
HONDURODENDRON, A NEW MONOTYPIC GENUS OF APTANDRACEAE FROM HONDURAS¹

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ABSTRACT

Hondurodendron C. Ulloa, Nickrent, Whitef. & D. Kelly, a new monotypic genus endemic to Honduras, is here described and illustrated. The new species, *H. urceolatum* C. Ulloa, Nickrent, Whitef. & D. Kelly, is a dioecious tree, distinguished by its minute flowers borne on densely tomentose inflorescences, unique anthers opening by three valves, and a characteristic fruit totally enveloped by the accrescent calyx, which projects beyond the fruit. A molecular analysis based on four genes (nuclear small subunit [SSU] ribosomal DNA [rDNA], chloroplast *rbcl*, *matK*, and *accD*) placed this genus in a clade with *Aptandra* Miers, *Harmandia* Pierre ex Baill., *Chaunochiton* Benth., and *Ongokea* Pierre in the family Aptandraceae Miers.

RESUMEN

Se describe e ilustra un nuevo género monotípico *Hondurodendron* C. Ulloa, Nickrent, Whitef. & D. Kelly endémico de Honduras. La nueva especie *H. urceolatum* C. Ulloa, Nickrent, Whitef. & D. Kelly es un árbol dioico, que se distingue por las flores diminutas en inflorescencias densamente tomentosas, las anteras únicas que se abren por tres valvas y un fruto característico totalmente encerrado por el cáliz acrescente que se proyecta sobre éste. Un análisis molecular con cuatro genes (SSU ADN ribosómico nuclear, *rbcl* del cloroplasto, *matK* y *accD*) ubica al género en un clado junto con *Aptandra* Miers, *Harmandia* Pierre ex Baill., *Chaunochiton* Benth. y *Ongokea* Pierre en la familia Aptandraceae Miers.

Key words: Aptandraceae, Cusuco National Park, Honduras, *Hondurodendron*, IUCN Red List, Olacaceae.

During a plot-based survey of the forest vegetation of Parque Nacional El Cusuco in northwest Honduras in 2004 and 2006, specimens of an unknown tree were collected that proved difficult to place into any known Central American genus or family. The plant had distichous leaves and fine pubescence on the very young inflorescences, features reminiscent of the genus *Acanthosyris* (Eichler) Griseb. (Santalaceae), but it also possessed a greatly enlarged (accrescent) calyx that projected beyond the fruit as a conspicuous flared limb, thus suggesting Olacaceae s.l. The plant was dioecious, with remarkable anthers opening by three valves. Neotropical olacaceous genera with

accrescent calyces include *Aptandra* Miers, *Chaunochiton* Benth., and *Heisteria* Jacq., but none of these genera possess the combination of morphological characters seen in the Honduran specimens.

Compared with other Central American countries, Honduras is poorly known botanically with no published flora. The country checklist of Molina (1975) and the new *Catálogo de las Plantas Vasculares de Honduras* (Nelson Sutherland, 2008) were examined, but none of the Olacaceae and relatives mentioned in those lists corresponded to the samples from Cusuco. Additional field observations and collections that included both flowers and

¹ All collections resulted from the survey of the biodiversity of Cusuco National Park, funded and organized by Operation Wallacea under the direction of Dr. T. Coles and Dr. R. Field. We are grateful for the support and assistance of the “Op Wall” team, especially J. Núñez-Miro, A. Tozer, and J. Hines. For assistance in the fieldwork, we thank in particular R. Fritch, K. Fagan, C. Lennkh, G. Sandoval, A. Bergoënd, and the students and teachers of South Bromsgrove School, Birmingham, and Beaumont School, St. Alban’s. For collecting permits, we thank Corporación Hondureña de Desarrollo Forestal (COHDEFOR) and its successor organization Instituto de Conservación Forestal (ICF). We gratefully acknowledge the assistance of our guides P. Cortés, M. Ramírez, and others. For photographs, we thank K. Snarr and J. Kolby. N. Robson kindly translated the diagnosis into Latin. A. L. Arbeláez prepared the beautiful line drawing. T. Distler and J. Hidalgo helped with determining the conservation status and P. Jørgensen with preparing Figures 5 and 6. Thanks to D. Gates and J. Bozzola (Southern Illinois University Carbondale Integrated Microscopy and Graphics Expertise [IMAGE]) for assistance with pollen scanning electron microscopy and to V. Malécot for providing the herbarium specimen of *Harmandia* and for assistance with pollen ultrastructure. Helpful comments from reviewers V. Malécot, Z. Rogers, and P. Stevens improved the manuscript.

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silica gel–dried leaf samples were obtained in 2008; these have allowed the phylogenetic position of this mysterious plant to be confirmed.

MATERIALS AND METHODS

PHYLOGENETIC ANALYSIS

The specimens used for DNA extraction are listed in Table 1. Samples were taken from herbarium specimens or from silica gel–dried leaves. The methods for DNA extraction, polymerase chain reaction (PCR) amplifications, and sequencing were generally the same as those reported in Rogers et al. (2008), except that the automated sequencer used to generate the new sequences reported here was an AB3130xl capillary system (Applied Biosystems, Carlsbad, California, U.S.A.). PCR primer sequences for nuclear small subunit (SSU) ribosomal DNA (rDNA) and chloroplast *rbcL*, *matK*, and *accD* were reported in Rogers et al. (2008). Eight ingroup taxa were used in this study, representing all genera of Aptandraceae. *Maburea trinervis* Maas (Erythropalaceae) and *Strombosiopsis tetrandra* Engl. (Strombosiaceae) were used as outgroups as guided by the topology of the tree in Malécot and Nickrent (2008). Nine of the 40 sequences used in the alignment were generated in the present study, whereas the rest were reported by Malécot and Nickrent (2008). The sequences were aligned manually using SeAl version 2.0 (Rambaut, 2004), and this alignment is available online under “Combinatorial Data Sets” at <<http://www.parasiticplants.siu.edu/Alignments/Alignments.html>>. Exhaustive maximum parsimony (MP) analyses were conducted on the concatenated four-gene data set using PAUP* 4.0b10 (Swofford, 2002). Nodal support was determined using MP bootstrap analysis (branch-and-bound search using 1000 replicates, taxon addition sequence set as “furthest”). In addition, a maximum likelihood (ML) bootstrap tree was generated using GARLI 1.0 (Zwickl, 2006). The nucleotide substitution model was general time reversible (GTR + G + I) using program defaults, except random starting trees were used instead of stepwise-addition starting trees for each analysis. Two analyses for each bootstrap replication were conducted and both found the same tree. A majority-rule consensus tree was constructed with the 100 bootstrap trees.

TAXONOMY

All measurements were taken from herbarium specimens, but flower measurements are from rehydrated herbarium material. Additional observations,

Table 1. Voucher information and GenBank accession numbers for 10 taxa used in the phylogenetic analysis. The DNA accession numbers refer to the collections by D. L. Nickrent archived at Southern Illinois University Carbondale. Sequences in boldface were newly generated for this study. NHN, National Herbarium of the Netherlands.

Taxon	Voucher	Herbarium	Country	DNA accession number			
				SSU rDNA	<i>rbcL</i>	<i>matK</i>	<i>accD</i>
<i>Anacolosa papuana</i> Schellenb.	<i>Regalado & Sirikolo 692</i>	MO	Solomon Islands	DQ790104	DQ790144	DQ790181	DQ790250
<i>Aptandra tubicina</i> (Poepp.) Benth. ex Miers	<i>van der Werff & Vasquez 13846</i>	MO	Peru	DQ790105	DQ790141	DQ790178	DQ790247
<i>Cathedra acuminata</i> (Benth.) Miers	<i>Ratter et al. 6782</i>	MO	Brazil	FJ848847	DQ790145	DQ790182	DQ790251
<i>Chaunochiton kappleri</i> (Sagot) Ducke	<i>Zamora 1928</i>	MO	Costa Rica	DQ790106	DQ790142	DQ790179	DQ790248
<i>Harmandia mekongensis</i> Baill.	<i>Koizumi 1411</i>	KYO	Indonesia	FJ848849	FJ848842	FJ848845	FJ848843
<i>Hondurodendron urceolatum</i> C. Ulloa, Nickrent, Whitef. & D. Kelly	<i>Fagan et al. DA2/MS 313-II</i>	MO	Honduras	FJ848848	FJ848841	FJ848846	FJ848844
<i>Maburea trinervis</i> Maas	<i>Zagst s.n.</i>	NHN	Guyana	DQ790114	DQ790165	DQ790201	DQ790268
<i>Ongokea gore</i> (Hua) Pierre	<i>Breteler et al. 14888</i>	NHN	Gabon	DQ790120	DQ790140	DQ790177	DQ790246
<i>Phanerodiscus capuronii</i> Malécot, G. E. Schatz & Bossier	<i>Schatz et al. 3439</i>	MO	Madagascar	DQ790122	DQ790143	DQ790180	DQ790249
<i>Strombosiopsis tetrandra</i> Engl.	<i>Wieringa 3300</i>	NHN	Gabon	DQ790125	DQ790155	DQ790191	DQ790259

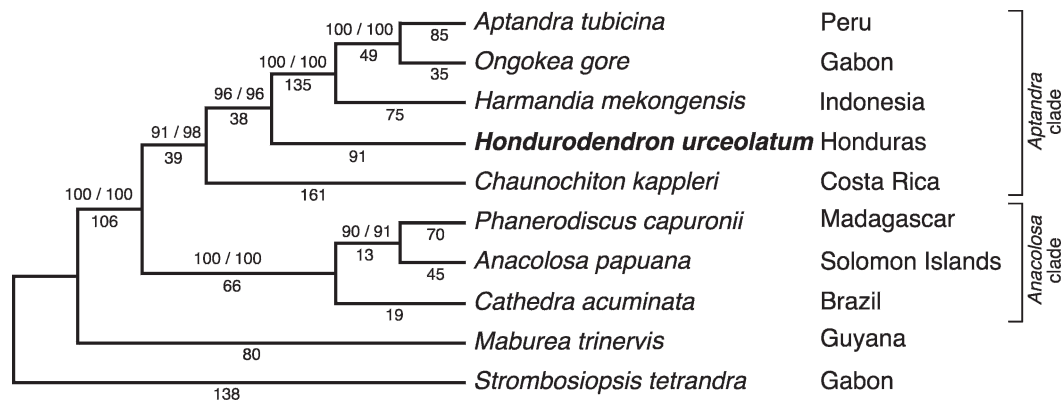


Figure 1. Phylogenetic tree derived from analysis of the concatenated four-gene data set (nuclear SSU rDNA, and chloroplast *rbcL*, *matK*, and *accD*) for genera of Aptandraceae (see Table 1 for vouchers). For maximum parsimony, one tree of length 1245 was found following an exhaustive search. The tree has a consistency index (minus uninformative sites) of 0.7473. Numbers above the branches are maximum parsimony bootstrap percentages (1000 replications, branch-and-bound search) followed by maximum likelihood bootstrap percentages; numbers below are branch lengths.

photographs, and ecological notes were taken in the field.

RESULTS

PHYLOGENETIC ANALYSIS

The exhaustive MP search of the concatenated four-gene matrix yielded one tree of length 1245 (Fig. 1). This tree was identical in topology to the maximum likelihood tree. Of the 5696 characters, 414 were parsimony informative. Trees with identical topologies were recovered when the nuclear SSU rDNA partition and a partition composed of the concatenated chloroplast genes were analyzed separately. Both MP and ML bootstrap support (MPBS and MLBS) for all ingroup nodes was high, as was the node defining Aptandraceae. As shown in the previous three-gene analysis (Malécot & Nickrent, 2008), Aptandraceae is composed of two clades, the first with *Anacolosa* (Blume) Blume, *Cathedra* Miers, and *Phanerodiscus* Cavaco, and the second with *Aptandra*, *Ongokea* Pierre, and *Chaunochiton*. The present analysis placed two additional taxa, *Harmandia* Pierre ex Baill. and *Hondurodendron* C. Ulloa, Nickrent, Whitef. & D. Kelly, gen. nov., in the second clade with strong support. *Chaunochiton* is resolved as sister to the second clade (91 MPBS, 98 MLBS). *Hondurodendron* is sister to the *Aptandra*–*Ongokea*–*Harmandia* clade (96 MPBS, 96 MLBS).

TAXONOMY

Hondurodendron C. Ulloa, Nickrent, Whitef. & D. Kelly. TYPE: *Hondurodendron urceolatum* C. Ulloa, Nickrent, Whitef. & D. Kelly.

Hondurodendron urceolatum C. Ulloa, Nickrent, Whitef. & D. Kelly, gen. et sp. nov. TYPE: Honduras. Cortés: Plot BC/3/MS, S of trail to Las Minas, ca. 200 m SE of jct. with Carretera Río Cusuco (trail BC4), W of 'Base Camp'/Campamento Parque Nacional El Cusuco, Sierra de Merendón, W of San Pedro Sula, 1656 m, UTM 0369210 1713408, 3–26 July 2006 (♀ fl., fr.), D. L. Kelly, R. Fritch, D. Brady, C. Whiteford, M. Ramírez BC/3/MS 233 (holotype, TEFH!; isotypes, BM!, MO!, TCD!). Figures 2, 3.

Hondurodendron C. Ulloa, Nickrent, Whitef. & D. Kelly, genus novum a generibus aliis Aptandracearum calyce accrescenti fructum omnino cingenti occultantique ultra fructum extensionem dilatam formanti, floribus staminatis disco succulento lobato lobis numerum staminum aequantibus eis alternantibus instructis, antheris valvis tribus longitudinalibus dehiscentibus atque surculis juvenibus inflorescentiaque indumento tenui ferrugineo vestitis differt.

Dioecious trees, to 12 m tall and over, to 23.6 cm DBH. Bark slightly rough, shallowly fissured, lenticellate, slash pink streaked cream, without exudates. Juvenile and smaller mature trees show a clearly defined architecture: main axis monopodial and orthotropic with spiral phyllotaxy and bearing rather evenly spaced branches; branches monopodial and plagiotropic with distichous phyllotaxy, corresponding to the model of Roux (Hallé & Oldeman, 1970; Bell, 1991). Second- and higher-order branches are freely produced, so that the foliage is arranged in flattened sprays. Twigs slightly zigzag toward the apices, longitudinally striate when dry. Reddish brown unicellular to uniseriate trichomes up to 0.3 mm densely covering young shoots, inflorescence rachis, bracts, and exterior of flowers; less dense on the

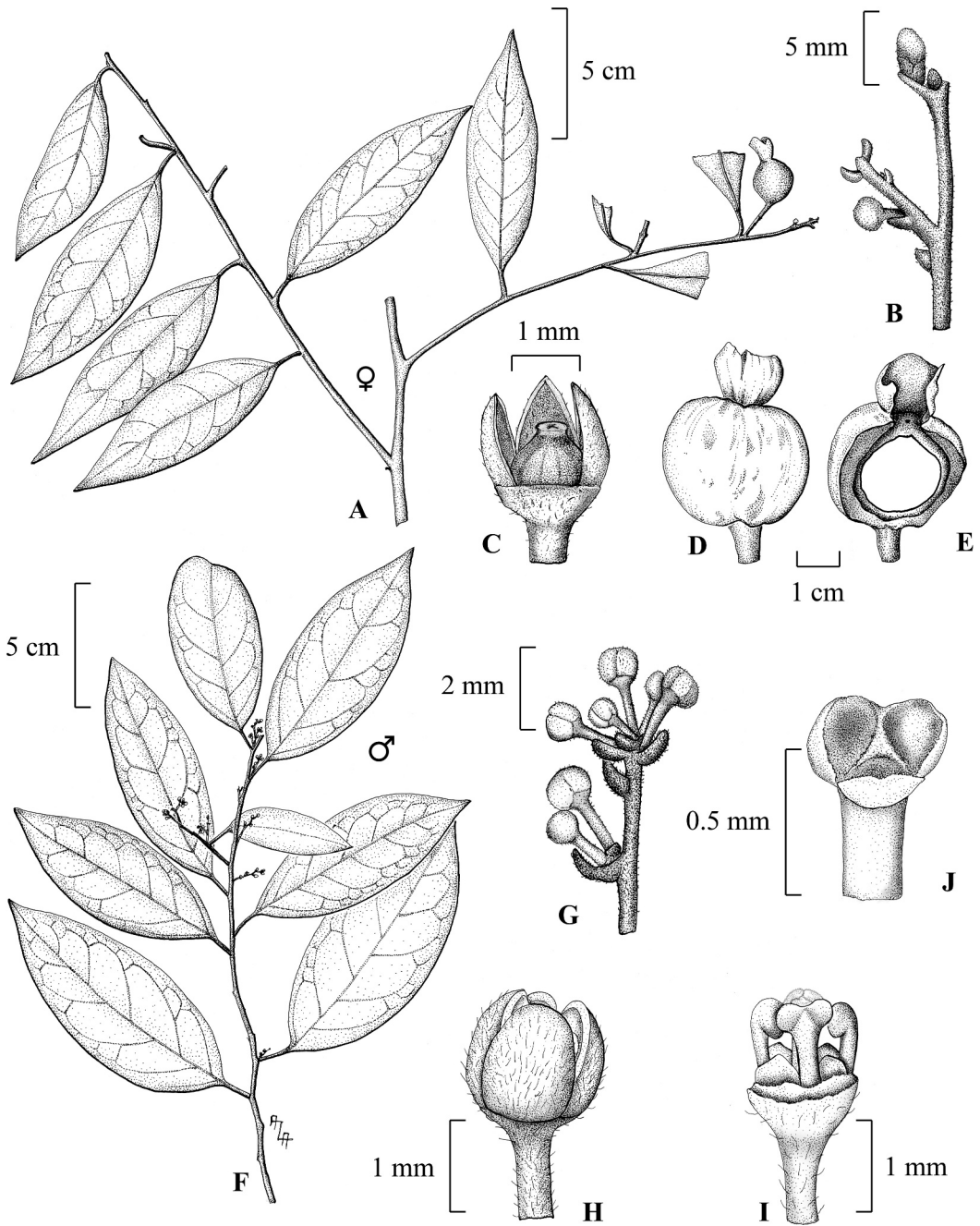


Figure 2. *Hondurodendron urceolatum* C. Ulloa, Nickrent, Whitef. & D. Kelly. —A. Fruiting branch. —B. Partial pistillate inflorescence in bud. —C. Pistillate flower, with cup-shaped calyx, one petal removed. —D. Mature fruit. —E. Fruit, cut lengthwise. —F. Staminate branch. —G. Staminate inflorescence (in bud). —H. Staminate bud. —I. Stamens and disk, petals removed. —J. Anther (with three longitudinal apically dehiscent valves). A, D, E from Kelly *et al.* BC/3/MS 233 (BM); B, C from Kelly *et al.* 13/304 (MO); F, G from Fritsch *et al.* GU/1/MS 869 (MO); H–J from Kelly & A. Fiallos DA/2/MS 313 (MO).

petioles, scattered along the midrib below and rarely on the surface of mature leaves. Leaves distichous; petiole 7–12.5 mm, slightly canaliculate above, rounded below; leaf blades usually elliptic, sometimes

slightly ovate to oblong, 6.5–12.5 × 1.5–4.6 cm, acute to acuminate at apex, acute to attenuate and slightly decurrent at base, margins entire, flat to slightly revolute when dried, midnerve flat to deeply im-



Figure 3. *Hondurodendron urceolatum* C. Ulloa, Nickrent, Whitef. & D. Kelly. —A. Branch with fruits (photograph D. L. Kelly, July 2008). —B. Longitudinal sections of fruit (photograph courtesy K. Snarr, June 2005). —C. Mature fruit (photograph courtesy J. Kolby, July 2010). Scale bars A–C = 1 cm.

pressed adaxially, raised and rounded abaxially, secondary venation brochidodromous with 5 to 8(to 11) pairs of nerves, raised abaxially, flat or slightly raised adaxially, tertiary venation reticulate, generally visible on both surfaces; blade texture slightly fleshy

when fresh, glabrescent. Inflorescences axillary, on the distal parts of leafy shoots. *Staminate inflorescences* 8–20 mm, up to ca. 20 flowers arranged in few-flowered cymose units, each unit subtended by a bract; bracts linear, 1–2 mm, densely reddish

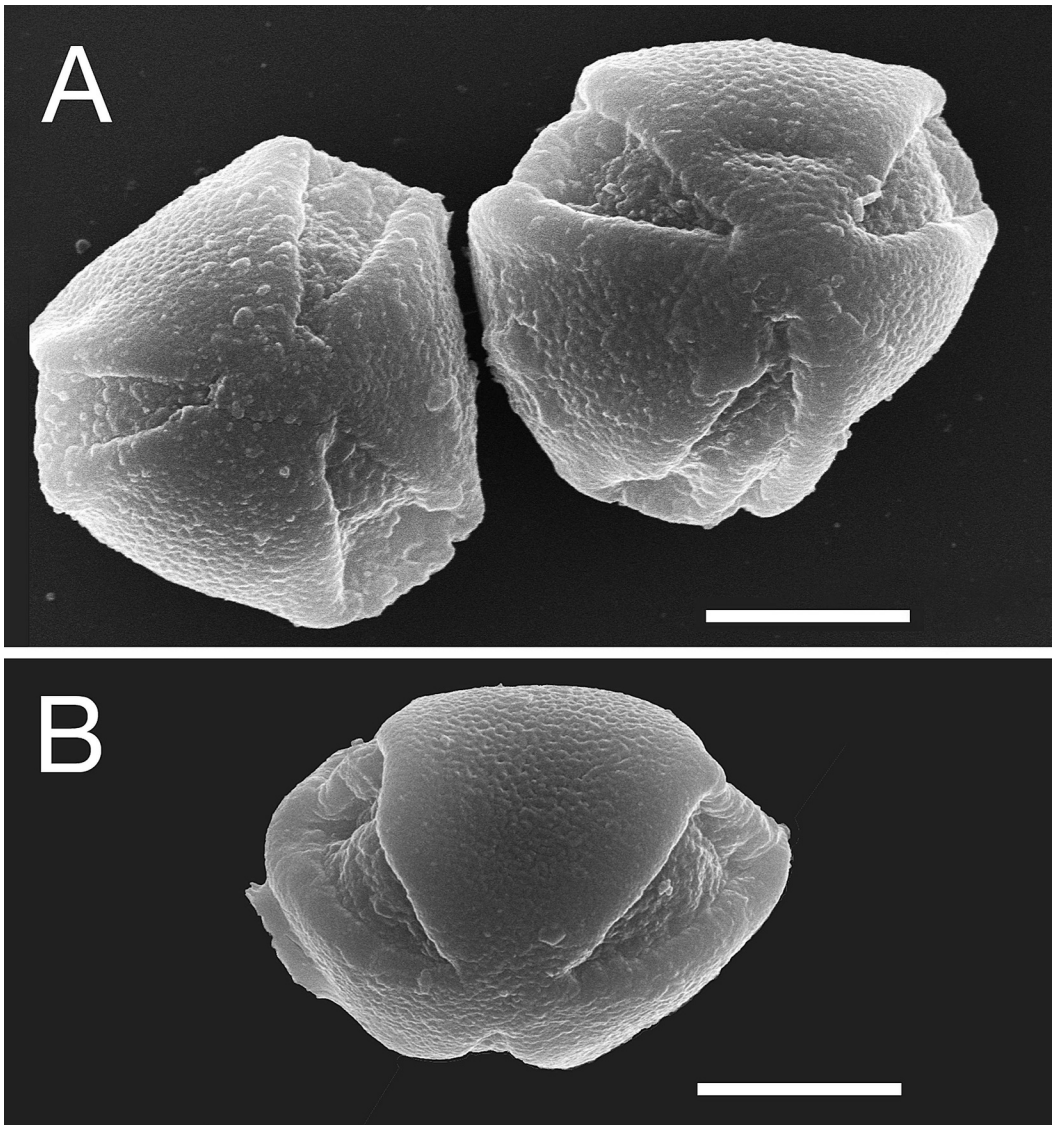


Figure 4. SEM images of the pollen of *Hondurodendron urceolatum* C. Ulloa, Nickrent, Whitef. & D. Kelly. —A. Polar views. —B. Oblique to nearly equatorial view. Scale bars = 6 μ m (2500 $\times$). (SEM images D. L. Nickrent.)

tomentose. Staminate flowers rounded in bud, ca. 1.8–2 mm diam., with short translucent hairs on the outside and scattered reddish hairs at the base, pedicels 1–2 mm, sparsely reddish tomentose; calyx cup-shaped, very short, ca. 0.5 mm tall, the rim minutely denticulate; petals attached to the rim, (3)4 to 5, ovate, ca. 1 $\times$ 0.8 mm, greenish cream, fleshy, glabrous within, thickened at the apex; stamens equal in number to and opposite the lobes, 0.6–0.8 mm, filaments free, ca. 0.3 mm long, thick, anthers 0.3–0.5 mm diam., basifixed, introrse, globose, 3-lobed, each lobe apically dehiscent by a longitudinal valve;

pollen brevaxial, radially symmetrical, isopolar, oblate in equatorial view, triangular, flat to convex in polar view, tricolporate, colpi long, apertural membrane granular or verrucose, apocolpium small, convex, mesocolpium large, flat to convex, exine of mesocolpium with a perforate tectum (Fig. 4); disk fleshy, 0.8–2 mm across, with lobes equal in number to the stamens and alternating with them; nectar not visible in partially opened flower, clearly visible at center of fully opened male flower. *Pistillate inflorescence* shortly spicate with up to 4 flowers, each flower subtended by a linear ca. 1.5-mm-long bract and 2

bracteoles ca. 0.5 mm long, densely reddish tomentose. Pistillate flowers (only a few open flowers observed) ovoid in bud, ca. 2.5×2.5 mm, pedicels ca. 2.5 mm; calyx cup-shaped, ca. 1 mm tall, densely pubescent, with a minute entire rim; petals attached just inside the rim, 4 or 5(6), deltate, ca. 1.5×0.8 –1 mm, greenish cream, thickened at apex, sparsely pubescent on both surfaces; ovary superior, 1–2 mm diam., slightly sulcate, densely pubescent, 1-celled at the summit, 2-celled at the base, with a free central placenta with 2 ovules pendant near its apex (one in each cell), the style very short, the stigma thick, round, ca. 1 mm diam. Fruits 1-seeded drupes, obovoid, 15 – 18×15 – 20 mm, each completely enclosed by the accrescent calyx, mostly free, conrescent at base, fruiting calyx leathery, slightly sulcate, completely surrounding and concealing the drupe, extending beyond with the accrescent lobes forming a flared, cuplike extension over the fruit, light green, sparsely pubescent, the part enclosing the fruit 20–27 mm diam., 2–3 mm thick, the cuplike extension 10–13 mm tall, ca. 1 mm thick; endocarp very thin, mesocarp ca. 1 mm thick, exocarp thin, smooth, yellowish green; fruiting pedicels 7–10 mm, 2–3 mm thick, articulate at base; seeds white, occupying the whole cavity, ca. 16 mm diam.

Distribution and ecology. *Hondurodendron urceolatum* is only known from Parque Nacional El Cusuco, west of San Pedro Sula, Cortés Province, in northwestern Honduras, where it appears to be widely but sparsely distributed within the “core zone” of the park. This species has been recorded between altitudes of 1240 and 1680 m in several kinds of montane rainforests: broad-leaved primary forest, mixed pine–broad-leaved primary forest, and broad-leaved secondary forest. It is found mainly as an understory tree under a high forest canopy, also in forests disturbed by natural tree-falls and alongside trails, growing in well-drained situations, on slopes and ridgetops. All sites are on strongly acidic soils (sampled pH 3.9 to 4.5) over siliceous bedrock (gneiss/schist).

Hondurodendron urceolatum was found as scattered individuals and in small groups; saplings and young trees were recorded at several locations. It was moderately plentiful in the vicinity of Guanales camp. A sample census was made to provide an overview of one characteristic population with a total of 19 individuals measured (Figs. 5, 6). The gender distribution is notable: male flowers were observed on juvenile individuals (as low as 2.3 m) as well as on larger trees of mature appearance, whereas female flowers and fruits were observed only on larger trees (4–10 m tall).

IUCN Red List category. The species is known only from scattered populations within a single mountain range—a forested area largely surrounded by agriculture lands. Some logging and grazing by livestock occur even within the bounds of the national park. The area of occupancy (AOO) of the species is 36 km² and the extent of occurrence (EOO) is 6.4 km² based on a 3×3 -km grid, with a measure of 0% continuing decline (percent of AOO that falls outside a protected area; IUCN Standard and Petitions Working Group, 2008). In terms of our current knowledge, the species is assigned a provisional IUCN (2001) conservation status of Endangered (EN).

Phenology. Flowers were collected in July and August, and fruits were found in July. The bark slash is recorded as having a cabbage-like (Kelly & A. Fiallos DA2/MS/313) or roselike (Fritch et al. GU/1/MS 869) smell and the leaves as having a toothpaste-like (Kelly et al. BC/3/MS 233) smell when crushed.

Etymology. The genus name, *Hondurodendron*, is a combination of the name of the country where these plants grow, Honduras, and the Greek word for tree, “dendron.” The Latin specific epithet “urceolatum,” meaning “shaped like a pitcher or urn,” refers to the striking form of the fruit with the projecting calyx limb.

Vernacular names. The fruit-bearing tree is known to the more experienced local guides under the names “guayabillo,” “guayabillo de montaña,” or “guayaba de montaña” (P. Cortés, M. Ramírez & R. Alvarenga, pers. comm.). The names are clearly variants of “guayaba” (guava, *Psidium guajava* L.), to which the fruits of *Hondurodendron* bear a superficial resemblance. The name “guayabillo” is recorded from Honduras for four tree species and one climber (Nelson Sutherland, 1986), none in Olacaceae. It is also recorded for various other species in Guatemala (Williams, 1977); however, in the Cusuco area the name was consistently applied to *Hondurodendron*. (Other local names were recorded for nonfruiting trees of *Hondurodendron*, which lack obvious distinctive features, but these names were also recorded for other, unrelated tree species.)

While anatomically a drupe, the fruit was not observed to become succulent. The thin mesocarp and large seed suggest that it is functionally a nut, adapted for dispersal by seed-hoarding vertebrates (van der Pijl, 1982). A cache of three fruits that had evidently been gnawed by mammals was found in the vicinity of the studied *Hondurodendron* population east of Guanales camp (28 July 2008). This supports the view of local guides that the fruits are eaten by small mammals: “tepescuinte” (paca, *Cuniculus paca* L.),

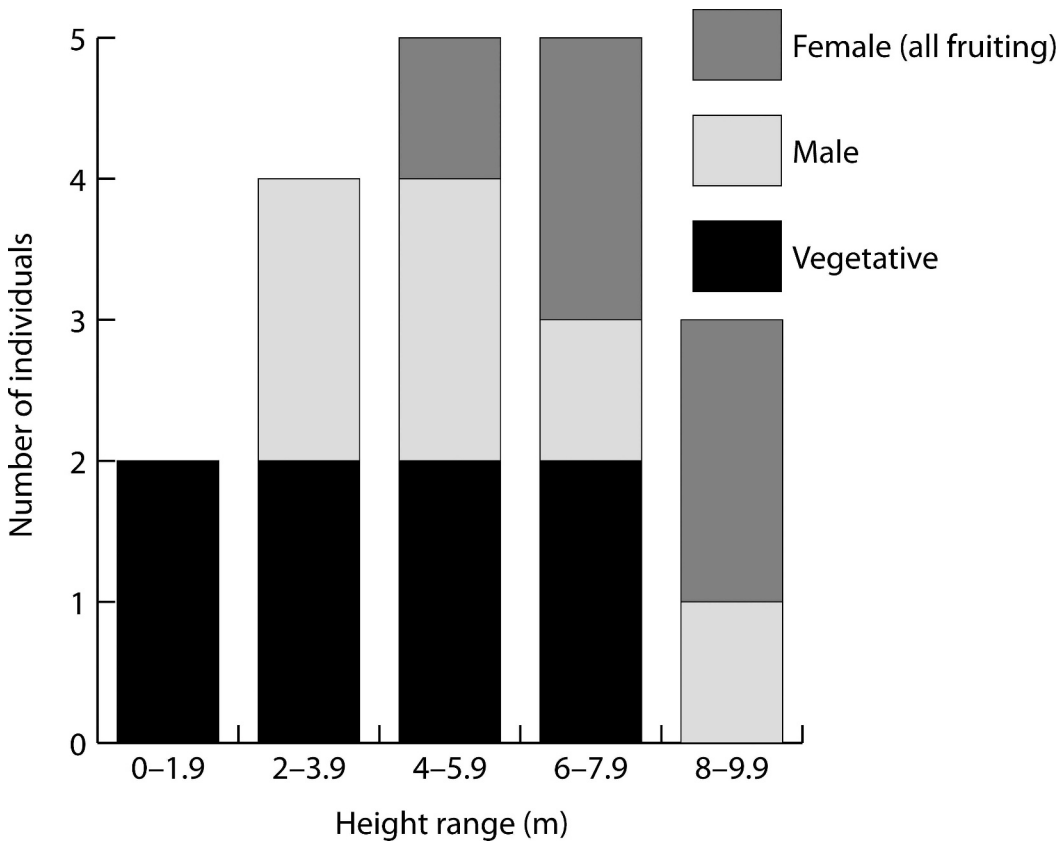


Figure 5. Plant sex and height distribution in a sample population ($n = 19$). Pooled data from two plots ca. 50 m apart; combined area 600 m². Population in tall mixed pine–broad-leaved forest east of Guanales camp, beside main trail to base camp (altitude ca. 1340 m).

“ardilla” (squirrels, species of *Sciurus* L.), and “pisote” (coatimundi, *Nasua narica* L.) according to P. Cortés (pers. comm.).

Paratypes. HONDURAS. **Cortés:** Parque Nacional El Cusuco, Sierra de Merendón: Plot GU/1/MS, NW of Guanales, 1415 m, 22 July 2006 (♂ fl.), R. Fritch, F. Laines & R. Fernández GU/1/MS 869 (BM, MO); Plot 7, trail E of Guanales, ca. 1680 m, 12 July 2004 (st.), D. L. Kelly & P. Cortés 7/23 (BM); Plot 13, Timbo trail, near Guanales, 1276 m, 2 Aug. 2004 (♀ fl.), D. L. Kelly, M. Ramírez & A. Alvarenga 13/304 (BM, MO); Plot DA/2/MS, S of El Danto campo site, 1530 m, 9 July 2006 (♂ fl.), D. L. Kelly & A. Fiallos DA/2/MS 313 (BM, HEH, MO); same tree, 6 July 2008 (♂ fl.), K. Fagan, A. Donnelly & P. Cortés DA/2/MS 313-II (HEH, TCD); on ridgetop, by trail CO3, S of El Cortecito camp site, ca. 1550 m, 17 July 2008 (♀ fl., fr.), D. L. Kelly, K. Fagan & P. Cortés 12036 (BM, HEH, MO, TCD); Guanales, ca. 1390 m, 28 July 2008 (♂ fl.), D. L. Kelly & P. Cortés 12074 (HEH, NY); Guanales, ca. 1330 m, 28 July 2008 (♂ fl.), D. L. Kelly & P. Cortés 12079 (EAP, F); Guanales, ca. 1330 m, 28 July 2008 (♀ fl., fr.), D. L. Kelly & P. Cortés 12075 (BM, EAP, F, NY); Guanales, ca. 1340 m, 28 July 2008 (♂ fl.), D. L. Kelly & P. Cortés 12082 (EAP); Guanales, ca. 1340 m, 28 July 2008 (♂ fl.), D. L. Kelly & P. Cortés 12090 (TEFH).

DISCUSSION

The molecular analyses clearly place *Hondurodendron* in a clade with seven other genera that have recently been classified in an expanded concept of Aptandraceae (Nickrent et al., 2010). Given the position of *Hondurodendron* on the tree, a new genus is necessitated. Traditional classifications, such as that of Sleumer (1984a, b), included these plants in a broadly defined Olacaceae, a practice still followed by some current workers (e.g., Mabberley, 2008). The Aptandraceae clade received high bootstrap support in a previous molecular study (Malécot & Nickrent, 2008) and was also recovered (albeit with low support) in a cladistic analysis of morphological features (Malécot et al., 2004). A 2-celled ovary (at least at the base), as well as several anatomical and palynological features, appear to be synapomorphies for the family (Malécot et al., 2004). The present molecular work also strongly confirms the placement of *Harmandia* in Aptandraceae as sister to *Aptandra* and *Ongokea*.

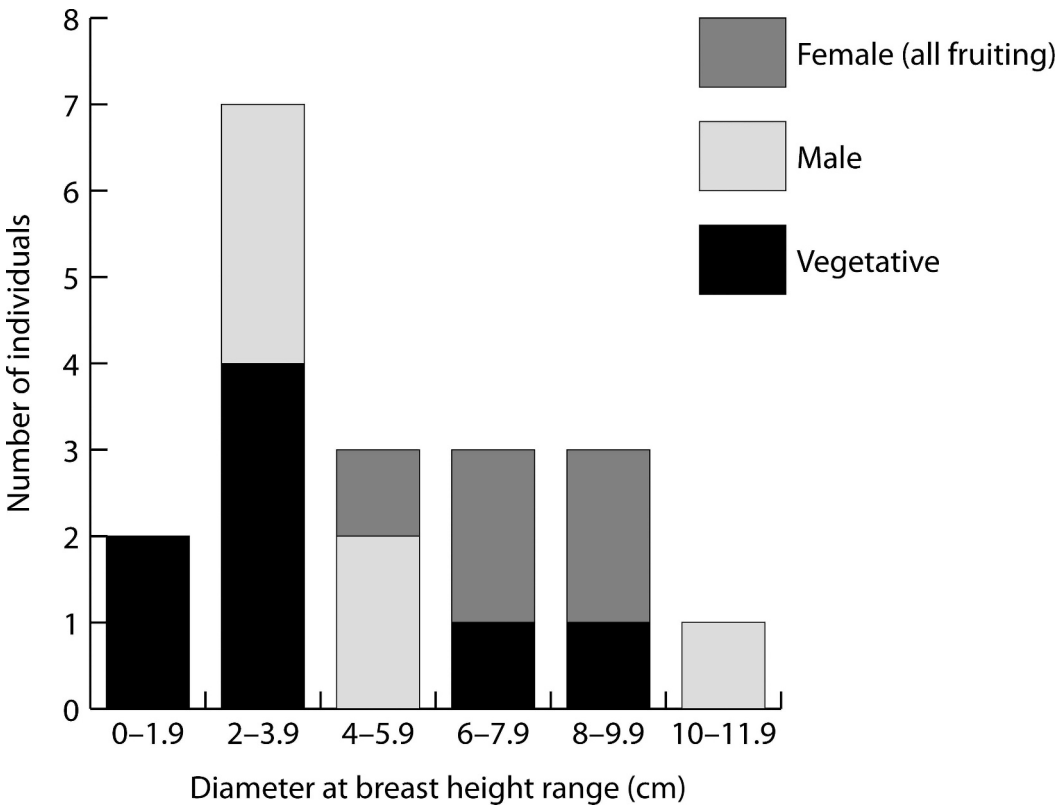


Figure 6. Plant sex and size class distribution in a sample population ($n = 19$). Pooled data from two plots ca. 50 m apart; combined area 600 m². Population in tall mixed pine–broad-leaved forest east of Guanales camp, beside main trail to base camp (altitude ca. 1340 m).

The phylogenetic tree (Fig. 1) shows that Aptandraceae is composed of two distinct clades that will here be referred to as the *Anacolosa* clade (*Anacolosa*, *Cathedra*, and *Phanerodiscus*) and the *Aptandra* clade (the remaining five genera). The former is characterized by several synapomorphies such as petals with apical thickenings, intrastaminal disk, and diploporate pollen (Malécot & Nickrent, 2008). In *Anacolosa* and *Cathedra*, the disk is accrescent, but only in the former genus is it fused to the ovary during fruit development. In *Phanerodiscus*, the disk is not accrescent; however, flowers possess an entire minute membranous lobed ring between the calyx and the disk which, through accrescence, forms a highly modified lobed vesicle that surrounds the fruit. Within the *Aptandra* clade, the disk is absent in *Chaunochiton*, alternating with stamens in *Hondurodendron*, and extrastaminal in the remaining three genera. The disk does not form a structure on the mature fruit on any of these genera. However, all five genera in the *Aptandra* clade possess fruits with an accrescent calyx. In *Chaunochiton*, the greatly accrescent calyx forms a large parachute-like structure that is apparently

involved in fruit dispersal. *Heisteria* (Olacaceae s.l.) also has an accrescent calyx, and in many classifications (e.g., Sleumer, 1984b) it is placed with *Chaunochiton* in tribe Heisterieae. The phylogenetic data show, however, that this feature has evolved independently in the two clades, Olacaceae s. str. and Aptandraceae (Malécot & Nickrent, 2008). In comparison to the other genera in the *Aptandra* clade, *Hondurodendron* is unique in that its calyx completely surrounds and conceals the drupe and bears a projecting flared limb at the apex.

The androecial morphology of the *Aptandra* clade is quite variable. *Aptandra*, *Ongokea*, and *Harmandia* all have staminal filaments connate into a tube (monadelphous) with terminal anthers fused into an annulus by their thick connectives. The anthers open longitudinally from the apex to the base by means of reflexed valves (Sleumer, 1984b). The filaments in *Chaunochiton* and *Hondurodendron* are free; however, the valvate anther dehiscence is reminiscent of the condition in the monadelphous taxa. In *Chaunochiton*, pollen is apparently dehiscid through apical slits between the valves, somewhat resembling the condi-

tion seen in *Cathedra* of the *Anacolosa* clade. In *Hondurodendron*, the anther has three valves that open from the top outward. To our knowledge, this is an extremely rare condition, perhaps unparalleled in the angiosperms. The basalmost genus of the *Aptandra* clade, *Chaunochiton*, possesses 4-lobed anthers that open by four longitudinal slits. Because the three loculi of *Hondurodendron* are slightly asymmetrical, it is possible this condition is derived from the fusion of two loculi.

The pollen in the *Aptandra* clade is also quite variable with 3-aperturate (*Chaunochiton*, *Hondurodendron*, *Aptandra* in part), 4-aperturate (*Harmandia*), and 4- and 5-aperturate (*Aptandra*, *Ongokea*) types seen. The pollen of *Hondurodendron* (Fig. 4) is rather unspecialized, most similar to that of *Chaunochiton* except that it is psilate, i.e., lacking elaborate sculpturing on portions of the exine.

The phylogenetic tree (Fig. 1) also provides evidence for the evolution of plant sexual conditions. Because members of the *Anacolosa* clade and *Chaunochiton* of the *Aptandra* clade have bisexual flowers, dioecy may be an apomorphy. *Hondurodendron* is dioecious with no apparent remains of staminodes or pistillodes. Similarly, *Harmandia* (Southeast Asia), *Ongokea*, and *Aptandra zenkeri* Engl. (both from West Africa) are dioecious. Surprisingly, the two closely related Amazonian species, *Aptandra tubicina* (Poepp.) Benth. ex Miers and *A. lirisomoides* Spruce ex Miers, have bisexual flowers, thus the topology of the tree suggests that this feature evolved secondarily from a dioecious ancestor.

Several biogeographic assumptions can be surmised by comparing the phylogenetic tree topology with distributions of the extant genera. The basalmost members of both the *Anacolosa* and *Aptandra* clades are New World tropical (*Cathedra* and *Chaunochiton*, respectively). Two dispersal events could then be proposed (New to Old World), one for each of the two clades. For *Aptandra*, a third dispersal must be assumed but in the opposite direction (Old to New World).

The four-gene matrix was used to generate uncorrected "p" distances using PAUP* (Swofford, 2002), and these values were used to assess the degree of genetic differentiation among the genera of Aptandraceae. Average intergeneric distances are lower in the *Anacolosa* clade (0.0193) compared with the *Aptandra* clade (0.0544); however, the average distance between these clades is similar to the latter (0.0574). The average distance between *Hondurodendron* and other ingroup genera is 0.0508 (range, 0.0391 to 0.0642), thus illustrating that this genus is as genetically distinct as others in the family.

The family Aptandraceae is now constituted as follows: the Neotropical genera *Chaunochiton* (three species, tropical America), *Cathedra* (five species, South America), and *Hondurodendron* (one species, Honduras); the Paleotropical genera *Anacolosa* (16 species, 14 in Asia, one in central Africa, one in Madagascar), *Harmandia* (one species, Southeast Asia), *Ongokea* (one species, West Africa), *Phanerodiscus* (three species, Madagascar), and *Aptandra* (three species in tropical America and one in tropical West Africa) (Villiers, 1973; Sleumer, 1984a, b; Malécot et al., 2003; Nickrent et al., 2010). This family is characterized by distichous, petiolate, simple leaves; stamens in one whorl and opposite the petals; hypogynous ovary; brevaxial pollen grains; and fruit with accrescent tissues derived from either the calyx or disk tissues.

Photographs of the taxa discussed above are available on the Parasitic Plant Connection web site (<<http://www.parasiticplants.siu.edu/>>).

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