

GENERIC RELATIONSHIPS AND TAXONOMY OF
ACAMPTOPAPPUS (COMPOSITAE: ASTEREAEE)

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ABSTRACT

Acamptopappus comprises *A. sphaerocephalus* var. *sphaerocephalus* and var. *hirtellus*, and *A. shockleyi*, taxa of the southwestern deserts of the United States. Characteristics shared by these taxa include extremely long-villous achenes, a pappus of long, somewhat erose scales with lanceolate to spatulate apices, deeply alveolate receptacles, short, funnelform disk corollas with deep sinuses and reflexed lobes, very broad phyllaries with very broad, scarious margins, and nearly globose capitula. Chromosome numbers of all taxa are $n = 9$. The probable closest relatives of this outlying genus are to be found among larger genera of Astereae having $x = 9$, particularly the *Chrysothamnus*—*Ericameria*—*Macronema* alliance.

Acamptopappus (A. Gray) A. Gray comprises three taxa of the Mojave and Sonoran deserts of the southwestern United States (Figs. 1, 2). The taxa are distinctive in appearance, with very light green foliage, whitish stems, nearly globose capitula, phyllaries nearly as broad as long, and the most villous achenes of all North American Astereae. No treatment encompassing all three taxa has previously been published, except in floras. This paper circumscribes these taxa, and discusses the possible relationships of *Acamptopappus* with other genera of Astereae.

TAXONOMIC HISTORY

Gray (1849) named sect. *Acamptopappus* of *Haplopappus* Cass. to accommodate *H. sphaerocephalus* Harvey & A. Gray in A. Gray (1849). It was based on a specimen collected by Thomas Coulter in 1832 that had been forwarded to Gray between 1846 and 1848 by W. H. Harvey, Coulter's successor as curator of the herbarium of Trinity College, Dublin (Coville 1895). Later, Gray (1873) accorded generic status to *Acamptopappus*, a move with which Hall (1928, p. 365) concurred. In 1882, Gray described *A. shockleyi*. Jones (1898) established *A. microcephalus*, which was placed in synonymy with *Ericameria cooperi* (A. Gray) H. M. Hall by Blake (1929), when he named *A. sphaerocephalus* var. *hirtellus*. No additions have been made to the genus as a result of the present study, although questions about the types are clarified in comments following the descriptions of taxa.

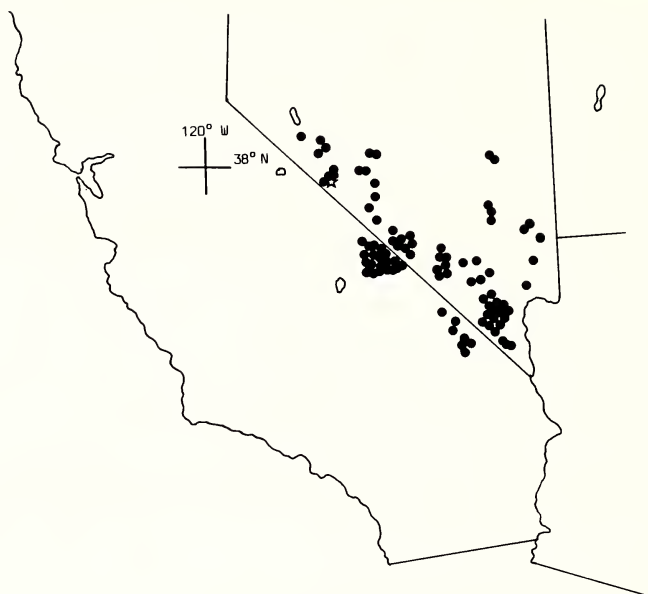


FIG. 1. Distribution of *Acamptopappus shockleyi*. Each symbol may represent one or more collections. Type locality indicated by star.

METHODS

Standard herbarium techniques were used to study 1182 specimens of the three taxa, including types, borrowed from or observed at ARIZ, ASU, CAS, COLO, F, GH, JEPS, K, LL, MO, NY, POM, RM, RSA, SD, TCD, TEX, UC, US, and UTC. For comparison of generic features, specimens of *Chrysothamnus*, *Eastwoodia*, *Ericameria*, *Petradoria*, *Stenotus*, and *Vanckleya* belonging to COLO, LL, RM, and TEX were studied. *Acamptopappus* taxa were observed in the field during trips taken in 1984 and 1986.

Achenes, style-branches, corollas and pappus members used for scanning electron microscopy were carefully removed from herbarium specimens (COLO, LL, RM, or TEX). Achenes and pappus were mounted on stubs with double-stick tape; style-branches and corollas were rehydrated by soaking in Wetter's solution (Wetter 1983), rinsed, and then mounted with double-stick tape. Stubs were sputter-coated with ca. 400 nm gold, and observed on an AMR 1000A at 20 kV.

DISCUSSION

Morphology. The two species of *Acamptopappus* are very similar to one another (Table 1, Fig. 3), except that *A. sphaerocephalus* plants

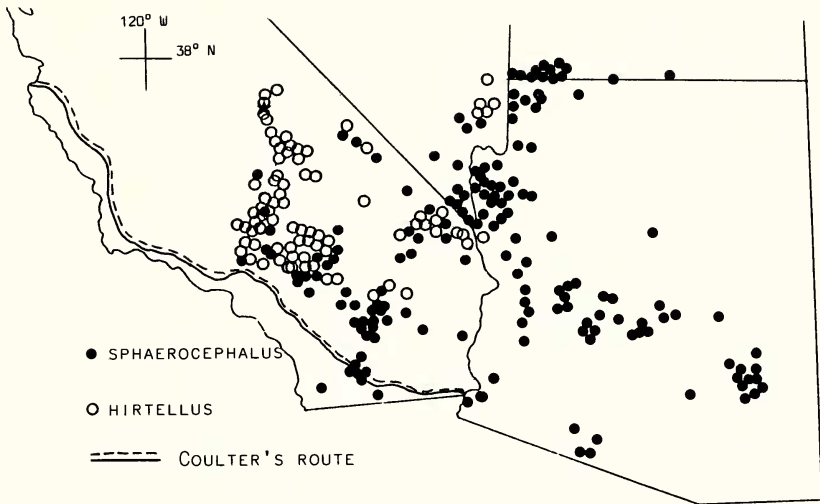


FIG. 2. Distribution of *Acamptopappus sphaerocephalus* var. *hirtellus* and var. *sphaerocephalus*. Each symbol may represent one or more collections. Type locality for var. *hirtellus* indicated by star. Route of Thomas Coulter (Coville 1895) indicated by double line; see comments under description of var. *sphaerocephalus* for explanation.

are usually slightly larger (to 4 dm) than those of *A. shockleyi* (to 3.3 dm), are more highly ramified, have narrower leaves, and have smaller, more numerous and occasionally clustered capitula that are eradiate and have fewer disk florets.

The pappus of *A. shockleyi* usually consists of 17–30 moderately erose, white scales. Ray floret pappus apices usually are lanceolate to acute, whereas those of the disk florets are more spatulate (Fig. 4a); the pappus elements of *A. sphaerocephalus* disk florets are spatulate.

Both species have narrowly triangular-lanceolate disk style-branch appendages that are acute and flattened on the adaxial face, and have collecting hairs that are of moderate length (Fig. 4a). Disk corolla epidermes (Fig. 5a) of the two species of *Acamptopappus* are identical. Ray-corolla epidermis of *A. shockleyi* is shown in Fig. 5b.

Achenes of *Acamptopappus* species are actually cylindric, but appear obconic in outline because they are covered with the longest and densest *zwillingshaares* that I have seen in any taxon of *Astereae*. Anderson and Weberg (1974) noted that there are “long, isotropic, non-glandular (shag) hairs” present with the “anisotropic duplex hairs” on *Acamptopappus* achenes. However, I found that all trichomes are of the normal “anisotropic duplex” type exemplified by those of *Stenotus acaulis* (Fig. 5c), except that some are twisted and contorted (Fig. 5d). The latter are usually concealed by a layer of

TABLE 1. DISTINGUISHING MORPHOLOGICAL FEATURES OF *Acamptopappus* SPECIES, *Amphipappus*, *Eastwoodia*, AND *Vanceleva*. Adapted in part from Anderson and Weberg (1974).

	<i>Acamptopappus shockleyi</i>	<i>Acamptopappus sphaerocephalus</i>	<i>Amphipappus fremontii</i>	<i>Eastwoodia elegans</i>	<i>Vanceleva stylosa</i>
Leaves	Narrowly obovate, spreading-ascendant, uninervate, non-resinous	Mostly linear, spreading-ascendant, uninervate, non-resinous	Obovate or elliptic, spreading, uninervate, scarcely resin-dotted	Linear to lanceolate, ascendant, uninervate, glandular-punctate	Linear-lanceolate, spreading to falcate, trinervate, resinous
Capitulescence	Solitary (Fig. 3a)	Solitary or occasionally cymosely clustered (Fig. 3b)	Cymose clusters (Fig. 3c)	Solitary or open cymose panicle	Solitary to cymose
Capitulum shape	Hemispheric (Fig. 3a)	Hemispheric to nearly spheric (Fig. 3b)	Cylindric (Fig. 3c)	Broadly turbinate	Campanulate to campanulate with umbilicate base
Phyllaries	13-18(-23), 2-3 series, broad, flat, chartaceous; margins broad, scarious; apices rounded	11-18(-20), 2-3 series, broad, flat, chartaceous; margins broad, scarious; apices rounded	7-12, 2-3 series, broad, semi-plecate; margins broad, scarious; apices rounded	ca. 50, 4-5 series, narrow, flat to recurved; margins usually not scarious; apices acute-acuminate	50-60, 4-5 series, narrow, often squarrose; margins usually not scarious; apices acute-acuminate
Receptacle	deeply alveolate, with projections between florets	deeply alveolate, with projections between florets	alveolate	alveolate, paleaceous	alveolate
Ray florets	5-14	0	1-2, barely exceeding involucre	0	0
Disk florets	30-80, hermaphroditic	(13-)14-24(-27), hermaphroditic	3-7, functionally staminate	ca. 30-40, hermaphroditic	(31-)35-45(-48), hermaphroditic

TABLE 1. CONTINUED.

	<i>Acamptopappus shockleyi</i>	<i>Acamptopappus sphaerocephalus</i>	<i>Amphipappus fremontii</i>	<i>Eastwoodia elegans</i>	<i>Vanceleva stylosa</i>
Disk corollas	Broadly funnelform; sinuses deep; lobes spreading to reflexed	Broadly funnelform; sinuses deep; lobes spreading to reflexed	Broadly funnelform; sinuses deep; lobes reflexed to recurved	Tubular-funnelform; sinuses shallow to deep; lobes laxly erect	Tubular-funnelform; sinuses shallow; lobes erect to reflexed
Pappus	(15-)18-30(-38) flat, slightly erose scales, sometimes tortuous	(15-)17-26(-28) flat, slightly erose scales, sometimes tortuous	15-20 broad, flat, tortuous, deeply barbellate bristles	5-8 ascendant, awl-shaped, paleaceous awns	(12-)15-18 spreading, awl-shaped, thinly paleaceous awns
Achenes	Extremely densely long-villous; outer trichomes straight; inner ones tortuous	Extremely densely long-villous; outer trichomes straight; inner ones tortuous	Scantily long-villous; trichomes tortuous	Somewhat pubescent above	Nearly glabrous



FIG. 3. Line drawings of habits (left) and capitula (right): a. *Acamptopappus shockleyi* (Henrickson 9584, TEX); b. *A. sphaerocephalus* var. *sphaerocephalus* (M. E. Jones s.n., TEX); c. *Amphipappus fremontii* var. *fremontii* (Cronquist 10649, TEX). Scale bars = 2 cm.

straight trichomes, much as the downy underhairs of animal fur are covered by long, straight guard hairs. The adaptive significance of this arrangement is obscure, but may protect the achene from desiccation or overheating, or enhance dispersal (see discussion of ecology, below).

The two varieties of *A. sphaerocephalus* differ only in that stems and leaves of var. *sphaerocephalus* are typically glabrous, or some

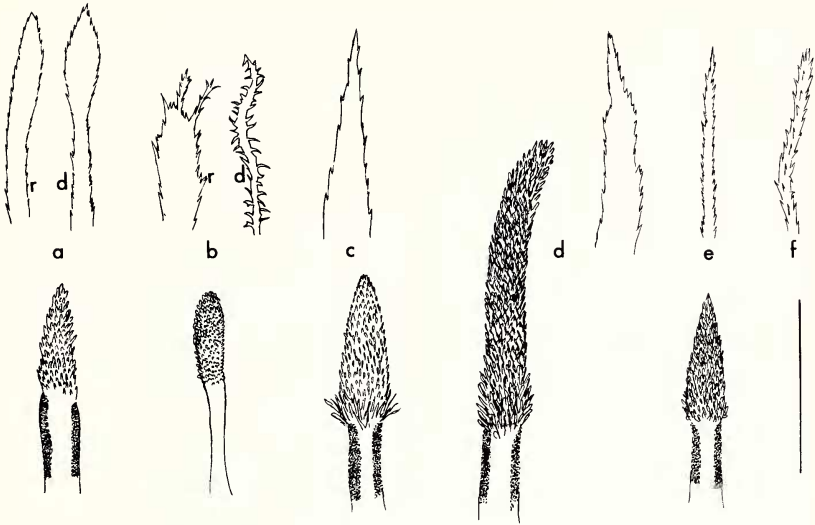


FIG. 4. Line drawings (traced from scanning electron micrographs) of pappus-member apices (above; r = ray, d = disk) and disk style-branch appendages (below): a. *Acamptopappus shockleyi* (style-branch appendage: *Henrickson 9584*, TEX; pappus member: *Clokey 8157*, TEX); b. *Amphipappus fremontii* var. *fremontii* (*Cronquist 10649*, TEX); c. *Eastwoodia elegans* (*Eastwood and Howell 5791*, TEX); d. *Vanckleya stylosa* (*Shultz and Shultz 7393*, COLO); e. *Ericameria cooperi* subsp. *cooperi* (*Gierisch and Esplin 3460*, COLO); f. *Stenotus acaulis* (*Weber and Salamun 12568*, COLO). Scale bar = 1 mm.

plants may have a very few, scattered trichomes on the leaf margins, whereas herbage of var. *hirtellus* is scabro-hirtellous (Blake 1929). This is a minor difference, although there is a geographic component to the variation (Fig. 2). Some populations in Los Angeles and San Bernardino cos., California, which lie in the area of overlap of the ranges of the varieties, have individuals with and without the vestiture. There are no intermediate individuals, either in these populations or elsewhere. This situation is parallel to that for the two varieties of *Amphipappus fremontii* (Porter 1943, Lane unpubl. data), in which var. *fremontii* is glabrous, and var. *spinus* is scabro-hirtellous.

Ecology. *Acamptopappus* is well-adapted to the arid climate of the Mojave Desert. The leaves are drought-deciduous, and the white stems reflect sunlight. In favorable years, the plants are in leaf by February, have flowered by late March, and are in fruit by late April to early June (Ackerman et al. 1980, pers. obs.). In unfavorable years, plants often do not bloom at all, or the capitula wither before achenes are matured or even set.

Achenes are dispersed by wind and/or rain, being blown "tum-

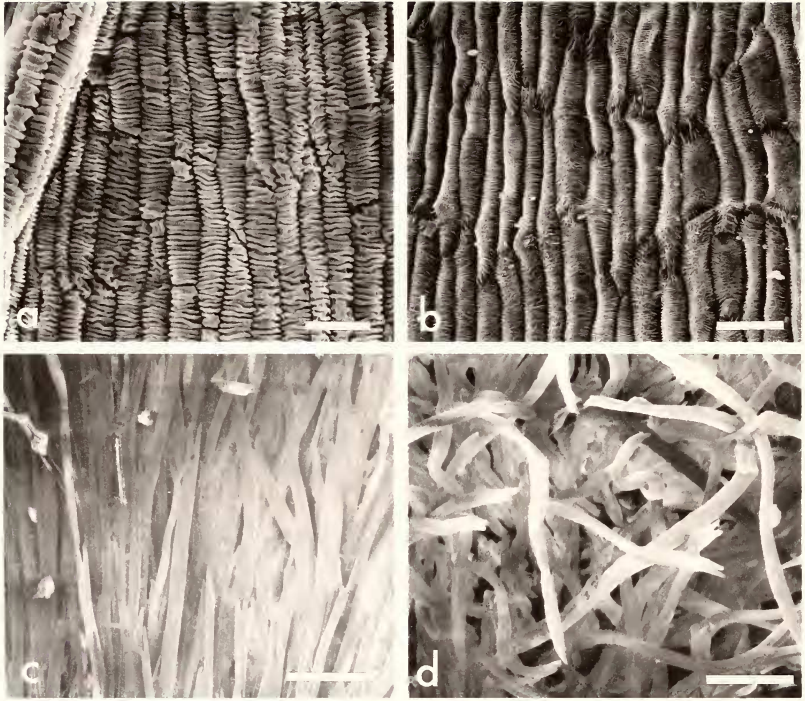


FIG. 5. Scanning electron micrographs of adaxial corolla epidermes and achene trichomes: a. disk corolla epidermis of *Acamptopappus sphaerocephalus* var. *sphaerocephalus* (M. E. Jones s.n., TEX); b. ray corolla epidermis of *A. shockleyi* (Henrickson 9584, TEX); c. achene trichomes of *Stenotus acaulis* (Weber and Salamun 12568, COLO); d. achene trichomes of *A. shockleyi* (Clokey 8157, TEX). Scale bar in a, b = 25 μm ; in c, d = 100 μm .

bleweed style" or carried in runoff across the soil surface. The achenes are moved either individually or clustered by the interdigitation of their pappus members and achene trichomes. This dispersal syndrome, together with a seedling mortality of only 28% over eight years of study (Wallace and Romney 1980) may account for the finding of Wallace and co-workers (1980d) that *A. shockleyi* is usually found growing in clumps of several individuals, and of Wallace and Romney (1980) that the species is a pioneer that initiates new "fertile islands" in bare desert areas.

Acamptopappus shockleyi has been one among several subjects of a number of ecological and ecophysiological studies conducted on shrubby taxa of the Atomic Energy Commission (Nuclear Regulatory Commission) test site in southern Nevada (unfortunately, comparable data are not available for *A. sphaerocephalus*). Wallace et al. (1980d) found 28–101 plants per hectare, although the relative den-

sity of the species was less than 1% (El-Ghonemy et al. 1980c). The mean stem weight per plant in these studies ranged from 35.2 to 68.0 g (Bamberg et al. 1980, El-Ghonemy et al. 1980a, Wallace et al. 1980a). Plants are not particularly salt-tolerant (Romney and Wallace 1980). Seventy-five percent of the root mass usually lies within 20 cm of the surface (Wallace et al. 1980b) of soils that have relatively low cation exchange capacity, low exchangeable sodium, a medium amount of moisture retention, and low potassium content (El-Ghonemy et al. 1980b).

Phytochemistry. *Acamptopappus* produces sesquiterpenoids (C-15 compounds) and labdane diterpenoids (C-20 compounds). Eight compounds of the latter type that are new to science were isolated and characterized from *A. sphaerocephalus* by Jolad et al. (1988); these compounds were also found in *A. shockleyi*. The terpenoids of *Acamptopappus* (Jolad et al. 1988) are similar to those produced by other genera of the tribe Astereae, such as *Chrysothamnus* and *Ericameria* (B. Timmermann pers. comm.).

Generic relationships. Distinguishing features of the two *Acamptopappus* species, *Amphipappus*, *Eastwoodia*, and *Vanclvea* (all monotypic) are presented in Table 1 and Fig. 4. I include *Amphipappus* in this discussion of the relationships of *Acamptopappus* because the two genera are placed near one another in floras (e.g., Keck in Munz 1959, Kearney and Peebles 1969), *Vanclvea* for the same reason and because of Steyermark's (1937) suggestion, and *Eastwoodia* because of its gross morphological similarity to these other genera. However, I suggest, based on the evidence presented below, that each of these genera is derived independently from an ancestral complex that also gave rise to *Chrysothamnus*, *Ericameria*, and *Macronema* (*Haplopappus* sects. *Ericameria* and *Macronema* sensu Hall), which in turn have been considered related by Hall (Hall and Clements 1923, Hall 1928), and other authors.

Steyermark (1937) placed *Acamptopappus* near *Xanthisma* and distinguished it from *Grindelia* in his discussion of the relationships of the latter genus. I agree that *Acamptopappus* and *Grindelia* are very dissimilar, but *Acamptopappus* also differs from *Xanthisma* in many features, such as disk-corolla shape and epidermis pattern, style-branch appendage shape, leaf shape and vestiture, habit, habitat, and distribution. These three genera also differ in base chromosome number. All *Acamptopappus* taxa have $n = 9$ (Raven et al. 1960, Keil and Pinkava 1976, Pinkava and Keil 1977, Kovanda 1978, Schaak et al. 1982), *Grindelia* has $x = 6$, and *Xanthisma* has $x = 4$ (or possibly $x = 5$, see Semple 1976). All of the genera listed in Table 1, and *Chrysothamnus*, *Ericameria*, and *Macronema*, have $x = 9$. Although chromosome number alone is insufficient evidence of relationship or lack thereof, the consistent correlation of mor-

phological characters with base chromosome number that is found in the Astereae supports its use as a character in a discussion such as this one.

Acamptopappus and *Amphipappus* are found in the Mojave and Sonoran deserts (Figs. 1, 2, and Porter 1943), and *Vancleavea* in the southeastern extension of the Great Basin desert in Utah and Arizona (Anderson and Weberg 1974). *Eastwoodia* occurs along the xeric western and southern rim of the San Joaquin Valley (Brandege 1894) on the eastern slopes of the South Coast Ranges and northern slopes of the Transverse Ranges of California (Lane in Hickman in prep.). All share certain features such as low, shrubby habit, greenish- or yellowish-white new growth, and white, sometimes varnished stems that become gray and shreddy with age.

Among the genera detailed in Table 1, *Acamptopappus* is most similar to *Amphipappus* (Fig. 3). Shared characters include those of the foliage, phyllary shape, color, and texture, disk-corolla shape, and the tortuous nature of the achene trichomes (Fig. 5d). These genera differ in capitulum size and shape, floret number, receptacle features, sexuality of the disk florets, style-branch appendage shape, pappus type, and degree of achene pubescence.

Steyermark (1937) saw a resemblance between *Eastwoodia* and *Acamptopappus* on the basis of receptacular projections between the florets. However, those of *Eastwoodia* are true paleae, whereas those of *Acamptopappus* are merely the extended rims of the alveolae. Both *Eastwoodia* and *Acamptopappus* have hermaphroditic disk florets and prominent ray florets in at least one taxon, but these are plesiomorphic conditions and therefore do not necessarily indicate relationship. Differences are found in the leaves, capitulum shape, phyllary shape and texture, disk-corolla shape, style-branch appendages and pappus type (Fig. 4), and degree of achene pubescence (Table 1).

Vancleavea differs from *Acamptopappus* in characters of the foliage, phyllaries, disk-corolla shape, style-branch appendages and pappus (Fig. 4), and degree of achene pubescence (Table 1). Very few similarities with *Acamptopappus*, except for those listed above for all four genera, can be found.

I suggest that although the four genera probably share a common heritage, they are independently derived because there are so few synapomorphies among them. Because each genus is so distinctive, indications of the nature of their common heritage must be sought in a large grouping of extant taxa. Of the Astereae genera that might be considered, the genera having $x = 9$ and comprising shrubby taxa of the southwestern deserts include *Chrysothamnus* (sensu Anderson 1984), *Ericameria* (sensu Urbatsch and Wussow 1979), and *Macronema* (= *Haplopappus* sect. *Macronema* sensu Hall 1928). *Petroria* (sensu Anderson 1963) and *Stenotus* (*Haplopappus* sect. *Steno-*

tus sensu Hall 1928), although herbaceous, are nonetheless perennial with woody caudices and share general habitat preference and distribution with the other members of this alliance.

Many members of this group have greenish-white young stems that become white and then gray with shredding bark in age, as do all the genera of Table 1. Some members have the light green, non-resinous leaves of *Acamptopappus* and *Amphipappus*, and others have the dark green, resinous leaves of *Eastwoodia* and *Vancklevea*. A complete intergradation between the short, broadly funnellform disk-corolla shape of *Acamptopappus* and *Amphipappus* and the tubular-funnelform one of *Eastwoodia* and *Vancklevea* is found in this alliance as well.

The disk style-branch appendages of the *Chrysothamnus*-*Ericameria*-*Macronema* alliance, represented in Fig. 4e by that of *Ericameria cooperi*, are generally lanceolate-acute, although some species have more lanceolate ones. Those of *Acamptopappus* (Fig. 4a) are similar, whereas *Eastwoodia* (Fig. 4c) has broader ones, and *Vancklevea* (Fig. 4d) has the largest style-branch appendages of any taxon of Astereae that I have studied. *Amphipappus* (Fig. 4b) has lost female fertility in its disk florets, and this is reflected in absence of stigmatic lines on its style branches, which also have obtuse appendages. A reasonable interpretation of these data is that the style branches of *Amphipappus*, *Eastwoodia*, and *Vancklevea* are each, but separately, apomorphic with respect to those of the *Chrysothamnus*-*Ericameria*-*Macronema* alliance.

The pappus of members of this phylad is generally composed of barbellate bristles that are more or less round in cross section as are those of *Stenotus acaulis* (Fig. 4f), although *Ericameria cooperi* (Fig. 4e) and other members have flattened bristles. Porter (1943) suggested that the ray pappus of *Amphipappus* (Fig. 4b) is formed by fusion of bristles like those of the disk pappus (Fig. 4b) into scales. The same process, extended over evolutionary time, may account for the origin of the pappus scales of *Acamptopappus*, *Eastwoodia*, and *Vancklevea* (Fig. 4a, c, d) from those of ancestor(s) with broad, flat bristles such as those found in *Ericameria cooperi* (Fig. 4e) today. The pappus of *Amphipappus* (Fig. 4b) is always tortuous, but this may result from compression within the tightly imbricate involucre, much as the pappus of some florets within an *Acamptopappus* head may become twisted because it is compressed by surrounding florets during development. Thus, the similarity between these two genera with respect to tortuous pappus may be a parallelism rather than a synapomorphy.

Corolla epidermis patterns have been found to be useful characters at the generic and infrageneric levels in the Astereae (Lane 1982, 1985). *Acamptopappus*, *Amphipappus*, *Eastwoodia*, *Vancklevea*, *Chrysothamnus*, *Macronema*, and *Petradoria* have the same disk

corolla epidermis pattern (Fig. 5a). *Acamptopappus*, *Amphipappus*, and *Macronema* also share the same ray corolla epidermis pattern (Fig. 5b), whereas *Petradoria*, *Ericameria*, and *Stenotus* have a different one (Lane unpubl. data). It is difficult to polarize the epidermal pattern characters, but it would seem that one or the other of these two groups of three genera is synapomorphic in this respect.

It would be desirable to have a cladistic analysis of the relationships of the genera discussed above. However, to present a cladogram at this time would be premature because such an analysis requires that all taxa belonging to a lineage be included in the analysis. The scope of the current study has not ensured that this is the case; neither has it yet been possible to determine an appropriate out-group.

Future studies leading to thorough phylogenetic analysis have been designed to test the hypothesis that *Acamptopappus* has been derived from the ancestral complex that gave rise more directly to the *Chrysothamnus*-*Ericameria*-*Macronema* phylad. The single taxon of this group to which *Acamptopappus* is most similar is *E. parrasana*. With this species, *Acamptopappus* shares capitulum shape, phyllary features, and reflexing involucre in addition to the overall similarities of the genera given above. The similar but separate derivation of *Amphipappus*, *Eastwoodia*, and *Vancleavea* is another hypothesis to be tested in future. The distinctiveness of *Acamptopappus* and each of these genera may be accounted for by elapsed time since separation of the lineages, and the strong selection pressures of their desert habitats.

TAXONOMIC TREATMENT

Acamptopappus (A. Gray) A. Gray. Proc. Amer. Acad. Arts 8:634. 1873. — *Aplopappus* Cass. sect. *Acamptopappus* A. Gray, Mem. Amer. Acad. Arts (ser. 2) 4:76 [Pl. Fendler. 76]. 1849. — TYPE: *Acamptopappus sphaerocephalus* (Harv. & A. Gray in A. Gray) A. Gray.

Shrubs to 4 dm high, scraggly or rounded (Fig. 3); taproots woody, vertical or usually laterally spreading; stems decumbent, divergent or erect, striate; young stems greenish-white or -yellow, becoming white; old stems gray, usually with shredding bark; leaves pale green to light gray-green, borne singly, rarely in axillary fascicles below, spreading-ascendent to appressed-erect, linear to lanceolate or narrowly obovate or spatulate, 1-nervate, entire, glabrous or scabro-hirtellous at margins, generally minutely spinulose at apices, glabrous or scabro-hirtellous on both surfaces; capitula borne singly or occasionally in cymose clusters; buds expanding rapidly just prior to anthesis; involucre broadly campanulate-hemispheric to nearly spheric; phyllaries in 2–3 series, broadly ovate to ovate-elliptic, chartaceous, brittle, cream-yellow at bases, green at apices, with broad,

scarious, erose margins, all distinctly reflexing at maturity to release achenes; receptacle deeply alveolate, with projections between florets but not chaffy; heads radiate or eradiate, corollas yellow; disk corollas broadly funnellform, sinuses deep, lobes spreading to reflexed; style-branch-appendages narrowly triangular-lanceolate (Fig. 4a), somewhat exceeding the stigmatic portion; achenes obconic, extremely densely long-villous; trichomes white, bronze, rufous, or brownish, outer straight, inner contorted or tortuous (Fig. 5d); pappus of 1-seriate, white, scarcely erose scales with acute-lanceolate to narrowly spatulate apices (Fig. 4a), slightly exceeding achenes; base chromosome number: $x = 9$. Flowering (Mar-)Apr-May(-Jun) (Ackerman et al. 1980, Lane hoc. loc.).

KEY TO TAXA OF *Acamptopappus*

1. Heads radiate, involucre campanulate to hemispheric *A. shockleyi*
1. Heads eradiate, involucre hemispheric to globose.
 2. Stems and leaves scabro-hirtellous *A. sphaerocephalus* var. *hirtellus*
 2. Stems and leaves glabrous, or only leaf margins scabro-hirtellous *A. sphaerocephalus* var. *sphaerocephalus*

Acamptopappus shockleyi A. Gray, Proc. Amer. Acad. Arts 17:208. 1882. — TYPE: USA, Nevada, Esmeralda Co., Candelaria, 1881, *Shockley 34* (GH!).

Stems decumbent to ascendent, (1.5-)2-3(-3.3) dm, usually spinescent with age, surfaces usually scabro-hirtellous; leaves spreading-ascendent, narrowly obovate to narrowly spatulate, (0.7-)1-1.6 (-2) cm long, (2-)3-4(-5) mm wide, scabro-hirtellous; capitula borne singly; involucre campanulate to hemispheric, 7-11(-13) mm high, (10-)13-19 mm wide; phyllaries 13-18(-23), (3.5-)5-9(-11) mm long, (1.8-)2-4(-6) mm wide; ray florets 5-14, corollas (3.5-)6-17(-19.5) mm long, (1.5-)2.5-6.5 mm wide; disk florets 30-80, corollas (2.3-)3.2-5(-5.5) mm high; achenes (1-)1.5-3.5(-4.7) mm long, (0.4-)0.8-1.8(-2.9) mm wide; pappus scales (15-)18-30(-38), less spatulate in rays than disks, (2.7-)3-4.5(-5) mm high.

Distribution and habitat. Mojave Desert areas of southeastern California and southern Nevada (Fig. 1); 500-2000 m. Mesas, slopes, ravines, and washes in *Larrea* and *Yucca brevifolia* communities, in association with *Atriplex*, *Amphipappus*, *Artemisia*, *Lycium*, *Grayia*, *Encelia*, *Psilostrophe*, *Thamnosma*, *Hymenoclea*, *Eurotia*, and/or *Hilaria*.

Comments. Gray's (1882) description of *A. shockleyi* was based on a specimen numbered *Shockley 34*, collected in 1881. Other

specimens with this number are at CAS and UC (but these are from Rhyolite or Tonopah and dated 1883 or 1907), and another at NY (dated 1886). Clearly these specimens cannot be considered isotypes, though the NY specimen presumably is a topotype. Isotypic status for a sheet at RSA is doubtful because it gives only "Apr-May" for collection date, even though it bears the correct locality and number. Given Shockley's re-use of the number 34, I doubt that it was collected in 1881.

Representative specimens. USA, California, Inyo Co., Payson Canyon, White Mts., 14 Jun 1932, *Duran 3295* (CAS, NY, GH, F, MO, NY, RM, RSA, UC, US, UTC). San Bernardino Co., 4 mi e. of Horse Spring, Mojave Desert, Kensington Mts., 15 May 1935, *Wolf 6848* (CAS, COLO, MO, NY, RSA, UC). Nevada, Clark Co., Old Kyle Canyon fan, 11 May 1938, *Clokey 8157* (ARIZ, CAS, F, GH, K, MO, NY, RM, RSA, SD, TEX, UC, UTC). Esmeralda Co., Candelaria, 22 Jun 1882, *Jones 3895* (CAS, F, MO, NY, POM, RSA, NY, UC, UTC). Lincoln Co., 11 mi s. of Alamo, 6 Apr 1934, *Maguire et al. 5033* (GH, MO, RM, UC, UTC). Mineral Co., near Mina, 5 Jun 1906, *Heller 8368* (CAS, F, GH, MO, NY, US). Nye Co., Smokey Valley, 9 Jun 1945, *Maguire and Holmgren 25362* (ARIZ, GH, NY, US, UTC).

Acamptopappus sphaerocephalus (Harvey & A. Gray in A. Gray) A. Gray.

Stems usually many, much-branched, ascendent to erect, (1.5-)2-3.5(-4) dm, with surfaces scabro-hirtellous or glabrous; leaves ascendent-appressed, linear to narrowly oblanceolate, 0.5-2(-2.8) cm long, (1-)1.5-3(-4) mm wide, scabro-hirtellous or glabrous; capitula very numerous, borne singly or in clusters; involucre hemispheric to spheric, 4-7 mm high, (1.5-)6-11 mm wide; phyllaries 11-18(-20), (2.5-)3.2-5.5(-6.5) mm long, (1.5-)1.9-3(-3.6) mm wide; heads eradiate; disk florets (13-)14-24(-27), corollas (2.1-)2.5-4.3(-4.7) mm high; achenes (1.2-)1.7-3.3(-3.7) mm high, (0.6-)0.8-1.9(-2.2) mm wide; pappus bristles (15-)17-26(-28), (1.7-)2.1-3.7(-4.4) mm high, apices narrowly spatulate.

Distribution and habitat. Mojave and Sonoran desert areas of southern California, southern Nevada and Utah, and south-central Arizona (Fig. 2); 5-2000 m. Gravelly, rocky soils on slopes and flat areas in grasslands, deserts, and *Juniperus* woodlands; in association with *Larrea*, *Yucca*, *Viguiera*, *Eriogonum*, *Salsola*, *Ambrosia*, *Artemisia*, *Chrysothamnus*, *Coleogyne*, *Ephedra*, *Canotia*, *Hymenoclea*, *Cercidium*, *Fouquieria*, *Carnegia*, *Opuntia*, and/or *Ferocactus*.

Comments. Some populations in the area of overlap of the two varieties of this species (Fig. 2) are mixed with respect to the distinguishing pubescence character. Representative collections from

this area include: California, Los Angeles Co., Lancaster, Jun 1902, *Elmer 3621* (CAS, F, GH, K, MO, NY, RSA, US). San Bernardino Co., Mojave Desert, May 1882, *Parish and Parish 139* (CAS, F, GH, MO, NY, SD, UC, US); Cima, Mojave Desert, Jun 1915, *Bran-degee s.n.* (F, GH, MO, NY, RM, UC); Mojave Desert, Spring 1927, *Hutchinson s.n.* (LL, TEX).

Populations of *A. sphaerocephalus* may very rarely contain individuals with vestigial ray florets (D. Keil pers. comm., M. Lane pers. obs.). This condition might result from one of two phenomena: 1) hybridization with the radiate *A. shockleyi* or 2) partial expression of ray-floret genes that were suppressed during the evolution of *A. sphaerocephalus* from a radiate ancestor. Either explanation is plausible, but neither is more strongly supported than the other by evidence available at this time. There are infrequent cases of co-occurrence of the two *Acamptopappus* species where their ranges overlap (Figs. 1, 2) and hybridization may occur, although I have seen no specimens that I would suspect to be of hybrid origin. Vestigial rays occasionally occur in eradiate taxa of other genera of Astereae that I have studied (for example, *Isocoma*), indicating that loss of rays is an apomorphic condition but that their suppression is not absolute.

Acamptopappus sphaerocephalus (Harv. & A. Gray in A. Gray) var. *hirtellus* S. F. Blake, J. Wash. Acad. Sci. 19:270. 1929.—TYPE: USA, California, Inyo Co., near Lone Pine, 7 Jun 1891, *Coville and Funston 890* (US!).

Stems (1.5–)2.5–3.3(–3.8) dm high, scabro-hirtellous; leaves (0.6–)0.8–1.3 cm long, 1.5–3(–4) mm wide, scabro-hirtellous; involucre 6–7 mm high, (1.5–)8–11 mm wide; phyllaries (14–)15–18(–20), (2.8–)3.7–5.4(–5.7) mm long, (1.5)2–2.8(–3.1) mm wide; disk florets (13–)16–24(–27), corollas 2.8–3.6(–4.5) mm high; achenes 1.7–3.2(–3.7) mm long, 0.7–1.7(–2.2) mm wide; pappus bristles 15–24, (2.1–)2.8–3.3(–3.7) mm high. Gravelly soils in deserts and *Juniperus* woodlands; 5–1600 m.

Representative specimens. USA, Arizona, Mohave Co., Fort Mohave, Apr 1884, *Lemmon s.n.* (UC, US). California, Inyo Co., Alabama Hills, 3 mi w. of Lone Pine, 23 May 1958, *Rose 58061* (CAS, COLO, GH, JEPS, NY, RSA, US). Kern Co., near Searles, 28 May 1932, *Duran 3224* (CAS, COLO, F, GH, MO, NY, RM, RSA, UC, UTC, US). Los Angeles Co., near Lancaster, 11 Jun 1906, *Hall and Chandler 7388* (ARIZ, F, K, MO, NY, RM, RSA). San Bernardino Co., Mojave River district, Apr [or 23 May or 1 Jun?] 1876, *Palmer 219* (F, MO, NY, US). Nevada, Clark Co., 15 mi e. of Glendale, 19 May 1933, *Maguire and Blood 4487* (MO, RM, RSA, UC, UTC). Lincoln Co., Moapa, 12 May 1905, *Kennedy 1077* (F).

Acamptopappus sphaerocephalus (Harv. & A. Gray in A. Gray) A. Gray var. *sphaerocephalus*, Proc. Amer. Acad. Arts 8:634. 1873.—*Haplopappus sphaerocephalus* Harvey & A. Gray in A. Gray, Mem. Amer. Acad. Arts, ser. 2, 4:76 [Pl. Fendler. 76]. 1849.—TYPE: USA, California, [San Diego Co.?], [without locality], [1832], Coulter s.n. exsic. no. 281 (GH!; isotypes K!, TCD!).

Stems (1.8–)2.4–3.5(–3.8) dm high, glabrous; leaves (0.5–)1–2(–2.8) cm long, (1–)1.5–3(–4) mm wide, glabrous; involucre 4–7 mm high, (1.5–)6–10 mm wide; phyllaries 11–18(–19), (2.5–)3.2–5.3(–6.4) mm long, 1.9–3(–3.6) mm wide; disk florets (13–)14–22(–26), corollas (2.1–)2.5–4.3(–4.7) mm high; achenes (1.2–)1.7–3.2(–3.7) mm long, (0.6–)0.8–1.9(–2.2) mm wide; pappus scales (15–)17–28, (1.7–)2.1–3.7(–4.4) mm high. Gravelly, rocky soils in grasslands, deserts, and woodlands; 60–2000 m.

Comments. Coulter's specimen bears no date, but it probably was collected sometime during his excursion from Monterey to Yuma, Arizona, by way of San Diego, between 20 March and 19 July 1832 (Coville 1895, McKelvey 1955). The route followed by Coulter's party (Fig. 2) passed through or near three possible collection areas. 1) Northeastern Los Angeles Co. According to Coville (1895), the route was on the southwestern side of the San Gabriel Mountains, between San Fernando and San Gabriel. The only known localities for *A. sphaerocephalus* in or near the San Gabriels (Pallett Creek, Little Rock Creek, and Bob's Gap) are on the northeastern side of the mountains. 2) East-central San Diego Co. Coulter passed through either the San Felipe Valley or the next valley south between 30 April and 8 May, and again between 17 and 27 May on the return trip (Coville 1895). There are a number of specimens from this area, and the dates of Coulter's visit during the outbound trip coincide with those for collections that are in the same state of maturity as the type. 3) Area of Yuma, Arizona. Coulter was in this area 8 through 17 May (Coville 1895); however, specimens from that portion of the range of the species have completely mature achenes by that date, and the type specimen has only partially mature achenes. This information suggests that the type locality is one of the valleys of east-central San Diego Co.

Representative specimens. USA, Arizona, Coconino Co., Glen Canyon National Recreation Area, Glen Canyon, ca. 1 mi due s. of Wahweap Marina, 26 May 1983, *Welsh 22066* (BRY, RM). Gila Co., between Roosevelt Dam and Tonto Basin, 15 May 1935, *Nelson and Nelson 1933* (GH, K, MO, NY, RM, UC, US, UTC). Graham Co., 2 mi below San Juan Mine, Gila Mts., 8 Apr 1935, *Maguire and Maguire 10546* (ARIZ, GH, MO, NY, UTC). La Paz Co., 1 mi s. of Alamo State Park boundary on road to Wenden, 10 Mar 1973,

McLeod and Pinkava 10326 (ARIZ, ASU, LL, NY, SD, TEX). Maricopa Co., roadside s. of Cañon, 21 Apr 1938, *Foster and Arnold 338* (CAS, GH, UC, US). Mohave Co., Yucca, 15 May 1884, *Jones 3911* (ARIZ, CAS, F, GH, POM, RM, UC, US, UTC). Pima Co., Walls Well, Organ Pipe Cactus National Monument, 28 Apr 1939, *Nichol s.n.* (ARIZ). Pinal Co., Camp Grant, 14 May 1867, *Palmer 114* (GH, MO). Yavapai Co., Black Canyon P.O., 14 Apr 1960, *Demaree 42241* (ARIZ, NY, TEX). Yuma Co., Yuma, 21 Apr 1938, *Crooks and Darrow s.n.* (ARIZ, NY). California, Imperial Co., Mountain Springs Grade, 17 Apr [without year], *Orcutt s.n.* (UC). Inyo Co., Dante's View above Death Valley, 11 Jun 1930, *Peebles 302* (ARIZ, NY). Kern Co., 8 mi ne. of Mojave, 12 May 1930, *Howell 4913* (CAS). Los Angeles Co., Pallett Creek, San Gabriel Mts., 27 May 1923, *Munz 6896* (CAS, NY, RSA). Riverside Co., San Jacinto Mts., e. base along the borders of the Colorado Desert, Jun 1901, *Hall 2108* (CAS, K, MO, NY, POM, UC, US). San Bernardino Co., Baker, Mohave Desert, 2 May 1933, *Jones s.n.* (GH, K, RM, RSA, UC, UTC). San Diego Co., Yaqui Wells, Colorado Desert, 14 Apr 1913, *Eastwood 2800* (CAS, GH, K, NY, US). Nevada, Clark Co., St. Thomas Gap area sw. of Whitney Ridge, 0.9 road mi n. of Grand Gulch Rd on Reservoir Rd, 14 May 1982, *Tiehm 6867* (MO, RSA, UTC). Lincoln Co., Moapa, 5 May 1909, *Kennedy 1808* (F). Utah, Kane Co., ca. 2 mi s. of Nun Butte, ca. 20 mi e. of Glen Canyon City, 24 May 1972, *Atwood 4062* (MO, US). Washington Co., e. slope of Black Hill, St. George, 24 May 1942, *Gould 1772* (CAS, COLO, F, GH, NY, POM, UC, UTC).

EXCLUDED TAXON

Acamptopappus microcephalus M. E. Jones, *Contr. W. Bot.* 8:33. 1898. = *Ericameria cooperi* (A. Gray) H. M. Hall subsp. *cooperi*.

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