Leaf Hairs in Encelia (Asteraceae)

J. R. Ehleringer, C. S. Cook

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LEAF HAIRS IN ENCELIA (ASTERACEAE)[1]

J. R. EHLERINGER[2] AND C. S. COOK

Department of Biology, University of Utah, Salt Lake City, Utah 84112

ABSTRACT

Four different kinds of leaf hairs occur in *Encelia* species. These are unicellular-based and multicellular-based uniseriate hairs, moniliform hairs, and biseriate glandular hairs. The unicellular-based uniseriate hairs appear responsible for increased leaf spectral reflectance by species within the genus. In particular, it appears that elongation of the distal cell of the uniseriate hair is necessary for increased leaf reflectance.

ENCELIA is a genus of approximately seventeen species, subspecies and varieties. All are perennial shrubs found in the arid regions of western North America and South America (Blake, 1913; Munz, 1959; Shreve and Wiggins, 1964). One of the primary morphological features distinguishing species of *Encelia* is leaf pubescence; leaves of different *Encelia* species range from essentially glabrate to heavily pubescent (Table 1).

The presence of this leaf pubescence can have significant effects on leaf spectral characteristics, resulting in reflectance values ranging from 8% to 71% for different species (Ehleringer, Björkman, and Mooney, 1976; Ehleringer and Björkman, 1978; Ehleringer, 1981, 1983). The consequence of these leaf reflectance differences is an altered leaf energy balance, which reduces leaf temperatures. The adaptive and ecological significance of leaf pubescence changes appears to be that it allows leaves to avoid high, potentially-lethal leaf temperatures and to maximize net carbon gain under arid conditions (Ehleringer and Mooney, 1978; Ehleringer, 1980; Ehleringer and Werk, 1986).

Numerous kinds of hairs have been described on the surfaces of leaves of different taxa from many plant families (Theobald, Krahulik, and Rollins, 1979). However, it is unclear which hair types (if any particular one) are functionally associated with increased leaf surface reflectance. Since hair morphology is often distinct between closely-related species and has in the past been used to distinguish among different taxa (Theobald et al., 1979), it may be that within *Encelia* changes in hair morphologies are the basis for the observed differences in leaf reflectance patterns.

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[2] Send correspondence to this author.

The purpose of this study is to describe the leaf hair morphologies and frequencies found within *Encelia* and to relate these results to observed spectral reflectance patterns. An additional aspect of this study was to determine groupings of hair morphology types within *Encelia* that might lead to information on the evolutionary relations within the genus and to compare these results with observed species patterns based on floral UV-reflectance patterns as observed in *Encelia* by Clark and Sanders (1986).

MATERIALS AND METHODS—Leaf samples for scanning electron microscopy were collected from plants in the field or from greenhouse-grown plants. The leaves were fixed in 3% glutaraldehyde for 24 hr, then rinsed with distilled water and stored in 0.1 M phosphate buffer (pH 7.0). The fixed samples were taken through an acetone dehydration series and critical point dried using CO_2 (Bomar Model SPC-900/EX critical point dryer). The dried samples were fractured, mounted with high purity silver paint onto Hitachi stubs and then gold coated to a thickness of 250 A using a Denton Desk I sputter coater. The prepared samples were examined with a Hitachi 450 scanning electron microscope set at 20 KV and with a 15 mm working distance. Scanning electron micrographs were taken with a Polaroid CU-5 camera using Polaroid Type 55 positive/negative film.

Field or greenhouse leaf materials for *E. actoni* and *E. ventorum* were not collected at the time the other species were sampled. As a consequence, the hair morphologies and densities presented for these species are based on herbarium voucher materials collected the previous growing season. Thus, while the hair morphology information is quite useful in determining their relations to other *Encelia* species, the specific hair densities should be interpreted as being only approximate. *Encelia*

TABLE 1. Encelia *species and the extent of their leaf pubescence development as described by Blake (1913), Munz (1959), Shreve and Wiggins (1964), and Wiggins (1980)*

Species	Leaf pubescence
North America	
Encelia actoni Elmer	densely canescent
Encelia asperifolia (S.F. Blake) Clark and Kyhos	scabrous
Encelia californica Nutt.	lightly appressed pubescent
Encelia farinosa Gray	silvery-tomentose
Encelia farinosa var. *phenicodonta* (S.F. Blake)	silvery-tomentose
Encelia farinosa var. *radians* (Brandegee) S.F. Blake	soon glabrate
Encelia frutescens (Gray) Gray	scabrous with pustulate-based hairs
Encelia halimifolia Cav.	somewhat pubescent with incurved hairs
Encelia palmeri Vasey and Rose	hispid-canescent
Encelia ravenii Wiggins	densely white-tomentose
Encelia ventoum Brandegee	glabrous
Encelia virginensis A. Nels.	finely canescent
South America	
Encelia canescens Lam.	canescent
Encelia canescens var. *lanuginosa* Johnston	thick cottony tomentum
Encelia canescens var. *oblongifolia* (D.C.) S.F. Blake	puberulent
Encelia hispida Anderss.	appressed-hirsutulous

ravenii has a very limited geographical distribution and field plant materials could not be found for analysis.

RESULTS AND DISCUSSION—Four basic hairs can be seen on the leaves of *Encelia*. These are a multicellular-based uniseriate hair (Fig. 1), a moniliform hair (Fig. 2), a unicellular-based uniseriate hair (Fig. 3), and a biseriate glandular hair (Fig. 4). No other hair type was observed on any of the *Encelia* leaf surfaces. Although the descriptors differ slightly, the latter three hair types have been previously noted on the floral parts of *Encelia* by Clark (1984).

The unicellular-based uniseriate hairs were found on all *Encelia* species with the single exception of *E. frutescens* (Table 2). These uniseriate hairs tended to consist of 4–6 cells with the distal cell often being much longer than the more proximal cells. This was very much so the case for *E. palmeri* (Fig. 9), *E. farinosa* (Fig. 12), and *E. canescens* (not shown), where the distal cell was typically an order of magnitude or more longer than proximal cells. There was a second grouping of species for which the distal cell was approximately five to ten times the length of the proximal cells. This grouping included *E. asperifolia* (Fig. 8), *E. californica* (Fig. 5), *E. farinosa* var. *radians* (Fig. 11), *E. frutescens* (Fig. 7), *E. halimifolia* (Fig. 6), and *E. ventorum* (not shown). The third grouping consisted of species in which the distal cell was of approximately equal length to the proximal cells. In this third category were *E. virginensis* (Fig. 10) and *E. actoni* (not shown).

To help interpret these patterns, it is useful to consider what is known about the evolutionary relationships within the genus *Encelia*. Based on the preliminary species patterns within *Encelia* as discussed by Clark (1986) and Clark and Sanders (1986), two distinct group-

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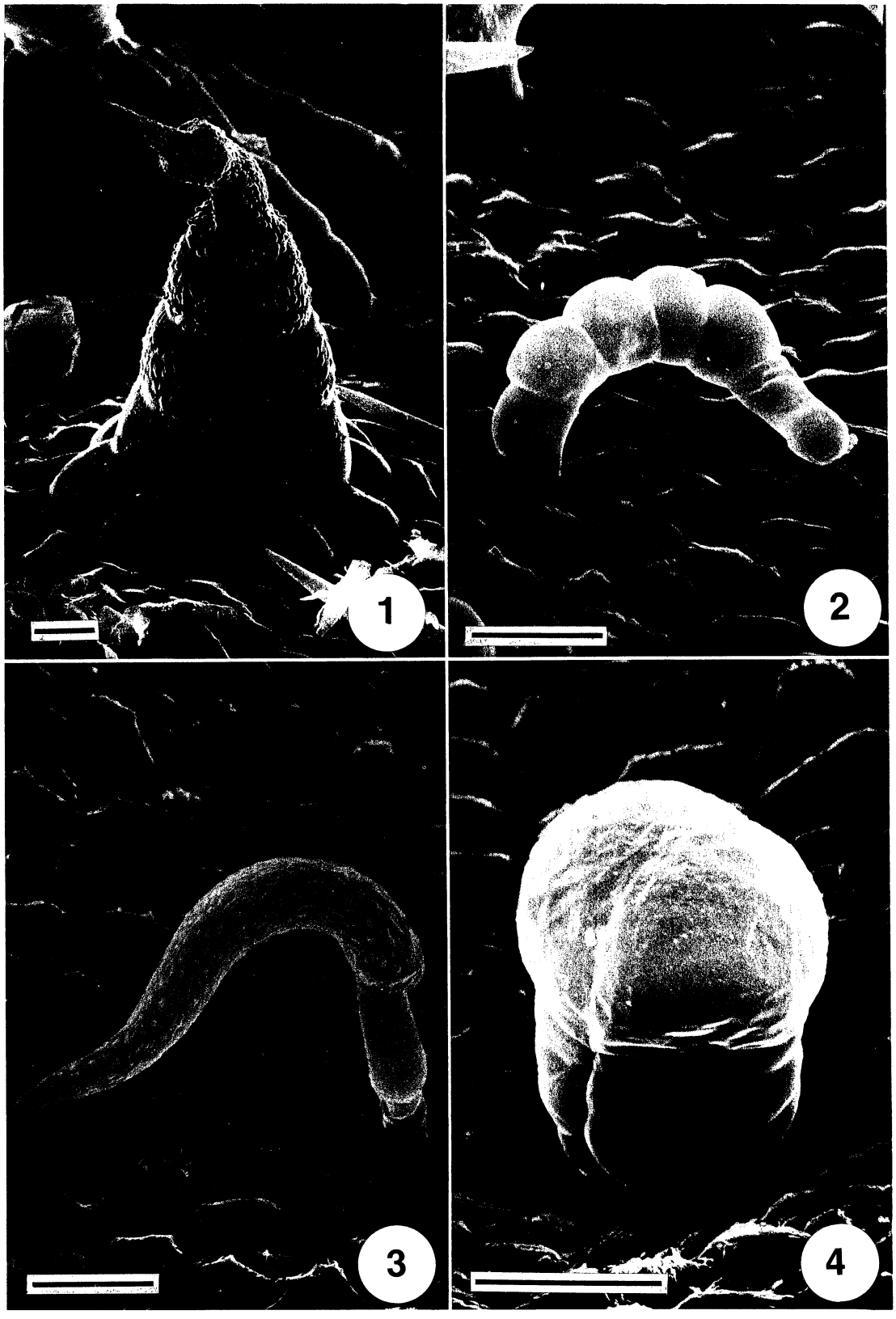
Fig. 1–4. The different hair types observed on leaf surfaces of *Encelia* species. Bar is 25 μm for each plate. Multicellular-based uniseriate hair from *Encelia virginensis* (Fig. 1). Moniliform hair from *Encelia halimifolia* (Fig. 2). Unicellular-based uniseriate hair from *Encelia farinosa* var. *radians* (Fig. 3). Biseriate glandular hair from *Encelia farinosa* var. *radians* (Fig. 4).

Fig. 5–8. Unicellular-based uniseriate hairs as observed on leaf surfaces of *Encelia* species. Bar is 50 μm for each plate. *Encelia californica* (Fig. 5), *Encelia halimifolia* (Fig. 6), *Encelia frutescens* (Fig. 7), and *Encelia asperifolia* (Fig. 8).

Fig. 9–12. Unicellular-based uniseriate hairs as observed on leaf surfaces of *Encelia* species. Bar is 25 μm for each plate. *Encelia palmeri* (Fig. 9), *Encelia virginensis* (Fig. 10), *Encelia farinosa* var. *radians* (Fig. 11), and *Encelia farinosa* var. *farinosa* (Fig. 12).

Fig. 13–14. Dorsal surfaces of *Encelia farinosa* var. *radians* (Fig. 13) and *Encelia farinosa farinosa* (Fig. 14). Bar is 500 μm for each plate.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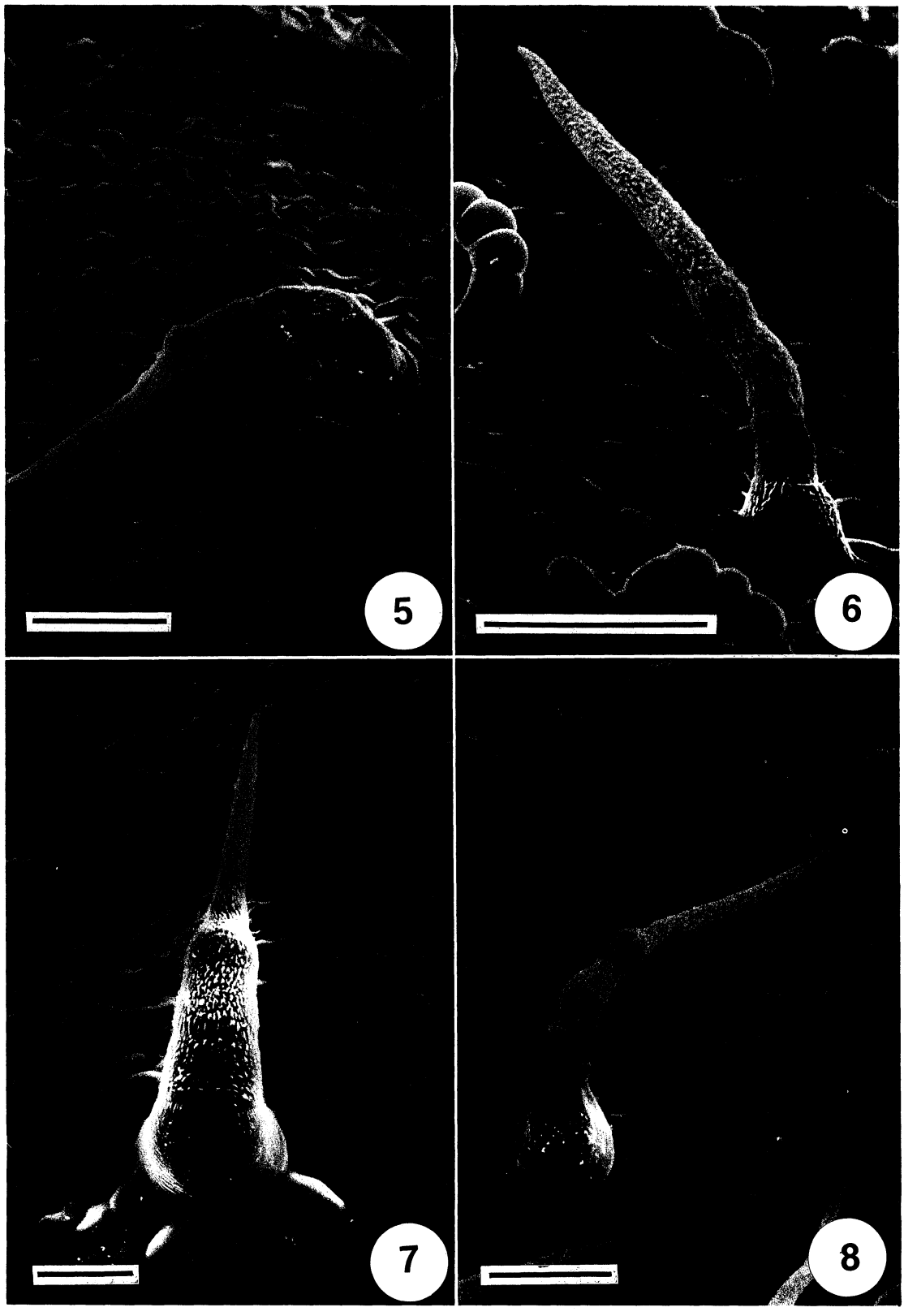
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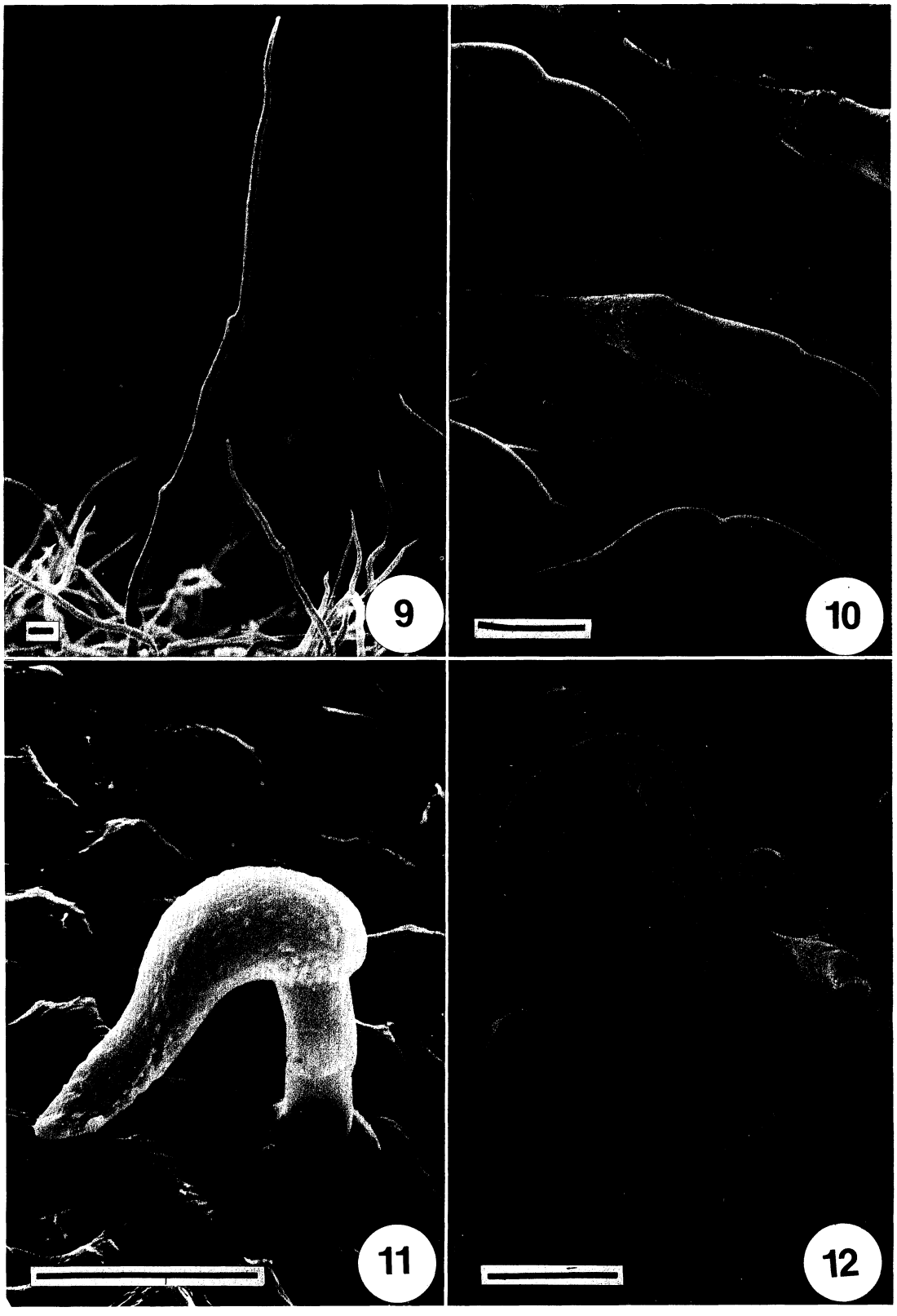
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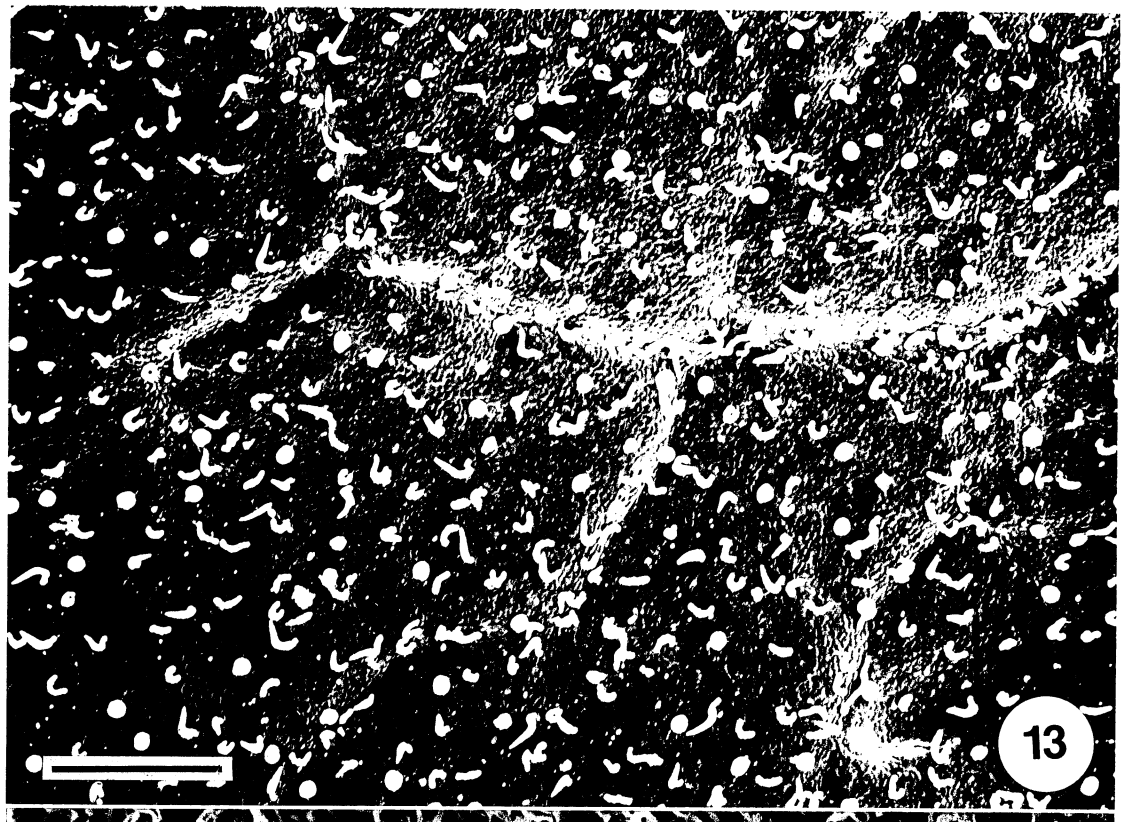
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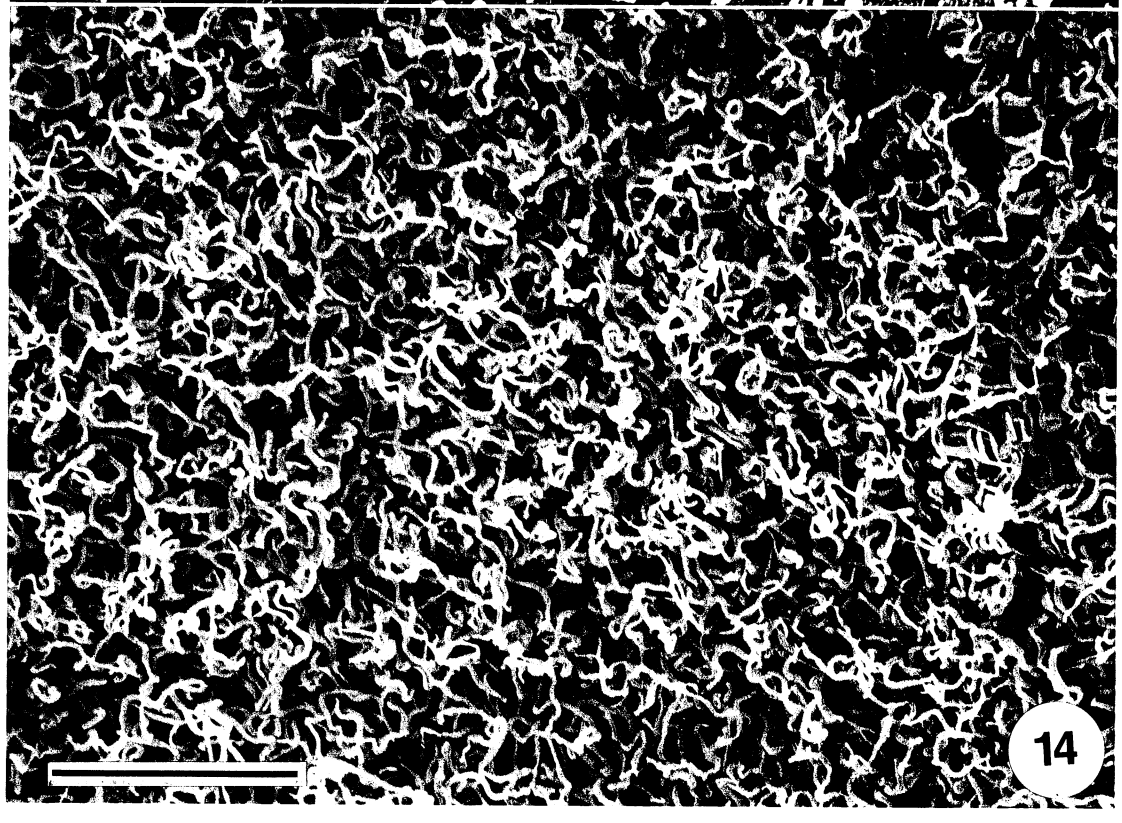
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TABLE 2. *Densities of various hair types on leaf surfaces of different* Encelia *species. The four hair types are the same as shown in Fig. 1. Data are means ± 1 SE and densities are expressed per square millimeter. Sample size is in parentheses. "ND" is not detected*

	Densities of different hairs				
	Multicellular based uniserate	Moniliform	Unicellular based uniseriate	Biseriate glandular	Total
E. actoni (8)	ND	ND	78.9 ± 27.5	2.8 ± 2.7	81.7 ± 26.5
E. asperifolia (6)	ND	15.4 ± 2.5	11.3 ± 1.1	9.4 ± 1.7	36.1 ± 2.5
E. californica (13)	ND	22.1 ± 2.7	2.8 ± 0.2	0.5 ± 0.2	25.4 ± 2.6
E. canescens lanuginosa (8)	ND	ND	53.6 ± 10.9	ND	53.6 ± 10.9
E. farinosa (50)	ND	ND	1,450.7 ± 79.1	ND	1,450.7 ± 79.1
E. farinosa mutant (50)	ND	0.7 ± 2.0	80.7 ± 11.9	60.8 ± 9.5	142.2 ± 18.9
E. farinosa var. *radians* (10)	ND	15.0 ± 7.1	29.0 ± 7.1	10.6 ± 0.7	54.6 ± 3.6
E. frutescens (13)	3.3 ± 0.6	ND	ND	ND	3.3 ± 0.6
E. halimifolia (7)	ND	58.3 ± 3.6	53.1 ± 3.6	ND	111.4 ± 2.7
E. palmeri (6)	ND	ND	121.8 ± 13.1	ND	121.8 ± 13.1
E. ventorum (100)	ND	ND	0.2 ± 0.6	ND	0.2 ± 0.6
E. virginensis (10)	12.0 ± 1.0	ND	76.8 ± 7.5	5.8 ± 0.7	94.7 ± 8.3

ings are thought to occur within *Encelia.* One grouping is characterized by UV-absorbing ray corollas and includes *E. actoni, E. frutescens, E. ravenii,* and *E. virginensis.* The second grouping is characterized by UV-reflecting ray corollas and includes *E. asperifolia, E. californica, E. canescens, E. farinosa, E. halimifolia, E. palmeri* and *E. ventorum.* Furthermore, Clark and Kyhos (1979) and Clark, Thompson, and Kyhos (1980) have suggested that two *Encelia* species are of hybrid origin: *E. asperifolia* (from *E. frutescens* and *E. californica*), and *E. virginensis* (from *E. actoni* and *E. frutescens*).

From the analyses of unicellular-based uniseriate hairs, it would appear that species with UV-absorbing ray corollas either have hairs in which the distal cell is relatively short in length with respect to proximal cells or this type of hair is lacking completely. In contrast, species with UV-reflecting ray corollas have hairs in which the distal cell is much longer than the proximal cells. The distal cell of the unicellular-based uniseriate hairs was straight in most species, but tended to be distinctly quite curly in *E. canescens, E. farinosa,* and *E. palmeri.* From our analyses, *E. canescens, E. farinosa,* and *E. palmeri* were the species characterized as having distal cells many times the length of the proximal cells in the unicellular-based uniseriate hairs, and thus might be considered more advanced than the other members of this grouping.

The other uniseriate hair observed in the *Encelia* leaves was a large, multicellular-base hair (Fig. 1). This hair type was not found in high densities (Table 2) and was limited to only two species, *E. frutescens* and *E. virginensis.* Given that *E. virginensis* is thought to have been derived by hybrid origin from *E. frutescens* (Clark et al., 1980), it is perhaps not too surprising to see the presence of multicellular-based uniseriate hairs in *E. virginensis.*

Moniliform hairs (Fig. 2) were detected in four of the species (Table 2). All were members of the UV-reflecting ray corolla grouping. The moniliform hairs were not observed in any species with UV-absorbing ray corollas.

Biseriate glandular hairs (Fig. 4) were observed in five of the species investigated (Table 2). There was no consistent pattern of occurrence with this hair type. In *E. farinosa,* the biseriate glandular hair was observed in both *E. farinosa* var. *radians* and *E. farinosa* mutant (Ehleringer, 1983), but not in the *E. farinosa* leaves examined. However, these glandular hairs do appear in micrographs of lightly pubescent *E. farinosa* leaves from plants in Tucson, Arizona (Ehleringer and Björkman, 1978). It may be that there are population-based differences for the presence of this hair type.

Increased leaf reflectance appears to be associated with the presence of unicellular-based uniseriate hairs with high densities being necessary to increase reflectance (Fig. 13, 14; Table 2). Table 3 presents leaf absorptance data for the different *Encelia* species. For many species, these absorptance values span a broad range, reflecting the fact that the distal cell can elongate under water stress conditions causing a substantial change in reflectance characteristics (Ehleringer, 1982). Comparing the observations of Tables 2 and 3, it becomes evident that only in species whose leaves have a high density of the unicellular-based uniseriate hairs is there substantial change in leaf absorptance. The multicellular-based uniseriate, moniliform and glandular hairs appear to contribute little if any to changing leaf spectral properties, because species possessing these hair types and

TABLE 3. *Leaf absorptance (400–700 nm) in percent for leaves of* Encelia *species*

Species	Leaf absorptance	Reference
E. actoni	68–80	Ehleringer (unpublished observations)
E. asperifolia	75–79	Ehleringer (1981); Ehleringer et al. (1981)
E. californica	85	Ehleringer et al. (1976); Ehleringer and Björkman (1978)
E. canescens	44–82	Ehleringer et al. (1981)
E. farinosa	29–81	Ehleringer et al. (1976); Ehleringer and Björkman (1978)
E. farinosa mutant	86	Ehleringer (1983)
E. farinosa var. *radians*	79	Ehleringer (1981)
E. frutescens	79	Ehleringer (1981)
E. halimifolia	79	Ehleringer (1981)
E. palmeri	45–82	Ehleringer (1981); Ehleringer et al. (1981)
E. virginensis	79	Ehleringer (1981)

lacking the unicellular-based uniseriate hair had high leaf absorptances.

For the two species suggested to be of hybrid origin by Clark and Kyhos (1979) and Clark et al. (1980) (*E. asperifolia* and *E. virginensis*), only one of the two species possessed the combined hair types present on the leaves of both putative parents. That is, *E. virginensis* leaves possessed both unicellular-based and multicellular-based uniseriate hairs and biseriate glandular hairs. The multicellular uniseriate hairs would be derived from the *E. frutescens* parent (which lacks all of the other hair types) and the unicellular uniseriate and biseriate glandular hairs would be derived from the *E. actoni* parent (which lacks both multicellular-based uniseriate and moniliform hairs). In *E. asperifolia,* the three hair types represented are those characteristic of the putative *E. californica* parent; the multicellular-based uniseriate hair of the putative *E. frutescens* parent was not observed in *E. asperifolia* leaves.

Based on the hair morphologies observed in the present study, the following conclusions can be made about evolutionary patterns in *Encelia*: 1) biseriate glandular hairs are present in both UV-absorbing and UV-reflecting ray corolla groupings of *Encelia* (Clark and Sanders, 1986) and thus can be considered as an ancestral hair type within the genus; 2) multicellular-based uniseriate leaf hairs appear in the UV-absorbing ray corolla group, while moniliform hairs appear on the leaves of UV-reflecting ray corolla group; the two hair types do not occur together in any single species. Yet because hairs of similar shapes are known to occur in other closely related genera of the Heliantheae (Kyhos, 1967), their absence from different *Encelia* groupings may be considered to be a derived condition; and 3) increased spectral reflectance appears to be associated with unicellular-based uniseriate hairs and, in particular, with those hairs in which the distal cells of the uniseriate hair can greatly elongate in length relative to the proximal cells.

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