SPINELESS PETIOLES IN *WASHINGTONIA FILIFERA* (ARECACEAE)

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SPINELESS PETIOLES IN *Washingtonia filifera* (ARECACEAE).—The flattened petioles of the desert fan palm, *Washingtonia filifera* (Lindl.) Wendl. are described as being more or less spiniferous (Munz, A flora of Southern California, Univ. California Press, 1974) or as having spines along either edge (Shreve and Wiggins, Vegetation and flora of the Sonoran Desert, Stanford Univ. Press, 1964). Spines are usually assumed to aid in the protection of plant tissue from herbivore attacks (Louw and Seely, Ecology of desert organisms, Longman Group, 1982). In *W. filifera,* spine density is greatest around the apical meristem where the emergent, spine-covered petioles are in closest proximity to each other.

I have examined over 300 specimens of *W. filifera* and found that petiole spines are absent or nearly so in individuals exceeding 14 m in height (Fig. 1). The spines also are absent on distal ends of petioles in trees exceeding 8 m in height and cover a decreasing percentage of the petiole in taller trees (Table 1). These tendencies persist regardless of whether the trees are growing under cultivated or natural conditions.

If the spines function to deter herbivores from consuming vital plant tissues, then it can be assumed that petiole spines in small to intermediate individuals of *W. filifera* have evolved as a result of the protection afforded the apical meristem. (Extensive damage to this portion results in death of the tree because *Washingtonia* does not produce vegetative offshoots as do some palms.) It appears, however, that the utility of this protection decreases or is lost as *W. filifera* exceeds 14 m in height. Palms that develop spines only when small to intermediate may be at a selective advantage if energy for spine development is utilized for a more beneficial trait as the trees become taller and the utility of armament decreases.

Other than the infrequent nibbling of seedlings by desert cottontails (*Sylvilagus audubonii*) and the browsing of leaf tips by domestic cattle (in the three locations where livestock and native palms occur together), no known herbivores consume the foliage of *W. filifera* today. During past geological epochs, numerous mammals existed within the present range of *W. filifera,* and some probably browsed upon palms. No known species, however, could have browsed upon palms exceeding 12 m in height. The giant camel, *Titanotylopus,* occurred throughout southern California during the Pliocene and Pleistocene epochs, but had a vertical reach of just 5 m (D. Whistler, pers. comm.). Ground sloths were widespread in western North America during the Pliocene and Pleistocene (Anderson, *In* Martin and Klein, eds., Quaternary extinctions, Univ. Arizona Press, 1984). The largest sloth known from the southern half of California is the big-tongued sloth, *Glossotherium* (Stock, Rancho La Brea, Los Angeles Co. Mus. Nat. Hist., 1956). When erect, this sloth could not reach more than 5 m (G. Jefferson, pers. comm.). Mastodons (*Mammut*) appeared in the Miocene and persisted into the early Holocene in southern California. Some stood 3 m at the shoulder and had a vertical reach of about 6 m (Anderson 1984). Mammoths (*Mammuthus*) were the largest terrestrial herbivores to occur in western North America from the Pliocene forward. Their fossils are abundant and widespread throughout the West (Agenbroad, *In* Martin and Klein 1984). They are believed to have fed upon a tremendous variety of plant material, including palms, but did not have a vertical reach of more than 9 m (G. Jefferson, pers. comm.).

Whether or not these herbivores were sympatric with *Washingtonia,* and thus able to provide the selective pressure behind the development of spined petioles in young palms, is conjecture. No fossils attributable to *Washingtonia* have been identified. Natural populations of *W. filifera* are presently confined to the Sonoran Desert of southeastern California, Baja California, and western Arizona (Vogl and McHargue,

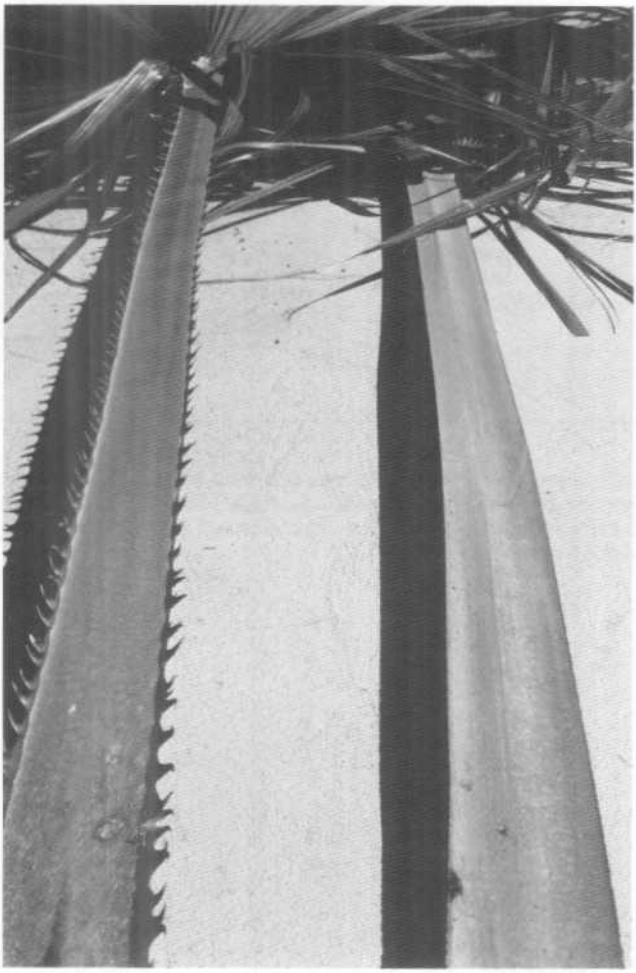

FIG. 1. Leaves of *Washingtonia filifera*: left, spines on a petiole from a 4 m palm; right, a spineless petiole from a 12 m palm.

Ecology 47:532–540, 1966; Brown et al., J. Ariz. Acad. Sci. 11:37–41, 1976). Axelrod (*In* Barbour and Major, eds., Terrestrial vegetation of California, Wiley and Sons, 1977) implies that *Washingtonia* had a broader range in past epochs than at present. In addition, palm fossils of Pliocene age, assigned to the genus *Sabal,* occur over much of the southern half of California including what is now the Mojave Desert (Axelrod, Evolution 2:127–144, 1948). These fossils may be misidentified. The taxonomic affinity of fossil palm leaves from California is based (in part) upon the presence or absence of spines on the petioles (Axelrod, pers. comm.). As I have shown, however, the petioles of *Washingtonia* may lack spines and therefore could be assigned erroneously to the genus *Sabal.*

TABLE 1. PERCENT OF SAMPLED TREES OF *Washingtonia filifera* (BY HEIGHT CATEGORY) WITH SPINES ON ALL OR PART OF PETIOLES. n = number of trees in each catergory.

Palm height categories (meters)	n	Percent of petiole length covered with spines										
		100	90	80	70	60	50	40	30	20	10	0
0–4	20	100										
4–6	18	72	11	6		6			6			
6–8	33	55	6	6	3	3	12		9	3	3	
8–10	24	4		8	8		13	8	4	29	25	
10–12	43			2	2	2	4	4	2	12	58	12
12–14	34								3	21	50	26
14–16	45									4	42	53
16–18	59										25	75
18–20	29										10	90

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