

A New Endemic *Ceratozamia* from Honduras (Cycadales: Zamiaceae)

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ABSTRACT

Ceratozamia hondurensis J.L. HAYNES, WHITELOCK, SCHUTZMAN & R.S. ADAMS, a broad-leafleted Honduran endemic cycad most similar to *C. euryphyllidia* VÁZQUEZ-TORRES, SABATO & D.W. STEV. from Oaxaca, Mexico, is described.

Key words: *Ceratozamia miqueliana* species complex, Mesoamerica, disjunct

INTRODUCTION

According to most published accounts, the genus *Ceratozamia* BRONGNIART is confined to Mexico and adjacent Belize and Guatemala (*e.g.*, Stevenson *et al.*, 1986; Norstog & Nicholls, 1997; Jones, 2002; Stevenson *et al.*, 2003; Hill *et al.*, 2007). The center of diversity of the genus is southern Mexico (González & Vovides, 2002; Whitelock, 2004), and 22 currently recognized species occur in that country (Hill *et al.*, 2007; Pérez-Farrera *et al.*, 2007; Osborne *et al.*, *in press*). Two of these species also occur outside Mexico: *C. robusta* MIQUEL is reported from Guatemala and Belize, and *C. matudae* LUNDELL extends from Chiapas into western Guatemala (Hill *et al.*, 2007). *Ceratozamia*

euryphyllidia VÁZQUEZ-TORRES, SABATO & D.W. STEV. has also been reported from Guatemala (Stevenson *et al.*, 2003), but its presence there remains controversial (see Chemnick, 2005; Hill *et al.*, 2007).

Anecdotal reports of a broad-leafleted *Ceratozamia* in Honduras have appeared over the past decade. Some of these reports provided photos of cultivated plants and referred to the species as an undescribed *Zamia* L. (*e.g.*, Kyburz, n.d.). The oldest known voucher of this species was collected in northwestern Honduras in the late 1920's by the renowned Mesoamerican botanist Paul C. Standley (*P.C. Standley 56779*). Currently residing in the Smithsonian Institution herbarium (USNH) in Washington, D.C., its label bears the

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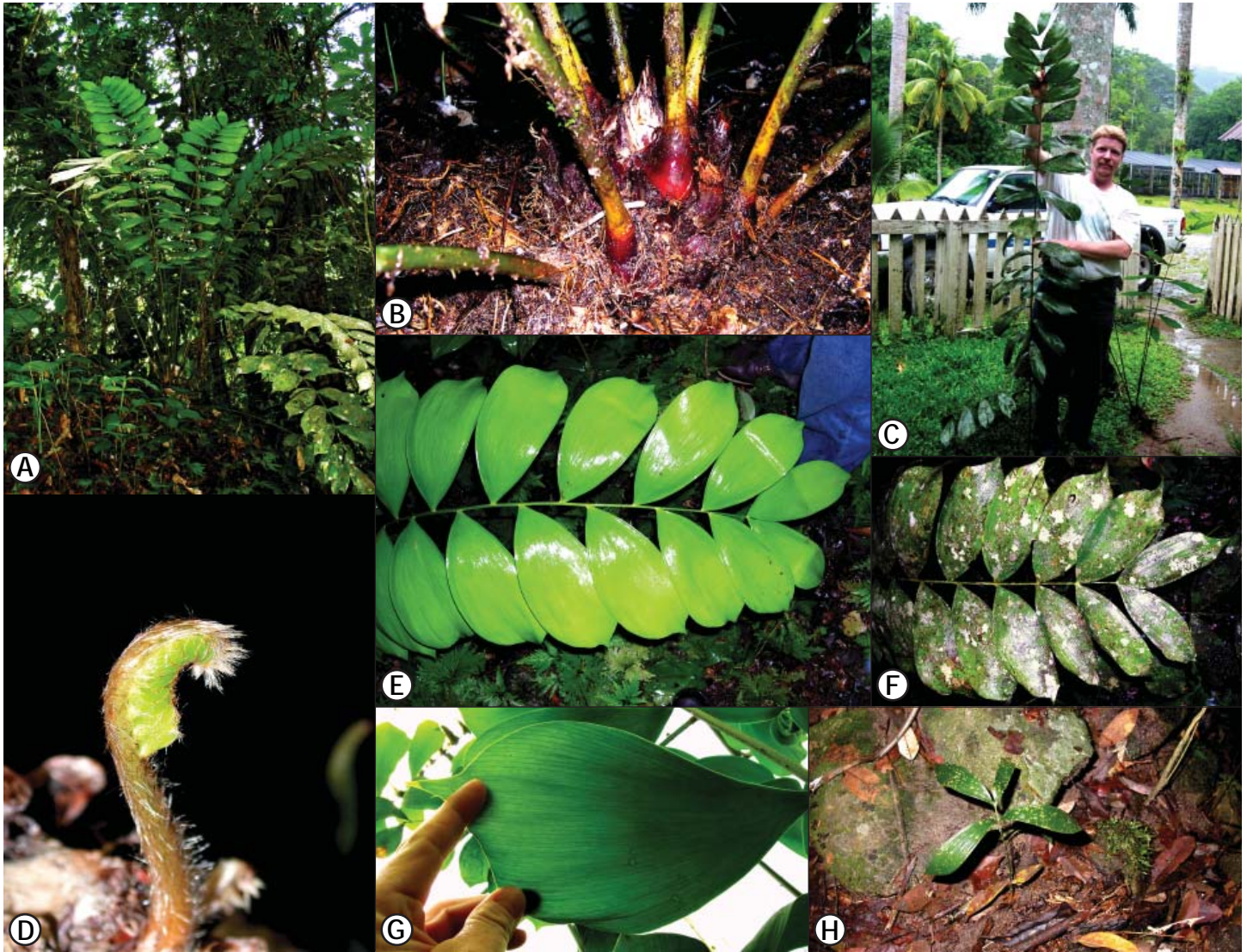


Fig. 1. Distinguishing vegetative traits of *Ceratozamia hondurensis*. A. Habit and habitat. B. Caudex, illustrating stipulate, pubescent, acuminate cataphylls, as well as glabrous, non-glaucous petioles and stipulate, wine-red to purplish-maroon, glabrous leaf bases. C. Mature leaf, illustrating overall size, as well as arrangement, spacing, and orientation of leaflets (with first author for scale). D. Newly emerging leaf, illustrating lanate rachis and petiole, lime-green coloration, and circinate vernation. E. Fully expanded new leaf, illustrating glossy, non-glaucous, lime-green coloration, as well as shape, spacing, and orientation of median and apical leaflets. F. Mature leaf, illustrating typical covering of lichens and bryophytes, as well as shape, spacing, and orientation of median and apical leaflets. G. Closeup of median leaflet, illustrating typical shape and relative size, as well as opaque veins and translucent, membranous disposition. H. Eophyll, illustrating number, shape, and orientation of leaflets. (Photo A by G. Holzman; B, C, E, F by M. Bonta; D, G taken in cultivation.)

original determination of "*Zamia*," with a later determination of *Z. tuerckheimii* DONNELL SMITH by D.W. Stevenson (n.d.), and a third determination of "*C. telensis* Schutzman & Vovides ined." by B. Schutzman (1998). The latter name refers to the town of Tela in northwestern Honduras, near which the only known population was originally thought to exist. Also at USNH is a specimen collected by Standley from the same region of Honduras twenty years later (*P.C. Standley 7593*); originally labeled *Z. tuerckheimii*, it was also determined by B. Schutzman in 1998 as "*C. telensis*." This latter collection number also appears on a specimen labeled *Z. tuerckheimii* in the Paul C. Standley Herbarium (EAP) at

the Pan-American Agricultural School at El Zamorano, Honduras—along with several additional specimens also mistakenly identified as *Z. tuerckheimii* (see list of other specimens examined below).

In 2003, M. Bonta and the first author conducted an expedition to Honduras with the primary goal of determining the distribution and population status of *Dioon mejiae* STANDLEY & L. O. WILLIAMS. Along the way, several other cycad taxa were also observed: *Zamia standleyi* SCHUTZMAN, two (then) undescribed species of *Zamia* (= *Z. sandovalii* C. NELSON [Nelson Sutherland, 2006] and *Z. bussellii* SCHUTZMAN, R.S. ADAMS, J.L. HAYNES, & WHITELOCK [Schutzman *et al.*, 2008 - this issue]), and the

herein described *Ceratozamia* sp. nov. At the time, the latter was known from only two disjunct localities—representing the western and eastern known extremes of its range, respectively—in the Caribbean littoral region of the Department of Atlántida. During the course of the expedition, both of the known populations were determined to be nearly extirpated: the first from habitat destruction and the second from illicit harvesting by collectors. Fortunately, a healthy population was discovered within a few km of the first population, and three years later several plants, including a coning female, were discovered within a few km of the second population (Sandoval, 2006; R. Steiner,

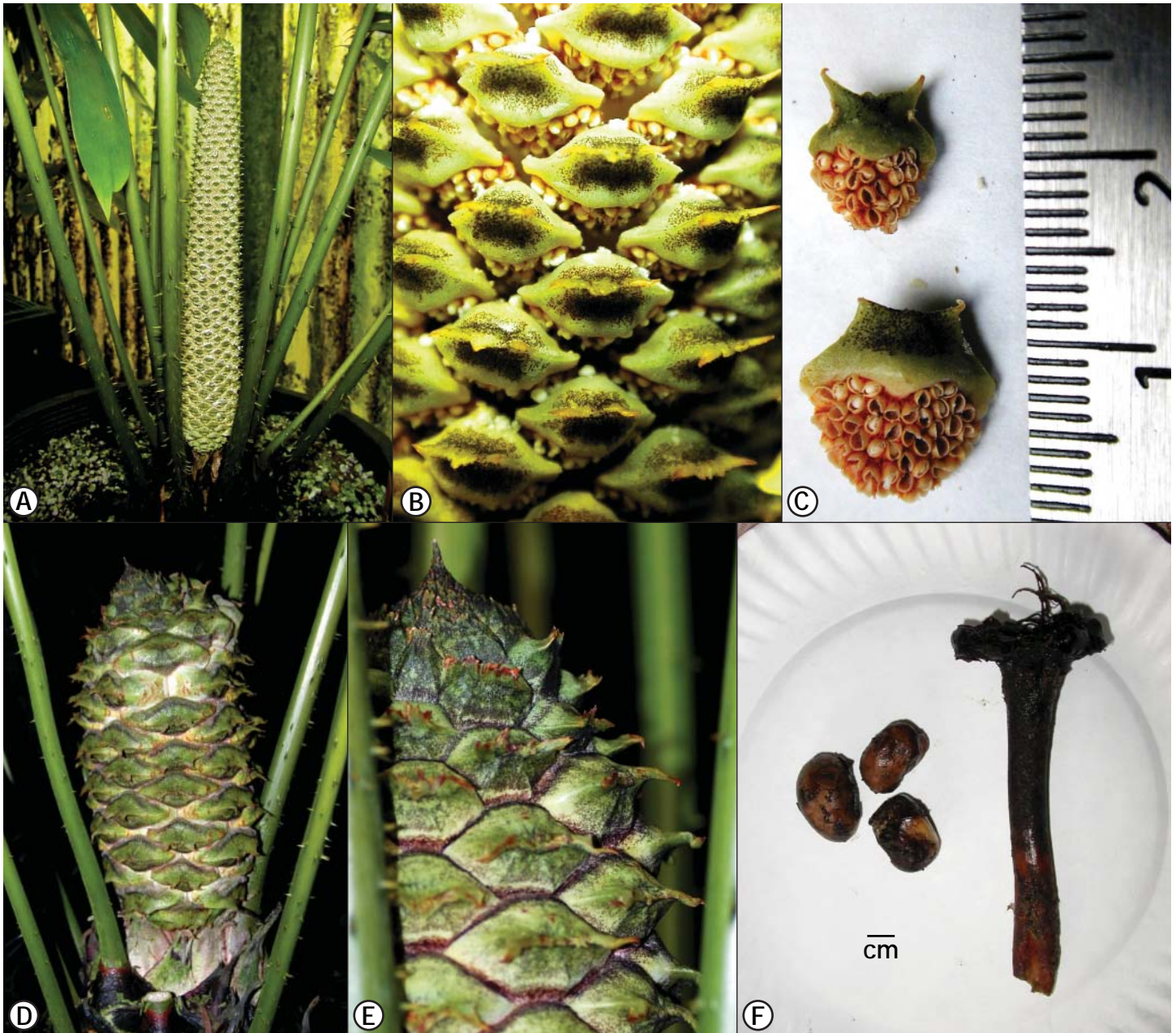


Fig. 2. Distinguishing reproductive traits of *Ceratozamia hondurensis*. A. Mature male cone, illustrating shape, coloration, and sessile disposition. B. Closeup of mature male cone, illustrating shape, color, and orientation of microsporophylls. C. Abaxial view of microsporophyll, illustrating size, shape and color, as well as distribution of microsporangia. D. Nearly mature female cone, illustrating shape, coloration, and erect disposition. E. Closeup of nearly receptive female cone, illustrating shape, color, and orientation of megasporophylls. F. Seeds (including sarcotesta) and ovulate cone peduncle, illustrating shape and size of both, as well as persistent pubescence of mature peduncle. (All except F taken in cultivation.)

pers. comm.). Thus, it appears that the species is not completely eliminated from either end of its range. Two additional localities in the middle of the known range were documented by herbarium vouchers in 1994, but the current status of these populations is unknown.

DESCRIPTION

Below is the formal description of this new Honduran endemic cycad. Every effort has been made to adhere to the recommendations for new species descriptions outlined in Osborne and Walters (2004) and Whitelock (2004), including providing as much detail as possible about vegetative and reproductive morphology, biology, life history, habitat, ecology, ethnobotanical importance, threats, and conservation status. Unfortunately, nothing is known of its pollinators, pests or diseases, so these will not be addressed. Specific locality information has been withheld for conservation purposes.

Ceratozamia hondurensis J.L. HAYNES, WHITELOCK, SCHUTZMAN & R.S. ADAMS *sp. nov.* (Figs. 1-2).

Ceratozamia euryphyllidia affinis, a qua imprimis differt folioliis medianis plus symmetricis, folioliis emergentibus flavovirentibus, micro- et megastrobilis maturis viridibus.

Plant an understory shrub (Fig. 1A). Stem 15-25 cm diam., acaulescent, solitary, covered by persistent cataphylls and leaf bases (Fig. 1B); cataphylls 4.5-6.5 cm long, 4.5-9 cm wide, triangular, stipulate, pubescent, wine red to purplish-maroon, base appressed, tip acuminate and erect to reflexed (Fig. 1B). Leaves to 20 or more per crown, 1.4-2.8 m long, erect to

arching (Figs. 1A,C); vernation circinate (Fig. 1D); emerging lanate, bright green, and slightly glaucous to non-glaucous; expanding to glossy lime green and glabrous (Fig. 1E); maturing to glossy dark green, later becoming covered with lichens and other epiphytes (Fig. 1F); rachis 80-180 cm long, 0.5-1 cm diam., terete, not twisted, armed with small prickles in lower half to two-thirds; 6-16 leaflet pairs, widely spaced, not fasciculate; basally keeled, medially and apically flat to slightly declinate; basally alternate, medially alternate to subopposite, apically subopposite to opposite (Figs. 1E,F); petiole 60-70 cm long, 1-2 cm diam., terete, lightly to moderately armed, non-glaucous to slightly glaucous, initially lanate, maturing sparsely pubescent or glabrous (Fig. 1B); leaf base 2.5-5.5 cm wide, stipulate, wine red to purplish-maroon, glabrous (Fig. 1B); leaflets 24-30 cm long, 9-13 cm wide (median), membranous, nearly symmetric to slightly asymmetric, oblanceolate, not falcate, flat to slightly convex adaxially, may be slightly upturned toward the edges; margins subrevolute, apically entire to slightly scalloped and smooth to slightly undulating; tip 1-2 cm long, slightly to moderately asymmetric, abruptly acuminate; articulation 0.5-1 cm wide, green, attenuate; veins 40-55, parallel, basally dichotomous, opaque, raised abaxially (Fig. 1G); eophylls typically with four equal-sized, slightly asymmetric, oblanceolate leaflets 4-5 cm long, 0.5-1 cm wide, basally slightly keeled, apically flat to slightly declinate (Fig. 1H). Microsporangiate strobilus 27-35 cm long, 4-5 cm diam., solitary, fusiform-cylindrical, erect, appearing sessile, green with numerous small black trichomes localized in the center of each sporophyll (Figs. 2A,B); peduncle 1.8-3.5 cm long,

1.5-2.5 cm diam., lanate, not curved, hidden by surrounding cataphylls (Fig. 2A); microsporophylls 1-1.2 cm long, 0.7-1.2 cm wide, 0.5-0.6 cm tall, deltoid to cuneate, slightly peltate, spirally arranged in 18-20 columns and 75-85 rows, each bearing two outward- and downward-turning, red-tipped horns 1-2 mm long, with one to several small, jagged protrusions between them (Figs. 2B,C); microsporangia in clusters of 2-5 equally distributed over entire unexposed abaxial surface, dehiscent longitudinally (Fig. 2C). Megasporangiate strobilus 18-21 cm long, 10-12.5 cm diam., solitary, cylindrical to barrel-shaped, dull green with a light scattering of small, blackish-brown trichomes, each sporophyll edged in darker, purplish-maroon trichomes (Figs. 2D,E), erect to leaning at maturity, not pendent; apex rounded-acute, 3-5 cm tall, consisting of reduced, sterile sporophylls (Fig. 2E); peduncle 5-15 cm long, 1.5-3 cm diam. (Fig. 2F), densely tan to brown tomentose; megasporophylls 3.5-4.5 cm long, 4.2-5.5 cm wide, 2-2.5 cm tall, transversely hexagonal, spirally arranged in 12-14 columns and 10-12 rows, each bearing two stout, outward- and downward-turning, red-tipped horns 3-5 mm long, with one to several jagged protrusions between them (Figs. 2D,E); seeds 2-2.5 cm long, 1.5-2 cm diam., 200 or more per cone, smooth, ovoid to globose; sarcotesta white when ripe, quickly aging to brown (Fig. 2F).

Type: Honduras. Atlántida: 1.5 m leaves, 50 masl, disturbed primary forest on steep slope along river bank, 13 April 1994, A.E. Brant & R. Zúñiga 2830 (holotype, EAP!; isotype, MO!).

Other specimens examined. HONDURAS. Atlántida: 6 December 1927-20

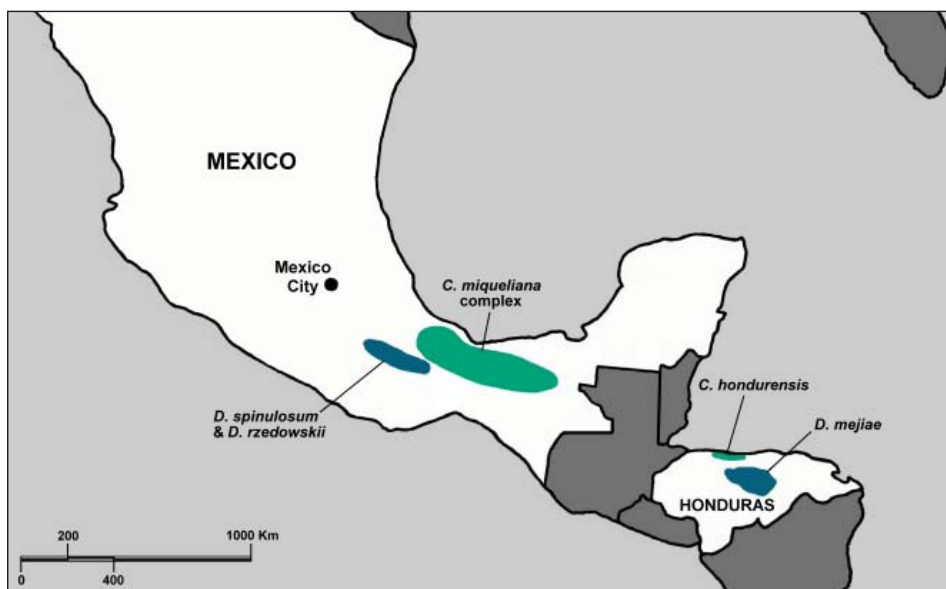


Fig. 3. Geographic distribution of the *Ceratozamia miqueliana* species complex.



Fig. 4. Comparison of apical (top), median (middle), and basal (bottom) leaflets of *Ceratozamia hondurensis* (left) and *C. euryphyllidia* (right). (Leaflets taken from cultivated plants.)

March 1928, *P.C. Standley 56779* (USNH); 22-27 April 1947, *P.C. Standley 7593* (EAP, USNH); 12 May 1993, *R.L. Liesner & D. Mejía 26238a* (EAP), *26239* (MO); 9 April 1994, *D.L. Hazlett, A.E. Brant & R. Zúñiga 8036* (EAP, MO); 14 April 1996, *D.R. Hodel & S. Schleder 1485* (NY); 31 July 2003, *J. Haynes, M. Bonta, G. Sandoval, C. O'Reilly, I. Zúñiga & J. Mendoza JLH03-040, JLH03-047* (TEFH).

Etymology. The specific epithet was chosen to honor the country of endemicity.

Distribution and habitat. This species is distributed along the Caribbean versant of the Cordillera Nombre de Dios, Department of Atlántida, Honduras (Fig. 3). Plants typically grow at 20-600 masl on steep river banks under dense canopy in wet tropical evergreen forest, but are occasionally found in the open near the stream bed (Fig. 1A).

Geology and soils. Intrusive granite dominates the North Coast region of Honduras (Kozuch, 1991; R. Rogers, pers. comm.), and the soils in the area of endemicity are

typically weathered from this rock, causing them to be somewhat acidic. These soils are also rich in humus derived from rapid degradation of copious amounts of leaf litter typical of wet tropical forests.

Climate. The climate of the north coast is tropical, with relatively consistent rainfall throughout the year. Mean annual precipitation ranges from 1,800-2,800+ mm, with a drier season extending from March-June. The climate is so humid year-round that older leaves are often covered with lichens and bryophytes (Fig. 1F).



Fig. 5. Distinguishing traits of *Ceratozamia euryphyllidia*. A. Habit and habitat, illustrating remarkable similarities with *C. hondurensis*. B. Fully expanded new leaf, illustrating persistently glaucous, 'pea green' leaflets. C. Median leaflet, illustrating relative size and strongly asymmetric, widely obovate shape. D. Male cone, illustrating shape, coloration, and disposition, as well as pubescent, intensely glaucous, emergent petioles. E. Receptive female cone, illustrating shape, coloration, and disposition, as well as pubescent peduncle, petioles, leaf bases, and cataphylls. (Photos A-C by J. Chemnick; D,E taken in cultivation.)

Reproductive phenology. An immature female cone was observed in September 2006 (R. Steiner, pers. comm.), and disarticulating female cones were observed in January 2005 (Fig. 2F). No other phenological information is available *in situ*.

Population structure. This species occurs in small, discrete, widely separated populations distributed along the North Coast region of Honduras. The largest known population consists of perhaps as many as 100 plants. This population is successfully reproducing, as seedlings (Fig. 1H) were observed within 1 m of a mother plant bearing a disarticulating seed cone.

Ethnobotanical uses and vernacular names. Along with the zamias of the Caribbean coast of Honduras, this species is known locally as ‘camotillo’ and is thought to be poisonous. After a fairly extensive survey of central and northern Honduras, no evidence of any local human use was revealed among mestizo or indigenous populations. One unfortunate non-local use is as an illicit export ornamental (Bonta, 2007).

Threats. Because of its startling beauty, this species is likely to become one of the most sought-after ceratozamia in the illicit cycad trade. Over-collecting has already nearly devastated one population within a protected area (ironically this population was also adversely affected by clearing activities in the boundary zone surrounding the protected area). Its native range is also subject to deforestation for migrant subsistence agriculture as well as export-driven agro-industry and cattle ranching. Habitat and elevation requirements also restrict it to one of the most environmentally hazardous landscapes of Honduras. In particular, its propensity to grow along river banks puts it in the path of potentially destructive floods of Hurricane Mitch-like proportions, making most populations particularly vulnerable (Haynes & Bonta, 2003).

Conservation status and recommendations. This species occurs within two protected areas and possibly a third. However, based on the discovery of two nearly extirpated populations—one of which occurs partly within a protected area—and the continuing threat of illicit collecting and habitat destruction, in addition to its limited extent of occurrence and area of occupancy, a listing of Critically Endangered (CR) is recommended according to the most recent IUCN Red List categories and criteria (IUCN, 2001). The complete proposed Red List assessment is CR A2acd+3cd B1b(i-v) C1+2a(ii). At present, all species of *Ceratozamia* are included in

CITES Appendix I (Donaldson, 2003), and this new species should be no exception. The following actions are recommended in an effort to conserve and protect this critically endangered species:

- Development of local and national legislation specifically targeting the protection of all known populations of *Ceratozamia hondurensis*.
- Careful monitoring of existing populations and comprehensive surveys of other areas with similar habitats.
- Creation of *ex-situ* conservation and propagation collections in well-established, world-class botanical gardens with a documented track record of supporting such efforts and with a written, long-term commitment to continue to do so.

TAXONOMIC & BIOGEOGRAPHIC AFFINITIES

Several workers have attempted to categorize the extant species of *Ceratozamia* into morphologically distinct groups. Moretti *et al.* (1980) recognized *C. mexicana* BRONGNIART and *C. matudae* LUNDELL species complexes, while Stevenson *et al.* (1986) proposed a *C. mexicana* group, with long, narrow leaflets, and a *C. euryphyllidial C. miqueliana* H. WENDLAND group, with shorter, wider leaflets. Vovides *et al.* (2004) later subdivided the genus into seven species complexes based on similarities in gross morphology, geographic proximity, and habitat preference. The latter authors subsumed *C. euryphyllidia* and included the more recently described *C. zoquorum* PÉREZ-FARRERA, VOVIDES & IGLESIAS and *C. becerrae* VOVIDES in their *C. miqueliana* complex. They also stated the following about *C. hondurensis*: “Recently a taxon related to the *C. miqueliana* complex has been found in northern Honduras, hence the range of the genus has been extended” (Vovides *et al.*, 2004).

Morphologically, *Ceratozamia hondurensis* most closely resembles *C. euryphyllidia*. Chemnick (2005) stated it best: “Indeed, to see the Honduran plant is to be struck at how very similar the two species are in spite of the considerable geographical distance between them.” This morphologic similarity is matched only by the remarkable biogeographic parallel between the *C. miqueliana* and *Dioon spinulosum* DYER & EICHLER species complexes (Fig. 3)—which leads one to wonder whether the geographic congruence in these two cycad genera resulted from similar vicariance events, or if the intervening region has simply not been adequately surveyed (Chemnick, 2005; Haynes, 2005).

Based on its similarity to *Ceratozamia euryphyllidia*, it is herein concluded that *C. hondurensis* should be formally added to the *C. miqueliana* complex. Another species that shares morphologic features with the members of this group is *C. whitelockiana* CHEMNICK & T.J. GREGORY (Chemnick & Gregory, 1995; Whitelock, 2002). Although Vovides *et al.* (2004) placed this species in their *C. robusta* complex, the authors of *C. whitelockiana* suggested that it is most closely allied to *C. miqueliana* based on shared cone, caudex, and leaf traits (Chemnick & Gregory, 1995); thus it, too, is herein considered a member of the *C. miqueliana* complex.

DIAGNOSTIC TRAITS

Ceratozamia hondurensis differs from *C. euryphyllidia* vegetatively by having thicker-textured, nearly symmetric, and oblanceolate, rather than very thin-textured, strongly asymmetric, and widely obovate median leaflets; glossy to slightly glaucous, lime-green rather than glaucous pale light green to bluish new leaves; non-glaucous to slightly glaucous rather than intensely glaucous emergent petioles; glabrous rather than persistently pubescent leaf bases; larger median leaflet length-to-width ratio (2.65:1 as opposed to 1.85:1; see Fig. 4); and acuminate rather than acute cataphylls. The Honduran species differs from *C. zoquorum* and *C. becerrae* by having membranous rather than coriaceous leaflets, armed rather than unarmed petioles, and opaque rather than transparent veins, and it can be readily distinguished from *C. whitelockiana* by its many more leaves, smooth rather than rough-textured caudex, glossy rather than glaucous emergent leaves, and smaller petiole length-to-leaf length ratio. Finally, *C. hondurensis* differs from *C. miqueliana* by having fewer, wider, and membranous rather than papyraceous leaflets.

Ceratozamia hondurensis differs from *C. euryphyllidia* reproductively by having male cones that are larger overall (both longer and wider) but with shorter peduncles (1.5-3.5 cm as opposed to 6-8 cm); male cones that remain green with small, black trichomes on each sporophyll from emergence through maturity, rather than emerging greenish-red and maturing to light gray; and female cones that are green with small, evenly distributed, brown to black trichomes, and with each sporophyll edged in darker, purplish-maroon trichomes, from emergence through maturity, rather than emerging wine red and maturing to brown or dark brown. Female cones of *C. hondurensis* also lack the pronounced mucronate tip of *C. euryphyllidia*. Also of note are the unique red-tipped and outward- and downward-turning horns of the micro- and

megasporophylls of *C. hondurensis*. The male cones of the remaining four species in the group are also quite distinct. In both *C. miqueliana* and *C. whitelockiana*, the apex of the cone is mucronate and the color is olive green, but, unlike the latter, the sporophylls of the former are sparsely covered with black tomentum and the horns are directed straight out from the sporophyll. In *C. zoquorum* and *C. becerrae*, the male cones emerge light green and mature light yellow or cream-colored, but the former has much longer peduncles as well as reddish tomentum on the peduncle (as opposed to brown) and on the sporophylls surrounding the horns. While the dark green-emergent and decumbent mature female cones of *C. zoquorum*, the beige-emergent female cones of *C. becerrae*, and the large, solid apiculum of the female cones of *C. whitelockiana* are distinguishing traits for these species, the size and orientation of the horns on the megasporophylls are also diagnostic in each of the remaining species: *C. becerrae* has 3-4 crests near the base of the horns; the horns of *C. miqueliana* are bent downward, and there is a small, rudimentary horn between the two main horns; the horns of *C. whitelockiana* are divergent to either side of the sporophyll, are up to 1 cm long, and are joined by a raised, wrinkled ridge; and the horns of *C. zoquorum* are surrounded by reddish-brown tomentum.

TAXONOMIC KEY

The dichotomous key in Table I below separates *Ceratozamia hondurensis* from the other members of the *C. miqueliana* species complex. It excludes reproductive structures because these are rarely seen in habitat.

ACKNOWLEDGMENTS

T. Walters, former executive director of Montgomery Botanical Center, supported and sponsored the HN03 expedition and a later HN05 study tour; M. Bonta coordinated and led the HN03 expedition, co-organized the HN05 study tour, and provided habitat photos; I. Zúñiga, G. Sandoval, C. O'Reilly, and J. Mendoza assisted with data and specimen collection; G. Holzman provided a habitat photo and helped locate plants and a mature female cone during the HN05 study tour; J. Chemnick provided habitat photos of *Ceratozamia euryphyllidia*; M. Bonta, J. Chemnick, T. Gregory, G. Holzman, and A. Taylor reviewed the manuscript prior to submission.

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Table I. Dichotomous key to the *Ceratozamia miqueliana* species group

- | | | |
|-----|---|-------------------------|
| 1a. | Petioles unarmed, leaflets coriaceous, veins transparent..... | 2 |
| 2a. | Leaflets pruinose emergent, length-to-width ratio 5:1 to 7:1..... | <i>C. zoquorum</i> |
| 2b. | Leaflets not pruinose emergent, length-to-width ratio 2:1 to 3:1..... | <i>C. becerrae</i> |
| 1b. | Petioles armed, leaflets papyraceous or membranous, veins opaque..... | 3 |
| 3a. | Median leaflets 30-50 cm long, petioles generally > 50% of overall leaf length..... | <i>C. whitelockiana</i> |
| 3b. | Median leaflets typically < 30 cm long, petioles < 50% of overall leaf length..... | 4 |
| 4a. | Leaflets papyraceous, 5-8 cm wide..... | <i>C. miqueliana</i> |
| 4b. | Leaflets membranous, ≥ 9 cm wide..... | 5 |
| 5a. | Median leaflets strongly asymmetric and widely obovate, new leaves glaucous pale light green to bluish with intensely glaucous petioles .. | <i>C. euryphyllidia</i> |
| 5b. | Median leaflets nearly symmetric and oblanceolate, new leaves glossy to slightly glaucous lime green with non-glaucous to slightly glaucous petioles..... | <i>C. hondurensis</i> |