Evidence of Hybridization Between *Rhus integrifolia* and *R. lentii* (Anacardiaceae) on Cedros Island, Baja California, Mexico

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INTRODUCTION

The tendency among island plants to hybridize has been noted by many authors (*e.g.*, Carlquist 1966) and this phenomenon is exemplified by several plants of the California Islands (Thorne 1969). Examples of hybridization on the California Islands can be found in genera such as *Quercus* (Muller 1967), *Rhus* (Young 1974a), *Opuntia, Dudleya, Salvia, Helianthemum, Cercocarpus,* and *Ceanothus,* to mention a few. At the same time, even though the California Islands, like most fringing archipelagos, often serve as refugia for relict plant taxa (Axelrod 1967, Thorne 1969), they also are possible sites of autochthonous evolution, although they certainly are not comparable in this respect to oceanic islands (Carlquist 1974). Some possible examples of autochthonous evolution in plants of the California Islands can be found in *Hemizonia* (Carlquist 1965) and *Dudleya* (Moran 1959), as well as in *Lavatera, Solanum, Eriogonum,* and *Malacothrix*. The objective of this study was to determine whether *Rhus integrifolia* (Nutt. in T. & G.) Brew. & Wats. var. *cedrocensis* Barkl., an endemic of Cedros Island, represents an example of autochthonous insular evolution or whether it actually is of hybrid origin, representing a hybrid between *R. integrifolia* and *R. lentii* Kell., as suggested by Barkley (1937).

Cedros Island is the largest of the California Islands, with a total land area of 348 km² (134 mi²) (Philbrick 1967); it is located 23 km (14 mi) off the coast of Baja California near Punta Eugenia (Fig. 1). In 1967, the total number of native plant taxa on Cedros Island was estimated at 205 (Raven 1967). Although probably a conservative estimate, it is still a fairly low number of taxa, given the size of the island, compared with the other large California Islands. For example, Santa Cruz Island (249 km² or 96 mi²) has approximately 420 native plant taxa (Raven 1967). The depauperate nature of the flora of Cedros Island probably is due to the very arid nature of the Vizcaino Desert that covers most of the island and the adjacent mainland (Shreve and Wiggins 1964).

Rhus integrifolia, a perennial shrub with typically simple evergreen leaves, is a prominent member of the coastal sage scrub and chaparral communities of coastal southern California and Baja California (Fig. 1). On Cedros Island, *R. integrifolia* occurs on the west side and northern end of the island in a vegetation type that would best be termed island coastal sage scrub-chaparral. *Rhus lentii* also is a perennial shrub with simple evergreen leaves and is another example of a near island endemic (Axelrod 1967) (Fig. 1). On Cedros Island, *R. lentii* is a distinctive element of the Vizcaino Desert vegetation that covers the island at lower elevations.

MATERIALS AND METHODS

Population samples.—Field studies on Cedros Island were conducted in March and April of 1972 and 1973. Collections of "pure" *R. lentii* were made from lower elevations around the village and on the southwest and southeast ends of the island. A previously studied population of *R. integrifolia* from Santa Barbara County, California (Young 1974a; population 4, nos. 711-725) was used to represent a "pure" population of this taxon. In addition, collections of

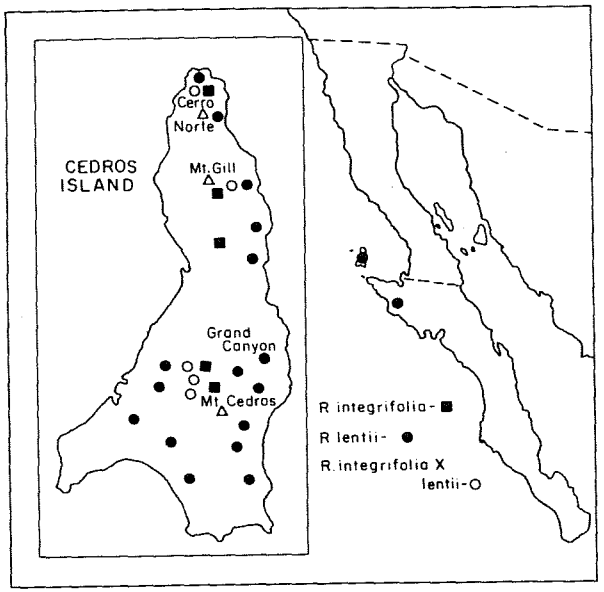


FIGURE 1. *Distribution of* R. lentii, R. integrifolia, *and the putative hybrid* R. integrifolia x R. lentii *on Cedros Island (based upon herbarium specimens and personal collections).*

both taxa were made on the west side of the island (near the main water-pumping station) along a transect that began in coastal sage scrub-chaparral (*R. integrifolia*), descended through transitional or ecotonal vegetation, and ended in the lower elevation Vizcaino Desert vegetation (*R. lentii*). Voucher specimens of the plants sampled from Cedros Island are deposited at Rancho Santa Ana Botanic Garden; duplicates are located at the University of Illinois. Vouchers of *R. integrifolia* from Santa Barbara County, California are deposited in the California State University at Fullerton.

Comparative morphology.—Based upon examination of numerous herbarium specimens and analysis of descriptions of the two taxa, several morphological features were selected that could be used to characterize them. Features considered to be diagnostic were: leaf length/width ratios, leaf pubescence (mean number of simple trichomes per mm² on the lower leaf surface), sepal color and pubescence, and inflorescence morphology. Values for each quantitative feature consisted of an average of three measurements per plant. The number of trichomes per mm² was determined by making collodion peels of leaves and counting the number of trichomes using a compound microscope. In addition, cuticular relief patterns for the two taxa were observed using scanning electron microscopy (SEM). Dried leaves were obtained from herbarium specimens for SEM studies. The portion of each leaf examined came from an area midway between the base and apex and extending laterally from the midvein to the margin of the leaf. Leaf specimens were prepared in two ways. Leaf surfaces were peeled using cellulose acetate paper and acetone (Payne 1968). Both the peeled leaf surface and the peel (cast) of the surface were examined. Leaf surfaces also were examined directly as obtained from the herbarium sheets. All specimens were affixed to aluminum stubs with silver conducting paint or Microstik prior to coating with gold-palladium. SEM micrographs were made on a Cambridge Mark II Stereoscan, operated at 15KV. Populational variation of these morphological features was analyzed with the aid of pictorialized scatter diagrams and hybrid index (*HI*) values (Table 1) (Anderson 1949).

TABLE 1. Characters used and values assigned to them in constructing the morphological hybrid index (*HI*).

Character	Hybrid index value 0	1	2
Sepal color	green	pinkish	deep rose
Leaf pubescence (= mean no. trichomes/mm² on lower leaf surface	< 10	10-150	> 150
Mean leaf length/width ratio	1.45-2.00	1.31-1.44	1.15-1.30
Sepal pubescence	glandular trichomes	mixed glandular/ simple trichomes	simple trichomes
Inflorescence	compact spike	intermediate	open panicle

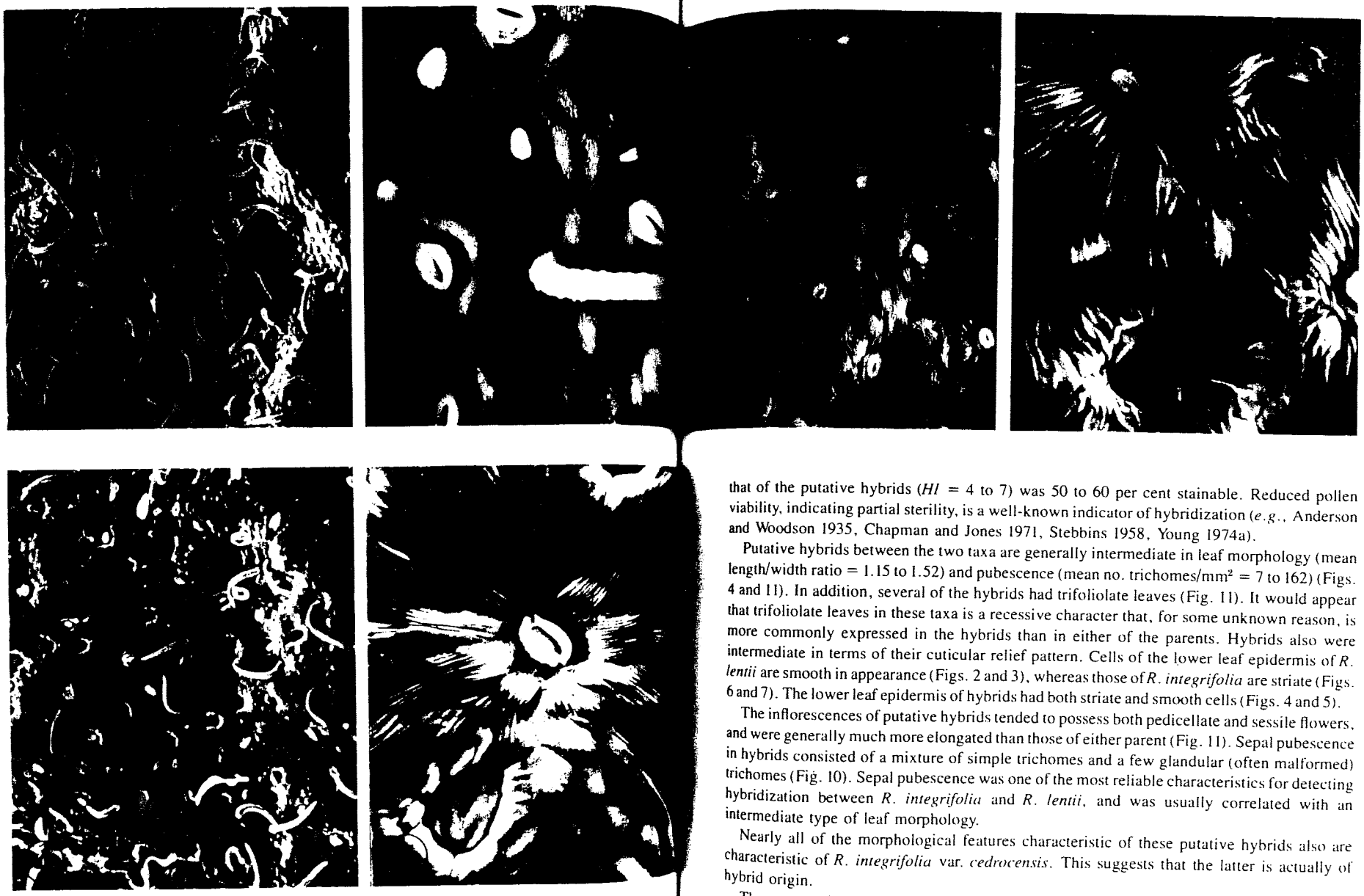
Pollen stainability.—Pollen stainability was determined for functionally male individuals (see Young 1972) of each species and their putative hybrids. Pollen was stained in 1 per cent aniline blue in lactophenol ("cotton blue") for 24 hours. Three different flowers from each plant were utilized and a minimum of 600 grains (per plant) counted. Those pollen grains that stained dark blue were assumed to be viable and those that stained faintly or not at all, inviable (however, see Jones 1976).

RESULTS AND DISCUSSION

Comparative Morphology and Analysis of Population Samples

Although the two species superficially are quite similar, several features distinguish them. Distinctive features of *R. integrifolia* include: (1) its leaves, which are generally elliptic in shape (length/width ratio ≥ 1.5), glabrous (usually < 10 simple trichomes/mm² on the lower leaf surface; Fig. 6), entire to serrate, and simple (rarely trifoliolate [Young 1974a]); (2) its flowers, which are sessile and borne in dense, terminal, compact spikes (with persistent bracts); and (3) its sepals, which are greenish in color and ciliate with an abundance of orange, glandular, uniserriate, multicellular trichomes (Fig. 8). Characteristic features of *R. lentii* include: (1) its leaves, which are more or less deltoid in shape (length/width ratio ≤ 1.3), densely hairy on the lower leaf surface (usually > 200 simple trichomes/mm²; Fig. 2), entire, and always simple; (2) its flowers, which are pedicellate and borne in short, somewhat open panicles (with deciduous bracts); (3) its sepals, which are deep rose in color and ciliate with uniserriate, unicellular, simple trichomes (Fig. 9); and (4) its large fruits (11 to 14 mm in diameter compared with 8 to 10 mm in *R. integrifolia*), which are the largest in the genus (Young 1975).

Variation of morphological features measured for the population samples is presented in Figures 12 and 13. Based upon the morphological features analyzed in this study, the two species are easily distinguished and morphologically are quite distinct. Those individuals which were morphologically intermediate between the two species were found growing in the transitional, or ecotonal, vegetation along the elevational transect. The results of pollen stainability studies supported the interpretation that these morphologically intermediate individuals were putative hybrids between *R. integrifolia* and *R. lentii*. Pollen of individuals of *R. integrifolia* (*HI* = 0) and *R. lentii* (*HI* = 10) was 95 to 99 per cent stainable (viable), whereas



FIGURES 2-7. *SEM photographs of the lower leaf surfaces of the* Rhus *taxa studied.* **Figures 2-3:** R. lentii, *"peeled" surface (see text for explanation of "peeled" and "unpeeled"); Figure 2* ca. *200×; Figure 3* ca. *600×.* **Figures 4-5:** R. integrifolia × R. lentii; *Figure 4 "unpeeled" surface,* ca. *200×; Figure 5 "peeled" surface,* ca. *700×.* **Figures 6-7:** R. integrifolia *"peeled" surfaces; Figure 6* ca. *300×; Figure 7* ca. *600×.*

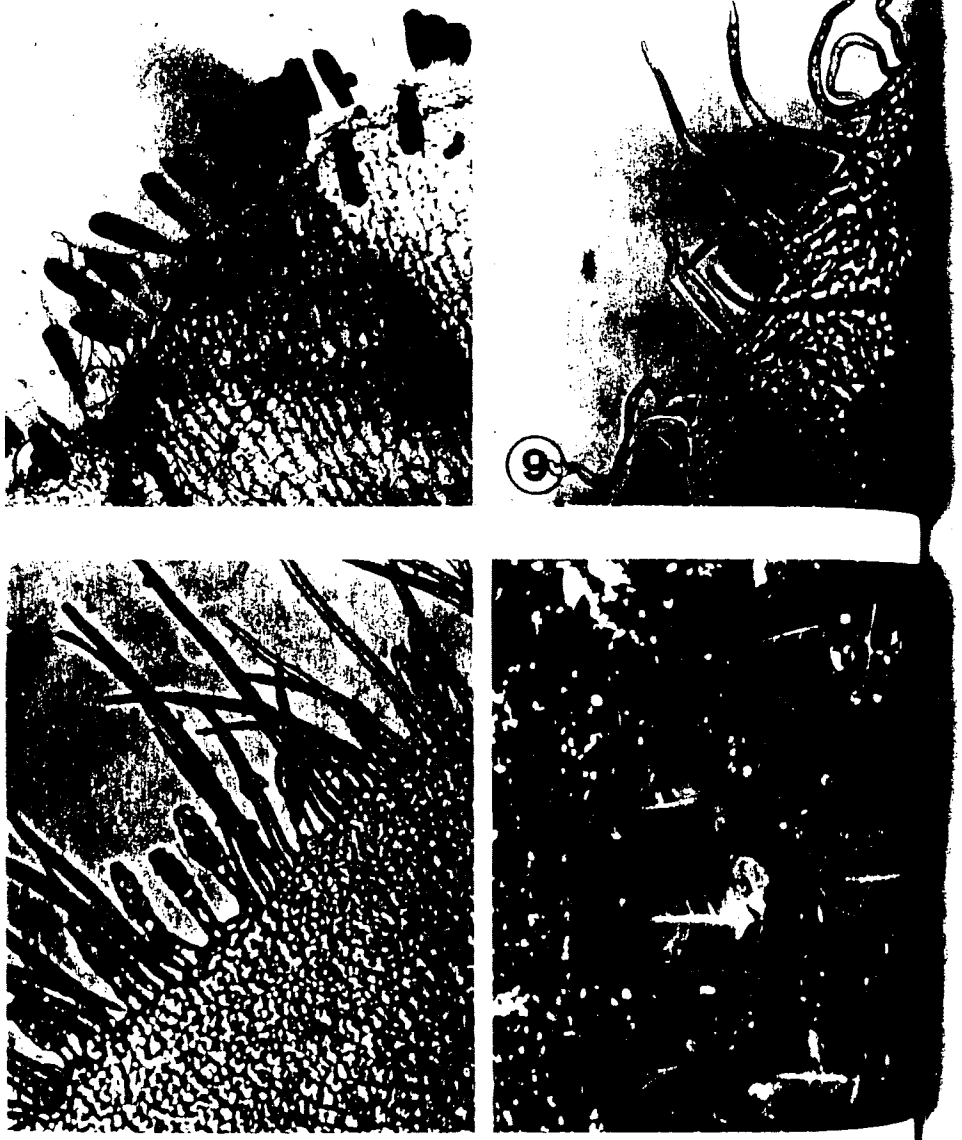
that of the putative hybrids (*HI* = 4 to 7) was 50 to 60 per cent stainable. Reduced pollen viability, indicating partial sterility, is a well-known indicator of hybridization (*e.g.*, Anderson and Woodson 1935, Chapman and Jones 1971, Stebbins 1958, Young 1974a).

Putative hybrids between the two taxa are generally intermediate in leaf morphology (mean length/width ratio = 1.15 to 1.52) and pubescence (mean no. trichomes/mm² = 7 to 162) (Figs. 4 and 11). In addition, several of the hybrids had trifoliolate leaves (Fig. 11). It would appear that trifoliolate leaves in these taxa is a recessive character that, for some unknown reason, is more commonly expressed in the hybrids than in either of the parents. Hybrids also were intermediate in terms of their cuticular relief pattern. Cells of the lower leaf epidermis of *R. lentii* are smooth in appearance (Figs. 2 and 3), whereas those of *R. integrifolia* are striate (Figs. 6 and 7). The lower leaf epidermis of hybrids had both striate and smooth cells (Figs. 4 and 5).

The inflorescences of putative hybrids tended to possess both pedicellate and sessile flowers, and were generally much more elongated than those of either parent (Fig. 11). Sepal pubescence in hybrids consisted of a mixture of simple trichomes and a few glandular (often malformed) trichomes (Fig. 10). Sepal pubescence was one of the most reliable characteristics for detecting hybridization between *R. integrifolia* and *R. lentii*, and was usually correlated with an intermediate type of leaf morphology.

Nearly all of the morphological features characteristic of these putative hybrids also are characteristic of *R. integrifolia* var. *cedrocensis*. This suggests that the latter is actually of hybrid origin.

There was no indication of introgression between the two species on the island (Fig. 13). Two possible explanations may account for this situation. The first is that the hybrids are sterile and are not reproducing. Pollen stainability data indicated that male fertility in the hybrids was greatly reduced compared with that of the parental species. However, many of the putative hybrids found during the course of the field studies were female plants. These plants did produce some seed, which appeared to have normally developing embryos, but no seedlings



FIGURES 8-11. *Whole mounts of sepals showing characteristic pubescence of taxa and leaves of the putative hybrid.* **Figure 8:** R. integrifolia *(725, HI=1) with predominantly glandular trichomes.* **Figure 9:** R. lentii *(125, HI=10) with simple trichomes only.* **Figure 10:** *Putative hybrid (108, HI=5) with mixture of malformed glandular and simple trichomes.* **Figure 11:** *Leaves of the putative hybrid; note the trifoliolate shape.*

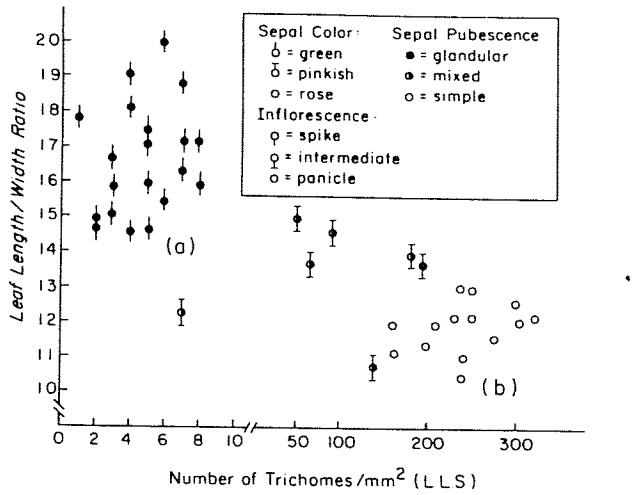


FIGURE 12. *Pictorialized scatter diagram for the populations of* R. integrifolia *and* R. lentii *studied. Grouping* (a) represents R. integrifolia; *grouping* (b) *represents* R. lentii. *(L.L.S. = lower leaf surface.)*

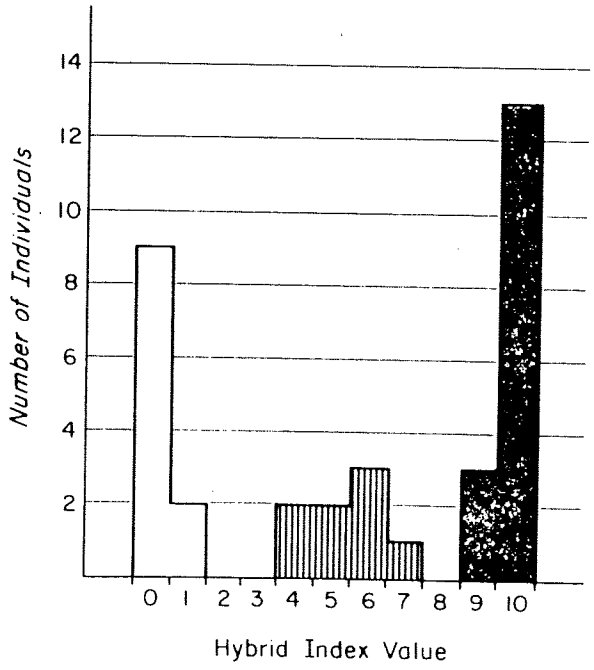


FIGURE 13. *Histogram of hybrid index values for "pure"* R. integrifolia *(clear), "pure"* R. lentii *(dotted), and the putative hybrid (vertical lines).*

were discovered. It has been shown that introgression between *R. integrifolia* and *R. ovata* probably occurs via fertilization of female hybrids with pollen from either of the parental species, due to decreased pollen viability of the hybrids (Young 1974a). It seems likely that this also is the case in *R. integrifolia* and *R. lentii*. The degree of fertility of female hybrids is not known; while it probably is lower than that of either of the parents, some viable introgressive seeds are likely to be produced by female hybrids. A second possible explanation for the absence of introgression may be that there simply are not any habitats available for the establishment of introgressive types. One of the characteristics of introgression is that the recombinant types ("hybrid swarms") typically are found in disturbed habitats which are often intermediate between the habitats of the parental taxa. In those regions on Cedros Island where *R. integrifolia* and *R. lentii* are sympatric there is relatively little disturbance and consequently few disturbed habitats. Clearly, the putative hybrids that were present occurred in a *natural* habitat that appeared to be intermediate between those of the parents. However, this habitat was not extensive and appeared to be occupied primarily by F_1 (or perhaps F_2) morphotypes (Figs. 12 and 13). In my opinion, the lack of suitable, *available* habitats for the establishment of introgressive types is the primary reason for the absence of introgression between *R. integrifolia* and *R. lentii* on Cedros Island.

Evolutionary Significance of Hybridization

The ultimate evolutionary importance of hybridization depends directly on the environment in which it takes place. For example, hybridization between *R. integrifolia* and *R. ovata* in coastal southern California has occurred under changing environmental conditions, most recently due in large part to manmade disturbances, which have afforded new habitats for the establishment and stabilization of recombinant types through introgression (Young 1974a). In this instance, hybridization probably has played, at least to some extent, a role in the evolutionary history of these species. However, hybridization between well-established and well-adapted taxa in a stable environment will generally have no significant effect on the evolutionary history of the taxa involved (Stebbins 1950). The most obvious effect of hybridization under such conditions is the breakdown or blurring of the distinctions between the species involved. This certainly appears to be the case concerning hybridization between *R. integrifolia* and *R. lentii* on Cedros Island.

TAXONOMIC TREATMENT

The results of this investigation indicate that *R. integrifolia* var. *cedrocensis* is actually of hybrid origin (*R. integrifolia* × *R. lentii*), and not the result of autochthonous insular differentiation. Formal taxonomic recognition of this hybrid seems unwarranted and is, in fact, misleading. The following taxonomic treatment is presented to help clarify the relationships between these taxa.

Key to *R. integrifolia*, *R. lentii*, and Their Hybrids

1. Leaves generally elliptic and glabrous; inflorescence a dense, terminal spike with persistent bracts; flowers sessile; sepals green, ciliate with orange, glandular trichomes ..... *R. integrifolia*
1. Leaves deltoid to elliptic, puberulent to densely tomentose; inflorescence a terminal panicle or spike-like with deciduous bracts; flowers pedicellate or sessile; sepals pinkish to deep rose, ciliate with simple and orange, glandular trichomes.
   2. Leaves deltoid, glaucous, puberulent above, densely tomentose below; inflorescence a terminal panicle, with deciduous bracts; flowers short pedicellate; sepals deep rose, ciliate with short, simple trichomes ..... *R. lentii*

   2. Leaves more or less elliptic, more or less glabrous above, pubescent below; inflorescence intermediate between spike and panicle, with more or less deciduous bracts; some flowers short pedicellate; sepals pinkish, ciliate with a mixture of simple and orange, glandular (often malformed) trichomes ..... *R. integrifolia* × *R. lentii*

Rhus integrifolia (Nutt. in Torr. & Gray) Brewer and Watson. Bot. California 1: 110. 1876. HOLOTYPE: San Diego, *Nuttall s.n.* (BM!). [A complete discussion of the nomenclature, synonyms, and description of *R. integrifolia* can be found elsewhere (Young 1974b).]

In order to conserve space, a list of representative specimens examined will not be included for *R. integrifolia*, but are presented only for *R. lentii* and hybrids. Upon written request to the author, a complete list may be obtained.

Rhus lentii Kellogg, Proc. California Acad. Sci. 2: 16. 1863; Just's Bot. Jahresb. 21: 158. 1893, as *R. leutii* [sic].—*Schmaltzia lentii* (Kell.) Barkley, Amer. Midl. Natur. 24: 650. 1940.—*Toxicodendron lentii* (Kell.) Kuntze, Rev. Gen. Pl. 1: 154. 1891.—HOLOTYPE: Cedros Island, *Veatch s.n.*, 1859 (CAS! Photo: MO!).

Rounded evergreen shrub, 1 to 3 m high, with stout, often red-maroon, puberulent twigs with scattered reddish-brown lenticels. Leaves simple, coriaceous, entire, often with subrevolute, whitish margins, distinctly pallid-veined with a fine reticulum of distinctly visible smaller veins, upper surface brownish-green to gray-green, glaucous, lower surface lighter green to tan, less often glaucous; lvs. 2.0 to 6.0 cm long, 1.5 to 4.5 cm wide, deltoid, orbicular to subovate, apex rounded-obtuse to subacute, base rounded-obtuse, less often cordate, upper surface minutely pubescent, lower surface densely tomentose-villous. Petioles often reddish-maroon, stout, pubescent, 2.0 to 8.0 mm long. Inflorescence a terminal, open panicle, *ca.* 5 cm long, slightly narrower; bracts deciduous, ovate, *ca.* 3 mm long, *ca.* 2 mm wide, whitish, pubescent, apex acute; flowers short pedicellate, pedicel *ca.* 2.5 mm wide, pilose on outer surface and ciliate with simple trichomes; petals whitish-pink to deep rose (rose to yellow when dried), ovate-deltoid, *ca.* 3 mm long and 3.5 mm wide in hermaphrodites, glabrous on outer surface, pilose at base of inner surface, ciliate with simple trichomes; stamens shorter than sepals in female flowers, slightly exserted in hermaphrodites. Fruit a drupe, *ca.* 14 mm in diameter, pubescent with red, glandular and simple trichomes.

Representative specimens:

MEXICO: Baja California Sur: Cedros Island: *Anthony 98 & 305* (MO, SD, UC); *Brandegee s.n.* (SD, UC); Grand Canyon, 3 mi E from coast, *Haines & Hale s.n.* (LA, UC); wash bottom 0.5 mi W of village, *Haines & Hale 183* (CAS, LA, MO, SD, UC); North Head, *Lindsay 2151* (SD, UC); spring above village, *Moran 10600* (SD, UC); arroyo in middle of E coast, *Moran 10695* (SD); canyon on E side 4 mi from N end, *Moran 15167* (SD, UC). Mainland: Aguaje de San Andrés S of Cerro Elefante, *Gentry 7465* (ASU, SD, UC); mountains SE of Aguaje de San José, *Gentry 7786* (SD, UC); arroyo 4 mi N of San Andrés, *Moran & Reveal 19809* (RSA, SD).

Rhus integrifolia (Nutt. in Torr. & Gray) Brew. & Wats. × Rhus lentii Kell.

Rhus integrifolia var. *cedrosensis* Barkley, Ann. Missouri Bot. Gard. 24: 363. 1937.—*Schmaltzia integrifolia* var. *cedrosensis* (Barkl.) Barkley, Amer. Midl. Natur. 24: 651. 1940.—HOLOTYPE: Cedros Island, Baja California, Mexico, 11 March 1911, *Rose 16134* (NY! Photo: MO!).

Hybrids between the species are similar in general habit to that of the species. Major diagnostic features are: leaves simple to trifoliolate, coriaceous, entire, more or less intermediate in shape to that of parents, subglabrous to puberulent, 3.0 to 6.0 cm long, 2.0 to 4.0 cm wide. Petioles 3 to 12 mm long. Inflorescence much looser and more elongate than in either

parent, with more or less deciduous bracts; flowers short pedicellate to sessile. Sepals pinkish-rose and ciliate with simple and glandular (often malformed) trichomes. Occasional on the west side and northern end of Cedros Island at the interface of the Vizcaino Desert and chaparral-coastal sage scrub vegetations.

Representative specimens:

MEXICO: Baja California: Cedros Island: Mt. Katherine, *Haines & Hale s.n.* (UC); edge of pine grove near summit of main divide, *Haines & Hale s.n.* (UC); *Mason 2039* (CAS).

SUMMARY

Populations of *Rhus integrifolia* (Nutt. in T. & G.) Brew. & Wats. and *Rhus lentii* Kell. on Cedros Island were studied and, based upon morphological features, a number of putative hybrids were found in areas where the two species were sympatric. On the west side of the island, hybrids were almost entirely restricted to an ecotone (intermediate habitat) between island chaparral-coastal sage scrub (*R. integrifolia*) and Vizcaino Desert vegetation (*R. lentii*), and there was little evidence of introgression. Diagnostic features of value in distinguishing the species and their hybrids are leaf pubescence and morphology, sepal pubescence, and inflorescence morphology. Although this interspecific hybrid has been formally recognized as a variety (*Rhus integrifolia* var. *cedrosensis* Barkl.), as was true for the hybrid between *R. integrifolia* and *R. ovata* Wats. on Santa Catalina Island (*Rhus ovata* var. *traskiae* Barkl.), such recognition is misleading.

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