

DISCOVERY OF *ARDISIA* SUBGENUS *ACRARDISIA* (MYRSINACEAE) IN MESOAMERICA: ANOTHER BOREOTROPICAL ELEMENT?

John J. Pipoly III

Fairchild Tropical Garden

11935 Old Cutler Road, Coral Gables (Miami) FL 33156-4299, U.S.A.

jjpipoly@fairchildgarden.org; clusia@latinmail.com

Jon M. Ricketson

Missouri Botanical Garden

P.O. Box 299, St. Louis MO 63166-0299, U.S.A.

jon.ricketson@mobot.org

ABSTRACT

Ardisia rarescens, native to the border area of SE Chiapas, Mexico and SW Guatemala, was studied in preparation for a treatment of Myrsinaceae for the *Flora Mesoamericana* project. Its dextrorsely imbricate petals, extremely short free apical portions of the filaments, anthers whose wide longitudinal slit from each theca meet apically to form a subcontinuous opening at anthesis, short and broadly conical flower buds, and relatively numerous ovules on the rather thick placenta, precluded its placement in any known neotropical subgenus of *Ardisia*. Curiously, the aforementioned features comprise the diagnostic character states unique to the Indo-Malesian *Ardisia* subgenera *Acrardisia* and *Stylardisia*. Because subgenus *Stylardisia* is defined by its protogynous flowers (the style piercing the bud apex long before the bud opens), *Ardisia rarescens* can be excluded from that group and therefore placed in subgenus *Acrardisia* Mez. We suggest that *Ardisia rarescens* is a member of *Ardisia* subgenus *Acrardisia* and that this represents another species whose distribution may be attributable to the logical extension of the Boreotropics Hypothesis, previously explained in our work on the discovery of the genus *Hymenandra* in Mesoamerica. *Ardisia rarescens* is described, newly illustrated, its distributions, phylogenetic relationships, ecology and conservation status, are discussed.

RESUMEN

Ardisia rarescens fue estudiada para el tratamiento taxonómico de la familia Myrsinaceae para la Flora Mesoamericana. Sus pétalos dextrorsamente imbricados, porciones apicales libres de los filamentos que son muy cortas, anteras con dehiscencia comprendida por hendiduras longitudinales anchas y continuas en el ápice, botones corto- y anchamente cónicos en perfil, y óvulos relativamente numerosos y insertados en una placenta gruesa, se combinaron para indicar que no fue posible ubicar ésta especie dentro de un subgénero previamente conocido en el neotrópico. Sin embargo, los caracteres susodichos comprenden los que se define el género *Ardisia* subgéneros *Acrardisia*, y *Stylardisia*, ambos provenientes de la región Indo-Malesia. Debido al hecho de que se define el subgénero *Stylardisia* por sus flores protóginas, y que *Ardisia rarescens* no tiene esa cualidad, ubicamos la especie dentro del subgénero *Acrardisia*. Surgerimos que *Ardisia rarescens* es otro elemento, tanto como el género *Hymenandra* previamente reportado, cuya distribución se atribuya a la extensión lógica de la Hipótesis Boreotropical. Se describe, se ilustra y se discute su distribución, parentesco, ecología y estatus en cuanto a la conservación se refiere.

INTRODUCTION

The pantropical genus *Ardisia* Sw. is by far the largest in the family Myrsinaceae, containing perhaps as many as 500 species (Chen & Pipoly 1996). Its circumscription has been problematic owing to a lack of comprehensive treatment since that of Mez (1902) in Engler's *Pflanzenreich*, almost a century ago. While reviewing the status of *Ardisia rarescens* Standl., we observed the combination of: dextrorsely imbricate petals, extremely short free apical portions of the filaments; anthers whose longitudinal slits from each theca meet apically to form a subcontinuous opening at anthesis; short, broadly conical buds, and relatively numerous ovules on the rather thick (thicker than long) placenta, all characteristics of *Ardisia* subgenus *Acrardisia* Mez. With subgenus *Acrardisia*'s distribution from Sri Lanka eastward through Malaysia and Indonesia to the Philippines and New Guinea, it is strikingly similar to that of *Hymenandra* (A. DC.) A. DC. ex Spach, a group that we suspect is of boreotropical origin (Pipoly and Ricketson 1999). A distribution such as this, most closely fits those groups cited as partial evidence to support what Wendt (1993) discovered in his study of lowland Mexican wet forests, and what Lavin and Luckow (1993) attributed to the Boreotropics Hypothesis, proposed by Wolfe (1975) and Tiffney (1985a, b) to explain the distribution of the "boreotropical flora." The hypothesis proposes that the biotas of North America and Europe, including tropical North America, were once more widespread in the northern hemisphere and transgressed the North Atlantic by direct land connections or over limited water gaps until the late Eocene or early Oligocene (Lavin & Luckow 1993). A logical extension to Wolfe's and Tiffney's concept, presented by Wendt (1993) and Lavin and Luckow (1993) is that the boreotropical flora not only existed in the Eocene, but also left a significant number of direct descendant lines in present lowland tropical floras of northern Latin America. Therefore, we would expect that many of the early Tertiary fossil taxa from both North America and Europe were most closely related to extant species from tropical southeast Asia, and to some extent, Central America and the Greater Antilles (Lavin & Luckow 1993). It is the latter notion that is congruent with the Amphipacific distributional pattern like that found in our new concept of *Ardisia* subg. *Acrardisia*. This extension to the boreotropics hypothesis was cited by Wendt (1988, 1989, 1993), in discussing the relationships of *Chiangiodendron* (Flacourtiaceae), and by Zona (1990) in discussing the biogeography of *Sabal* (Arecaceae). A similar distribution for the genus *Alstonia* (Apocynaceae) was cited by Gentry (1983), but he did not invoke the hypothesis *per se*. Conran (1995), in his study of the Liliiflorae, found that three taxa defining the Southeast Asian/northern Australasian clade (Stemonaceae, Hanguanaceae and Uvulariaceae) were widespread northern taxa that have spread southwards.

The geographic distribution of subgenus *Acrardisia* is entirely consistent with the area cladogram presented by Lavin and Luckow (1993, Fig. 1), where Central and South American elements are ultimately derived from among diverse North American lineages, these lineages having a sister group relationship to paleotropical groups. While Wolfe's

(1975) hypothesis could be correct even if no modern descendants of the boreotropical flora were found in the Neotropics owing to extinction, the three criteria proposed by Lavin and Luckow (1993) to test the hypothesis were: 1) a center of diversity in North America (including "tropical North America" as they define it), 2) an early Tertiary fossil record in North America, and 3) a pantropical distribution.

For the first test criterion, "North America" includes both tropical and temperate elements, the tropical ones south of the Tropic of Cancer. In the case of subgenus *Acrardisia* it is clear that only one species is presently known, but until we have tested hypotheses of phylogenetic relationship among other related *Ardisia* species, in particular the group described by Lundell as *Ibarrea*, and containing the rather common species *Ardisia paschalis* Donn. Sm., we cannot be sure. Subgenus *Acrardisia* itself may be paraphyletic, because the only characteristics separating it from the extremely closely related subgenus *Stylardisia* Mez are that it does not have a stigma that perforates the flower bud and is receptive before the flower opens (thus protogynous), and that its ovules are pluri-rather than uniseriate. A group even partially defined by the lack of a structure can be problematic because it is not clear if protogynous flowers have occurred more than once within the genus *Ardisia* as a whole.

Unfortunately, no data is available for use in the second test criterion owing to lack of fossils known for the group. As for the last criterion, a pantropical distribution, the closest related group, *Ardisia* subgenus *Stylardisia*, is concentrated in Borneo, but occurs from northern India and Bangladesh through Indochina, eastward through Malesia as far as Sulawesi, with no neotropical members known at this time. However, the entire genus *Ardisia* is truly pantropical, as is the tribe Ardisieae. Until a phylogenetic analysis is complete for the tribe, a rigorous test cannot be performed. Despite the absence of a cladogram, the pattern of distribution among the genera of the tribe Ardisieae fit the general pattern one would expect if the distribution was boreotropical.

In summary, we hypothesize that *Ardisia* subgenus *Acrardisia* appears to fit the overall pattern consistent with a boreotropical distribution. We must emphasize that until a phylogenetic analysis among the subgenera of the genus *Ardisia*, and more importantly, among the genera of Myrsinaceae is complete, there is no reliable way to unequivocally determine if the group is boreotropical or Gondwanan. However, at this point in our work, we find it useful to point out the strong correlation and call attention to the value of examining generic limits on a worldwide basis when preparing treatments for a large flora such as *Flora Mesoamericana*.

Ardisia rarescens is known only from 27 herbarium specimens, and apparently is restricted to the eastern slope of the Sierra Madre de Chiapas, from central-southernmost Chiapas, Mexico, along the slope and into northern San Marcos and Quetzaltenango Departments, Guatemala. This region, including the famous Volcán Tacaná, houses many endemics and a myriad of taxa with boreotropical affinities, particularly in the pine-oak and *Liquidambar* forests in the region.

NOTES ON DESCRIPTION AND TERMINOLOGY

Quantitative and qualitative data in the description for floral parts and bracts were taken from organs rehydrated from herbarium specimens by boiling in water. Measurements from these range from 10% to 15% greater than those measurements taken directly from dried material. Data regarding stem diameters, inflorescence rachises, pedicels, leaf and fruit shape and size were taken from dried herbarium specimens.

Morphological terms in this treatment follow Lindley (1848) and Pipoly (1987, 1992) for the inflorescence, rachis pedicels and floral parts. Description of leaf morphology follows Hickey (1984), trichome description follows Theobald et al. (1984) and basic cell and tissue terminology follow Metcalfe (1984).

TAXONOMIC TREATMENT

Ardisia Swartz subgenus **Acrardisia** Mez, Pflanzenr. IV. 236(Heft 9):116. 1902.

Subshrubs to small trees. Branchlets glandular-papillate, glandular-hirtellous, ferruginous tomentose or rarely, glabrous. Leaf blades mostly entire or obscurely crenulate, but never regularly serrate. Inflorescence terminal, subtended by a foliaceous bract, the branches corymbose to umbellate or rarely racemose in fruit. Flowers 5-merous; buds short and broadly conical; sepals and petals dextrorsely imbricate; stamens with extremely short apical portions of the filaments, anthers dehiscent by wide, apically confluent longitudinal slits; pistils not protogynous, the ovules numerous, pluriserial.

Distribution.—Approximately 35 species, throughout Indo-Malesia, with one disjunct at the border of Mexico and Guatemala.

Ecology.—Premontane to montane humid to wet forest, often on calcareous or sandstone-derived soils, 500–2400 m elevation.

Ardisia rarescens Standl. (**Fig. 1**), Publ. Field Columbian Mus., Bot. Ser. 4:248. 1929. *Amatlanian rarescens* (Standl.) Lundell, Wrightia 7:40. 1982. TYPE. MEXICO. CHIAPAS: Cerro del Boquerón, without elevation, Sep 1913 (fl) C.A. Purpus 7032 (HOLOTYPE: F, F neg. no. 68247; ISOTYPES: BM, GH, MO, NY, US).

Shrub to small trees 3–12 m tall. *Branchlets* slender, terete, 2–5 mm in diam, densely glandular-papillate, glabrescent. *Leaves* loosely pseudoverticillate; *blades* chartaceous, elliptic to slightly oblanceolate, 3.5–16.2 cm long, 1.1–5.3 cm wide, apically acuminate, the acumens 0.5–1.4 mm long, basally acute to cuneate, decurrent on the petiole, midrib impressed above, prominently raised below, the secondary veins 15–27 pairs, slightly raised above and below, prominently black punctate and conspicuously punctate-lineate, glabrescent above and below, the margins entire, revolute; petioles slender, canaliculate, 3.5–10.2 mm long, glabrescent above and below. *Inflorescence* terminal, erect, bipinnately or tripinnately paniculate, 6–22.5 cm long, 5.5–20 cm wide, pyramidal, usually longer than the leaves, densely, erect glandular-papillate, the branches terminally congested into 7–12-flowered corymbs; peduncles 0.3–2.2 cm long; inflorescence bract unknown; inflorescence branch bracts foliaceous, chartaceous, ovate to oblong, 2.3–3.7 cm long,

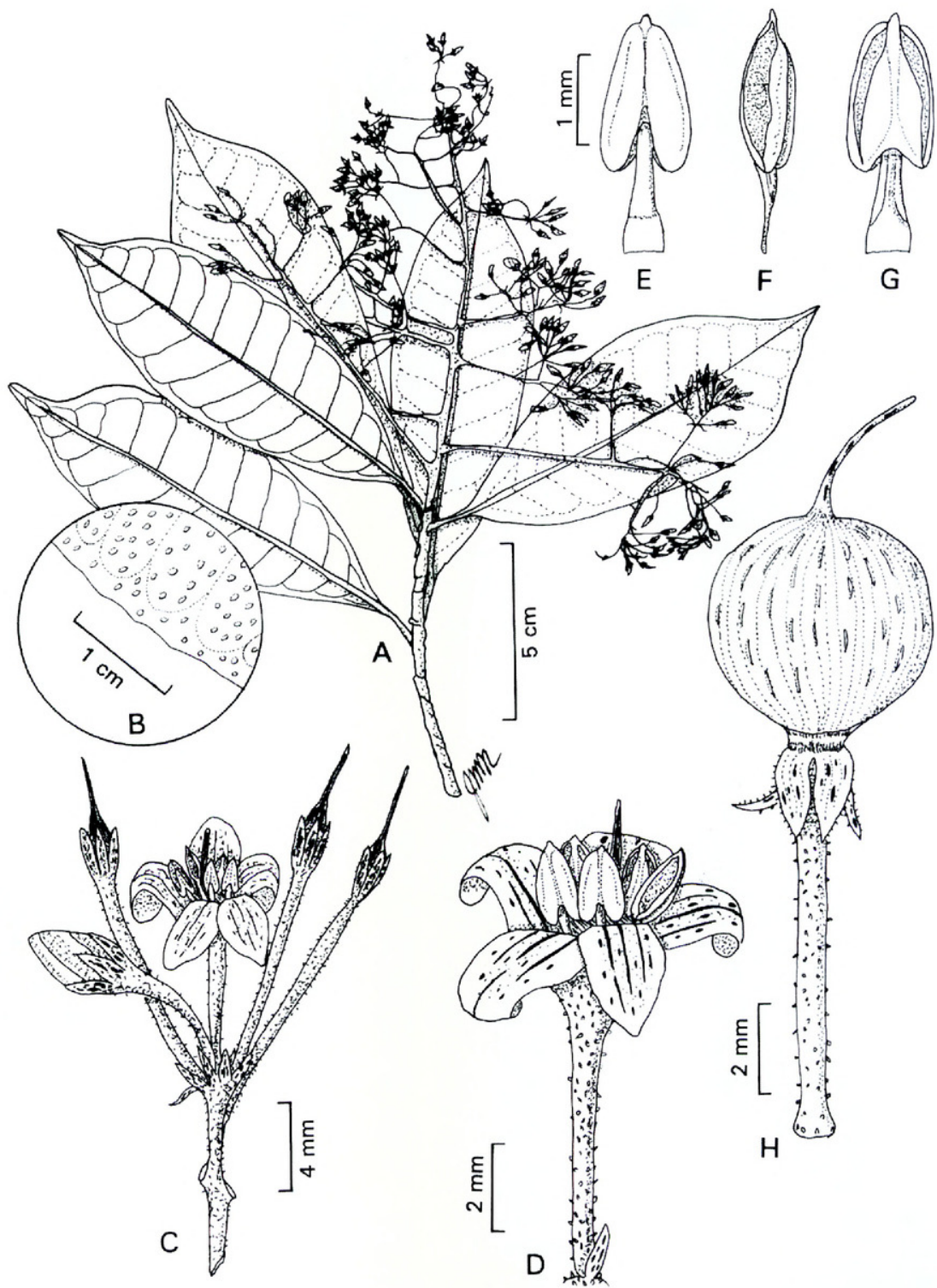


FIG. 1. *Ardisia rarescens* Standl. A. Flowering branch. B. Detail of abaxial leaf surface. C. Detail of inflorescence. D. Detail of flower. E. Detail of stamen, showing adaxial surface. F. Detail of stamen, showing lateral margin. G. Detail of stamen, showing abaxial surface. H. Fruit. A–B drawn from isotype, *C. Purpus* 7032 (BM). C–G drawn from isotype, *C. Purpus* 7032 (GH). H drawn from *L. Williams et al.* 26002 (F).

1.3–1.9 cm wide, apically acute, early caducous; secondary branches similar to the peduncles, but 0.9–2.2 cm long; floral bracts persistent, membranaceous, ovate to oblong, 0.7–1.8 mm long, 0.3–0.7 mm wide, apically acute, the midrib inconspicuous, the secondary veins obscure, densely and prominently punctate and punctate-lineate, glabrous above, sparsely erect glandular papillate below, the margins entire, hyaline, sparsely glandular-ciliate; pedicels slender, terete, 6.7–10.3 mm long, inconspicuously punctate and punctate-lineate, densely, erect glandular papillate. *Flowers* 5-merous, membranaceous, pink to reddish-violet; calyx 1.6–1.8 mm long, the tube 0.3–0.5 mm long, the lobes ovate to lanceolate, 1.1–1.5 mm long, 0.6–0.8 mm wide near the base, asymmetric, apically acute to rounded, prominently punctate and punctate-lineate, glabrous within, tomentum of scattered, erect glandular papillae, the margins entire, minutely erose, hyaline, sparsely glandular-ciliate; corolla 5–5.3 mm long, the tube 0.9–1.1 mm long, the lobes connate basally, ovate to lanceolate, 3.9–4.4 mm long, 2.5–2.8 mm wide near the base, apically acute to rounded, prominently punctate and punctate-lineate, glabrous throughout, the margins entire; stamens 3.1–3.3 mm long; the filaments 1.9–2.1 mm long, apically free, 0.3–1.7 mm long, connate basally into an elobate tube, 0.4–0.6 mm long, free from the corolla tube, epunctate, glabrous, the anthers free, ovate, 1.4–1.7 mm long, 0.8–0.9 mm wide near the base, apically apiculate, basally sagittate, dehiscent by wide, apically continuous longitudinal slits, the connective epunctate; pistil obturbinate, 4–4.2 mm long, glabrous; ovary 0.9–1.1 mm long, the style 2.9–3.3 mm long, slender, erect, inconspicuously punctate; stigma punctiform; ovules 11–15, pluriseriate. *Fruit* globose, 5–6.4 mm in diam., conspicuously and prominently punctate, the style base persistent.

Distribution.—*Ardisia raescens* is restricted to the extreme SE corner of Chiapas in the Sierra Madre Mountains, and in the adjacent area in the Departments of San Marcos and Quetzaltenango in Guatemala, growing at 1,300–2,400 m elevation.

Ecology and conservation status.—*Ardisia raescens* occurs in montane rain forest and cloud forests. Because of its restricted distribution, it should be considered threatened.

Etymology.—The specific epithet comes from the combination "rare" meaning far apart, sparsely and "-escens" to indicate a process of becoming without full attainment reached, referring to the sparse tomentum.

Common Name.—"Cereza morada" (*J. Steyermark* 33656).

Specimens examined. **MEXICO. CHIAPAS:** Mpio. Motozintla de Mendoza, 45–50 km NE of Huixtla along road to Motozintla, 1,900 m, 17 Nov 1971 (fr), *D. Breedlove & A. Smith* 22592 (LL, MO); 28 Dec 1972 (fr), *D. Breedlove & R. Thorn* 31017 (LL, MO); Municipio of Motozintla de Mendoza, SW side of Cerro Mozotal, 11 km NW of the junction of the road to Motozintla along the road to El Porvenir and Siltepec, 2,100 m, 21 Nov 1976 (fr), *D. Breedlove* 41608 (MO); 23 Nov 1981 (fr), *D. Breedlove & B. Bartholomew* 55740 (LL, NY); Municipio of Motozintla de Mendoza, between El Rosario and Ojo de Agua along road to Niquivil, 1,770 m, 10 Jun 1988 (fl), *D. Breedlove* 69114 (CAS); Above El Rosario, 8 mi S of Motozintla, 1,800 m, 10 Jul 1977 (fl), *T. Croat* 40740 (LL, MO); Mt. Ovando, without elev., 24 Dic 1936 (fr), *E. Matuda* 0680 (US); Mt. Pasitar, without elev., 3–4 Aug 1937 (fl), *E. Matuda* 1641 (LL); 4 Aug 1937 (fl), *E. Matuda* S-206 (A, K, LL, MO, NY, US); Mt. Ovando, 2,100 m, 14–18 Nov 1939 (fl), *E. Matuda* 3942 (A, NY); Mt. Ovando, Escuintla, without elev., 1–16 Jul 1940 (fl), *E. Matuda* 4180 (A, GH, LL, MO, NY); Saxchanal, Sierra Madre, 2,700 m, 1 Jul 1941 (fl), *E. Matuda* 4306 (A, F, LL, MO, NY); Carlas, near

Motozintla, 2,176 m, Apr 1945 (fl), *E. Matuda 5511* (LL 2-sheets, TEX); San Juan Panama, Escuintla, 1,834 m, 23 Jul 1948 (fl), *E. Matuda 18148* (F); Along the dirt road to Siltepec, past Ejido Benito Juárez, ca. 12 km from the turnoff from Mexican highway 190, S of Motozintla, 15° 20' N, 92° 15' W, 2,100 m, 9 May 1987 (fl), *J. Miller & J. Myers 2778* (BRIT, F, MEXU, MO); Tapachula, Finca Chinincé, 1,500 m, 17 Aug 1961 (fl, fr), *H. Schwabe s.n.* (B 2-sheets); Municipio of Motozintla de Mendoza, track from Ejido Boquerón to Cerro Boquerón, 15°?15' N, 92° 17' W, 2,400 m, 9 Feb 1990 (fr), *P. Stafford et al. 347* (BM, MO); Municipio of Motozintla, Buenos Aires, 1,900 m, 31 Jul 1986 (fl), *E. Ventura y E. López 3985* (MO). **GUATEMALA. QUEZALTENANGO:** Volcán Zunil, 6,100 ft [1,859 m], 5 Aug 1934 (fl), *A. Skutch 948* (F, NY); Lower S-facing slopes of Volcán Santa María, between Santa María de Jesús and Calahuaché, along great barranco between Finca Pirineos and San Juan Patzulín, 1,300–1,500 m, 6 Jan 1940 (fr), *J. Steyermark 33656* (F, LL). **SAN MARCOS:** 6 mi SW of town of Tajumulco, NW slope of Volcán Tajumulco, along Río Malacate, 2,300–2,800 m, 26 Feb 1940 (ster.), *J. Steyermark 36666* (F); Above Finca El Porvenir, between "Todos Santos Chiquitos" and "Loma de la Paloma", S-facing slopes of Volcán Tajumulco, 1,400–1,700 m, 8 Mar 1940 (ster.), *J. Steyermark 37283* (F, LL); 1,300–1,500 m, 16 Mar 1940 (ster.), *J. Steyermark 37981* (F, LL); Near Aldea Fraternidad, between San Rafael Pie de la Cuesta and Palo Gordo, W-facing slope of the Sierra Madre Mountains, 1,800–2,400 m, 10–18 Dec 1963 (fr), *L. Williams et al. 26002* (F); (fl, fr), *26004* (F 2-sheets); (fr), *26101* (NY); Outer slopes of Tajumulco Volcano, Sierra Madre Mountains about 8–10 km W of San Marcos, ca. 2,300 m, 31 Dec 1964–1 Jan 1965 (fr), *L. Williams et al. 26799A* (US).

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LIST OF EXSICCATAE

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