TAXONOMIC STATUS OF BARROETEA GLUTINOSA (ASTERACEAE, EUPATORIEAE) AND ITS ALLIES: MORPHOLOGICAL EVIDENCE FOR THE TRANSFER OF BARROETEA TO BRICKELLIA

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ABSTRACT

The phyletic position of the taxonomically controversial Barroetea glutinosa T. Brandegee, is investigated using microcharacters of flowers and fruits. It is concluded that the species stands somewhere between the genera Barroetea and Phanerostylis (sensu King & Robinson). Since the latter taxon is positioned within the genus Brickellia by several recent workers, all of Barroetea is transferred to Brickellia. This has necessitated the following name changes: Brickellia problematica B. Turner, nom. nov. (= Barroetea glutinosa T. Brandegee; non Brickellia glutinosa A. Gray); Brickellia laxiflora (T. Brandegee) B. Turner, comb. nov.; Brickellia pavonii (A. Gray) B. Turner, comb. nov.; and Brickellia subuligera (Schauer) B. Turner, comb. nov.

KEY WORDS: Barroetea, Brickellia, Eupatorieae, Asteraceae, México

Treatment of the small genus Barroetea for the Asteraceae of México (Turner & Nesom, in prep.) has led the senior author to pursue at some length a problem relating to the position of an anomalous member of this genus, B. glutinosa. The latter was first described by Brandegee (1908) who noted that it was "a very distinct species, differing from the others of the genus in having alternate leaves and being glandular." He also called attention to the enlarged style branches and corollas which "are campanulate rather than tubular." Indeed, on an isotype of B. glutinosa (GH!), Brandegee appended a hand written notation, "Biclavella glutinosa Brandg.," as if he had contemplated the erection of a new genus, Biclavella, to accommodate the species. Nevertheless, B.L. Robinson (1911) retained the species, along with four others, in his revisionary treatment of Barroetea.

Barroetea glutinosa was maintained in Barroetea until King & Robinson (1972) transferred the species into their newly erected Phanerostylis (A. Gray)

King & H. Robins., a small genus of four or five species which was originally described as a subgenus within Eupatorium by A. Gray, but subsequently transferred to Brickellia by Turner (1978), following the suggestions of Harcombe & Beaman (1967). King & Robinson (1987), however, maintained all three genera: Brickellia, a large, mostly shrubby, desert group of about 100 species; Barroetea with six annual species; and Phanerostylis, except for the annual, P. glutinosa, a perennial, suffruticose or subshrubby group of four species. These several genera are accommodated next to each other in their treatment of the tribe Eupatorieae.

According to King & Robinson (1987), Barroetea glutinosa "has precisely those characters that were given by King & Robinson for Phanerostylis, distichous pappus barbulae, flaring corollas, rather large sinuous hairs on the basal stylar node, comparatively triangular and papillose corolla lobes, and densely papillose style branches." They maintain that these characters "are all foreign" to the genus Barroetea, especially the form of the corolla."

While most of their morphological observations regarding Barroetea glutinosa are valid, what they have not called to the fore are those characters which relate the species to Barroetea itself. Table 1 lists those characters which B. glutinosa shares with the three taxa, Barroetea, Phanerostylis, and Brickellia (sect. Bulbostylis). Casual examination of this listing will show that the species in question is closer to Barroetea in habit, capitulescence, and characters of the mature fruit; however, it appears closer to Phanerostylis in characters of the corolla and style. In short, all three genera are certainly closely related and should probably be positioned together, but it would appear that Barroetea and Phanerostylis are especially close. Indeed, Barroetea glutinosa appears to stand somewhere between Barroetea and Phanerostylis, but where? and how might these best be treated taxonomically?

The above taxonomic dilemma is not uncommon among the numerous genera recognized by King & Robinson (1987) in their monumental treatment of the closely knit tribe Eupatorieae. Most generic segregates of these authors have one or more species which are difficult to position because they stand somewhere between their neatly demarcated groupings. King & Robinson often recognize this themselves, but draw upon the belief that "intergeneric hybridization is common in the family [meaning tribe, we think]."

In any case, the senior author, in his preparation of a treatment of the Eupatorieae for México, is faced with several taxonomic options: 1.) to retain Barroetea glutinosa; 2.) position this in Phanerostylis as part of Brickellia but maintain Barroetea; or 3.) to merge all of Barroetea in an expanded subgenus Phanerostylis of Brickellia. While there are yet other taxonomic options, we view these as excessive. The purpose of the present paper, then, is to choose from among the several options posed above.

METHODS AND EXPERIMENTAL

Since much emphasis is placed upon the microfeatures of floral and fruit characteristics by King & Robinson (1987; Grashoff & Turner 1970), we documented the characteristics of achene, pappus, style, corolla, and leaves using scanning electron microscopy (SEM). Leaves and flowers were removed from herbarium specimens (Table 1), hydrated in a modified Hoyer's solution (3:1:1: 10; Aerosol OT: Glycerin: Chloral hydrate: H₂O; v:v:v:w), fixed in FAA solution, dehydrated by a graded ethanol series, and critical point dried. The dried samples were then mounted on a stub with double sided cellophane tape and vacuum coated with gold (25-35 nm thickness). The specimens were observed with a Phillips 515 SEM (10-20 KeV) and photographed using Polaroid Type 55 P/N film. For achene observation, mature seeds were soaked in 50% acetone, dehydrated through a graded acetone series and then dried at room temperature. Dusts on the seed surface were removed by 3-4 minutes of ultrasonification. The subsequent steps were the same as described for the preparation of leaf and flower materials.

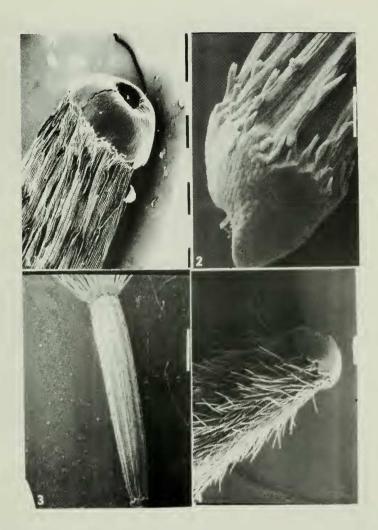
We have examined the following taxa, vouchers for which are given below in Table 2 (deposited in TEX). For convenience, except for *Barroetea glutinosa*, these are listed by their treatments in King & Robinson (1987).

RESULTS

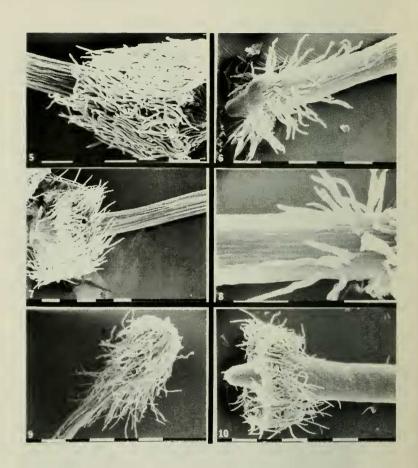
Achenes - The achenes of Brickellia (Fig. 23a, 23b) are characteristically columnar or prismatic, 4-5 sided; possess 8-9 pronounced ribs; and the exocarp is firmly fused to the achene, and does not normally peel, as is characteristic for Barroetea and Phanerostylis. The latter is also true for Brickellia coulteri and the annual, Brickellia diffusa both of which superficially resemble Barroetea in habit. Phanerostylis also has prismatic or columnar achenes, but these are mostly 4 or 5 ribbed, with achenal walls very much like those of Barroetea (Figs. 24b, 25b). Achenes of the latter, including Barroetea glutinosa, differ from those of Phanerostylis in being tangentially flattened with 4-5 major ribs (or with 8-10 ribs when intercalary ribbing occurs).

The carpopodium of all species of *Brickellia* examined were characteristically rather symmetrical and "stopper shaped" (Fig. 1-3), but occasional species such as *Brickellia veronicifolia* may have asymmetrical carpopodia (Fig. 4); carpopodia of *Phanerostylis* are similar but markedly asymmetrical, composed of thick walled cells, and from a side view much resemble the profile of an open jawed shark (Figs. 24, 25); those of *Barroetea*, including *Barroetea glutinosa*, differ from both of the aforementioned, in having a flattened carpopodium with thinner, less pronounced cells (Figs. 11, 14a, 20a, 21a, 22a).

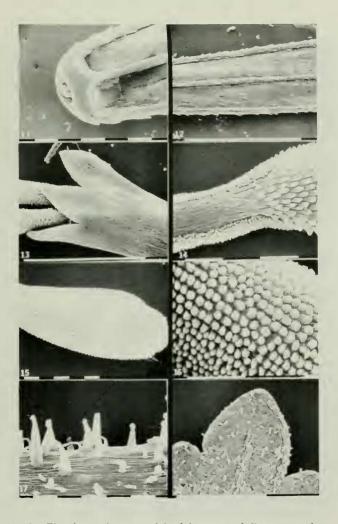
The pappus bristles found in Brickellia vary from nearly ebarbellate to plumose. The bristles of both Phanerostylis and Barroetea are mostly evenly



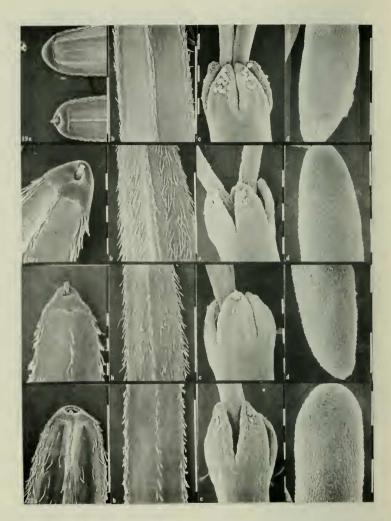
Figs. 1-4. Achenes of *Brickellia*, showing carpopodia - 1. *B. cordifolia*; 2. *B. coulteri*; 3. *B. lanata*; 4. *B. veronicifolia*. The size of the bar units shown for each figure is 0.5 cm except for the following: fig. 1, 1 cm.



Figs. 5-10. Basal stylar shafts showing pubescent nodes - 5. Brickellia coulteri; 6. Brickellia (Phanerostylis) coahuilensis; 7. Brickellia (Phanerostylis) pedunculosa; 8. Barroetea glutinosa; 9. Barroetea glutinosa (lower portion of shaft, basal node excluded); 10. Brickellia sonorana ined. The size of the bar units shown for each figure is 0.5 cm.



Figs. 11-18. Floral, vestiture, and leaf features of Barroetea glutinosa - 11. carpopodium; 12. midportion of adaxial surface of achene; 13. upper portion of corolla with protruding style branches; 14. upper portion of stigmatic lines, where these join the appendage; 15. apical portion of stylar appendages; 16. closeup of surface of Fig. 15; 17. glandular trichomes along stem; 18. apical portion of leaf. The size of the bar units shown for each figure is 0.5 cm except for the following: fig. 18, 1 cm; figs. 12 and 13, 2 cm.



Figs. 19-22. Fruit and floral details of Barroeteoid species of *Brickellia* (top to bottom: a. carpopodia, adaxial surfaces; b. midportion of achenes, adaxial surfaces; c. corolla lobes; d. stylar appendages) - 19. *B. sonorana* ined.; 20. *B. laxiflora*; 21. *B. subuhgera*; 22. *B. pavonii*. The size of the bar units shown for each figure is 0.5 cm except for the following: figs. 19a, 19b, 20b, 21c, 22a, and 22b, bar = 2 cm.

Table 1. Comparison of Barroetea glutinosa with selected related taxa.

	Barroetea	B. glutinosa	Phanerostylis	Brickellia coulteri
				(Sect. Bulbostylis)
1.	annuals	annual	strong perennials	shrublets
2.	leaves setose	not setose	not setose	not setose
3.	leaves punctate	punctate	punctate or not	not punctate
4.	heads in cymules	in cymules	solitary	in cymules
5.	corolla tubular	flaring	flaring	tubular
6.	corolla lobes	large	large	minute
	minute			
7.	style branches	a. broad,	a. broad,	a. narrow,
	a. narrow b. smooth	b. papillose	b. papillose	b. smooth
8.	shaft abruptly	gradually	gradually	abruptly
	nodular	swollen	swollen	nodular
9.	pappus short	long ciliate	long ciliate	variously ciliate
	ciliate or			
	eciliate			
10.	pappus w/o cup	strong cup	strong cup	w/o cup
11.	achenes flat	achenes flat	4-5 sided	4-5 sided
12.	achenes with	3 ribbed	4-5 ribbed	8-10 ribbed
	6-8 ribs			
13.	carpopodium	flattened	rounded	rounded
	flattened			symmetrical
14.	Achene outer	peeling	peeling	not peeling
	surface			
L	peeling			

Table 2. Specimens and taxa examined by SEM for micromorphological features.

Тахоп	Voucher
Brickellia cordifolia Ell.	Correll 10558
Brickellia coulteri A. Gray	Correll 30626
Brickellia diffusa (M. Vahl) A. Gray	King 3888
Brickellia lanata (DC.) A. Gray	Paray 3410
Brickellia sonorana ined.	Flyr 110
Brickellia veronicifolia (H.B.K.) A. Gray	Flyr 258
Barroetea glutinosa T. Brandegee	Tenorio 4751
Barroetea pavonii A. Gray	Sundberg 3029
Barroetea laxiflora (T. Brandegee) B. Turner	Lott 3409
Barroetea subuligera (Schauer) A. Gray	Sundberg 2821
Phanerostylis coahuilensis (A. Gray) King & H. Robins.	Lundell 5384
Phanerostylis nesomii (B. Turner) King & H. Robins	Lavin 4888
Phanerostylis pedunculosa (DC.) King & H. Robins	Mc Vaugh 176

ebarbellate with fringed, apically acute hairs along the margins. Towards the apices of the bristles, the marginal hairs lose their neat arrangement, becoming contorted or twisted.

In summary, the achenes of Barroetea and Phanerostylis are very similar, those of the latter differing primarily in their columnar shape with relatively massive carpopodia. The achenes of Barroetea glutinosa resemble more closely those of Barroetea in that they are tangentially flattened with very similar

carpopodia.

Corollas - The corolla lobes of Barroetea (s.s.) characteristically possess glandular hairs (Figs. 19, 20, 21, 22). Corollas of Barroetea glutinosa are eglandular (Fig. 13), like those of most species of Brickellia examined. In addition, the upper portion of the tube tends to flare in Barroetea glutinosa, much as in Phanerostylis; most species of Brickellia, however, tend not to flare, as is the case for all species of Barroetea (s.s.).

Styles - The base of the stylar shafts of Barroetea, Brickellia, and Phanerostylis are very similar in possessing pubescent nodes (Figs. 5-10). The nodes are not as pronounced in Phanerostylis and Barroetea glutinosa as they are in most species of Brickellia and Barroetea, but this appears to be more a matter of vestiture restriction than nodal size, the hairs of Phanerostylis and Barroetea glutinosa being more loosely arranged along the base of the shaft (Fig. 6-10).

The stylar appendages of Barroetea glutinosa (Figs. 14-16) are very similar to Phanerostylis (Figs. 24d, 25d), both possessing markedly papillate surfaces. Those of the remaining species of Barroetea, and those species of Brickellia

examined, have relatively smooth surfaces (Fig. 19d, 21, 22, 23d).

In summary, the microfeatures of the corolla and styles of Barroetea glutinosa are more like those of the Phanerostylis group of Brickellia than they are to the genus Barroetea (s.s.), the latter having essentially the same features as those of typical Brickellia.

Vegetative features - The leaves of Barroetea (s.s.) differ from most species of Brickellia, Phanerostylis, and Barroetea glutinosa in possessing callous prickles at the leaf apex and upon the apices of denticulations along the margins of the blade. This character, taken alone, can be used to distinguish Barroetea (s.s.) from Phanerostylis. Nevertheless, Barroetea glutinosa does tend to develop a callosity at the apices of its leaves (and often on denticulations), but these do not form obvious prickles (Fig. 18). Thus, leaf morphology, as relates to callosity, remains ambiguous.

In its annual habit and branching aspect, Barroetea glutinosa is much more similar to Barroetea than it is to Phanerostylis, the latter being composed of

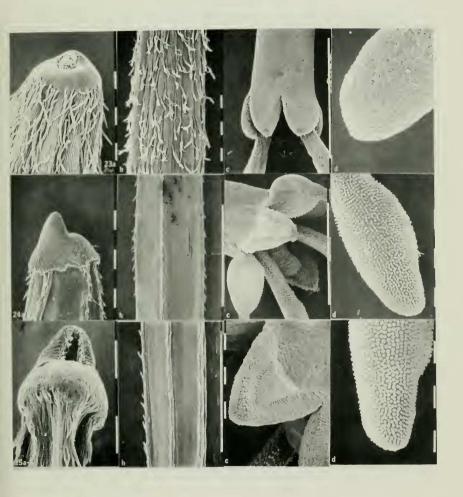
few headed, often rhizomatous, perennials.

DISCUSSION

As can be seen by the comparison of characters given in Table 1, Barroetea glutinosa stands somewhere between Barroetea and Phanerostylis: floral and stylar characters suggest a close relationship with Phanerostylis, while achenal features and habit suggest a closer relationship with Barroetea. Both Barroetea and Phanerostylis appear closely related to Brickellia, so much so that some workers (Beaman & Harcombe 1967; Turner 1978; McVaugh 1984) have included Phanerostylis in Brickellia. So treated, it would be difficult to exclude Barroetea from Brickellia since Barroetea glutinosa marks the two taxa as sister groups.

Barroetea, Brickellia, and Phanerostylis have base chromosome numbers of x=9, share numerous similar microfeatures, and all are centered in mostly xeric habitats of central and northern México. Indeed, a preliminary cladistic analysis (Nesom & Turner, in prep.) of Brickellia (sensu King & Robinson), using the characters touted here, strongly suggests that Barroetea and Phanerostylis are readily imbedded within Brickellia, regardless of the position of Barroetea glutinosa. Thus, the generitype of Brickellia is a shrublet with flaring corollas, large corolla lobes, as in Phanerostylis; the style branches also flare as in the latter taxon, but their surfaces are essentially smooth, as in Barroetea. In short, the inclusion of Barroetea in the subgenus Phanerostylis within a broadly conceived Brickellia makes good phyletic sense, both on morphological and biogeographical grounds. The following nomenclature to accomplish this arrangement is proposed by the senior author:

- Brickellia problematica B. Turner, nom. nov. Based upon Barroetea glutinosa T. Brandegee, Zoe 5:262. 1908. Not Brickellia glutinosa A. Gray, Proc. Amer. Acad. Arts 21:385. 1886.
- Brickellia laxiflora (T. Brandegee) B. Turner, comb. nov. BASIONYM:
 Barroetea laxiflora T. Brandegee, Univ. Calif. Publ. Bot. 4:93. 1910.
 My concept of this taxon includes Barroetea brevipes B.L. Robins.
- Brickellia pavonii (A. Gray) B. Turner, comb. nov. BASIONYM: Barroetea pavonii A. Gray, Proc. Amer. Acad. Arts 17:206. 1882. My concept of this taxon includes Barroetea sessilifolia Greenm.
- Brickellia subuligera (Schauer) B. Turner, comb. nov. BASIONYM: Bulbostylis subuligera Schauer, Linnaea 19:718. 1847. My concept of this taxon would include Barroetea setosa A. Gray.



Figs. 23-25. Fruit and floral details of - 23. Brickellia coulteri; 24. Brickellia (Phanerostylis) nesomii; and 25. Brickellia (Phanerostylis) coahuilensis (a. carpopodium; b. midsection of achene, adaxial surface; c. corolla lobes; d. stylar appendages). The size of the bar units shown for each figure is 0.5 cm except for the following: figs. 23b, 23c, 24b, and 24c, bar = 2 cm.

ACKNOWLEDGMENTS

The SEM work for this paper was performed solely by the junior authors. The senior author conceived of the work, wrote the paper, and is responsible for the taxonomic judgments rendered. We are grateful to Dr. Guy Nesom and Dr. A.M. Powell for reviewing the paper.

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