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NONGLANDULAR TRICHOMES OF CALIFORNIAN AND HAWAIIAN  
TARWEEDS: SURFACE ULTRASTRUCTURE AND  
ITS SIGNIFICANCE

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ABSTRACT

The purpose of this paper was to demonstrate the diversity in nonglandular trichome morphology of tarweeds at the ultrastructural level, and to propose categories for the morphologies reported for such trichomes. Using light and scanning electron microscopy (SEM), the authors surveyed 31 species of 11 genera of tarweeds from California and three genera of tarweeds from Hawaii. Trichome cell wall thickness in the Californian species ranged from 1 to 6  $\mu\text{m}$ , whereas in the Hawaiian species trichome cell wall thickness ranged from 1 to 14  $\mu\text{m}$ . Based on their surface appearance using SEM, trichomes were grouped into four categories: grooved; smooth + grooved; smooth; and verrucose. The verrucose surface of trichomes is an innate feature of the cell wall and is not due to resinlike deposits. The ecology and growth form of the plants in each group were compared to the trichome surface structure. Ecologically, members of the grooved group were alike in experiencing prolonged exposure to solar irradiation; eight of the nine plants in this group are perennial. The smooth + grooved group of trichomes was found on tarweeds that inhabit various types of habitats. This is likely a transitional group. The smooth trichome group is composed of mostly low-elevation Californian annuals. No Hawaiian tarweed surveyed had completely smooth trichomes. Tarweeds having verrucose-surfaced trichomes were mostly found in regions of moderate moisture. The trichomes observed in *Dubautia platyphylla* were unique and could not be placed into any of the four groups; the surface of these trichomes was a combination of verrucose and smooth.

Key words: Asteraceae, California, Hawaii, nonglandular trichomes, silverswords, Madiinae, SEM studies, tarweeds, ultrastructure.

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INTRODUCTION

Recent chloroplast DNA data indicate that the mainland tarweeds of southwestern United States gave rise to the Hawaiian tarweeds (Asteraceae tribe Heliantheae, subtribe Madiinae) (Baldwin, Kyhos, Dvorak, and Carr 1991). With reference to the evolutionary diversification of Hawaiian tarweeds, there may have been important founder effects associated with each of the estimated 14 major dispersal and colonization events (Robichaux, Carr, Liebman, and Pearcy 1990).

Immigrant Hawaiian tarweeds radiated into diverse ecological niches. The ecology of the mainland and Hawaiian tarweeds is quite different. Mainland tarweeds inhabit lowlands with some xeric habitats; only a few grow in areas above tim-

berline (Kyhos, Carr, and Baldwin 1990). The Hawaiian tarweeds inhabit lava flows, cinder cones, dry scrub, dry forests, mesic forests, rainforests, and bogs (Kyhos et al. 1990). The morphology may have been influenced by the environment. For example, the diverse leaf length (5–500 mm; Robichaux et al. 1990) of the Hawaiian tarweeds can be related to the diverse ecology of these plants. Alternatively, the morphology of the trichomes of the Hawaiian tarweeds may result from founder effect. The role of the founder effect is expressed in the limited gametic chromosomal number of the Hawaiian tarweeds, as compared to the immense range of mainland tarweeds. The range of mainland chromosomal numbers is  $n = 4$  to  $n = 34$  with prominent modes at  $n = 7$ ,  $n = 8$  and  $n = 14$ , whereas the Hawaiian chromosomal numbers are all  $n = 14$ , except for a few species with  $n = 13$  (Kyhos et al. 1990).

One would expect morphological diversity to be correlated with physiological factors. Water use, temperature regulation, and leaf absorbance are physiological features of the Hawaiian tarweeds that relate to various leaf sizes and shapes (Robichaux et al. 1990). Robichaux et al. (1990) found that the difference in leaf pubescence between *Argyroxiphium sandwicense* and the *Dubautia menziesii* is correlated with a large difference of leaf absorbance.

When Robichaux et al. (1990) correlated the relative amount of leaf pubescence to a wide range in leaf absorption, they considered the number of trichomes, but they did not consider other characteristics of the trichomes (e.g., trichome length or trichome surface) that would have an affect on leaf absorption. The trichomes that comprise the pubescence of the Hawaiian tarweeds exhibit morphological diversity. The purpose of this paper is to examine the morphology of nonglandular trichomes of tarweeds at the ultrastructural level, and to propose categories for the morphologies reported for the nonglandular trichomes. We also will examine the nonglandular trichome morphology with respect to growth form and ecology of Hawaiian and Californian tarweeds. In addition, we will discuss the morphological diversity of the nonglandular trichomes with relation to possible physiological and ecological significance.

#### MATERIALS AND METHODS

In our survey of Hawaiian and Californian tarweed trichomes, we examined 31 species using the scanning electron microscope (SEM). The survey covers all 11 genera of tarweeds of California and the three Hawaiian genera of tarweeds. The specimens were selected from the RSA-POM herbarium. Leaf surfaces were observed using standard SEM techniques. The specimens used are listed in Table 1.

The verrucose surface group was at first only tentative, because the verrucose surface appeared to be either a resin or a part of the cell wall. If the verrucose surface was due to a resin, then the resin would have to be removed to observe the trichome surface. We used two methods to discover whether the verrucose surface observed on some of the trichomes was part of the cell wall or a resinlike deposit. First, we tried to dissolve away the warty surface on *Raillardiopsis scabrida* trichomes. The solvents used included acetone, 95% ethyl alcohol, water, and aqueous sodium hydroxide. Leaves of *R. scabrida* were left in 2.5% aqueous NaOH for two days at 60 C. The leaves were then infiltrated and embedded according standard paraffin techniques. The embedded leaves were sectioned with

a rotary microtome; sections were stained with a combination of safranin and fast green. The specimens treated by the various methods were observed under a light microscope to see if the warty surface was an integral part of the cell wall.

Using a light microscope, we observed trichome cell number and cell wall thickness from slide preparations. These slides were originally used in an earlier paper by Carlquist (1959).

Table 1 gives the growth form and ecology of the tarweeds. These data were not collected in connection with this study, but were compiled for the discussion of the four groups of trichomes. Data on growth form and ecology of the specimens were taken from Munz and Keck (1965), Wagner, Herbst, and Sohmer (1990), and Robichaux et al. (1990).

## RESULTS

Nonglandular trichomes of the Californian and Hawaiian tarweeds are diverse. However, the Hawaiian tarweed trichomes showed a greater diversity with respect to the trichome cell wall thickness. The Californian trichome cell wall thickness ranged from 1 to 6  $\mu\text{m}$ , whereas the Hawaiian trichome cell wall thickness ranged from 1 to 14  $\mu\text{m}$ . The nonglandular trichomes of *Argyroxiphium caliginis*, *A. grayanum*, *A. sandwicense*, *A. virescens*, *Lagophylla ramosissima*, and *Wilkesia gymnoxiphium* have a cell wall thickness of 1  $\mu\text{m}$ . Cell walls of nonglandular trichomes of *Madia sativa* and *Raillardella scaposa* were 2  $\mu\text{m}$  thick. The nonglandular trichomes of *Achryachaena mollis*, *Blepharizonia plumosa*, *Hemizonia clementina*, *Holocarpa heermannii*, and *Layia platyglossa* have a cell wall thickness of 3  $\mu\text{m}$ . *Hemizonia fitchii*, *Holozonia filipes*, *Madia bolanderi*, and *Raillardiaopsis muirii* have nonglandular trichome cell walls that were 4  $\mu\text{m}$  thick. The cell wall thickness of nonglandular trichomes of *Dubautia ciliolata*,<sup>1</sup> *Raillardella argentea*, and *Raillardiaopsis scabrata* was 5  $\mu\text{m}$ . Cell walls of nonglandular trichomes of *Blepharipappus scaber*, *Calycadenia multiglandulosa*, *Dubautia laxa*, and *Dubautia paleata* were 6  $\mu\text{m}$  thick. *Dubautia platyphylla* had nonglandular trichomes with cell walls 7  $\mu\text{m}$  thick. *Dubautia linearis* had nonglandular trichomes with cell walls 11  $\mu\text{m}$  thick. *Dubautia menziesii* had nonglandular trichomes with cell walls 14  $\mu\text{m}$  thick. In our rather limited survey of Hawaiian species nonglandular trichomes were comprised of three to five cells (for *Hemizonia clementina*, *D. linearis*, *D. laxa*, *D. ciliolata*, *W. gymnoxiphium*, and *Argyroxiphium caliginis*).

We grouped nonglandular trichomes into four categories, based on their surface appearances studied by SEM. The four categories are: grooved, smooth + grooved, smooth, and verrucose. The grooved group (samples of which are displayed in Fig. 1, 2, 3, 5 and 6) consisted of *Argyroxiphium caliginis*, *A. kauense*, *A. sandwicense*, *Dubautia paleata*, *Hemizonia clementina*, *H. fitchii*, *Raillardella argentea*, *R. minima*, and *Wilkesia gymnoxiphium*. The smooth + grooved (samples of which are shown in Fig. 4, 7, and 8) group consisted of *A. grayanum*, *C. multiglandulosa*, *D. ciliolata*, *D. menziesii*, *D. scabra*, and *Holozonia filipes*. Trichomes were placed in the smooth + grooved group if the trichome was partly grooved and partly smooth. The smooth group (samples of which are displayed in Fig. 9, 10, and 11) consisted of *Blepharizonia plumosa*, *Blepharipappus scaber*, *Holocarpa heermannii*, *Lagophylla ramosissima*, *Layia platyglossa*, *Madia sativa*, and *Raillardiaopsis muirii*. The verrucose group (samples of the which are illus-

Table 1. Growth form, ecology and elevation of the Hawaiian and Californian tarweeds observed.

Species studied Ecology	Growth form Elevation
<i>Achryachaena mollis</i> Schauer Moist grassy fields with heavy soils	Annual Below 305 m
<i>Argyroxiphium caliginis</i> Forbes Bog	Rosette subshrub 1350–1650 m
<i>Argyroxiphium grayanum</i> (Hillebrand) Degener Bog	Rosette shrub 1200–2050 m
<i>Argyroxiphium kauense</i> (Rock and Neal) Degener and Degener Bog and lava	Rosette perennial 1625–1900 m
<i>Argyroxiphium sandwicense</i> DC. Dry scrub, woodland, cinder and lava	Rosette Perennial 2700–3750 m
<i>Argyroxiphium virescens</i> Hillebrand Wet scrub and forest	Rosette perennial 1600–2300 m
<i>Blepharipappus scaber</i> Hook Arid plain	Annual 915–2740 m
<i>Blepharizonia plumosa</i> (Gray) Jepson Grassland and occasionally dry ground	Annual Low elevations
<i>Calycadenia multiglandulosa</i> (DC.) Gray Grassy valleys and ridges	Annual Below 305 m
<i>Dubautia ciliolata</i> (DC.) Keck Dry shrubland, woodland, cinder and lava	Shrub 900–3200 m
<i>Dubautia laxa</i> Hook and Arnott Wet forest and bogs	Shrub 360–1700 m
<i>Dubautia menziesii</i> (Gray) Keck Subalpine shrubland, alpine desert, subalpine woodland, cinder and lava	Small shrub 1800–3075 m
<i>Dubautia paleata</i> Gray Margins of bogs	Shrub to small tree 1100–1550 m
<i>Dubautia platyphylla</i> (Gray) Keck Wet bogs to dry inner walls of Haleakala crater	Shrub 1900–2750 m
<i>Dubautia scabra</i> Keck Lava flows and in wet forest	Shrub 75–2500 m
<i>Hemizonia clementina</i> Brandegee Open rocky plains	Perennial 100 m or below
<i>Hemizonia fitchii</i> Gray Dry hills and plains	Annual Up to 915 m
<i>Hemizonia pallida</i> Keck Plains and hills	Annual Up to 671 m
<i>Holocarpa heermannii</i> (Greene) Keck Hard-baked soil of valley flats	Annual Up to 1220 m
<i>Holozonia filipes</i> (H. & A.) Greene Dry alkaline clays, grassland and woodland	Perennial Below 610 m
<i>Lagophylla ramosissima</i> Nutt. Open places, often with hard dry soils	Annual Sea level to 1585 m
<i>Layia platyglossa</i> (F. and M.) Gray Grassy flats near coast	Annual Below 92 m
<i>Madia bolanderi</i> Gray Damp mountain meadows	Rhizomatous perennial 1068–2045 m
<i>Madia sativa</i> Molina Close to the coast	Annual Up to 305 m
<i>Raillardella argentea</i> Gray Dry open places	Acaulescent rosette 2745–3660 m
<i>Raillardella minima</i> Rydberg Dry granitic sand	Acaulescent rosette 3050 m

Table 1. Continued.

Species studied Ecology	Growth form Elevation
<i>Raillardella scaposa</i> (Gray) Gray Dry stony places on the edge of meadows	Rosette perennial 1990–3398 m
<i>Raillardiopsis muirii</i> (Gray) Rydberg Open slopes	Subshrub 1220–2135 m
<i>Raillardiopsis scabrada</i> (Eastw.) Rydberg Open stony places	Subshrub 1985–2290 m
<i>Wilkesia gymnoxiphium</i> Gray Sunny slope of forest	Unbranched rosette shrub 610 m

trated in Fig. 13, 14, 15, and 16) consisted of *Achryachaena mollis*, *Argyroxiphium virescens*, *D. laxa*, *Hemizonia pallida*, *M. bolanderi*, and *R. scabrada*. *Dubautia platyphylla* (Fig. 12) had a smooth to verrucose appearance and therefore did not fit into any of the four groups.

*Raillardiopsis scabrada* leaves were treated with water, acetone, 95% ethyl alcohol, and 2.5% aqueous sodium hydroxide to see if these reagents would remove the warty surface on trichomes. However, this surface was not removed. Even exposure to 2.5% aqueous NaOH for two days did not remove the warts. Safranin and fast green stained the trichome walls the same color as the warts. These tests indicated that the verrucose surface is an integral part of the trichome cell wall.

#### DISCUSSION

Using the SEM, we viewed herbarium specimens that had been dried and pressed. Hypothetically, drying of specimens might be supposed to increase grooving in the trichome surface, because of loss of water from the trichome. If the grooving was caused by the specimens being dried and pressed, then all the specimens should be affected. However, over half of them did not exhibit grooves. If the grooves had been caused by the collapse of the cell wall, then all the thin-walled specimens should have grooves. *Lagophylla ramosissima* has an extremely thin trichome cell wall (1  $\mu\text{m}$  thick), but does not exhibit grooves. The trichome walls of *Madiá sativa*, and *R. scaposa* are 2  $\mu\text{m}$  thick and lack grooves on the trichome. Therefore, the trichome grooves were actually part of the ultrastructure and not an aberration.

Trichome cell wall thickness also shows some general trends. The trichome walls of all species of *Argyroxiphium* and of *W. gymnoxiphium* were 1  $\mu\text{m}$  thick. Trichome cell walls of *Dubautia* are at least 5  $\mu\text{m}$  thick, and those of most Californian annuals were 3, 4 or even 6  $\mu\text{m}$  thick. Trichome cell walls of Californian perennials were mostly 4–5  $\mu\text{m}$  thick.

The systematic distribution of trichome types shows interesting taxonomic distinctions. The genus *Raillardella* is not in the same group as *Raillardiopsis*. The *Raillardella* species were in the grooved group, whereas *Raillardiopsis scabrada* is in the verrucose group and *Raillardiopsis muirii* is in the smooth group.

After the specimens had been grouped by their appearance under the SEM, we looked for correlations between the ecology or growth form and trichome surface. The ecology of the grooved group (Table 1) had a similar characteristic of exposure to high solar irradiation. The primary habitat of *Argyroxiphium* is high alpine,

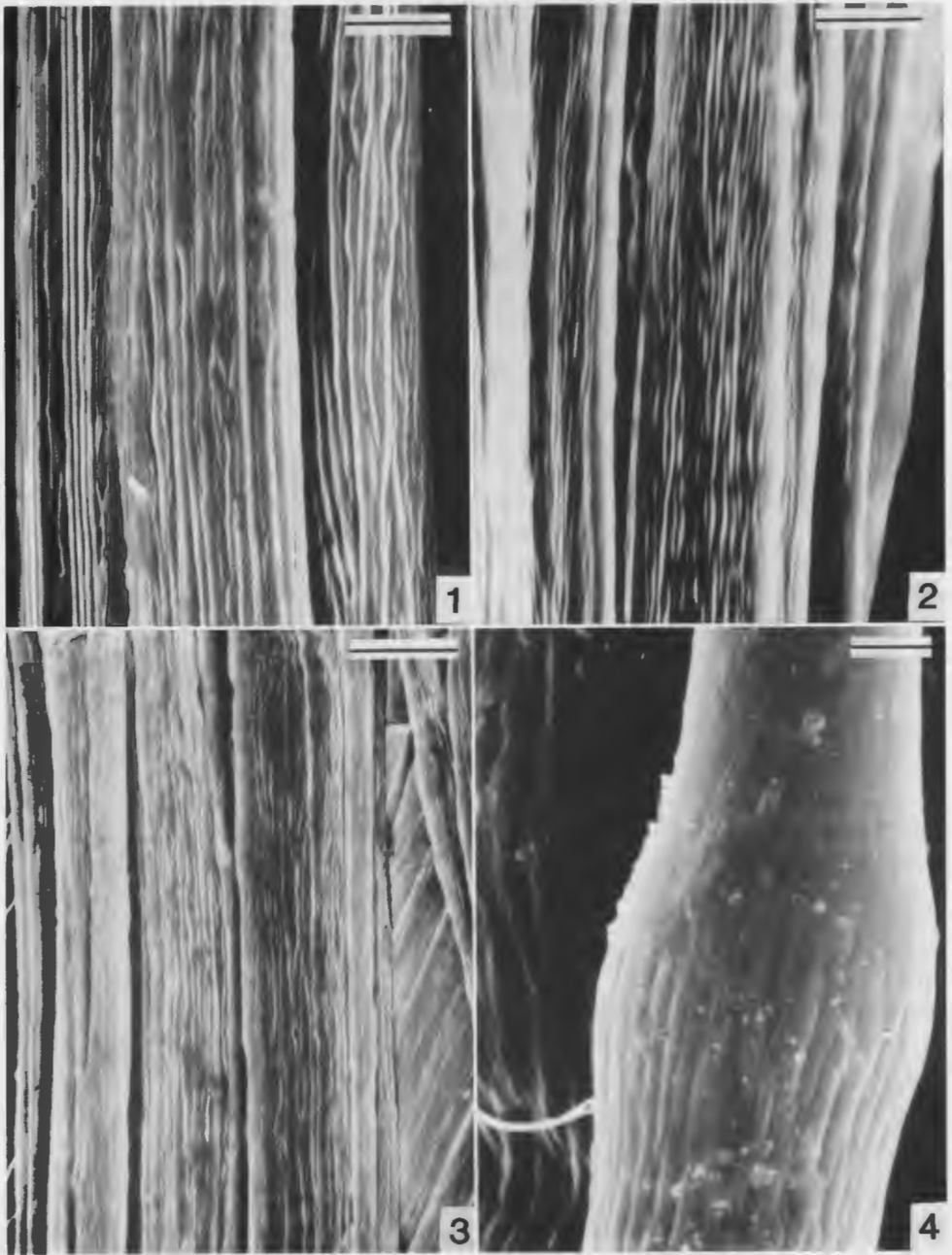


Fig. 1-4. SEM photomicrographs of trichome ultrastructure of *Argyroxiphium*.—1. Grooved trichome surface of *A. sandwicense* (Carlquist 544, RSA).—2. Grooved trichome surface of *A. kauense* (Carlquist 2110, RSA).—3. Grooved trichome surface of *A. caliginis* (Carlquist 550, RSA).—4. Smooth + grooved trichome surface of *A. grayanum* (Carlquist 2140, RSA). The bar on the figures indicates 5  $\mu$ m.

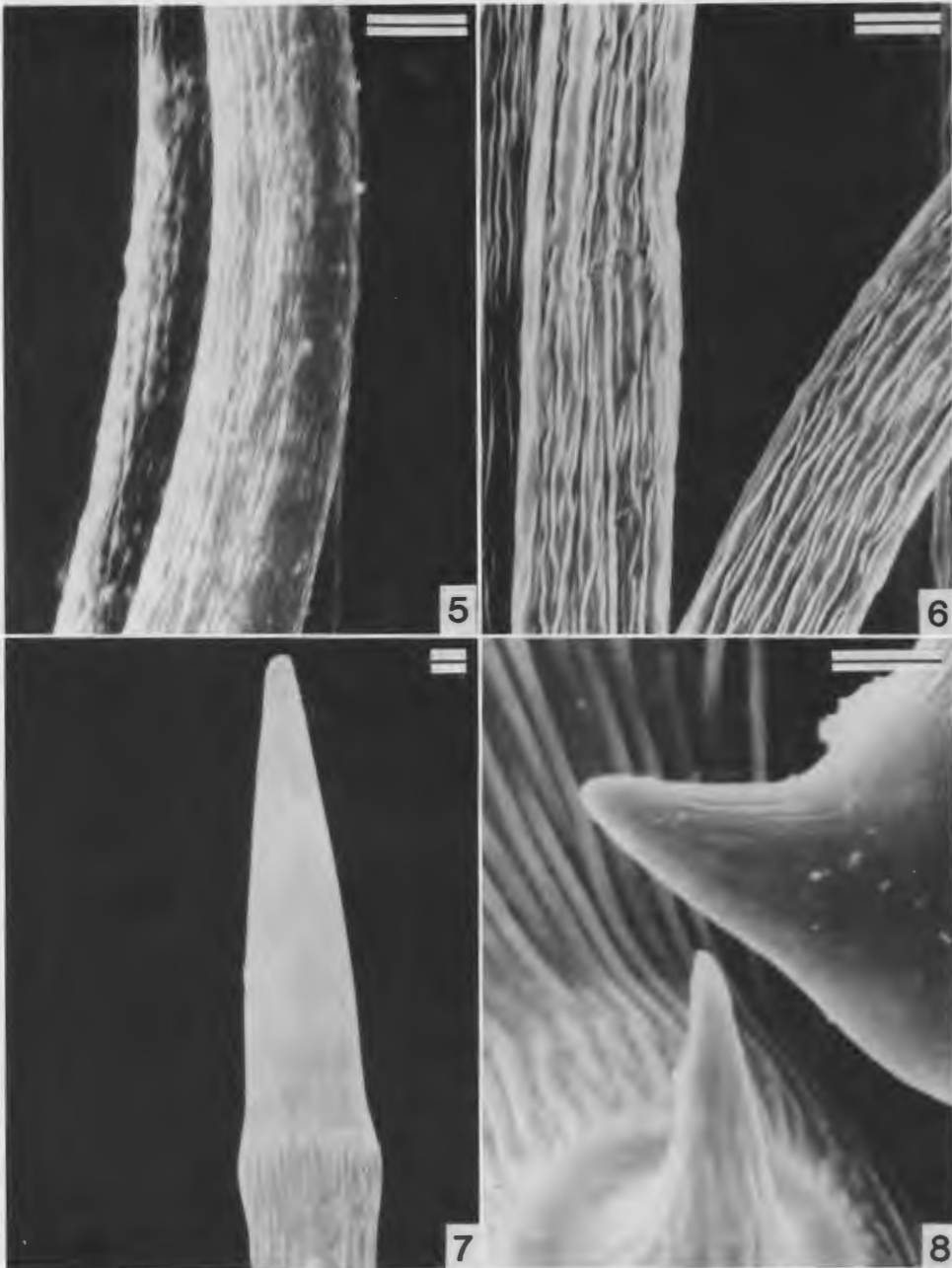


Fig. 5-8. SEM photomicrographs of trichome ultrastructure.—5. Grooved trichome surface of *Wilkesia gymnoxiphium* (J. Henrickson 4039, RSA).—6. Grooved trichome surface of *Raillardella argentea* (R. F. Thorne 32334, RSA).—7. Smooth + grooved trichome surface of *Dubautia menziesii* (R. Gustafson & C. Briel Aug. 19, 1975, POM).—8. Smooth + grooved trichome surface of *Calycadenia multiglandulosa* (L. S. Rose 41268, POM). The bar on the figures indicates 5  $\mu$ m.



and bogs are probably a secondary habitat (Baldwin unpublished). Alpine areas receive high solar irradiation. Although bogs receive only a fraction of the solar irradiation that alpine areas do, Hawaiian bogs often receive intense sunlight during the morning before clouds ascend over the bogs (Carlquist, personal observation). *Dubautia paleata* probably does not receive as much sunlight as the other species in the grooved group. *Dubautia paleata* inhabits a bog that is more generally cloudy and therefore does not receive as much sunlight. Also, eight of nine species in the grooved group are perennial. If perennial growth form and sunny habitat are correlated with grooved trichomes, then trichomes may be involved in reducing leaf temperature. Trichome grooves may act to radiate heat or reflect sunlight in perennial species and in species of sunny habitats. A ridged area has more surface area than a smooth surface and this serves to radiate excess heat (Johnson 1975). A rough surface reflects more sunlight than a smooth surface (Johnson 1975). Reduction of light energy by radiation of excess heat and surface reflection are selective advantages in areas of intense light, because reducing light energy would lower leaf temperature. In areas of intense light, high leaf temperatures can be lethal and therefore a cooling mechanism is of selective value.

The smooth + grooved group of trichomes included tarweeds that inhabit various types of habitats (Table 1). Habitats of these species range from wet to dry and from high elevation to low elevation. This group is likely a transitional group. The range of trichome sculpture is possibly adaptive in a wide range of habitats. Another explanation for the mixed condition of the trichome surfaces in the plants in this group is that these species have relatively sparse trichomes compared to the other groups. Relatively reduced sculptured trichomes may have heat exchange capabilities equal to those of a large smooth trichome. Almost all specimens in this group are perennials and have leaves that persist through all seasons. *Calycadenia multiglandulosa*, the only annual of this group, has relatively short trichomes (Fig. 8). The shortness and sparseness of the *C. multiglandulosa* trichomes might be correlated with a greater degree of sculpture than seen in species with longer and more abundant trichomes. Also, *C. multiglandulosa* flowers in late summer and thereby the leaves experience more heating than do those of species that flower earlier (e.g., *Achryachaena*, *Layia*). This extra heat would need to be dissipated, or reflected by the grooves.

The smooth group is composed of mostly low-elevation Californian annuals. No Hawaiian tarweed has completely smooth trichomes. These relatively smooth surfaced trichomes are on annual tarweeds that inhabit areas relatively dry compared to habitats of plants in the other three groups (Table 1). Smooth surfaces would not reflect as much light as a uneven surface (Johnson 1975). In this group the trichome surface might not be as important as the trichome structure itself. The presence of trichomes is associated with arid conditions (Fahn 1986), and trichome presence has been linked with water economy (Fritsch and Salisbury 1965). The tarweed trichomes could function to trap air near the leaf, to form boundary-layer resistance as has been demonstrated in various species (Woolley 1964; Gates 1968). Boundary layer resistance occurs when the water vapor from the saturated leaf interior must pass through the still air before reaching the drier air outside of the trichome (Woolley 1964). It has even been suggested that trichomes can absorb water from the surrounding air (Lyshede 1977; Galati 1982).

The smooth group is not perfectly correlated with ecology and elevation. The

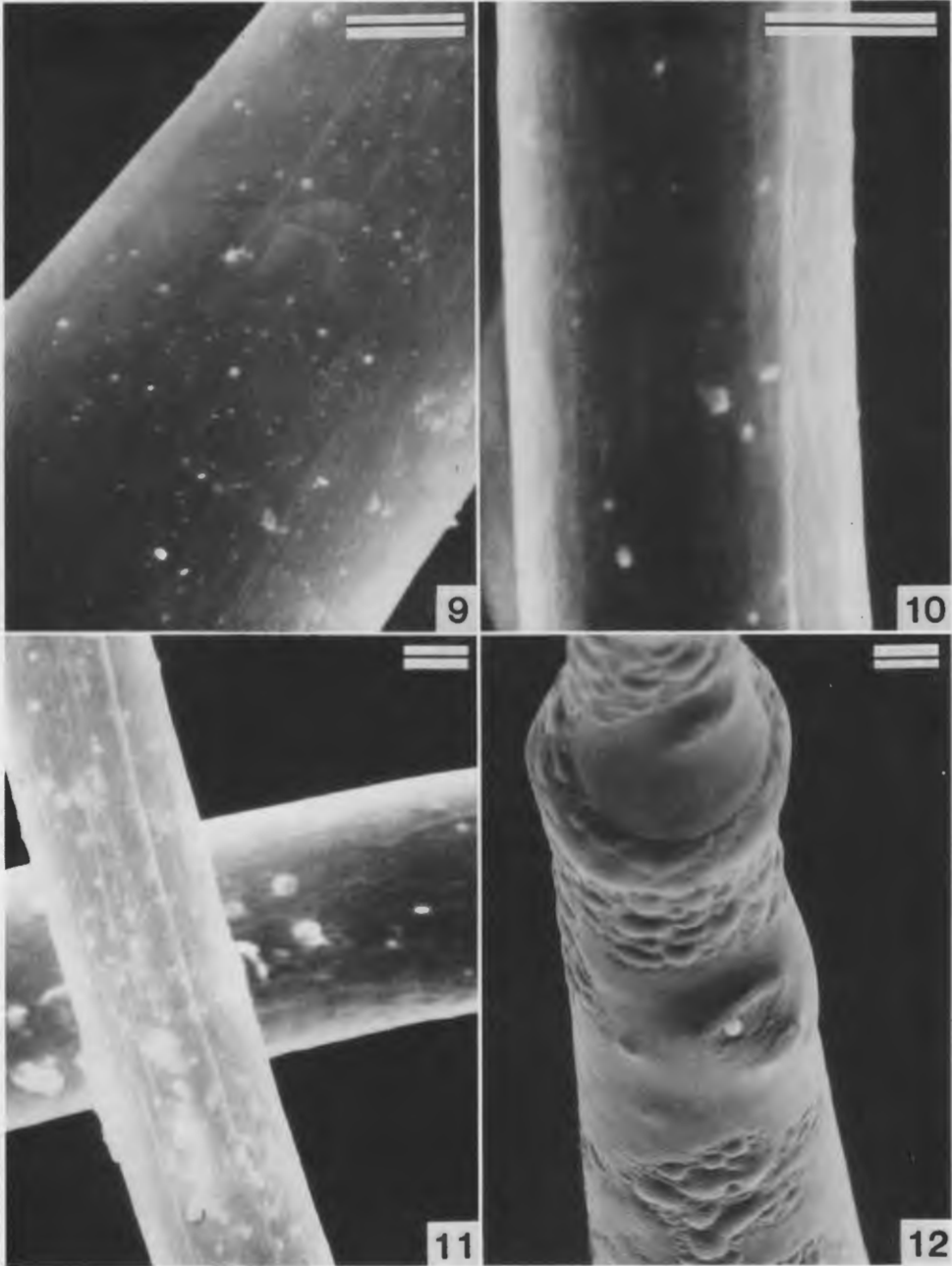


Fig. 9–12. SEM photomicrographs of trichome ultrastructure.—9. Smooth trichome surface of *Layia platyglossa* (E. S. Steele & H. S. Pratt April 9, 1934, POM).—10. Smooth trichome surface of *Raillardiopsis muirii* (J. T. Howell 33960, RSA).—11. Smooth trichome surface of *Hemizonia fitchii* (P. Tracy 2264, POM).—12. Smooth + verrucose trichome surface of *Dubautia platyphylla* (J. Herrickson 3848, RSA). The bar on the figures indicate 5  $\mu$ m.

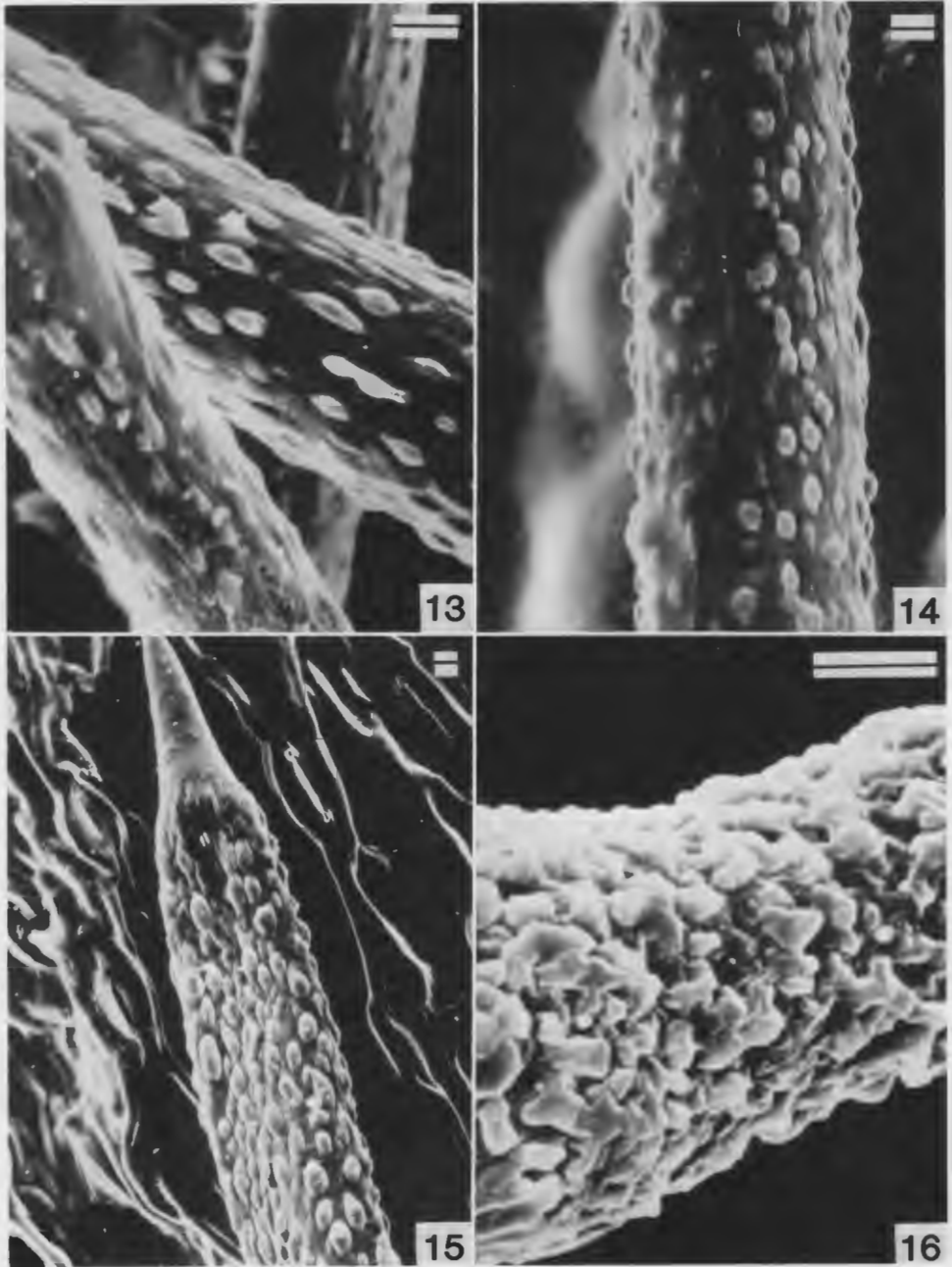


Fig. 13–16. SEM photomicrographs of trichome ultrastructure.—13. Verrucose trichome surface of *Achyrrachaena mollis* (Q. P. Sinnott & K. A. Sinnott 649, RSA).—14. Verrucose trichome surface of *Madia bolanderi* (W. M. Hiesey 255, POM).—15. Verrucose trichome surface of *Dubautia laxa* (R. Gustafson 2056, POM). Note that the terminal cell of the *D. laxa* has a smooth surface.—16. Verrucose trichome surface of *Raillardiopsis scabrada* (J. L. Strother 1282, RSA). The bar on the figures indicates 5  $\mu$ m.

growth form and elevation of *Raillardiopsis muirii* are different from those of the other members of the group. *Raillardiopsis muirii* is a perennial and inhabits higher elevations than do other tarweeds in this group. Another anomaly of the group is that *Blepharipappus scaber* is found not only at low elevations but up to 2740 m.

The fourth group, verrucose, was tentative because the protuberances on the surface of the trichome at first appeared to be a resinlike deposit. However, because solvents could not remove the protuberances and they stained the same color as the trichome cell wall, the verrucose surface was determined to be part of the trichome cell wall. Therefore, the verrucose group was accepted as valid.

The verrucose group is a mixture of annuals and perennials as well as both Californian and Hawaiian tarweeds with similar ecology. These tarweeds are mostly found in regions of moderate moisture (Table 1). *Raillardiopsis scabrada* inhabits dry areas and is an exception to this rule. Also, the verrucose surface on *R. scabrada* trichomes is relatively more textured than are trichome surfaces in other members of the verrucose group (compare Fig. 16 with Fig. 13, 14, and 15). The ecology of *R. scabrada* suggests that the protuberances might have less to do with moisture, and more with light intensity. A verrucose surface is a form of surface texture alternative to grooved surfaces. The rough surface would serve the same function as the grooved surface (i.e., radiate excess heat and reflect sunlight). A verrucose surface is, however, relatively smooth compared with surfaces of the grooved group. Therefore, trichomes of the verrucose group would reflect less light, which corresponds with the fact that the plants of the verrucose group receive on the average less light than do those of the grooved group.

The trichomes observed in *Dubautia platyphylla* are unique and cannot be placed into any of the four groups. The surface of these trichomes (Fig. 12) is a combination of verrucose and smooth. The ecology of this species ranges from bogs and wet forests to dry inner walls of Haleakala crater. The habitat of *D. platyphylla* is most like that of the smooth + grooved group. *Dubautia platyphylla* often grows in close association with *D. menziesii* (Robichaux, personal communication). The nature of habitat and close spatial association between *D. platyphylla* and *D. menziesii* support the idea that verrucose surfaces represent a trichome surface alternative to a grooved surface.

Trichomes do not have a single function. They may be involved in shading the leaf from the sun, dispersing light that strikes the leaf surface, in radiating heat, in absorbing moisture (Lyshede 1977; Galati 1982), in deterring herbivores (Poos 1929; Poos and Smith 1931), or in forming a boundary layer. The function of the trichome depends on the environment. When adapting to the environment, one environmental factor might be more significant than another. Variation in trichome number, trichome length, and trichome cell wall thickness as well as trichome surface structure may represent adaptations to particular ecological requirements.

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## FOOTNOTE

<sup>1</sup> The trichome cell wall had separated into the outer and inner layers, because of exposure to NaOH. Therefore, the outer and inner cell wall were added together to give an estimate.