

Kanaloa, a New Genus of Fabaceae (Mimosoideae) from Hawaii

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ABSTRACT. *Kanaloa kahoolawensis* Lorence & K. R. Wood, a new genus and species of Fabaceae subfamily Mimosoideae tribe Mimoseae, is described from the Hawaiian Island of Kaho'olawe. Based on morphology, wood anatomy, pollen structure, and chromosome number ($2n = 28$), *Kanaloa* is described as a monotypic genus of shrubs allied to genera belonging to the *Leucaena* and *Dichrostachys* groups of Mimoseae, from which it is differentiated by its tergeminate leaves, monospermous fruits inertly dehiscent along two sutures with the valves separating into inner and outer envelopes, and large cordiform seeds. The new genus is extremely rare and currently known from only two remaining plants on Kaho'olawe, a small, arid, and highly disturbed island. Fossil pollen attributable to *Kanaloa* has been found in core samples from low-land sites on O'ahu dating to the early Pleistocene.

Because of their great isolation and considerable age, the Hawaiian Islands harbor a unique and remarkable flora with a higher degree of endemism—about 90% of the angiosperms—than any comparable area of the world. These islands have been relatively well botanized, and the angiosperm flora of Hawai'i is well known from a modern floristic treatment (Wagner et al., 1990). Therefore, the discovery of an unusual leguminous shrub not assignable to any genus known from Hawai'i was an unexpected surprise, particularly on an island as small and degraded as Kaho'olawe.

Kaho'olawe is the smallest of the major Hawaiian Islands (Fig. 1), with a surface area of 116 km² and a maximum elevation of 450 m. The island is arid due to its low elevation and location in the rain shadow of the much larger Maui. Study of the numerous archaeological sites on Kaho'olawe indicates it was inhabited by Hawaiians from about A.D. 1000, and by the time of Western contact in 1779 much of the island's vegetation had been cleared for agriculture (Kirch, 1985: 144–154). Kaho'olawe was used as a penal colony by the Hawaiian monarchy from 1826 to 1853 after which it was leased for ranching (Perlman, 1992). Although Kaho'olawe proved too dry and barren for successful ranching operations, feral goat and sheep populations became established and devastated the island's little remaining vegetation, resulting in massive soil erosion (Kirch,

1985). During World War II the island was appropriated by the U.S. military for training troops and as a target for ship-to-shore guns and aerial bombing. It is still used as a bombing target by the U.S. Navy. The central plateau of Kaho'olawe now consists of a barren lateritic hardpan whose soil has been lost by erosion. Conservation efforts to restore the island's vegetation and control feral animals are now being undertaken by the Department of Land and Natural Resources of the State of Hawai'i and the Protect Kaho'olawe 'Ohana, a native Hawaiian activist organization. There is currently a movement to return the island to the State of Hawai'i for management by ethnic Hawaiians, practice of Hawaiian culture, and educational purposes.

While participating in a botanical survey of Kaho'olawe conducted by The Nature Conservancy of Hawaii in March 1992, the second author and Steve Perlman, field collectors for the Hawaii Plant Conservation Center (HPCC) of the National Tropical Botanical Garden, found an unusual shrubby Fabaceae. Subsequent visits revealed a second individual located nearby. Both plants were confined to native coastal shrubland on 'Ale'ale Stack (Fig. 1), a steep rocky spire almost separated from the main island by erosion (Perlman, 1992). Herbarium specimens were studied by botanists familiar with the Pacific islands' flora and Fabaceae specialists, none of whom recognized the plant. It was also run through the keys in treatments for Hawaiian Fabaceae (Geesink et al., 1990; Rock, 1920) and for all known genera of Mimosoideae (Lewis & Elias, 1981) without arriving at a satisfactory generic placement. An examination of specimens at the BISH, NY, and PTBG herbaria yielded nothing comparable to this extraordinary plant. Subsequent study of the plant's morphology, wood anatomy, chromosome number, and pollen has convinced us that it represents a new genus with unclear affinities belonging to subfamily Mimosoideae, tribe Mimoseae.

Kanaloa kahoolawensis Lorence & K. R. Wood, gen. et sp. nov. TYPE: Hawaiian Islands. Kaho'olawe: Makawao District, 'Ale'ale stack, near Pu'u Koa'e, mixed native coastal shrubland, 45 m, 18 Mar. 1992, K. R. Wood, S. Perlman, J. Lau & C. Rowland 1733 (holotype, PTBG; isotypes, BISH, US). Figure 2.

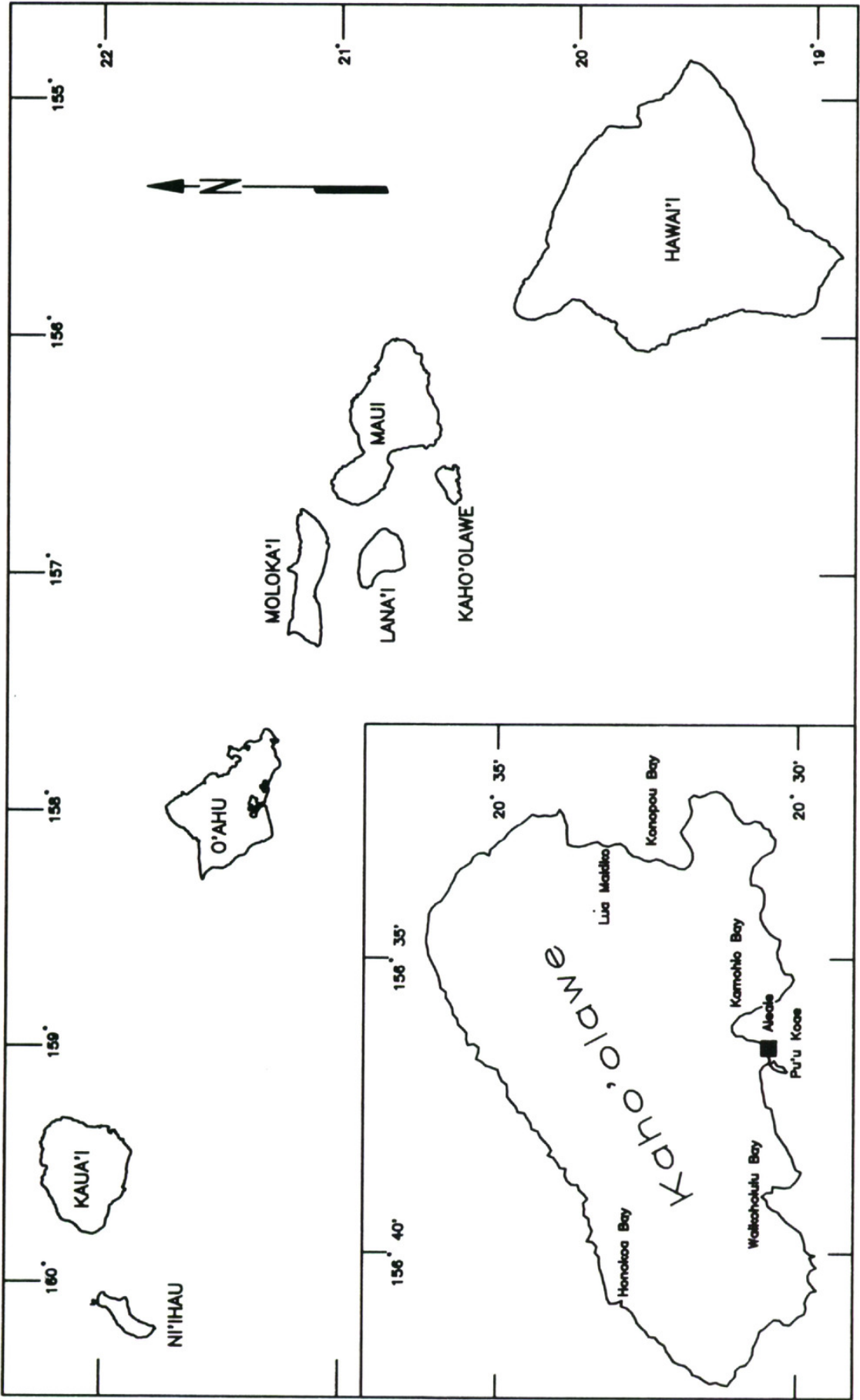


Figure 1. Map of main Hawaiian Islands, with inset of Kaho'olawe showing location of *Kanaloa* population.

Frutices inermes. Folia stipulis liberis, ovatis, crassis, persistentibus; petiolo apice nectarium cupuliforme sessile unicum adaxialiter gerenti; lamina tergeminata, i.e., pinnis duabus utraque apice foliolorum par unum etiam basi foliolum proximale unicum gerenti. *Flores staminati* numerosi in capitulos globosos dispositi, 5-meri, unusquisque bractea peltata subtentus; calyce obconico, lobulis parvis alabastro valvatis; petalis alabastro valvatis, oblanceolatis; staminibus 10 exsertis, basi connatis, antheris ellipsoideis dorsifixis glabris extrorse dehiscentibus, polline tricolporatum in monates disperso. *Flores hermaphroditi* non visi. *Fructus* breviter stipitati bivalvati compressi, ex obovatis suborbiculares, utrinque dehiscentes, ut videtur uniseminales; endocarpio papyraceo ab exocarpio secedenti; semine compresso irregulariter cordiformi, pleurogramum humile immersum gerenti.

Shrubs 0.75–1 m tall, unarmed, densely branched, the branches decumbent, 0.75–1.5 m long, the new growth densely brown hirtellous-villosulous with straight and curly, white and brown simple trichomes 0.1–0.3 mm long, the twigs 2–4 mm diam., brown, longitudinally ribbed or angled, becoming whitish gray with corky fissures, knobby with large rounded buds and persistent stipules and leaf bases, the leaves clustered near twig tips, brachyblasts absent; stipules free, paired, ovate, 1.5–2 mm long, 1.2–1.5 mm wide, densely villosulous, the apex acute, antrorsely curved, the thickened bases persistent, transversely fissured; leaves tergeminate bipinnate, the petiole 6–24 mm long, 0.8–1 mm diam., white hirtellous and brown villosulous, apically with a single leaf nectary adaxially at junction with pinnae, 0.5–0.8 mm diam., ellipsoid, sessile, the margin hirtellous, the concavity glabrous; pinnae one pair, 22–55 mm long, each pinna bearing a pair of terminal leaflets and a single smaller proximal leaflet basally, the pulvinules hirtellous, 1–1.5 mm long, the rachis terminated by a short, acute brown appendage; leaflets unequal-sided, ovate-elliptic, $1.4\text{--}4.2 \times 0.9\text{--}3.2$ cm, the base truncate to subcordate, the apex obtuse or rounded, stiffly chartaceous, discolorous, finely strigillose below when young, the margin ciliate, the 2° veins 3–4 on a side, the ultimate venation finely reticulate, visible to 5° on both surfaces. Inflorescences 1–3 per leaf axil, developing with a flush of new leaves, the peduncle $8\text{--}30 \times 0.4$ mm, hirtellous, the capitula 6–8 mm diam. including stamens; bracteoles 1–1.5 mm long, the peltate apex villosulous. Flowers white, 20–54 per capitulum. Staminate flowers with calyx limb obconic, 1–1.3 mm long, densely white villosulous in apical $\frac{1}{3}$; calyx lobes 5, valvate in bud, 0.1–0.2 mm long, triangular, incurved, brown-villosulous; corolla valvate in bud, the petals $1.5\text{--}1.8 \times 0.5\text{--}0.7$ mm, oblanceolate, cucullate, apiculate, 1-veined, externally hirtellous apically, separate at base; stamens 10, exserted, the filaments 2–3 mm long, glabrous,

connate at base, the anthers dorsifixed, ellipsoid, 0.6–0.8 mm long, glabrous, lacking glands, the dehiscence extrorse; vestigial gynoeceum subsessile, 0.5–0.7 mm long, the stigma truncate; disc absent. Hermaphroditic flowers not seen. Pollen tricolporate, in monads. Fruits on a stipe 4–5 mm long, up to 4 per capitulum, $2.4\text{--}3.2 \times 2\text{--}2.3$ cm, obovate or subcircular, compressed, coriaceous, externally hirtellous basally, with transverse cross veins, 2-valved, inertly dehiscent along both thin margins, the valves separating into inner and outer envelopes, the slender brown seed funicle 2–3 mm long; seed 1 per fruit, cordiform, brown, $1\text{--}1.3 \times 1.1\text{--}1.6$ cm, with a low inset pleurogram. $2n = 28$.

Distribution. Known only from Kaho‘olawe, where two plants were found growing on a small, spirelike peninsula known as ‘Ale‘ale stack located at Kamohio Bay on the island’s south coast at $20^{\circ}30.79'N$, $156^{\circ}36.30'W$.

Habitat. Kanaloa occurs on steep, rocky talus slopes at 45–60 m elevation with a substrate consisting of oxisols derived from basaltic lavas. The area harbors intact mixed native coastal shrubland with *Sida fallax* Walpers, *Senna gaudichaudii* (Hooker & Arnott) H. Irwin & Barneby, *Bidens mauiensis* (A. Gray) Sherff, *Lipochaeta lavarum* (Gaudichaud-Beaupré) DC., and *Portulaca molokiniensis* Hobdy as dominant species. Other associates include *Heteropogon contortus* (L.) P. Beauvois ex Roemer & Schultes, *Chamaesyce celastroides* (Boissier) Croizat & Degener var. *amplectens* (Sherff) Degener & I. Degener, *Capparis sandwichiana* DC., *Waltheria indica* L., *Doryopteris decipiens* (Hooker) J. Smith, *Portulaca villosa* Chamisso, *Ipomoea tuboides* Degener & Ooststroom, *Mariscus phleoides* Nees ex Kunth subsp. *phleoides*, *Eragrostis atropioides* Hillebrand, *Panicum fauriei* Hitchcock var. *latius* (St. John) Davidse, and *P. torridum* Gaudichaud-Beaupré. Some of these native plants are rare Hawaiian endemics, the only alien species being *Emelia fosbergii* Nicolson, *Chloris barbata* (L.) Swartz, and *Nicotiana glauca* R. C. Graham. The area is also a nesting site for Bulwer’s petrels and wedge-tailed shearwaters. The fact that ‘Ale‘ale stack is almost separated from Kaho‘olawe by a gap too steep for goats to cross explains the existence of the intact mixed coastal shrubland at this site.

Phenology and reproduction. The plants were observed to be briefly deciduous in October, after which a flush of new leaves was produced and partial expansion of the flower buds occurred. Brief flowering periods, apparently lasting only a few days, took place after heavy rains in November and again

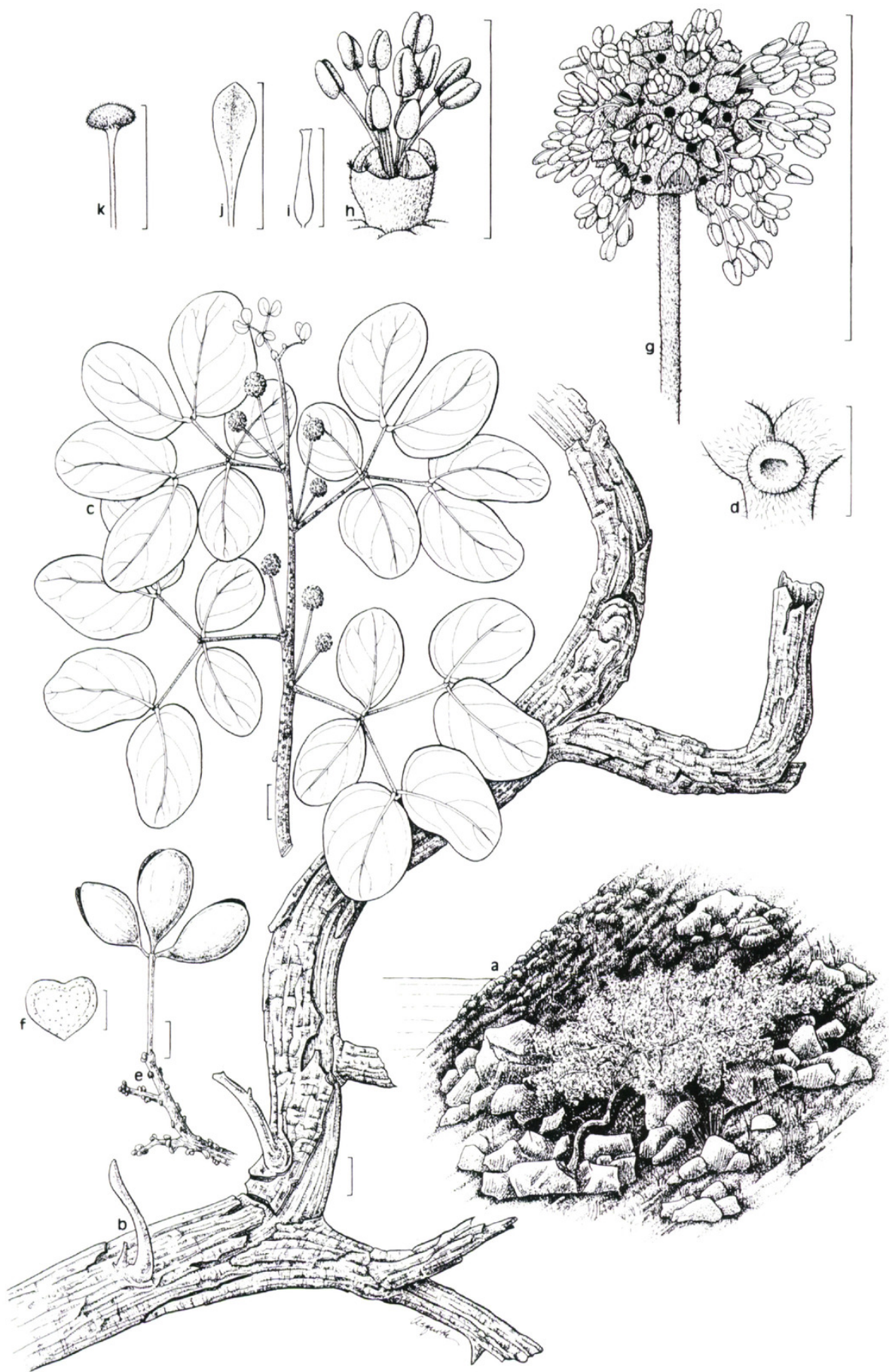


Figure 2. *Kanaloa kahoolawensis* Lorence & K. R. Wood. —a. Habit and habitat. —b. Branch. —c. Flowering twig. —d. Nectary on petiole apex. —e. Infructescence. —f. Seed. —g. Head of staminate flowers at anthesis. —

in April or May. No young plants were observed, although old stems of approximately 12 to 15 dead individuals were seen nearby. No hermaphroditic flowers were found among the numerous capitula examined (mostly fallen dried capitula, plus several fresh ones from cuttings in the HPCC nursery). The paucity of hermaphroditic flowers may account for the plants' low fruit set and fecundity; only four fruits were found on one plant and one old fruit under the other. Environmental conditions or stress appear to influence the proportion of hermaphroditic versus male flowers produced in *Desmanthus* Willdenow (M. Luckow, pers. comm.), and this also may be the case in *Kanaloa*.

Paratypes. HAWAIIAN ISLANDS. **Kaho'olawe:** Makawao District, 'Ale'ale stack, near Pu'u Koa'e, 50° NE aspect, 45–60 m, 17 May 1992, *Wood et al.* 1922 (PTBG), 14 July 1992, *Wood & Perlman* 2006 (NY, PTBG), 2 Sep. 1992, *Wood* 2070 (K, PTBG), 16 Oct. 1992, *Wood & Perlman* 2121 (NY, OXF, PTBG), *Wood & Perlman* 2122 (PTBG), 14 May 1993, *Lorence et al.* 7379 (BH, PTBG), *Lorence et al.* 7380 (PTBG).

Nomenclature. The discovery of this new genus was first alluded to in an article by its co-discoverer in June 1992 (Perlman, 1992). Subsequently Yoshioka & Gon (1993) used our name *Kanaloa kahoolawensis* [but without author, Latin diagnosis, citation of a type or other specimens] when referring to the plant in a popular article on Kaho'olawe published in March 1993. Although Yoshioka and Gon obviously did not intend to validly publish the name, its premature and unauthorized use was unfortunate, resulting in publication of a nomen nudum.

Etymology. *Kanaloa* is the name of a major Hawaiian deity closely associated with Kaho'olawe. According to Hawaiian legend, *Kanaloa* used the island as a place where he could rest and recoup his energies. Consequently, the island is dedicated to *Kanaloa*, which was used as an alternate name for Kaho'olawe: "kohe malama malama o *Kanaloa*," meaning the place or womb for the resuscitation of *Kanaloa* (Abraham Piianaia, pers. comm., 1992). *Kanaloa* also means "secure, firm, immovable, established, unconquerable" (Pukui & Elbert, 1986). Such attributes are certainly essential for this plant to have survived despite the severe degradation of the island.

Pollen morphology (contributed by Jerome V. Ward). A pollen sample was obtained from fallen

capitula collected in the litter layer beneath one of the plants (*Wood & Perlman* 2006, voucher PTBG). Anthers were removed from flowers, treated with KOH and acetolysis solution, mounted in glycerine jelly (Erdtman, 1960), and examined in light microscopy (LM). For scanning electron microscopy (SEM), pollen residue in alcohol was strewn onto a stub, coated with gold-palladium, and viewed in a Hitachi S570 scanning electron microscope. Samples for transmission electron microscopy (TEM) were prepared using the technique outlined by Skvarla (1966, 1973) except that the pollen was concentrated in SeaPlaque agarose, and after dehydration the material was embedded in Spurr's resin. Thin sections were collected on 200 mesh copper grids, stained with 10% uranyl acetate in 100% methanol and 0.4% aqueous lead citrate, and examined with a Philips 301 transmission electron microscope.

The pollen of *Kanaloa kahoolawensis* (Fig. 3a–h) is spheroidal to subspheroidal, with the polar and equatorial diameter range of 26–41 μm and a mean of 31 μm ($n = 30$). The grains are tricolporate monads with conspicuous subcircular annulate endoapertures (ora) visible in light microscopy (Figs. 3c, d). The colpi are long with distinct margins, revealing a finely granular membrane. In SEM the surface sculpturing is seen to be comprised of anastomosing muri forming a finely rugulate pattern, with their loose ends extending slightly from the exine surface.

In TEM the exine structure has a tectal and a columellar or interstitium layer of about equal thickness, each comprising about 27% of the total exine. The lower tectal surface also shows a finely rugulate pattern in TEM (Fig. 3h), but the elements are finer than those found on the outer surface. The columellae are intermediate in complexity, being irregular in shape, of varying thickness, and occasionally branched. In some sectional views (Fig. 3h) interstitial muri can be seen to project vertically from the foot layer and merge with the tectal sculpture above. The foot layer comprises about 35% of the exine, while the endexine at equatorial mesocolpium is thinner than any other layer at around 11% of the total thickness. In the lower portion of the foot layer, thin lamellae are visible which intergrade into the upper endexine and become more evident there due to the contrast difference. The lower endexine is irregular over much of the surface. Under the

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h. Staminate flower. —i. Vestigial pistil from staminate flower. —j. Petal. —k. Peltate floral bract. Scales b, c, e, f, g = 1 cm, d = 2 mm, h = 3 mm, i = 1 mm, j, k = 1.5 mm. (Composite drawing based on type, cited specimens, and photos.)

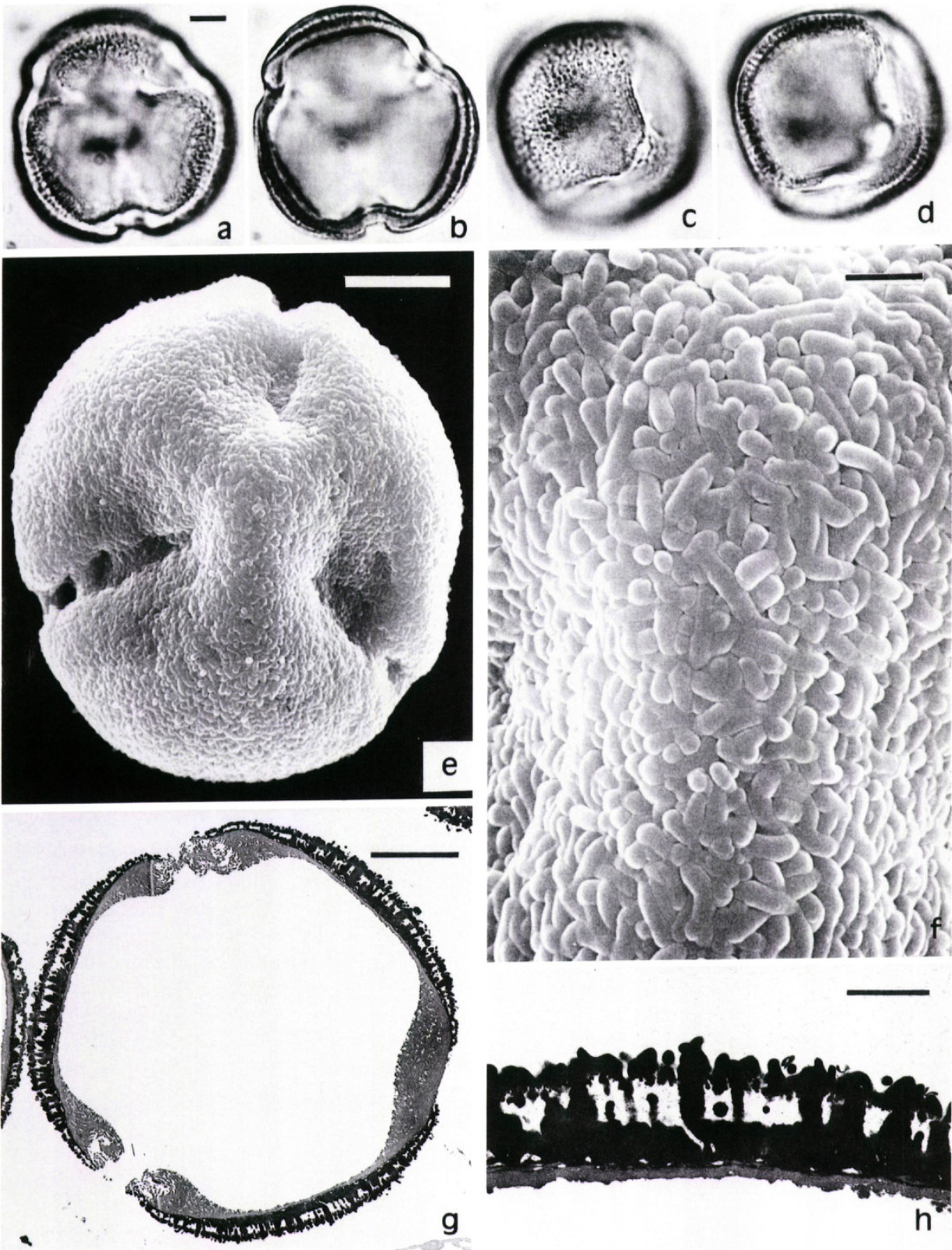


Figure 3. Pollen of *Kanaloa kahoolawensis* Lorence & K. R. Wood in light and electron microscopy. a–d. Light micrographs in high and mid foci. —a, b. Polar view. —c, d. Equatorial view showing prominent os. —e. SEM in polar view. —f. SEM of surface showing detail of finely rugulate sculpture. g, h. TEM, transverse section. —g. Whole grain. —h. Close-up of same section showing exine stratification. Scales a–e, g = 5 μ m, f, h = 1 μ m. (From Wood & Perlman 2006, PTBG.)

apertures the endexine becomes much thicker and is lamellated, while the foot layer thins.

The pollen of Mimosoideae has been shown to be tectate, predominately occurring in compound units with a granular infratectal structure and porate apertures (Guinet, 1981a, 1981b). The tricolporate single grain is probably the basic or unspecialized type within the subfamily (Guinet, 1981a). Single tricolporate pollen with tectate columellar structure is uncommon within the Mimosoideae but occurs more frequently in certain genera (Guinet, 1981a). This condition is typical of the *Dichrostachys* (DC.) Wight & Arnott group (including *Desmanthus*, *Dichrostachys*, *Gagnebina* Necker ex DC., and *Neptunia* Loureiro), and the *Leucaena* Benth group (including *Leucaena* and *Schleinitzia* Warburg) sensu Lewis & Elias (1981). Both *Dichrostachys* and *Gagnebina* have mostly compound pollen (tetrads or polyads), although monads with coarsely verrucate sculpture occur in the *Dichrostachys cinerea* (L.) Wight & Arnott group. *Schleinitzia* has large compound grains that are loosely attached (acalymmate), as shown by Nevling & Niezgoda (1978). The remaining three closely related genera, *Desmanthus*, *Neptunia*, and *Leucaena*, show the closest resemblance to the new taxon in pollen morphology. *Neptunia* and *Desmanthus* produce exclusively tricolporate monads, and nearly all species have striate to rugulo-striate sculpture pattern; *Neptunia* has, in addition, annulate endoapertures. Both genera have well-developed columellae, which would be expected, since Guinet (1981a) has shown this character to correlate with the tricolporate condition. Of the approximately 40 species of *Leucaena*, only two (*L. glabrata* Rose and *L. gregii* S. Watson) form tricolporate monads with rugulate to subrugulate sculpture similar to grains of *Kanaloa*.

Remarkably, fossil pollen attributable to *Kanaloa* (Unknown Tricolporate Type 1 of Athens et al., 1992, and Legume Type of Athens & Ward, 1993) was recovered from Quaternary lowland deposits on Maui and O'ahu, which indicates *Kanaloa* once had a more widespread distribution (Jerome Ward, pers. comm., 1994). On O'ahu, pollen data confirm the presence of *Kanaloa* from early Pleistocene to about 800 years B. P., when it was extirpated as a result of human destruction of the lowland forest (Athens et al., 1992; Athens & Ward, 1993).

Chromosome number (contributed by Michael Kiehn). *Kanaloa kahoolawensis* has $2n = 28$ chromosomes. This mitotic number has been established from two different chromosome fixations: a field fixation (Wood 2070, voucher PTBG) and a fixation from cuttings of the same collection at the National Tropical Botanical Garden nursery (MK-920902-

1/4). The fixations were made in a fresh 3:1 mixture of 96% ethanol and glacial acetic acid. After hydrolysis in 5 N HCl for 50 minutes at 20°C, chromosomes were stained using the Feulgen method, as other staining methods (e.g., aceto-carmine or Giemsa) gave only poor results. Counts were carried out on several cells from young flower buds: meristematic cells of developing corolla lobes from very young buds, and cells from young anthers before the first meiotic division. In prometaphase most of the chromosomes measure between 1.4 μm and 2.0 μm , but one pair is longer (ca. 2.4–2.6 μm). All chromosomes are clearly structured and most are metacentric to submetacentric. Besides having prominent centromeres, at least two of the chromosomes of the diploid set seemingly have secondary constrictions, and at least one pair of NOR-chromosomes is present.

A base number of $x = 14$ is indicated for the Mimosoideae (Goldblatt, 1981). In the *Leucaena* group counts of $2n = 36, 52, 56$, and 104 have been published for *Leucaena*, and $2n = 52$ and 54 for *Schleinitzia* (Lewis & Elias, 1981; Geesink et al., 1990). In the *Dichrostachys* group the following numbers have been reported (Lewis & Elias, 1981; Goldblatt, 1981): $2n = 26$ for *Gagnebina*, $2n = 28$ for *Desmanthus*, $2n = 28, 36, 54, 56, 78$ for *Neptunia*, and $2n = 50, 56$ for *Dichrostachys*. Although a count of $2n = 28$ for *Kanaloa* is consistent with base numbers of $x = 14$ for a number of genera in Mimoseae, a comparison of chromosome morphology may further elucidate affinities of *Kanaloa* with other genera.

Wood anatomy (contributed by Regis B. Miller). The wood anatomy description is based on a branch sample (Wood et al. 1922, MADw 46696). All features listed in the IAWA Standard List (IAWA Committee, 1989) were examined. Features not specifically mentioned are either absent or not applicable. No main stem heartwood was available, and thus several macroscopic features could not be analyzed. The following description treats only the microscopic features.

Growth rings distinct (separated by marginal bands of parenchyma and the crowding of vessels in the earlywood); diffuse-porous. Vessels in short radial multiples; 85–120 per mm^2 ; 42–66 μm in tangential diameter; 140–340 μm in element length. Perforation plates simple. Intervessel pits vestured; alternate; circular or oval; 5–6 μm diam.; vessel-ray pitting with distinct borders; similar to intervessel pits in size and shape. Helical thickenings absent. Tyloses infrequent or absent. Fibers septate; thin-to thick-walled; 413–679 μm in length; pits simple to minutely bordered. Vascular or vasicentric tra-

cheids absent. Paratracheal parenchyma vasicentric, aliform, and confluent (confluent parenchyma only occasionally present). Aliform parenchyma winged type. Banded parenchyma in marginal (or seemingly marginal) bands. Axial parenchyma mostly 2–4 cells per parenchyma strand (sometimes fusiform parenchyma cells also present). Rays homocellular, typically procumbent; 4–12 per mm (mostly 9–15); exclusively uniseriate (rarely in part biseriate); 125–233 μm in height. Storied structure not observed. Prismatic crystals abundant and in chambered axial parenchyma (very long chains); one crystal per cell or chamber. Silica absent.

The wood anatomy of *Kanaloa* falls within the range of variability exhibited by *Leucaena* (material of the other genera in the *Leucaena* and *Dichrostachys* groups was not available for comparison). Features similar in both genera include septate fibers, similar sized and shaped intervessel and vessel-ray pits, general parenchyma pattern, and non-storied homocellular rays. The major difference between the two genera is ray width; exclusively uniseriate in *Kanaloa* and multiseriate (generally 2–5 cells) in *Leucaena*. However, most quantitative features such as vessel diameter and frequency, ray height and width, and vessel element and fiber length are smaller, more numerous, or shorter than those of *Leucaena*. These trends may be attributed to habit (*Leucaena* usually a tree vs. *Kanaloa* a shrub), habitat, or the fact that the only sample of *Kanaloa* studied is from a branch.

Affinities. Using the Mimoseae treatment of Lewis & Elias (1981), *Kanaloa* keys out to their *Leucaena* group (which includes *Leucaena* and *Schleinitzia*) or *Dichrostachys* group (which includes *Desmanthus*, *Dichrostachys*, *Gagnebina*, *Neptunia*, and the recently described *Calliandropsis* H. Hernández & Guinet). Nevertheless, *Kanaloa* does not fit readily into genera of either group. Features which *Kanaloa* shares with one or more members of these two groups include: lack of spines or prickles; presence of sessile foliage glands; sepals valvate; petals valvate and free to the base; stamens connate only at base; anthers glabrous and eglandular; pollen grains tricolporate monads; ovary sessile or shortly stipitate; fruit unjointed; and seeds compressed. *Kanaloa* shares the following specialized characters with certain of these genera: inflorescence a head (with *Leucaena*, *Schleinitzia*, and *Desmanthus*); absence of an involucre (with the *Dichrostachys* group); flowers subtended by persistent peltate bracts (with *Desmanthus* and *Leucaena*). Specialized characters unique to *Kanaloa* include its tergeminate leaf formula, large cordiform seeds, and fruits that are small, apparently monospermous, coriaceous, unwinged, and inertly dehiscent along two sutures

with the valves separating into inner and outer envelopes.

Members of the *Leucaena* group have heads with persistent peltate floral bracts, apical bisexual flowers, and basal staminate flowers. Although only staminate flowers were observed in available inflorescences of *Kanaloa*, this character may be environmentally induced as fruit development requires at least occasional production of perfect flowers. *Schleinitzia* differs from *Kanaloa* in having anther-glands, acalymmate compound pollen grains, and slightly winged fruit valves that split at the edges but do not separate over the seed-chambers. *Kanaloa* most closely resembles *Leucaena* in lacking anther-glands and having unwinged fruits with valves splitting along both sutures at maturity. However, *Kanaloa* differs from both these genera in lacking an involucre under the capitulum and having unique monospermous fruits and cordiform seeds. Pollen of *Leucaena* is usually compound, but two species have pollen in monads like *Kanaloa*. Although the specialized tergeminate leaf formula of *Kanaloa* is unknown in the *Leucaena* and *Dichrostachys* groups, it has arisen independently in several other mimosoid genera including *Acacia* Miller, *Mimosa* L., and *Calliandra* Benth, and consequently represents a weak generic character with regard to the subfamily (R. Barneby, pers. comm., 1993).

The *Dichrostachys* group is characterized by: the presence of neuter or nonfunctional staminate flowers with showy staminodia toward the base of the inflorescence (sometimes caducous), a middle zone of staminate flowers, and hermaphroditic flowers toward the apex; free petals and stamens; a subsessile ovary; unjointed fruits; and the absence of a nectary disc. These features all occur in *Kanaloa*, although it differs by the absence of neuter staminodial flowers, extreme rarity or lack of hermaphroditic flowers (may be environmentally induced), and presence of peltate floral bracts. *Dichrostachys* differs from *Kanaloa* in having short shoots with spines or persistent fused stipules, spikes with sterile basal flowers and bisexual terminal ones, and pollen in tetrads or polyads, rarely in monads. *Gagnebina* differs in having elongate upper flowers in bud, basifixed linear anthers, compound pollen grains, and usually winged, indehiscent fruits. *Desmanthus* is distinguished from *Kanaloa* by its subsessile, generally linear fruits with multiple oblique or longitudinal seeds and subulate stipules usually with auricles. *Neptunia* differs from *Kanaloa* by its fruits with usually transverse seeds and ovate to lanceolate, striately nerved stipules. The stipules of *Kanaloa* look most like those found in the monotypic Mexican genus *Calliandropsis*, although the latter has very different floral bracts (M. Luckow, pers.

comm., 1993). Persistent stipule bases also occur in *Desmanthus* and *Dichrostachys* but are structurally quite different from those of *Kanaloa*. *Kanaloa* is set apart from genera in the *Dichrostachys* group by having large rounded buds, capitula with virtually all staminate flowers, peltate floral bracts (present in *Desmanthus*), inertly dehiscent monospermous fruits, and cordiform seeds. Unfortunately, we have not been able to locate hermaphroditic flowers of *Kanaloa* to study the style tip and ascertain whether or not the gynoeceum is truly uniovulate—a feature that would be unique in the Mimosoideae—or whether the fruits are monospermous by abortion.

In summary, *Kanaloa* shares certain morphological, wood anatomical, chromosomal, and palynological features with a number of genera in the *Dichrostachys* and *Leucaena* groups, but its unique combination of characters precludes its placement in any known genus. In terms of its chromosome number and pollen structure, *Kanaloa* is most similar to *Desmanthus*, *Neptunia*, and particularly *Leucaena*. Interestingly, Goldblatt (1981) noted a strong correlation between the occurrence of $x = 14$ and the primitive mimosoid condition of monad pollen. Wood anatomy of *Kanaloa* resembles that of *Leucaena* (but comparison to other genera is lacking). DNA studies of *Kanaloa* are currently in progress (Melissa Luckow, pers. comm., 1994), and these may shed more light on the phylogenetic affinities of this fascinating plant.

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