SYSTEMATICS CHAPTER 26

An Emended Description of Dioon mejiae Standl. & L. O. Williams (Zamiaceae)

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Abstract

Cycad taxonomy and systematics are plagued by insufficient and inconsistent species descriptions. Problems associated with the inadequate description of *Dioon mejiae* were perpetuated for more than 50 years. These include (1) unfounded and inaccurate reports of mature plant size, species distribution, and population numbers; (2) incomplete and/or erroneous descriptions of the type source locality; and (3) inaccurate designation of conservation status. In this chapter, the description of *D. mejiae* is emended following, to the extent possible, Walters and Osborne's (2004) taxonomic description guidelines. Included herein are (1) name, location, number of adult plants, area encompassed, habitat type, geology/soil type, and reproductive status of all known populations; (2) emended Latin description; (3) taxonomic key of the species and its closest relatives; (4) designation of a standard vernacular name; (5) brief overview of human uses; (6) estimates of the number of domestic plants in Honduras and Nicaragua and cultivated plants in ex situ collections worldwide; and (7) discussion of threats, conservation status, and in situ conservation recommendations.

Resumen

La taxonomía y la sistemática de las especies de Cycadales son plagadas por descripciones escasas y contrarias. Los problemas asociados a la descripción inadecuada de *Dioon mejiae* fueron perpetuados por más de 50 años. Éstos incluyen 1) los informes infundados e inexactos del tamaño de la planta adulta, de la distribución de la especie, y de los números de poblaciones; 2) descripciones incompletas y/o erróneas del lugar tipo; y 3) designación inexacta del estado de la conservación. En este artículo, la descripción de *D. mejiae* se enmienda, siguienodo al grado posible, las pautas taxonómicas de la descripción de Walters y de Osborne (2004). Se incluyen adjunto (1) el nombre, la localización, el número de plantas adultas, el área abarcada, el tipo de habitat, el tipo de geología/suelo, y el estado reproductivo de poblaciones conocidas; (2) descripción latina ampliada; (3) llave taxonómica de la especie y de sus parientes más cercanos; (4) designación de un nombre vernáculo estándar; (5) breve descripción de aplicaciones humanas; (6) estimaciones del número de plantas domésticas en Honduras y Nicaragua y plantas cultivadas en colecciones ex situ en el exterior; y (7) discusión de amenazas, del estado de la conservación, y de recomendaciones "in situ" de la conservación.

Introduction

Inconsistent and inadequate species descriptions have led to confusion in cycad taxonomy and systematics. To rectify these issues, a Cycad Classification Concepts (CCC) Workshop was held in 2002 at Montgomery Botanical Center (MBC), Miami, FL. The product of this workshop was a book (Walters & Osborne, 2004) containing the following prime tenets: (1) "species" is the smallest taxonomically useful entity in cycad systematics; (2) cycad species are best designated by a geomorphological species concept; and (3) a standard set of guidelines for taxonomic descriptions is necessary and timely. The book then introduced a set of guidelines for cycad taxonomists to follow.

Dioon mejiae Standl. & L. O. Williams is an example of a species that was inadequately described, and its meager description had far-reaching effects for more than half a century. Paul C. Standley and Louis O. Williams described *D. mejiae* in 1950 from a plant growing in the garden of Dr. Isidoro Mejía H., of Danlí, El Paraíso, Honduras. Mejía had "brought seed home 40 years earlier from a dry rocky canyon in the Department of Olancho," and, although the authors never visited the population from which the seeds came, they reported its location as "on the road between Pueblo Nuevo and Olanchito" (Standley & Williams, 1950). They also reported that this population represented "the only locality at which [the species] has been found wild." These statements are problematic because there is no Pueblo Nuevo in the relevant area of Olancho and because references to this species in the literature mistakenly perpetuated the single-population concept without any direct supporting evidence.

This chapter provides a much-needed emended description of *D. mejiae* and is offered as a case study of and justification for a taxonomic description standard. It should be noted that this emended description does not affect the type specimen, taxonomy, or nomenclature of *D. mejiae* in any way. It is simply meant to supplement the original description by correcting some long-standing mistakes and clarifying some misconceptions about the species. Most of the data reported herein were gathered during an MBC-sponsored expedition to Honduras in 2003 (hereinafter referred to as HN03), and every effort has been made to conform to as many of the CCC taxonomic guidelines as possible.

Population Characteristics

GEOGRAPHIC LOCATION

Bonta's (2003) report of widespread populations of a large cycad known locally as "teocinte" (or "tiusinte"; see later) in Olancho was the first indication that the range, abundance, and status of the species as reported by Standley and Williams (1950) were questionable at best. Bonta (2003) suggested that confusion over the common name may explain why botanists had been unaware of this cycad's true range for so long. In eastern Honduras—and Olancho in particular—"teocinte" and "tiusinte" refer to *D. mejiae*, whereas throughout the rest of Mesoamerica the names are applied to members of the grass genus *Zea*. Standley and Williams (1950) were aware of this confusion, but stated that it was "futile to speculate" how the same name became affixed to such dissimilar plants. Most populations of *D. mejiae* are referred to locally as "teocintales" or "tiusintales." Once botanists understood this, it was not difficult to pinpoint their locations.

Table 26-1 Name, locality, altitude, habitat type, geology/soil type, and reproductive status for all known *D. mejiae* populations in Olancho and Yoro, Honduras. Gray rows indicate superpopulations or components thereof.

Popu No	lation information Name	*		Munici pality		Geology/ soil type	Reprod.	No. of adult plants	Area (ha)	TEFH specimens
1	Saguay/Río Grande	593	Gualaco	Gualaco	TDF	Hills along Río Grande and Quebrada de	R: s+j+♀+♂	168,000	600	-
		·		,		los Hornos composed of sandstone of the Agua Fría Formation, Jurassic Period; remainder of population occurs on first, second, and third terraces of Quaternary alluvium.				
2	Quebrada Zarca	620-638	Gualaco	Gualaco	TDF	Quaternary alluvium	5	50	3	
3	Teocintalito/ Quebrada del Quiscamote	700750	Gualaco	Gualaco	POT	Cacaguapa Schist . Formation (Paleozoic)—schists, phyllite, gneiss, marble, quartzes; oldest basement rock in Honduras	R: s+j+♀+♂	250	10	39,075
4	Talquezate/Río El Riachuelo	638	Gualaco	Gualaco	TDF	Quaternary alluvium, along boundary with Chindona Batholith	NR?	50	3	-
5	El Nance/ Quebrada El Manchon	580	Gualaco	Gualaco	TDF	Quaternary alluvium	?	50	3	

6	Camalotal/	698	Pueblo	Gualaco	TDF	Clastic sedimentary	R: s+j+ð	1000	15	39,078
•	Río Alao	020	Viejo	Guaraco	البا	rocks of the	10.31)10	1000		52,070
7	Los Encuentros/ Río de Oro	488	Pueblo Viejo	Gualaco	TDF	Valle de Angeles Formation.	R:j+♀+♂	12,000	200	
8	Jacaleapa de Guata	671	Pueblo Viejo	Guata	TDF	Cretaceous; bedrock is group known as "redbeds;" along boundary with Chindona batholith.	R: s+j+♀+♂	500	30	39,079
9	Coamapa/ Río Negro 1	698	Pueblo Viejo	Guata	TRF	Cacaguapa schist, along boundary	R: s+♀	5000	?	39,082
10	Coamapa/ Río Negro 2	700-800	Pueblo Viejo	Guata	TRF	with Valle de Angeles Group	?	?	?	-
Mame	Superpopulation: She	ets (S to N): (Guata, Pueblo	Viejo, Esquipulas	s del Norte,	Conf. Ríos Aguán-Mame	250,000	2700		
11	Río Tezapa/ Río Mame (S end)	574	Guata	Guata	POT	River cuts through Cacaguapa schist; some populations may	R: s	200	10	39,093
12	Quebrada de Tiscan/Río Mame (middle)	432	Pueblo Viejo	Guata	POT	occur within Chindona batholith, which covers the middle course of	R: s+j	250	25	39,080
13	Quebrada Agua Caliente/Río Mame (N end)	657	Esquipulas del Norte	Esquipulas del Norte	POT	the river (between . Tezapa and Pueblo Viejo)	?	500	?	
14	Las Labranzas/ Quebrada de Los Copantes	962	Guata	Jano	POT	Cacaguapa schist, along boundary with Chindona batholith	R: s+♀	58	10	39,085
15	Pueblo Viejo/ Quebrada del Carao	900-1000	Guata	Jano	?	Tertiary volcanics	?	200	?	-
16	El Quebrachal/ Río de Jano	704	Guata	Jano	TDF	Atima limestones of Yojoa Group, at edge of Chindona batholith	NR	200	2	39,086

Рори	lation information	Altitude	Торо	Munici	Habitat	Geology/	Reprod.	No. of	Area	TEFH
No	Name	(m)	sheet	pality	type	soil type	status	adult plants	(ha)	specimens
17	La Laguna/ Quebrada El Teocinte	829	Esquipulas del Norte	Esquipulas del Norte	POT	Cacaguapa schist, at boundary with Chindona batholith	R:s+♀	200	10	39,092
18	Río de Arenas/ Quebrada del Camalote	690	Esquipulas del Norte	Esquipulas del Norte	TDF	Same as 17	R:s+♀	5,000	400	39,095
19	La Suncuya/ Quebrada del· Repecho	500	Esquipulas del Norte	Esquipulas del Norte	TDF	Same as 17	R: \$	3,000	300	39,098
20	Cerro El Gorrión/ Quebrada del Coyol	500	Esquipulas del Norte	Esquipulas del Norte	TDF	Cacaguapa schist	NR?	100	5	_
21	Filo Mulón- Palmira	420	Esquipulas del Norte	Esquipulas del Norte	POT	Valle de Angeles Group	NR?	500	10	~~~
22	"Río Chiquito o Esquipulas"	500-800	Esquipulas del Norte	Esquipulas del Norte	?	? ^	?	?	?	
23	Palmira/ Quebrada del Teocintal	600	Esquipulas del Norte	Esquipulas del Norte	TDF	?	?	3	. ?	_
24	Cerro de la Cruz/Quebrada de la Cera	600–700	Olanchito	Esquipulas del Norte	?	?	NR?	?	?	
25	Calpules/Río de Calpules	400 +	Olanchito	Olanchito	?	Tertiary volcanics	. ?	?	?	_
Aguán	Superpopulation: She	ets (W to E):	Jimia, Arenal,	Olanchito,Yaru	ca, Sonaguera	ı		200,000	6000	
26	El Tamarindo/ Quebrada del Tamarindo (W end)	317	Arenal	Olanchito	TDF	In west is Cacaguapa schist; to east is Tertiary volcanics. Poorly	R: s+j	200	10	39,099
27	Agalteca/ Río de la Pimienta (middle)	380	Yaruca	Olanchito	TDF	mapped.	R: s+j	1000	20	39,097

. 28	Río Lepaca Œ end)	327	Sonaguera	Olanchito	TDF		R:s+j	1000	20	39,100
29	Cerro Teocinte/ Río San Pedro	120+	Saba- Tocoa	Tocoa, Colon	TRF	Probably Cacaguapa schist	?	500	50	
30	El Teocinte/ La Soledad	600	Parumble	Manto	TDF	Same as 21	NR	6	?	-
E1	La Unión/ Cerro Teocinte (extinct)	900-1300	La Unión	La Unión	N/A	Cacaguapa schist	_			<u></u>
E2	La Crucita/ Quebrada del Teocinte (extinct)	900	La Unión	Jano	N/A	Same as E1	_	_	_	
E3	Mocanquire/ Cerro del Teocintal (extinct)	850950	Pueblo Viejo	o Guata	N/A	Same as E1		<u></u>	***	
Totals	, ,			•			15 of 21 (71%) reprod. pops.	646,658 plants	10,351 ha	14 pop. vouchers

Most population names derive from a pairing of the name of the nearest village or human habitation and the river or stream with which the population is associated. "Habitat Type" codes: TDF=tropical deciduous forest, POT=pine/oak transition, TRF=tropical rain forest. "Reproductive Status" codes: R=reproductive; NR=non-reproductive; s=seedlings present; j=juveniles present; Q=female cone(s) present; d=male cone(s) present. "TEFH Specimens" refer to herbarium vouchers deposited in the Herbario Nacional de Honduras, Universidad Nacional Autónoma de Honduras. (Modified from Tables 3 and 4 of Haynes & Bonta, 2003.)

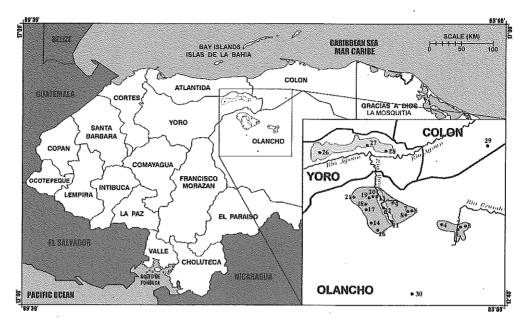


Figure 26-1. Location of known extant populations and three extinct populations of dioon mejiae.

Current Distribution

The distribution of the species, as it is known at present, extends from 14°48' to 15°32'N latitude and from 86°00 to 86°58'W longitude. A list of all known populations in Honduras is provided in Table 26-1, and the location of the known extant populations, in addition to three populations identified by map toponyms but confirmed to be extinct during HN03, is shown in Fig. 26-1. It is interesting to note that (1) most large populations are not reflected in place names on maps, (2) most extant high-altitude populations are quite small, and (3) three (of only seven) populations listed on topographical maps are extinct and all three occur at high elevations.

Most populations are found in the upper drainage basins of the Aguán and Sico rivers on the Caribbean slope in the departments of Olancho and Yoro (Fig. 26-1). In the Sico basin, the Saguay/Río Grande population (Pop. 1) and a few small satellite populations occur along the SW fringe of the Valle de Agalta, a Quaternary terrace plain. A large superpopulation—consisting of numerous small subpopulations distributed along smaller streams that empty into the larger river—skirts the northern edge of the Valle de Aguán

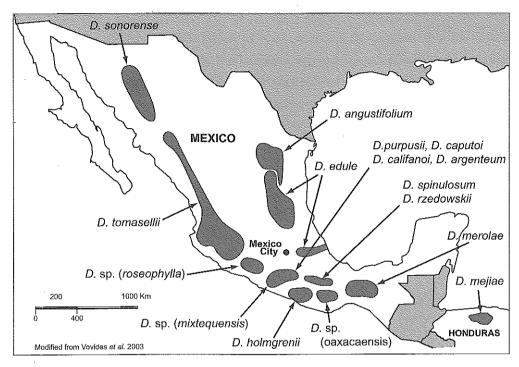


Figure 26-2. Distribution map of all known Dioon species.

terrace plain in Olanchito, Yoro. All but two of the remaining populations occur in the watershed of the Río Mame, a major tributary of the Aguán. Several of these are scattered along small streams entering the Mame—forming a second superpopulation—while the majority of the others occur in the watersheds of the Mame's major tributaries, the Chiquito and Negro rivers. Finally, one tiny disjunct population (Pop. 30) occurs in the upper Río Telica watershed (a tributary of the Río Patuca) in central western Olancho, while another disjunct population (Pop. 29) is found along the Río San Pedro, a stream that flows into the lower Río Aguán in the Department of Colón.

D. mejiae is the only Central American representative of this otherwise Mexican genus. Its distribution in relation to the other *Dioon* species is illustrated in Fig. 26-2. The nearest species is D. merolae, which occurs ca. 700 km to the west in Chiapas, while the other two tree dioons, D. spinulosum and D. rzedowskii, are greater than 1000 km disjunct in N. Oaxaca.

Other Locations

Anecdotal evidence and map toponyms suggest that *D. mejiae* may occur in central and west Honduras as well as north Nicaragua. An MBC-sponsored excursion by C. Nelson (Curator, Herbario Nacional de Honduras [TEFH], Universidad Nacional Autónoma de Honduras) to the San Juan de Opoa area of west Honduras in 2003 confirmed the existence of a *Zea×Tripsacum* hybrid called "teosinte" but no cycads (Haynes & Bonta, 2003). Though *D. mejiae* has been reported from gardens in Nicaragua and "teosintal" toponyms are also known from northern Nicaragua, whether these plants are descended from local wild populations or were brought there from Honduras is still unknown.

Type "Source" Locality

The exact locality/population from which the seed of the type specimen came remains a mystery. After much detective work, however, the most likely interpretation of Standley and Williams' (1950) locality reference is as follows:

- 1. Their report of the type source population being between Pueblo Nuevo and Olanchito is erroneous because (1) there is no Pueblo Nuevo in that part of Olancho, but there is a Pueblo Viejo and (2) the village name is written as "Pueblo Viejo" on the label of a herbarium voucher collected by Standley from plants in Mejía's garden around the same time the type specimen was collected—thus, it can safely be assumed that the name given in the formal description was a typographical error.
- 2. When Standley and Williams referred to a "road," if one assumes that they meant an automobile road, the La Suncuya/Quebrada del Repecho (Pop. 19) is the only population between Pueblo Viejo and Olanchito that is near such a road. However, no vehicular road existed in the region until after 1980; the main "road" was the "camino real," or old royal road. The main camino real route was preferred and was used during the dry season; the alternate route was used only during the rainy season.
- 3. The Cañón del Mame—the Río Mame Canyon—is one of only a handful of canyons in Olancho and is the only one that occurs along either the main or the

alternate camino real route from Pueblo Viejo to Olanchito. Because the main route runs along the Río Mame for much of its length, it is likely that this canyon is what Mejía (via Standley and Williams) was referring to. Also, because Standley and Williams referred to a "dry rocky canyon," one must assume that Mejía's trek occurred during the dry season, at which time the main route would have been preferred. Thus, the type source locality is most likely within the superpopulation that exists within the Río Mame Canyon, which extends for ca. 8 km in north-central Olancho. The precise locality will likely never be known.

PHYSICAL ENVIRONMENT

Habitat, Topography, and Climate

D. mejiae is typically an understory component of tropical broadleaf forests between 120 and 1000 masl and with average annual precipitation of 800–2,000 mm. Though it flourishes on steep slopes of 30–70 degrees, it also grows well on gentle and even flat terrain. Local habitat composition varies widely from lowland evergreen rain forest in Tocoa (Pop. 29), to deciduous mixed forests throughout NW Olancho, to arid thorn forest in Gualaco and Olanchito. It is rarely encountered in undisturbed habitat; rather, it is generally a hardy component of agro-pastoral habitats and modified forest zones, including pine/oak transition zones affected by anthropogenic fires. Habitat type and altitude for each population are listed in Table 26–1.

Geology and Soils

The soil type and underlying geology for each population are also provided in Table 26-1. Although many populations are restricted to rocky hillside terrain, the more intact populations spill down onto sandy Quaternary terraces above deeply incised water-courses. There is no single "preferred" soil type. Some populations thrive in sandy soil or sandy to clayey alluvial deposits, while others grow in loamy, limestone-derived soils; in soils weathered from metamorphics (schists, gneisses); etc. Most populations in Olancho lie along the edge of the Chindona batholith, a structurally homogeneous block of intrusive granite stretching across northwest Olancho (R. Rogers, pers. comm.). Analyses of

Table 26-2 Analyses of soil collected from eight *Dioon mejiae* populations across its range during the HN03 expedition.

Рорі	ılation information	pН	%	%	Available nutrients (ppm)				
No	Name	(H ₂ 0)	O.M.	$N_{_{ m Total}}$	P	К	Ca ,	Mg	
1	Saguay/Río Grande	6.71	2,26	0.11	29.58	402	1480	250	
3	Teocintalito/Quebrada del Quiscamote	6.69	3.42	0.17	15.81	144	1330	280	
6	Camalotal/Río Alao	8.05	18.94	0.95	11.69	360	14,500	450	
8	Jacaleapa de Guata	7.64	9.76	0.49	123.77	610	6000	420	
11	Río Tezapa/Río Mame	6.63	4.58	0.23	2,74	166	2720	430	
12	Quebrada de Tiscan/Río Mame	7.77	4.17	0.21	55.43	240	4750	370	
16	El Quebrachal/Río de Jano	7.95	15.74	0.79	5.86	410	9100	430	
26	El Tamarindo/Quebrada del Tamarindo	6.32	4.94	0.25	14.00	168	1730	360	

Analyses conducted at El Zamorano, the Panamerican School of Agriculture, Danlí, El Paraíso, Honduras.

soil collected from eight localities suggest a surprising adaptability with respect to soil physical properties and nutrient availabilities (Table 26-2).

POPULATION SIZES AND DENSITIES

Estimates of the number of adult plants and geographic area encompassed for most populations are provided in Table 26-1. A conservative estimate of the total number of adult plants in Honduras is greater than 650,000 growing in greater than 30 populations distributed in three main sites in central and north Olancho and east Yoro and covering greater than 10,000 ha of land area (Table 26-1; Fig. 26-2), making it by far the most abundant cycad in the New World. The Saguay/Río Grande population, alone, contains more plants than most other cycad species (n=ca. 168,000 mature plants). Estimates for the other *Dioon* species range from 200 to 20,000 (Stevenson et al., 2003), and the largest estimate for any species reported in the *IUCN/SSC Cycad Action Plan* is greater than 200,000 (*Cycas pectinata* and *C. panzhihuaensis*; Hill et al., 2004. Density estimates averaged 62.5 plants/ha but varied greatly, ranging from 10 to 280 plants/ha.

POPULATION ECOLOGY

Life History

Reproductive Status and Phenology

More than 70% of the populations visited during HN03 were reproducing, as evidenced by the presence of seedlings and juveniles (Table 26-1). Seedlings were commonplace in non-fire-damaged populations but were not observed in populations most heavily impacted by human burning regimes. Female plants have an average rate of production of one cone every 2–3 years and appear to outnumber male plants in most populations. Coning occurs early in the rainy season (late May/early June), and female cones become receptive from June to August. People harvest cones (with immature seeds) from January to May the following year. Cones that are not harvested ripen and the seeds fall to the ground in September to December. As few as 10% of cones actually mature naturally, given the heavy demand on seeds as a subsistence food (see later).

Pollination

Very little is known about the pollination biology of this species. In 2002, S. Wells and the second author collected a weevil from a male cone at the Saguay/Río Grande population. It was later identified by C. O'Brien (former Professor Emeritus, Florida A&M University) as *Rhopalotria* sp. nov. All known *Rhopalotria* species are associated with cycad cones, and those with a known biology actually breed in the microsporophylls (Norstog & Nicholls, 1997).

Seed Dispersal

Potential mechanisms of natural seed dispersal include gravity, water, and animal transport. It is not clear to what extent the current distribution is also due to human agency, because seeds have been transported long distances by people for many centuries. It is also unclear whether the species originated in the lowlands and spread upslope, or vice versa.

A model wherein a historic climate shift had allowed species to expand gradually upslope (such as Gregory & Chemnick's [2004] "dynamic habitat" hypothesis for Mexican *Dioon* species) would necessitate either dispersal by animals or slow advance through seedling recruitment. Thus far, only the Central American agouti, *Dasyprocta punctata*, has

been identified as a seed transporter, though it is possible that a now extinct specialized disperser existed in the past.

A downhill dispersal model would require only gravity or water transport, or both. The terrain of the region is extremely abrupt and subject to devastating flash floods that can rapidly transport seeds tens of kilometers. After the highest (i.e., 100+-year) floods, seeds might be safely deposited high above more frequent flood levels, allowing them time to germinate, mature, and gradually create new populations. More work needs to be done on seed dispersal in this and most other cycad species.

Growth Rate

Based on observations of garden plants in Juticalpa, Olancho, O. Flores Pinot estimated that *D. mejiae* grows only 70 cm per century at best (Bonta, 2003). If the assumption is made that plants in cultivation grow at least as fast as plants in habitat, Flores Pinot's growth rate would yield an estimated age of 1250–1400 years for the largest wild plants observed in Olancho—many of which had 8- to 10-m trunks (Fig. 26-3).

Predation

Insect Predators

During HN03, a brightly colored lepidopteran, was observed and photographed in every life stage exclusively on the leaves of *D. mejiae*. Newly emerging adults were collected at the Quebrada Agua Caliente/Río Mame population and were later identified as *Eumaeus childrenae* (R. Lehman, Butterfly & Insect Museum, La Ceiba, Atlántida). No record of this species using *D. mejiae* as a larval host plant is known.

A second caterpillar was observed burrowing into and feeding on the rachis of *D. mejiae* leaves at Talquezate/Río El Riachuelo. J. Heppner (Curator of Lepidoptera, Florida State Collection of Arthropods) identified it as an armyworm in the genus *Spodoptera*. Although armyworms are omnivorous, there is no record of a cycad being used as a larval host plant (J. Heppner, pers. comm.).

Non-insect Predators

At Saguay/Río Grande, cows were observed feeding on newly emerging leaves and tooth marks from an unidentified small mammal were observed on old sclerotestas. Domestic

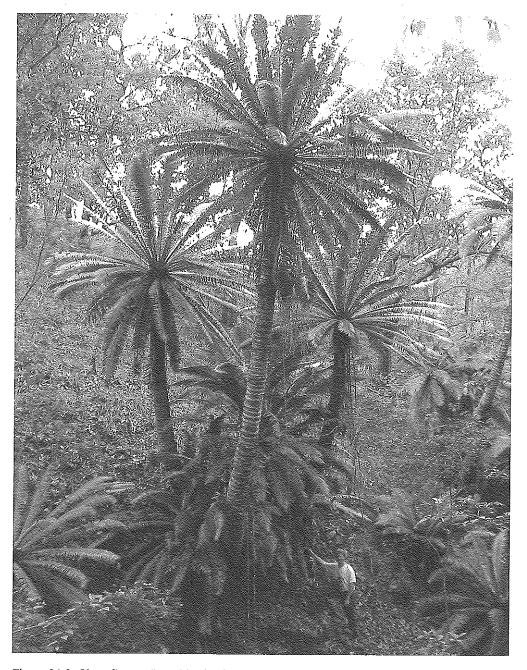


Figure 26-3. Giant dioon mejiae at Teocintalito, Olancho; first author at bottom right indicates scale.

geese have been observed eating new leaves and small seedlings in Juticalpa (O. Flores Pinot, pers. comm.). In addition, D. Graham (pers. comm.) reported that the Central American agouti (known locally as "guatuza") is recognized as a tiusinte seed hoarder in the community of Limoncito, Gualaco.

INTERPOPULATION VARIATION

Reports in the literature and discussions with experienced researchers suggest that interpopulation differences in vegetative characteristics are typical for *Dioon* species in Mexico (Gregory & Chemnick, 2004; T. Gregory, pers. comm.); thus, some level of variation was expected among populations in *D. mejiae* before HN03. Vegetative morphological variation was observed within each of the 20+ populations visited during HN03—and even within plants in any given population—but relatively little differentiation was noted between populations. A detailed analysis of intra- and interpopulation morphological variation is currently under way, and the results will be presented in a separate publication.

Species Characteristics

NOMENCLATURE, TAXONOMY, AND SYSTEMATICS

De Luca and Sabato (1978) are the only authors to address the nomenclature of *D. mejiae*, and they presented convincing arguments supporting specific rank for this taxon. With regard to taxonomy, Standley and Williams (1950) stated that, "on a geographic basis alone, it is quite safe to assume that the Honduran cycad is distinct" and that *D. mejiae* is "evidently related" to *D. spinulosum*. De Luca and Sabato (1978) echoed the latter testament, stating that *D. mejiae* is "probably more related to *D. spinulosum* Dyer (1883) than to *D. edule* Lindley (1843)." Sabato and De Luca (1985) supported these assumptions in their examination of evolutionary trends in *Dioon* and recognized the following three natural groups within the genus based on seed, seedling, and female cone morphology: (1) *D. mejiae*, (2) *D. spinulosum*, and *D. rzedowskii*, and (3) all other species.

With regard to systematics, the molecular work of Moretti et al. (1993) and De Luca et al. (1995) yielded two well-defined major clades within *Dioon*. The first consisted of the tree dioons (*D. mejiae* [*D. spinulosum & D. rzedowskii*] = "Spinulosum" clade) and the

second of the remaining species ("Edule" clade). The resulting cladistic phylogeny was broadly congruent with a phenetic analysis on the same data, with morphological data, and with biogeography. A more recent study using analyses of different molecular sequences further supported the distinction between the "Spinulosum" clade and the "Edule" clade (Bogler & Francisco-Ortega, 2004).

DISTINGUISHING TRAITS

The few authors who have reported vegetative or reproductive traits for D mejiae, or both, have done so primarily to distinguish it from the other two tree dioons. For example, Whitelock (2002) stated that, although D. mejiae is somewhat similar to D. spinulosum in outward appearance, adults can be separated by their "relatively stiff, straight, flat leaves, and leaflets without marginal spines." Whitelock (2002) further stated that D. mejiae seedlings have proximal leaflets reduced to prickles, whereas D. spinulosum seedlings have long, smooth petioles and lower leaflets that do not reduce to prickles. Sabato and De Luca (1985) reported that D. mejiae has the largest and most distinctive seeds, the most distinctive seedlings, and the largest male cones of any Dioon. The unpublished HN03 final report (Haynes & Bonta, 2003) provided extensive data on vegetative and reproductive traits for more than 200 plants from 14 populations. The distinguishing characteristics were used to develop an emended Latin description for this species as well as a diagnostic key that distinguishes the tree dioons from the more xeric Dioon species and from each other (see later). Vouchers from several populations were created during HN03 and deposited in the Herbario Nacional de Honduras [TEFH] at the Universidad Nacional Autónoma de Honduras, Tegucigalpa. They are listed in the far right column of Table 26-1.

Emended Latin Description

Planta arboriformis gigantea, trunco usque ad 6–10 m. vel ultra, saepe unius plantae multis magnis truncis erectis, his interdum crasse stipatis, folia numerosa rigida et coriacea, vel adscendentia vel declinantia, in statu juvenili tomentosa, cito glabrata, laete viridia, 87248 cm. longa vel ultra; rachis supra plana, subtus convexa, folii segmenta (pinnae) in uno latere rachidis 83–228 (i.e., omnino 163–456 in tota rachidi), segmenta media usque ad 8.5–30 cm. longa et 1.1–2.2 cm. lata, opposita, pungenti-attenuata, vel integra, vel

cum usque ad 4 serraturis in segmento; distalia sensim decrescentia, inferiora sensimque decrescentia, pauca pungenti-serrata, infima elliptica 1–2 cm. tantum longa; strobili feminei vel erecti vel dependentes, ovoidei, usque ad 21–47 cm. longi atque 25–32 cm. lati, apice subabrupte acuminato, ubique tomento densissimo pallide brunneo molli obtecti; squamae stipitem obtegentes lineari-lanceolatae, usque ad 6–14.5 cm. longae, anguste attenuatae, extus dense lanosae; squamae strobili feminei deltoideo-ovatae usque ad 8–12 cm. longae et 7–9 cm. latae, anguste obtusae, imbricatae, extus dense lanosae; strobili masculi erecti, fusiformi, circa 53 cm. longi atque 12 cm. lati, apice rotundato, squamae stipitem obtegentes lineareae, 8 cm. tantum longae; squamae strobili masculi deltoideo-ovatae, usque ad 1–1.3 cm. longae, 1.7–2 cm. latae; semina usque ad 250 in uno strobilo, 3.7–6.0 cm. longa et 3.0–4.0 cm. lata; sarcotesta flava, sclerotesta fissurata, chalaza appendix plana.

Diagnostic Key

1A	Median leaflets elliptic-acuminate, pungent; eophyll and seedling
	leaves resemble adult leaves, with petioles short or absent; female
	cones leaning to moderately pendulous at maturity; female cone
	peduncles \leq 14.5 cm long; seeds with prominent chalazal appendix
1B	Median leaflets lanceolate, not pungent; eophylls and seedling
	leaves with long, unarmed petioles; female cones completely
	pendulous at maturity, typically hanging below the leaves; female
	cone peduncles≥17.5 cm long; seeds lacking chalazal appendix
2A	Adult leaves lacking petioles (some or all leaves); leaflet margins
	serrated (some or all leaves); emerging leaves glabrous; female cone
	peduncles \geq 30 cm long; megasporophylls appressed at maturity
2É	Adult leaves with unarmed petioles, 10–15 cm long; leaflet margins
	entire; emerging leaves pubescent; female cone peduncles ≤ 20 cm
	long; megasporophylls unappressed, becoming deflexed distally
	at maturity

Human Aspects

THE NAME "TIUSINTE"

Derived from classic Nahuatl, "tiusinte" (and its variants) means "sacred ear of maize." "Tiusinte" is herein designated as the standard vernacular name for *D. mejiae*. Although the authors had used "teocinte" in earlier writings (Bonta, 2003; Haynes & Bonta, 2003)—following the spelling on topographic maps—it is now important to standardize "tiusinte" (pronounced "tee-oo-SEEN-tay") over "teocinte" ("tay-oh-SEEN-tay"), not only because the former more closely reflects local pronunciation, but also because this should help avoid confusion between this cycad and other plants known as "teocinte."

HUMAN USES

Despite being little known outside its native range, *D. mejiae* is of great importance to the diets of 30–40,000 people in the municipalities of Gualaco, Guata, Jano, and Esquipulas del Norte in the Department of Olancho; Olanchito and Arenal in Yoro; and Tocoa in Colón. In some villages, up to 80% of the human population relies on tiusinte seeds as a starchy staple during times of maize scarcity. Cone harvests have taken on such importance that in some historical cases tiusintes received government protection. The average harvest is six cones per year for a household of six. Processed, one cone can feed one person for up to 2 months on a near-starvation diet; under better circumstances, tiusinte is used as a dietary supplement to maize and *Phaseolus* beans. Foods prepared from tiusinte seeds include tamales, tortillas, atol (a beverage), rosquillas (unleavened pastry), rosquetes (leavened pastry), and bread. The former three foods are widespread while the latter three are uncommon and the last two are restricted to Gualaco. At least two processes exist for the removal of toxins. Although no cases of progressive neurological damage in humans have ever been reported or observed, it is possible that isolated cases have occurred.

Tiusinte has a secondary importance within and outside its native range as a decorative species. The use of leaves for Catholic rites—particularly for Day of the Dead (Nov. 2), Christmas Eve, and Holy Week (Semana Santa)—is more widespread than seed consumption. Leaf use is uncommon in tiusinte-consuming villages and most common in

larger towns and cities, where people grow tiusinte in dooryard gardens solely for the leaves—which are highly valued for their showiness, elasticity, and durability.

Tertiary uses are fading in importance, even while demand for tiusinte as a subsistence food is increasing in some areas. Early in the twentieth century, seeds were commonly made into whistles and "enchutes," or pin-and-target toys, while the mucilage from the cones was used to secure envelopes; mucilage and tomentum also had medicinal applications. (See Bonta, 2007 for a detailed discussion of human uses of this and other Honduran cycads.)

Conservation Status and Recommendations

THREATS

Though *D. mejiae* faces numerous threats, its worth in local culture is unprecedented in areas where it is valued for cone production. As a common-property resource, tiusinte cannot, in theory, be owned by an individual (in contrast with most other trees). One rarely finds tiusintes chopped down by harvesters; damage is done primarily through conversion of habitat to farmland and ranchland, and, to a lesser extent, by habitat damage through road-building and logging. Roads are harmful to tiusintales, both through direct damage and through the introduction of new threats—such as conversion to pasture—that are brought about by the improved access. These changes are largely a result of post-1980 economic modernization.

Destruction of tiusintales is often an unintended result of illegal (but widely tolerated) enclosure of public lands. Subsequent treatment of tiusinte on private farmland ranges from protection to intentional destruction, with the most common case being the progressive but nonmalicious degradation of tiusinte plants due to excessive use of fire. In one village, small farmers have devised a management scheme whereby they balance the requirements of tiusintes and maize growing in the same field. In another case, a cattle rancher provides strict protection to part of the Saguay/Río Grande population at the village of Río Grande, Gualaco. But such examples are not commonplace.

Conservation Assessments

Osborne (1995) reported estimates of the number of plants in the wild, in public gardens, and in private collections for 200 cycad species. Osborne's estimates for *D. mejiae* were 5,000, 33, and 52 plants, respectively. As a result of these estimates, this species was considered "Rare" or "Vulnerable" based on the IUCN "Red Data" categories of Lucas and Synge (1978) and Mace et al. (1992), respectively (Osborne, 1995). The 1997 IUCN Red List of Threatened Plants listed *D. mejiae* as "Vulnerable" (Walter & Gillett, 1998), whereas Stevenson et al. (2003) treated it as "Data Deficient." The conservative estimate of greater than 650,000 wild adult plants reported herein effectively elevates this species to "Least Concern," (IUCN, 2001). Even though *D. mejiae* may very well be the most abundant cycad in the New World, many populations have been seriously degraded and the number of adult plants has diminished by ca. 50% over the past 25 years. As a CITES Appendix II species, it still merits a protection program. More than anything, it is a marvelous plant, not only in the context of its beauty and its importance to local diets, but also because it is the only locally abundant cycad in Honduras.

REPRESENTATION IN EX SITU COLLECTIONS

In May 2004, the first author conducted a survey in an attempt to obtain a more accurate and current estimate of the representation of this species in public and private gardens and parks, private collections and seed colonies, and nurseries around the world. Survey responses indicated the existence of 371 plants in 18 public or private gardens or parks in seven countries, 319 plants in 32 private collections or seed colonies in six countries, and 4,963 plants in 21 nurseries in six countries. Reported age of plants in cultivation ranged from 0 from 100+ years, and reported size ranged from 0 to 250 cm trunk height. Overall maturity ratio was 199:1 (immature:mature), overall sex ratio of mature plants was 1.25:1 (male:female), and age at first coning was 7–10 years, with some 30-year-old plants reported to have never coned. Although the number of cultivated plants in Honduras and Nicaragua remains unknown, it is important to include an estimate here because *D. mejiae* is a popular garden plant in many areas of these countries. It is reasonable to assert that the number is in the low thousands. Therefore, a conservative estimate of the total number of plants in cultivation worldwide exceeds 8000.

IN SITU CONSERVATION RECOMMENDATIONS

The following recommended actions would guarantee a safe future for *D. mejiae* and would assist the slow process of recovery in damaged tiusintales, together with a generalized "rescue" of the cultural traditions associated with the plant:

- 1. Immediate protection of tiusintales by the Protected Areas and Wildlife Department of the Administración Forestal del Estado-Corporación Hondureña de Desarrollo Forestal (AFE-COHDEFOR) by any means possible in the short term. This could include training of AFE-COHDEFOR personnel in recognition of the plant, where it grows, monitoring it, and trying to protect it against damage without prohibiting traditional extraction of tiusinte products.
- 2. Training of schoolteachers in tiusinte zones so that they can, in turn, educate the human populations who affect the plants.
- 3. Promotion of tiusinte in the media, and by private as well as state-run cultural centers ("casas de cultura").
- 4. In addition to botanical studies, studies of the nutritional and commercial values of tiusinte should be carried out.
- 5. Delimitation of tiusintales and zoning into the micro-watersheds of villages and towns, with their protection turned over to the communities.
- 6. Incorporation of tiusintales into actual and proposed protected areas, as mentioned I the preceding text.
- 7. Legal declaration of tiusintales as reserves, preferably as extractive reserves.
- 8. Development of the ecotourism potential of tiusintales.
- 9. Promotion of the hacienda of María Sarmiento Colindres, Río Grande, Saguay, Gualaco, as a special protection and study zone, because, thanks to family tradition, a great effort has been made there toward the protection of tiusinte—and as a result of HN03, it is now the most studied population of this species.
- 10. Reestablishment of municipal protection (the "embargo" of the "finca") in Gualaco and mechanisms for protection in other municipalities, perhaps by trying to have them protected as municipal reserves.
- 11. Presidential decree for protection of tiusintales throughout Honduras, as well as all Zamiaceae.

- 12. Support of legislation in Honduran Congress for the long-term protection of tiusinte and all Zamiaceae in Honduras.
- 13. Strict control and regulation of traffic in the species outside its local range, whether to domestic nurseries and cities or to the exterior.
- 14. Revival of the use of tiusinte foods (given adequate knowledge of toxin removal).
- 15. Recovery of the traditions of using leaves for religious and decorative purposes, so that domestic plants will be better appreciated. Also, commerce could be developed in leaves, from tiusinte populations to the urban population centers, where they are needed for both religious and secular purposes.
- 16. Study of the problems associated with tiusinte seed storage (pests, for example).
- 17. Study of the effects of the *Eumaeus* caterpillar on the health of the plant and populations.
- 18. Complete inventory of populations.
- 19. Collection of living material, for ex situ preservation, from populations not covered during HN03.
- 20. Inclusion of tiusinte in sustainable agriculture projects and biodiversity protection projects.
- 21. Promotion of knowledge of tiusinte by way of school texts, stamps, websites, and other means, to give it a higher national profile as a recognized part of Honduran natural and cultural heritage.
- 22. With the Instituto Hondureño de Antropología y Historia (IHAH), archaeological study of zones where tiusinte grows.
- 23. Incorporation of tiusinte into socioeconomic development projects that affect the zones where it grows.

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