 19

*Schistocarpha liebmannii* Klatt, Leopoldina, 23:146, 1887. [Type: Mexico. *Liebmann 42*, holotype C, not seen; photo and fragment US.]  
*Neurolaena liebmannii* Schultz-Bip. ex Klatt, Leopoldina, 23:146, 1887. [Nomen nudum in synonymy.]

Stems dark brownish to slightly reddish, glabrous to slightly puberulous. Petioles 1–4 cm long, distinctly winged only in distal  $\frac{2}{3}$ – $\frac{1}{3}$ ; lamina ovate to elliptic, 6–20 cm long, 3–9 cm wide, glabrous above, slightly puberulous on veins below, pale below, mar-

gins minutely serrulate to remotely serrate. Inflorescence lax with numerous corymbose panicles; pedicels 2–13 mm long, sparsely to densely puberulous. Heads (Figure 19) ca. 7 mm high; involucre bracts 16–20 in ca. 3 series, mostly oblong, 1.5–4.0 mm long, 1.0–1.5 mm wide, tips rounded with fringe of minute hairs, outer surface glabrous; paleae irregularly lacerate, 2–3 mm long. Rays 8 in one series, white; tube 3.5–4.0 mm long, glabrous; limb ca. 4 mm long. Disk flowers ca. 12; corollas 4.0–4.5 mm long; tube ca. 1.5 mm long, glabrous or nearly glabrous; lobes with small 2- or 3-celled hairs; weak resin ducts sometimes present in middle of lobes; anther thecae ca. 1.5 mm long. Achenes ca. 1.5 mm long; pappus setae ca. 22–25, mostly 2.5–3.0 mm long, easily deciduous, not broadened below tips.

The species is restricted to the eastern escarpment area of Veracruz in Mexico.

ADDITIONAL SPECIMENS SEEN. — MEXICO. VERACRUZ: along the road to Coscomatepec, ca. 7 km SW of Coscomatepec, ca. 4400 ft. *King 6487* (US); Zacuapán. *Purpus 7753, 10662* (US).

The ovate leaf blades and the nearly glabrous surfaces of the stems and leaves make the species the most distinctive vegetatively in the genus. Only *S. pseudoseleri* has a smaller number of disk flowers in the head.

#### 14. *Schistocarpha platyphylla* Greenman

FIGURE 20

*Schistocarpha platyphylla* Greenm., Publ. Field. Columb. Mus., Bot., 2:274, 1907. [Type: Quezaltenango, Guatemala. *Kellerman 5295*, holotype F, not seen; isotype US.]  
*Schistocarpha kellermanii* Rydb., North American Flora, 34(4):306, 1927. [Type: Sacatepéquez, Guatemala. *Kellerman 7293*, holotype NY, isotype US.]

Stems brownish to slightly reddish, rather sparsely hirtellous, usually glabrescent. Petioles 2–9 cm long, sometimes winged nearly to base, wings wider above; lamina ovate to broadly ovate, 6–25 cm long and 3–22 cm wide, margins closely serrulate. Inflorescence broadly corymbose-paniculate; pedicels 2–17 mm long, densely pilosulous. Heads (Figure 20) 6–8 mm high; involucre bracts 16–20 in ca. 3 series, oblong to oblong-lanceolate, 2–6 mm long, 1.0–1.5 mm wide, tips of inner bracts often acute with dense fringe of hairs, outer surface glabrous or slightly puberulous near tip; paleae irregularly lacerate, 2.5–3.0 mm long. Rays ca. 10 or rarely 12 in

one series, white; tube 2.5–3.5 mm long, densely hispidulous; limb lacking or vestigial and linear to 2 mm long. Disk flowers 15–25; corollas 4.5–6.0 mm long; tube 1.5–2.5 mm long, densely hispidulous; outer surface of throat with sparse short hairs, with short mostly 2- or 3-celled hairs denser on lobes; with or without resin ducts in middle of lobes; anther thecae 1.5–1.7 mm long. Achenes ca. 1.5 mm long; pappus setae ca. 30, 3–5 mm long, easily deciduous, slightly broadened below the sharp tips.

The species is represented by numerous collections from southern Guatemala and also occurs in the following areas:

ADDITIONAL SPECIMENS EXAMINED. — EL SALVADOR. SANTA ANA: Slope of Ayeco, NW flank of Volcán de Santa Ana, ca. 1710 m. *Tucker 1280* (US). SONSONATE: Forest Finca La Cumbre, 1600 m. *Molina & Montalvo 21737* (US). MEXICO. CHIAPAS: Volcán Tacana north, 2100 m. *Matuda 2951* (US). OAXACA: Vicinity of Concordia, Distr. Pachutla, 600 m. *Makrinius 584* (US); vicinity of Concordia, Montecristo, 1100 m. *Makrinius 661* (US); vicinity of Cafetal Concordia, 400–650 m. *Morton & Makrinius 2552* (US).

Most specimens from Guatemala, including the types of both *S. platyphylla* and *S. kellermanii*, completely lack limbs on the rays. The specimens occurring disjunct in Oaxaca are most notable for the consistent presence of small, linear, sometimes deeply cleft limbs on the rays. The Oaxaca specimens also seem more inclined to have 12 rays in the head. The latter specimens do not seem otherwise distinct, and such patterns of disjunction have been seen in many other plants such as some species of *Ageratina* (King & Robinson, 1978). One of the specimens from El Salvador (*Molina & Montalvo 21629*) differs from all other species that were seen by the presence of a long, slender, central awn on each palea.

#### 15. *Schistocarpha pseudoseleri*, new species

FIGURE 21

A *S. seleri* differt bracteis involucris paucioribus acutis, floribus radii ca. 8, floribus disci 8–10.

Stems brownish, sparsely coarsely hirsute, sometimes glabrescent. Petioles 2–3 cm long, winged only in distal half; lamina ovate, 6–12 cm long, 3–7 cm wide, margins closely serrulate. Inflorescence of many dense corymbose panicles at ends of branches; pedicels 1–9 mm long, densely pilosulous. Heads (Figure 21) 6–7 mm high; involucre bracts 15–18

in ca. 3 series, oblong to oblong-lanceolate, 1.5–5.0 mm long, 1.0–1.4 mm wide, obtuse to acute, tips of inner bracts more acute and densely fringed with hairs, outer surface glabrous; paleae irregularly lacerate, 2.5–3.0 mm long. Rays usually 8 in one series, white; tube 3.0–3.5 mm long, densely hispidulous; limb 3.5–5.0 mm long. Disk flowers 8–10; corollas ca. 5 mm long; tube 2.0–2.5 mm long, densely hispidulous; outer surface of lobes with numerous small 1- or 2-celled hairs; resin ducts weak or lacking in middle of lobes; anther thecae ca. 1.3 mm long. Achenes 1.5 mm long; pappus setae ca. 30, mostly ca. 4 mm long, easily deciduous, slightly broadened below the sharp tips.

TYPE.—GUATEMALA. SAN MARCOS: Near Aldea Fraternidad, between San Rafael Pie de la Cuesta and Palo Gordo, west facing slope of the Sierra Madre Mountains, wet mountain forest, 1800–2400 m. 10–18 Dec 1963. Rays white, herb 4 meters tall. *Williams, Molina & Williams 26256* (holotype US).

The species has furnished at least part of the basis for reports of *S. seleri* from Guatemala. Differences are evident in the smaller numbers of involucre bracts, ray flowers, and disk flowers in the heads. Such a reduced number of flower parts is approached elsewhere in the genus only in *S. liebmanni* of central Mexico, but the latter differs by its distinctive nearly glabrous remotely serrate and abaxially paler leaves. The lack or near lack of resin ducts in the middle of the disk corolla lobes may be of some significance.

## 16. *Schistocarpha sinforosii* Cuatrecasas

FIGURES 4, 22

*Schistocarpha sinforosii* Cuatr., Trab. Mus. Cienc. Nat. Madrid, Bot., 29:43, 1935. [Type: Tolima, Colombia. Cuatrecasas 2879, holotype MA, not seen; photo US.]

*Liabum eupatorioides* Muschler, Bot. Jahrb., 50, Beibl., 3:83, 1913. [Type: Cajamarca, Peru. *Weberbauer 4084*, holotype B, destroyed; photo and fragment US; not *Schistocarpha eupatorioides* (Fenzl) O. Kuntze.]

Stems brownish yellow to slightly reddish, hirsute to villous. Petioles 2–9 cm long, winged in distal part, wing sometimes extending narrowly to base; lamina ovate to broadly ovate, 6–22 cm long, 3–18 cm wide, margin closely serrate. Inflorescence corymbose-paniculate, often widely spreading; pedicels 3–20 mm long, densely villosulous or hirtellous.

Heads (Figure 22) 7–10 mm high; involucre bracts 16–20 in 2–3 series, mostly oblong to oblong-lanceolate, 3–7 mm long, 1–2 mm wide, tips often sharply acute and densely fringed, outer surface glabrous to sparsely pilose; paleae irregularly lacerate, 3–4 mm long. Rays usually 8–10 rarely 12 in one series, white; tube 4–6 mm long, glabrous to densely hirtellous; limb 6–11 mm long. Disk flowers mostly 20–30; corollas 6–7 mm long; tube 2.0–2.5 mm long, with few to many small hairs above; lobes scabrid with short tapering 2- or 3-celled hairs (Figure 4); resin ducts usually present in middle of lobes; anther thecae ca. 1.7–2.3 mm long. Achenes 1.5–2.0 mm long; pappus setae ca. 30, mostly 4.0–5.5 mm long, moderately deciduous, slightly broadened below apex and tapered to sharp tips.

The species is represented by many collections from Colombia and occurs as a disjunct in the northern half of Peru, but no collections have been seen from intervening Ecuador.

The species has the reduced numbers of involucre bracts and ray flowers that indicate relation to the *S. platyphylla* group of Central America and Mexico. *Schistocarpha sinforosii* is most distinct from other species of the group by the longer limbs of the ray flowers and the generally larger size of the heads. There is some variation in the species. Specimens with more pointed inner involucre bracts, glabrous or sparsely pubescent tubes of the ray flowers, and hirtellous pedicels are restricted to Colombia, but specimens with less pointed bracts, densely pubescent tubes of the rays, and villosulous pedicels occur in both Colombia and Peru. A single Peruvian collection (Amazonia: Chachapoyas. *Hutchison & Wright 4923*, US) represents an extreme form with the undersurfaces of the leaves tending to be reddish and the involucre bracts being arranged in 3 or 4 markedly unequal series.

## Excluded Species

*Schistocarpha steyermarkiana* H. Robinson, Phytologia, 29:248, 1974. [Guatemala. = *Oteiza ruacophila* (J. Donn. Smith) Fay, Phytologia, 31:16, 1975.]

*Schistocarpha triangularis* Rusby, Bull. New York Bot. Gard., 4:392, 1907. [Bolivia. *Bang 2477*. Isotypes at US. = *Senecio alternifolius* (Schultz-Bip.)

Greenm., Ann. Missouri Bot. Gard., 10:76, 1923. Also known as *Gynoxys repanda* Wedd., Chlor. And., 1:77, 1856. The holotype at NY has not

been found and the original description mentions triangular leaves and multiseriate involucre bracts that are not present in the isotypes.]

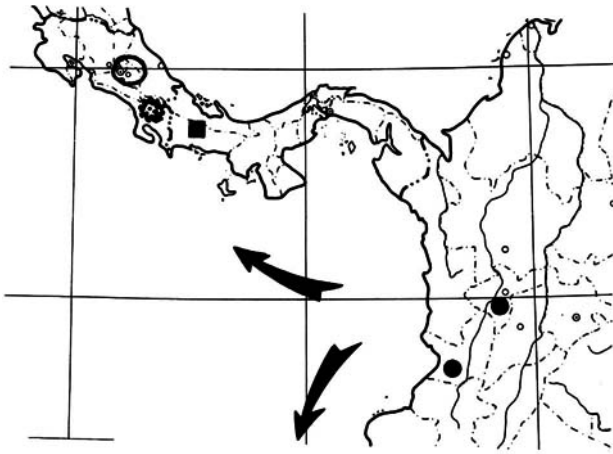


FIGURE 23.—Map showing *Schistocarpha* species having more than 20 ray flowers in the heads. (Solid line = *S. paniculata*; stipples = *S. wilburii*; square = *S. croatii*; solid dots = *S. margaritensis*; arrows = direction of dispersal of *S. eupatorioides* from presumed area of origin.)

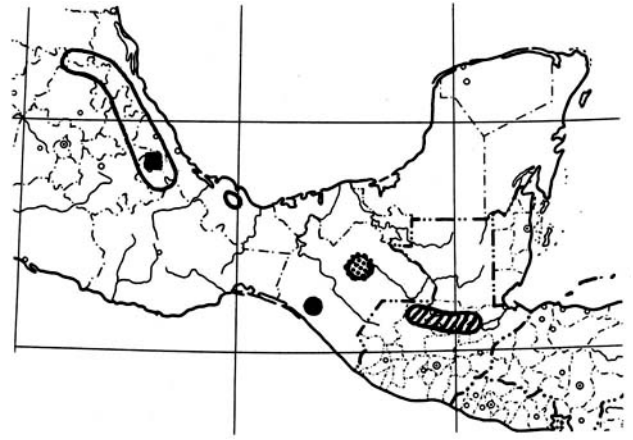


FIGURE 24.—Map showing *Schistocarpha* species having 12-18 ray flowers and 20-40 involucre bracts in heads. (Square = *S. pedicellata*; solid line = *S. bicolor*; stipples = *S. seleri*; stripes = *S. longiligula*; solid dot = *S. matudae*.)

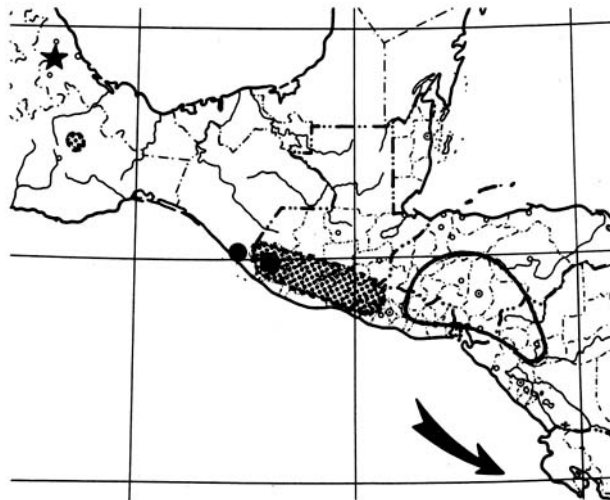


FIGURE 25.—Map showing *Schistocarpha* species having 8-12 ray flowers and 16-20 involucre bracts in heads. (Star = *S. liebmannii*; stipples = *S. platyphylla*; solid dot = *S. chiapensis*; square = *S. pseudoseleri*; solid line = *S. hondurensis*; arrow = presumed source of the South American *S. sinforosii*.)

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