

# DISCOVERY OF THE INDO-MALESIAN GENUS *HYMENANDRA* (MYRSINACEAE) IN THE NEOTROPICS, AND ITS BOREOTROPICAL IMPLICATIONS

JOHN J. PIPOLY III

*Botanical Research Institute of Texas*  
509 Pecan Street, Fort Worth, TX 76102-4060, U.S.A.  
*jpipoly@brit.org; clusia@latinmail.com*

JON M. RICKETSON

*Missouri Botanical Garden*  
P. O. Box 299, St. Louis MO 63166-0299, U.S.A.  
*jon.ricketson@mobot.org; jricketson@lehmann.mobot.org*

## ABSTRACT

The taxonomic revision of a neotropical group of taxa formerly placed by Lundell in *Auriculardisia*, *Chontalesia*, and *Icacorea*, resulted in the discovery that they were actually members of the otherwise Indo-Malesian genus, *Hymenandra*. The genus is defined by its filaments fused at least basally to form a staminal tube, the tube adnate to the base of the corolla tube and anthers connate along their longitudinal dehiscence sutures at least until anthesis. It is also noted that all species of the genus exhibit Fagerlind's Architectural Model, a model that is otherwise extremely restricted, and one whose vegetative vs. reproductive shoot dimorphism has led to taxonomic overdescription. Nine species of *Hymenandra* are recognized in the Neotropics, bringing the total number of species in the genus to 16. Owing to a lack of complete material for Indo-Malesian species, and previous workers' hesitancy to unequivocally assign all of those species to a subgenus, the neotropical group is transferred to the genus without circumscription of any subgenera. It is postulated that the geography of *Hymenandra*, now considered an amphipacific taxon, is consistent with that predicted by the Boreotropics Hypothesis, and its logical extension postulated by Wendt (1993) and Lavin and Luckow (1993), especially when viewed in light of the biogeography for the rest of the tribe Ardisieae. Each neotropical *Hymenandra* species is fully described, newly illustrated, and provided with citations for all taxonomic and nomenclatural synonyms. In addition to the general section on morphology, biogeography and ecology provided for the genus, each species is accompanied by a discussion of its distribution, ecology and conservation status, along with citation of specimens examined. Five binomials are newly relegated to synonymy, and one taxon, *Hymenandra pittieri*, is lectotypified. The following new combinations are made: *Hymenandra stenophylla* (Donn. Sm.) Pipoly & Ricketson, *H. calycosa* (Hemsl.) Pipoly & Ricketson, *H. sordida* (Lundell) Pipoly & Ricketson, *H. squamata* (Lundell) Pipoly & Ricketson, *H. wilburiana* (Lundell) Pipoly & Ricketson, *H. pittieri* (Mez) Pipoly & Ricketson, *H. callejasii* (Pipoly) Pipoly & Ricketson, *H. acutissima* (Cuatrec.) Pipoly & Ricketson, *H. crosbyi* (Lundell) Pipoly & Ricketson. A complete list of exsiccatae is provided at the end for all collections examined.



## RESUMEN

Al llevar a cabo una revisión taxonómica de un grupo comprendiendo taxa anteriormente clasificados por Lundell como pertenecientes a los géneros *Auricularia*, *Chontalesia*, y *Icacorea*, se reveló que todos pertenecen al género indo-malesiano, *Hymenandra*. El género se define por sus filamentos conados, formándose un tubo estaminal, por lo menos en su base, adnado a la base del tubo corolino y con anteras conadas a lo largo de las hendiduras longitudinales de dehiscencia. Se note que todas las especies del género se caracterizan por exhibir el Modelo Arquitectural de Fagerlind, un modelo bastante único y cuyo dimorfismo entre ramas vegetativas y reproductivas se ha ocasionado sobre descripción taxonómica. Se reconocen nueve especies neotropicales de *Hymenandra*, sumando el total para el género hasta 16. Debido al hecho de que el material indo-malesio es muy incompleto, no se han podido asignar a un subgénero todas las especies. Por lo tanto, se transfieren las especies neotropicales al género sin circumscribir subgéneros. Se postula que la geografía del género está de acuerdo con el patrón fitogeográfico proveniente del Hipótesis Boreotropical, especialmente en vista de la distribución y relaciones con el tribu Ardisieae. Además de la sección general sobre morfología, biogeografía, y ecología proveída para el género, se discute la distribución geográfica, ecología y estado de conservación, y se lista pliegos examinados para todos los taxa. Se relega cinco binomiales a la sinonimia, y se lectotipifica *Hymenandra pittieri*. Las nuevas combinaciones se incluyen a continuación: The following new combinations are made: *Hymenandra stenophylla* (Donn. Sm.) Pipoly & Ricketson, *H. calycosa* (Hemsl.) Pipoly & Ricketson, *H. sordida* (Lundell) Pipoly & Ricketson, *H. squamata* (Lundell) Pipoly & Ricketson, *H. wilburiana* (Lundell) Pipoly & Ricketson, *H. pittieri* (Mez) Pipoly & Ricketson, *H. callejasii* (Pipoly) Pipoly & Ricketson, *H. acutissima* (Cuatrec.) Pipoly & Ricketson, *H. crosbyi* (Lundell) Pipoly & Ricketson. Se provee una lista completa de exsiccata al final del trabajo.

## INTRODUCTION

The pantropical genus *Ardisia* Sw. is by far the largest in the family Myrsinaceae, containing perhaps as many as 500 species (Chen & Pipoly 1996). Its circumscription has been problematic owing to a lack of comprehensive treatment since that of Mez (1902) in Engler's *Pflanzenreich*, almost a century ago. Several genera have been separated from *Ardisia sensu lato* since the Mez monograph, including *Chontalesia* Lundell (1982), described as a monotypic genus to accommodate the Central American *Ardisia calycosa* Hemsley. *Ardisia calycosa* may be immediately recognized by its unique large, coriaceous, narrowly lanceolate to lorate sepals that are longer than the corolla. While examining *Ardisia calycosa* to determine its relationships, we noted that its vegetative characters, such as the punctate and punctate-lineate, nitid leaves, the branchlet apices with varying amounts of furfuraceous lepidote scales, and most notably, the unusual leaf dimorphism between the floral and vegetative shoots (now known as an artifact of its morphogenetic program that exhibits Fagerlind's Architectural Model, *sensu* Hallé et al. 1978), were similar to a Central American suite of species that includes *A. stenophylla* Donn. Sm., *A. oblanceolata* Standl., *A. calvarioana* Lundell, and *A. wilburiana* Lundell. Careful study of this group of species revealed that their androecia have filaments connate throughout their length to form a staminal tube (therefore mona-



delphous) basally adnate to the corolla, and anther thecae connate along the suture line, at least in the basal portion, prior to anthesis, at which time at least the distal (abaxial) portion of the theca opens to permit release of pollen, or the anthers split completely apart from each other. This structure was also reported by Pipoly (1992a) in the description of *Ardisia callejasii* Pipoly, a species endemic to the Antioquian Chocó of northern Colombia. Careful reexamination of additional material of *Ardisia callejasii* has revealed that the anthers are also basally connate up to full anthesis, when they split apart completely. In addition, the combination of long-pedunculate panicles terminating in very long-pedicelled flowers in corymbs to subumbels and large fruits with thick, juicy exocarps common to all the aforementioned taxa indicated that other neotropical species with the same features, including *Ardisia crosbyi* Lundell, *A. pittieri* Mez, and *A. acutissima* (Cuatrec.) Lundell might also belong to the alliance. Finally, with the sole exception of *Ardisia callejasii*, it was striking to note that for all species, the inflorescence was borne terminally or subterminally (but behaving terminally) on the end of a long sylleptic shoot, bearing leaves similar in shape to those of the vegetative shoots, except much smaller in size. The latter phenomenon was noted by Mez (1902) in *Ardisia* subgenus *Pyrgus* (Lour.) Mez, and by Stone (1991) in the genus *Hymenandra* A. DC. ex Spach. All of the aforementioned species except *Ardisia calycosa* have been referred by Lundell (1981) to his genus *Auriculardisia*, defined principally by the asymmetric sepals auriculate in outline. While surveying the rest of the neotropical *Ardisia* species attributed to *Auriculardisia*, we noted that *Ardisia squamata* (Lundell) J. F. Morales and *A. sordida* (Lundell) J. F. Morales possess all the features of the aforementioned group of taxa, but in a more diminutive form because they are subshrubs.

Given that *Ardisia* has traditionally been separated from its close congeners by filaments considered free from each other and from the corolla tube (Lundell 1966, 1971; Mez 1902; Ricketson & Pipoly 1997), the aforementioned group of species posed a serious problem in the circumscription of what was admittedly already a parapyletic group (Ståhl 1996). On the other hand, members of *Ardisia* subgenus *Graphardisia* (Pipoly & Ricketson 1998) have filaments basally fused for less than 1/5 their length, to form a short staminal tube free from the corolla tube, that is inconspicuous because of its thinly membranaceous texture, and anthers that are totally free from each other. If *Ardisia* is defined by stamens with free anthers and filaments free or variously connate, but totally free from the corolla tube, the group of species related to *Ardisia calycosa* discussed above would still not fit. The inclusion of *Ardisia calycosa* and its relatives in *Ardisia* would significantly amplify the morphological circumscription of the genus. To answer whether further enlargement of *Ardisia*'s circumscription was warranted to main-



tain *A. calycosa* and its relatives within *Ardisia*, a review of the related genera of the family was conducted. This led to the surprising conclusion that the relationships of this suite of species are clearly with the genus *Hymenandra*, heretofore considered an Indo-Malesian genus of seven species (Stone 1991).

#### THE GENUS HYMENANDRA

*Hymenandra* was described as a section of *Ardisia* by Alphonse de Candolle (1834, 1841) to accommodate two species, *A. hymenandra* Wall. and *A. glandulosa* Roxb., with filaments basally connate, but free apically, and anthers connate. De Candolle (1841) treated the group as a genus, a rank to which it had already been assigned by Spach (1840). Mez (1902) accepted the genus in his worldwide monograph of the family, using the same characters. Furtado (1958) transferred *Ardisia iteophylla* Ridley to the genus, on the basis of its fused filaments and anthers, but in the same paper described *A. calcicola* Furtado, distinguishing it from its sister species in subgenus *Pyrgus* by the fused filaments and anthers. Nayar and Giri (1975) described one new species, *Hymenandra narayanaswamii* Nayar & Giri, endemic to Myanmar (Burma). Stone (1991) revised the genus, transferred *A. calcicola* to *Hymenandra*, and described four new species, recognizing a total of seven species. Stone (1991) erected two subgenera, based on the degree of compaction of the inflorescence, the presence or absence of papillae on the adaxial calyx lobe surface, and general habit of the plants. *Hymenandra* subgenus *Lacrimophila* B. C. Stone was defined by caducous floral bracts, sepals hirtellous along the margins, glabrous or hirtellous (not papillose) within, but he included only *Hymenandra narayanaswamii* and *H. diamphidia* B. C. Stone in it, leaving the third species of the group from the second half of his key, *H. iteophylla* (Ridl.) Furtado, in subgenus *Hymenandra*. We have examined material of both groups and conclude that further material of the species will be necessary before accepting the subgeneric grouping.

*Hymenandra*, as defined by Stone (1991), is characterized by a staminal tube formed by filaments at least basally united and basally adnate to the corolla, concomitant with anthers connate, at least basally, by their longitudinal dehiscence sutures, until anthesis, at which time the distal flap of the theca may open or the anthers may split apart completely. All species have filaments basally connate and apically free, with anthers connate in anthesis along the entire length of the dehiscence sutures. In the Neotropics, the filaments are connate throughout their length, at least at first, and the anthers are connate in the basal half, separating early or just after the corolla lobes open, whereas in the paleotropical species, the filaments are connate in the basal half, free distally, and the anthers are connate along the



deshiscence sutures throughout their length. As far as is known, all members of the genus exhibit Fagerlind's Architectural Model, as defined by Hallé et al. (1978). Given the uniqueness of the androecial structure, we here transfer the aforementioned *Ardisia* species to *Hymenandra*.

With the addition of the neotropical species transferred in this paper, the total number of species in *Hymenandra* reaches 16, distributed from Assam, Bangladesh, Myanmar, Malaya, Borneo, and Nicaragua through the Colombian Chocó. Given the scarcity of material available for study, we defer reexamination of subgeneric delimitation until a later time.

#### MORPHOLOGY

The following descriptions are based on the genus as a whole, with particular emphasis and detail among neotropical taxa.

##### Habit, Architecture, "Trunk" and Shoots

Most members of neotropical *Hymenandra* are shrubs or small trees to 8 m tall with a maximum known diameter at breast height (dbh) of 8 cm, with the exceptions of *H. squamata* and *H. sordida*, which are subshrubs less than one meter tall. This is much like the case among the Indo-Malesian species, where seven of the nine species are also subshrubs. Therefore, when we refer to a "trunk" in the following architectural model discussion, it is the principal axis of the plant, or "vegetative stem." So far as is known, all species of *Hymenandra* are terrestrial (i.e., not epiphytes).

Careful study of herbarium specimens and examination of photographs lead us to postulate that all *Hymenandra* species exhibit Fagerlind's Architectural Model (Hallé et al. 1978). Fagerlind's Model describes those trees whose architecture is determined by a monopodial, orthotropic, readily distinguishable, rhythmically growing trunk that produces tiers of modular branches, each branch sympodial and plagiotropic by apposition, with spiral or decussate (never distichous) phyllotaxy. Branch modules are often hapaxanthic (dying after flower) or, as is the case in *Hymenandra*, they may exhibit sympodial growth by apposition, often branching several times without flowering. Deducing evidence we have pieced together from specimens, field observations, and collectors' notes, we might explain the morphogenetic program of *Hymenandra* individuals as follows: a) A "trunk" ("vegetative shoot") develops rhythmically, producing successive pseudoverticels of "vegetative" leaves until the apex loses dominance and latent lateral ("axillary") buds are released, producing successive, monopodial pseudoverticels of shoots, each of which is sylleptic (and rarely attaining 5 mm in diameter), with a long hypopodium and exhibiting rapid extension growth. b) The sylleptic branch shoots produce first a prophyll, then pseudoverticels of "reproductive shoot" leaves (similar to the leaves of the "vegetative shoot" but nota-



bly smaller), and then may either lose dominance and once again branch sympodially by apposition growth (repeating the module) without flowering, or produce a terminal or pseudoterminal (acting as a terminal) inflorescence. Therefore, like the other species exhibiting Fagerlind's Model, and unlike other models, inflorescence production is usually not acropetal along a set of modular plagiotropic branches (although it can be). c) When a shoot flowers, the apex of the reproductive shoot will gradually lose dominance and may produce the remaining flowers of the inflorescence, or support ongoing fruit development, or the remaining flowers may abort. Following flower, a branch sympodial by substitution growth may (or may not) be produced, that will very slowly generate leaves in a high phyllotactic spiral (a pseudoverticel) and eventually abort. It is interesting to note that the apical region of the principal plant axis ("trunk", or "vegetative shoot") does not produce an inflorescence, and as Hallé et al. (1978) noted, leaves associated with the trunk (here termed "vegetative shoot leaves") are considerably larger than those of the branches (here termed "reproductive shoot leaves"). It is precisely this rare leaf dimorphism that caused us to further investigate the dynamics associated with Fagerlind's Model to see if they were consistent with what we could surmise about the developmental biology (morphogenetic program) of *Hymenandra* species. Clearly, more intensive field studies are needed to determine if any other activity occurs in the plant body's development among species of the genus.

Mez (1902) described the branching dynamics and flowering phenomena associated with Fagerlind's Model when he discussed the "inflorescences on special branches, with the principal axis indeterminate, [the inflorescences] terminal on lateral apices, with large subtending leaves subverticillate" for *Ardisia* subgenus *Pyrgus*. Subgenus *Pyrgus* is Indo-Malesian in origin and its species often occur sympatrically with individuals of *Hymenandra*. Likewise, Stone (1991) made the same comparison when he described *Hymenandra lilacina* distinguishing between vegetative and flowering shoots in that species. While both Mez and Stone noted that the leaves of the vegetative shoot (trunk) are usually slightly different from those of the flowering shoot, it was not correlated with a model for growth. During the period Mez worked, the concept of architectural models did not exist, and the herbarium material available to Mez was rather fragmentary or restricted to flowering shoots, at times accompanied from a single leaf from the trunk or an axis in vegetative state. Stone (1991) noted similarities in the "position and form of the inflorescence" between *Hymenandra* and *Ardisia* subgenus *Pyrgus* but did not state this in terms of architectural models. While there are several other architectural models present in *Ardisia* and within the tribe Ardisieae (Maasart's, Scarrone's, Roux's, based on unpubl. data), very few taxa have been exam-



ined, and architectural models are not necessarily correlated with subgeneric or other taxonomic groups. While *Hymenandra* species may share the same architectural model with *Ardisia* subgenus *Pyrgus*, the free anthers with apical or subapical pores with minute filaments, and the numerous, pluriseriate ovules of *Pyrgus* clearly preclude inclusion of the *Hymenandra* species within it.

### Leaves

The leaves of *Hymenandra* are alternate, exstipulate and simple. As previously stated, leaves on the trunks ("stems" for small-statured taxa, "vegetative shoots" otherwise) are much larger than those of the reproductive ones, and also have a smaller length-to-width ratio. While both the "trunk" (or stem) and branches have spiral phyllotaxis, it is presumably by secondary twisting of the branches that make them plagiotropic, rather than by distichous arrangement. The blades may be chartaceous to coriaceous, elliptic, oblanceolate or oblong, apically acute to long-acuminate, basally cuneate to obtuse or rounded, decurrent on the petiole or not, conspicuously or inconspicuously black punctate and punctate-lineate, usually glabrous, but sometimes sparsely and minutely furfuraceous lepidote, the margins are entire, or rarely crenate (*Hymenandra calycosa*). The petioles are marginate and may bear the same tomentum as the branchlet apices, but they are glabrescent.

### Inflorescence, Flowers and Fruit

The inflorescence may be terminal or pseudo-terminal (but behaving terminal), and variously bi- or tripinnately paniculate, with branches ending in loose to tight corymbs of flowers. The panicles are mostly pyramidal, but may be reduced to a columnar panicle of corymbs, thus appearing racemose in fruit (e.g., *Hymenandra sordida*). The inflorescence bract is foliose, membranaceous, nearly sessile and early caducous. The peduncle, primary rachis and branches are glabrous or furfuraceous lepidote, then glabrescent. The floral bracts are ovate, lanceolate or narrowly elliptic, and membranaceous, sparsely to densely furfuraceous at first, then glabrescent. The pedicels are cylindrical and bear the same vestiture as the inflorescence branch. The flowers are perfect, bisexual, homomerous, and 5 (–6)-merous, and both perianth members may be membranaceous, chartaceous or coriaceous, with pellucid or black punctations and punctate-lineations. The calyx has lobes nearly free, lanceolate, linear-lanceolate, linear, oblong, or suborbicular, symmetrical or asymmetrical to slightly auriculate, apically acute, obtuse or rounded, the margin regular, irregular, or subapically notched, hyaline or scarious, sparsely glandular-ciliolate, minutely erose or entire (Fig. 1). The corolla is campanulate, the lobes nearly free, or free, ovate, lanceolate, oblong, or elliptic, symmetrical, apically acute or acuminate, erect or reflexed in anthe-



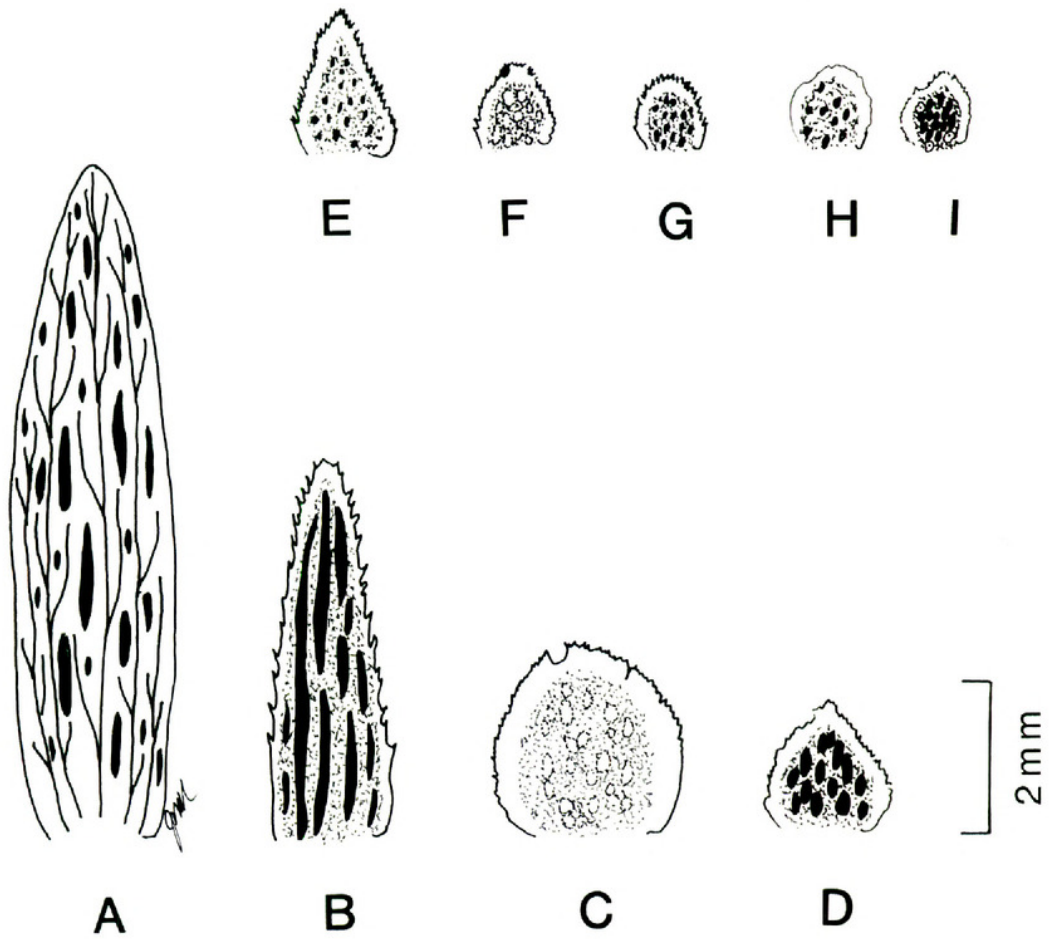


FIG. 1. Comparison of calyx lobes size, shape and punctations among the Neotropical species of *Hymenandra*. A. *Hymenandra calycosa*, drawn from M. chinchilla 93. B. *Hymenandra stenophylla*, drawn from B. Hammel 13717. C. *Hymenandra pittieri*, drawn from K. Sytsma, W. Hahn & T. Antonio 2453. D. *Hymenandra wilburiana*, drawn from G. Davidse & G. Herrera 31379. E. *Hymenandra callejasii*, drawn from R. Callejas et al. 5683. F. *Hymenandra crosbyi*, drawn from K. Sytsma, L. Andersson & R. Dressler 4279. G. *Hymenandra acutissima*, drawn from the holotype, J. Cuatrecasas 17219. H. *Hymenandra sordida*, drawn from the holotype, T. Croat 43538. I. *Hymenandra squamata*, drawn from the MO isotype, W. Burger & R. Stolze 5853.

sis, glabrous, the margin hyaline, and entire. The stamens are connate at least basally by their filaments to form a staminal tube, and by their anthers along the dehiscence sutures. The filaments are connate throughout their length in the neotropical species, but only basally in the Indo-Malesian species. The anthers are basifixed, connate along their dehiscence lines, either basally at first, or throughout their length, and lanceolate or ovate, apically long-attenuate to an acute or emarginate tip, or rounded with an apiculate tip, basally cordate, dehiscent by longitudinal slits, and with connectives ventrally darkened or prominently black punctate dorsally in the basal portion. The pistil may be obturbinate or ellipsoid, the style longer than the ovary,



attenuate to a punctiform stigma. The placenta is subglobose to ellipsoid with relatively few to numerous, pluseriate ovules in a high anthotactic spiral. The fruit is a globose to depressed-globose, one-seeded drupe, with a persistent style, sparsely or densely and prominently, conspicuously or inconspicuously pellucid or black punctate.

#### ECOLOGY

Neotropical *Hymenandra* species are mostly small trees, most commonly found along ridgetops in moist, wet, cloud or pluvial forests, from near sea level to 1,400 m elevation. Two species, *Hymenandra sordida* and *H. squamata*, are subshrubs less than one meter tall, but they are ecologically distinct, the former is known only from cloud forests, and the latter known from swamp forests. Only one species, *Hymenandra stenophylla*, is found in lowland moist forests. *Hymenandra wilburiana* and *H. pittieri* are both found in forests transitional between lowland and premontane wet forests, but the former species is restricted to ridgetops, while the latter is found along the forest margin, particularly along watercourses. In the Colombian Chocó, two species occur that are easily separated ecologically. *Hymenandra callejasii* is from the lowland pluvial forest of the northern Antioquian Chocó, while *H. acutissima* is a riparian species along major rivers along the shores of the Pacific Ocean. *Hymenandra calycosa* is known only from premontane wet forests, from Nicaragua to Panama.

In Mesoamerica, the altitudinal compression or expansion of life zones is largely a result of exposure to winds, rain and other meteorological events. Therefore, absolute altitude often has little to do with the life zone present at a given site. For example, many areas in Nicaragua support vegetation otherwise found only at much higher altitudes, because there are no taller mountains around. Fieldwork has shown that even a small mountain of 800 m can support cloud forest. Such appears to be the case of *Hymenandra crosbyi*, which is restricted to the Caribbean Slope of Panama, at the junction of the premontane and cloud forest life zones, even though the altitudinal range of the species is only 100–850 m.

#### BIOGEOGRAPHY AND IMPLICATIONS FOR THE BOREOTROPICS HYPOTHESIS

*Hymenandra*, as now defined, is amphipacifically distributed, occurring from Bangladesh eastward through Malaya to Borneo, and in the Neotropics from Nicaragua southward through Costa Rica and Panama to the Chocó of Colombia. A distribution such as this, in particular with the majority of the species centered in Central America, most closely fits those groups cited as partial evidence to support what Wendt (1993) discovered in his study of lowland Mexican wet forests, and what Lavin and Luckow (1993) attrib-



uted to the Boreotropics Hypothesis, proposed by Wolfe (1975) and Tiffney (1985a, b) to explain the distribution of the "boreotropical flora." The hypothesis proposes that the biotas of North America and Europe, including tropical North America, were once more widespread in the northern hemisphere and transgressed the North Atlantic by direct land connections or over limited water gaps until the late Eocene or early Oligocene (Lavin & Luckow 1993). A logical extension to Wolfe's and Tiffney's concept, presented by Wendt (1993) and Lavin and Luckow (1993) is that the boreotropical flora not only existed in the Eocene, but also left a significant number of direct descendant lines in present lowland tropical floras of northern Latin America. Therefore, we would expect that many of the early Tertiary fossil taxa from both North America and Europe were most closely related to extant species from tropical southeast Asia, and to some extent, Central America and the Greater Antilles (Lavin & Luckow 1993). It is the latter notion that is congruent with the Amphipacific distributional pattern like that found in our new concept of *Hymenandra*. This extension to the boreotropics hypothesis was cited by Wendt (1988, 1989, 1993), in discussing the relationships of *Chiangiodendron* (Flacourtiaceae), and by Zona (1990) in discussing the biogeography of *Sabal* (Arecaceae). A similar distribution for the genus *Alstonia* (Apocynaceae) was cited by Gentry (1983), but he did not invoke the hypothesis *per se*. Conran (1995), in his study of the Liliiflorae, found that three taxa defining the Southeast Asian/northern Australasian clade (Stemonaceae, Hanguanaceae and Uvulariaceae) were widespread northern taxa that have spread southwards.

The geographic distribution of *Hymenandra* is entirely consistent with the area cladogram presented by Lavin and Luckow (1993, Fig. 1), where South American elements are ultimately derived from among diverse North American lineages, these lineages having a sister group relationship to Paleotropical groups. While Wolfe's hypothesis could be correct even if no modern descendants of the boreotropical flora were found in the Neotropics owing to extinction, the three criteria proposed by Lavin and Luckow (1993) to test the hypothesis were: 1) a center of diversity in North America (including "tropical North America" as they define it), 2) an early Tertiary fossil record in North America, and 3) a pantropical distribution.

For the first test criterion, "North America" includes both tropical and temperate elements, the tropical ones south of the Tropic of Cancer. In the case of *Hymenandra*, it is clear that the majority of the neotropical members of the genus (*H. stenophylla*, *H. calycosa*, *H. sordida*, *H. squamata*, *H. wilburiana*, *H. crosbyi*) are centered in Nicaragua, Costa Rica, or the Caribbean slope of Panama, with only *H. pittieri* spanning the central montane of Costa Rica and Panama. *Hymenandra callejasii* and *H. acutissima* are restricted to the



Chocó of Colombia, a floristic province whose northern limit is southeastern Panama. Therefore, the pattern fits the first criterion.

Unfortunately, no data is available for use in the second test criterion owing to lack of fossils known for the group. As for the last criterion, a pantropical distribution, the closest related genus to *Hymenandra* appears to be the genus *Connandrium* Mez, known only from New Guinea, on the basis of possession of anthers fused along the sutures. In connection with New Guinea and adjacent Australia as significant sources of biota related to that of North America, Dobson (1996) cites the distribution of the termite genus *Mastotermes* and the sister poison frog genera, *Pitobui* and *Phylllobates*, as further evidence, but without citing the boreotropics hypothesis *per se*. It is unfortunate that the preliminary cladogram for genera of the family by Ståhl (1996) did not include *Hymenandra*. The other neotropical genera of the tribe *Ardisieae* include *Ardisia*, pantropically distributed with major centers of diversity in Malesia and Mesoamerica, *Ctenardisia* Ducke, with species from northern Mesoamerica and the Amazon Basin, *Synardisia* (Mast.) Lundell, a monotypic genus ranging from southern Mexico to Nicaragua, and *Gentlea* Lundell, with the majority of species in Mexico and Mesoamerica (only one, *G. venossissima*, in the Andes from Venezuela to Peru). Until a phylogenetic analysis is complete for the tribe, a rigorous test cannot be performed. However, the pattern of distribution among the genera of the tribe *Ardisieae* fit the general pattern one would expect if the distribution was boreotropical.

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

#### NOTES ON KEYS, DESCRIPTIONS, AND TERMINOLOGY

The keys are artificial and designed to expedite identification of herbarium specimens. An attempt has been made to emphasize vegetative characters to increase the keys' usefulness with sterile material. The numbers appearing before the taxa refer to their respective position in the key; any correlations with phylogenetic relationships are coincidental. Quantitative and qualitative data presented in keys and descriptions for floral parts and bracts were taken from organs rehydrated from herbarium specimens by boiling in water. Measurements from these range from 10% to 15% greater than those measurements taken directly from dried material. Data regarding shoot



diameters, inflorescence rachises, pedicels, leaf and fruit shape and size were taken from dried herbarium specimens.

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

Because of branchlet and leaf dimorphism between shoots in vegetative vs. reproductive phases, the primary orthotropic axes (stems if a small statured plant, trunks if a treelet), are shoots not bearing inflorescences and are termed "*vegetative shoots*," while those plagiotropic branches actually or potentially bearing flowers or fruit are termed "*reproductive shoots*". Likewise, the leaves on the trunk or on the branches when they are in a vegetative state, will be termed, "*vegetative shoot leaves*" while those leaves on the shoots while they are in the reproductive phase will be termed, "*reproductive shoot leaves*."

All types cited here have been seen by the authors unless noted as "n.v."

#### KEY TO GENERA OF MYRSINACEAE IN MESOAMERICA

1. Calyx closed in bud, irregularly opening into 2–8 lobes among flowers within the same inflorescence ..... **Geissanthus**
1. Calyx open in bud, with (3–)4–5(–6) lobes, the number of calyx lobes per flower consistent within one inflorescence.
  2. Calyx and corolla lobes valvate in bud; inflorescence axis never rufous glandular-papillate.
    3. Flowers bisexual; inflorescences paniculate, longer than the petioles; shoots tomentose with stellate or dendroid trichomes; calyx and corolla tomentose and glandular-papillose; anthers bright yellow; style elongate ..... **Parathesis**
    3. Flowers unisexual; inflorescences glomerulate, umbellate or rarely in reduced corymbs, much shorter than the petioles; shoots glabrous or when tomentose, then with simple trichomes; calyx and corolla glabrous or the corolla sometimes glandular-papillose along the margin within; anthers cream to white; style obsolete or reduced ..... **Myrsine**
  2. Calyx and corolla quincuncial, imbricate (although sometimes inconspicuously so), contorted or rarely valvate in bud, when valvate, the inflorescence rachis rufous glandular-papillate.
    4. Filaments connate basally to form a staminal tube adnate to the corolla tube.
      5. Inflorescence lateral (axillary); corolla tube glandular-granulose within at least at the junction of the tube and lobes; staminal tube adnate to corolla at least 1/5 its length ..... **Cybianthus**
      5. Inflorescence terminal or pseudoterminal functioning as terminal; corolla tube glandular-puberulent within at base; stamens free from or barely adnate to corolla at base.
        6. Anthers connate at least at base; filaments connate in a tube at least 1/2 their length; corolla lobes nearly free ..... **Hymenandra**



- 6. Anthers free; filaments connate less than 1/5 length; corolla lobes united up to 3/4 their length ..... **Synardisia**
- 4. Filaments free from each other and free from or variously adnate to the corolla tube, or filaments basally connate to form a staminal tube not adnate to the corolla tube.
- 7. Filaments adnate to the corolla; anthers less than 3 times longer than wide.
- 8. Filaments exerted, more than 6 times longer than the anthers; anthers obcordate; plants of elfin and cloud forests ..... **Gentlea**
- 8. Filaments included, shorter than or as long as the anthers; anthers ovate, lanceolate, elliptic or oblong; plants of montane to low land forests ..... **Stylogyne**
- 7. Filaments free from the corolla; anthers at least 3 times longer than wide.
- 9. Corolla lobes connate 1/4 their length; ovules uniseriate, the placentation free-central ..... **Ctenardisia**
- 9. Corolla lobes nearly free or connate to 1/5 their length; ovules pluriseriate, the placentation basal ..... **Ardisia**

#### TAXONOMIC TREATMENT

**Hymenandra** (A. DC.) A. DC. ex Spach, Hist. Veg. Phan. 9:374. 1840; A. DC., Ann. Sci. Nat., Bot., ser. 2, 16:79. 1841.; A. DC. in DC., Prodr. 8: 91. 1844. *Ardisia* sectio 2. *Hymenandra* A. DC., Ann. Sci. Nat., Bot., ser. 2, 2:297. 1834; Trans. Linn. Soc. London 17:126. 1837. TYPE: *Ardisia hymenandra* Wall. in Roxb. Fl. Ind. Ed. Carey 2:282. 1824, = *Hymenandra wallichii* A. DC., Ann. Sci. Nat. Bot., ser. 2, 16:79. 1841.

*Chontalesia* Lundell, Wrightia 7:41. 1982. TYPE: *Ardisia calycosa* Hemsl., Biol. Centr.-Amer., Bot. 2:292. 1882.

*Subshrubs* to small *trees* exhibiting Fagerlind's Architectural Model (Hallé et al. 1978) up to 8 m tall. *Leaves* pseudoverticillate, dimorphic; the blades of the orthotropic trunk or stem (i.e., primary axis) which are vegetative shoots larger with cuneate bases, those of the plagiotropic branches which are reproductive shoots basally obtuse to somewhat auriculate. *Inflorescence* terminal or pseudoterminal, bi- or tripinnately paniculate, pyramidal or columnar, the ultimate branches bearing flowers in loose to tight corymbs. *Flowers* perfect, bisexual, 5(–6)-merous, punctate and/or punctate-lineate; calyx lobes quincuncial, spreading at anthesis, nearly free, mostly papillose but sometimes hirtellous (Paleotropics) or glabrous (Neotropics), densely and prominently or conspicuously pellucid or black punctate, the margin glandular-ciliate; corolla white or pink, the lobes short-connate, quincuncial, lanceolate or oblong to ovate to narrowly ovate, glabrous or sparsely papillose within toward base, densely and prominently black punctate or inconspicuously pellucid punctate, the margin entire, erose or erose-fimbriate, sometimes subapically notched, glandular-ciliate or glabrous; stamens connate, shorter than the corolla lobes,



the filaments monadelphous, fused basally  $2/3$  their length and reunited apically, fused basally but with apical portions free, or fused along entire length, adnate basally to the corolla tube, the anthers connate basally for  $1/4$ – $2/3$ , or along entire length along the thecal margins, narrowly oblong, linear-lanceolate or lanceolate, the connectives darkened or prominently black punctate abaxially; pistil obturbinate, the ovary ovoid, the style slender, elongate, the stigma punctiform; placenta subglobose, 5–24 ovules, at times appearing uniseriate (but in a high anthotactic spiral), or clearly pluriseriate. *Fruit* 1-seeded, globose or depressed-globose, the exocarp densely and prominently or conspicuously punctate, the style base persistent.

*Distribution*.—A genus of 16 species, from Bangladesh eastward to Myanmar, south to Malaya and Borneo in the Paleotropics; Nicaragua southward through Costa Rica and Panama to the Chocó of Colombia in the Neotropics, from near sea level–1,400 m elevation.

*Ecology*.—Members of *Hymenandra* are subshrubs to small trees in the lowest level of the forest understory, from the lowland to premontane transition to cloud forest, frequently on ridge tops or steep slopes, and near small water-courses. They are at best locally common [see ECOLOGY section].

*Etymology*.—*Hymenandra* is a Greek compound, derived from the words *Hymen*, or membrane, and *andros*, of the anthers, to describe the membranaceous connective tissue joining the anthers at their dehiscence suture.

#### KEY TO NEOTROPICAL SPECIES OF *HYMENANDRA*

1. Calyx lobes oblong or narrowly oblong to narrowly lanceolate, at least 3–5 times longer than wide at maturity.
  2. Calyx lobes shorter than the corolla lobes, 2.3–4.7 mm long, 0.9–1.1 mm wide, the margins erose, hyaline, densely glandular-ciliolate; corolla lobes 5–6.5 mm long ..... 1. *Hymenandra stenophylla*
  2. Calyx lobes longer than the corolla lobes, 6–9 mm long, (1.6–)2–2.5 mm wide, the margins entire, glabrous; corolla lobes 7–8.2 mm long ..... 2. *Hymenandra calycosa*
1. Calyx lobes ovate or suborbicular, usually less than 2 times longer than wide at maturity.
  3. Inflorescence a columnar panicle of corymbs, often appearing racemose in fruit ..... 3. *Hymenandra sordida*
  3. Inflorescence a pyramidal panicle of corymbs, appearing paniculate in fruit.
    4. Calyx lobes asymmetric, notched subapically.
      5. Subshrubs, 0.2–1 m tall; abaxial leaf surface densely and minutely furfuraceous lepidote, appearing velutinous; stamens 2.6–3 mm long, the anthers apically rounded, apiculate at tip, 1.6–1.8 mm long, 0.8–0.9 mm wide ..... 4. *Hymenandra squamata*
      5. Trees, 1–8 m tall; abaxial leaf surface glabrous to sparsely and minutely furfuraceous lepidote, not appearing velutinous; stamens 6–9.5 mm long, the anthers apically long-attenuate to an acute or emarginate tip, 5.5–8 mm long, 1.4–2.2 mm wide.



6. Calyx lobes 1.4–1.8 mm long; stamens 6–6.5 mm long; anthers 5.5–5.8 mm long; vegetative shoot leaf blades 5.5–22.2 cm long, 1.3–7.8 cm wide, reproductive shoot leaf blades 7.2–17.3 cm long, 2.1–4.7 cm wide ..... 5. *Hymenandra wilburiana*
6. Calyx lobes 2.2–2.8 mm long; stamens 8.7–9.5 mm long; anthers 7.5–8 mm long; vegetative shoot leaf blades 33.7–72.2 cm long, 5.3–16.5 cm wide; reproductive shoot leaf blades 3.9–34.3 cm long, 1.2–11.8 cm wide ..... 6. *Hymenandra pittieri*
4. Calyx lobes symmetric, not subapically notched.
7. Vegetative or flowering shoots 7–10 mm in diam.; petioles (0.6–)1–1.2 cm long; calyx lobes 2–2.8 mm long ..... 7. *Hymenandra callejasii*
7. Vegetative or flowering shoots 1.5–5.5 mm in diam.; petioles 1.6–3.9 mm long; calyx lobes 0.9–1.6 mm long.
8. Calyx lobes 1.4–1.6 mm long; inflorescences terminal, 9–16.5 cm long, secondary branches 5–5.5 cm long; fruit 8–12 mm in diam. .... 8. *Hymenandra acutissima*
8. Calyx lobes 0.9–1.2 mm long; inflorescences subterminal, 2.7–8.8 cm long, secondary branches 1.3–3.5 cm long; fruit 4.5–6.5 mm in diam. .... 9. *Hymenandra crosbyi*

1. *Hymenandra stenophylla* (Donn. Sm.) Pipoly & Ricketson, comb. nov. (Figs. 1B, 2). *Ardisia stenophylla* Donn. Sm., Bot. Gaz. 24:395. 1897. *Icacorea stenophylla* (Donn. Sm.) Lundell, Phytologia 49:351. 1981. TYPE. COSTA RICA. LIMÓN: Forests of Shirores, Talamanca, 300 ft. [91 m], Feb 1895 (fl), H. Pittier & A. Tonduz 9173 (HOLOTYPE: US (LL Neg. # 71-109, US Neg. # 2388); ISOTYPES: CR n.v., US).

*Ardisia oblanceolata* Standl., Publ. Field Colombian Mus., Bot. Ser. 4:249. 1929, SYN. NOV. TYPE. PANAMA. BOCAS DEL TORO: Region of Almirante, without elev., Jan–Mar 1928 (fr), G. Cooper 370 (HOLOTYPE: F (F Neg. # 68229, LL Neg. # 1971-75); ISOTYPES: G (fragment), K, NY, US (US Neg. # 2378)).

*Tree* 2–6.1 m tall, to 7.5 cm in diam. *Trunk and vegetative shoots* terete, 7–9.5 mm in diam., minutely scattered furfuraceous lepidote, early glabrescent; *reproductive shoots* similar, but 1.5–4 mm in diam. *Vegetative shoot leaf blades* chartaceous, oblong to elliptic, 21.2–30.5 cm long, 3.5–8.5 cm wide, apically long-acuminate, the acumen 1–1.9 cm long, gradually tapering to a cuneate base decurrent to base of petiole, midrib slightly raised above, prominently raised below, secondary veins 22–32 pairs, slightly depressed or not visible above, slightly raised below, prominently punctate, scattered minutely furfuraceous lepidote, early glabrescent, the margins entire, flat; petioles marginate, 0.5–1.5 cm long, minutely scattered furfuraceous lepidote, early glabrescent; *reproductive shoot leaf blades* similar to the vegetative ones but 6.1–22.5 cm long, 2.1–5.2 cm wide, secondary veins 7–28 pairs; petioles similar to vegetative ones but 0.5–2.2 cm long. *Inflorescence* terminal, pinnately or bipinnately paniculate 3–10 (–15.5) cm long, pyramidal, secondary branches 0.8–3 (–6.2) cm long, minutely scattered furfuraceous lepidote, early glabrescent, the branches ending in 4–8-flowered corymbs; inflorescence bracts early caducous, membranaceous, oblong, 5.6–8.8 mm



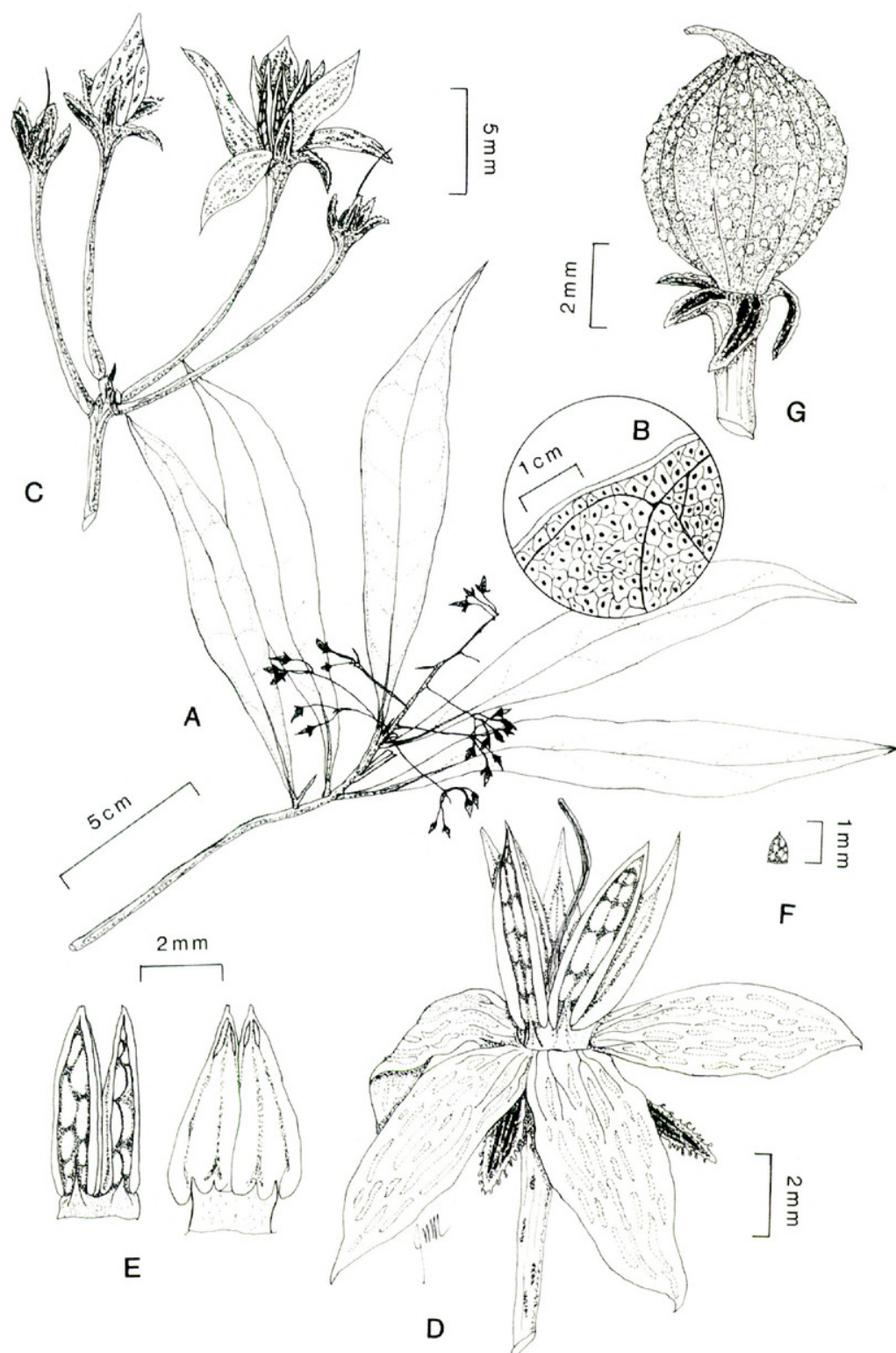


FIG. 2. *Hymenandra stenophylla* (Donn. Sm.) Pipoly & Ricketson. A. Reproductive shoot. B. Detail of abaxial leaf surface. C. Detail of inflorescence. D. Detail of flower. E. Detail of stamens, showing abaxial (left) and adaxial (right) surfaces. F. Ovules. G. Fruit. A–B drawn from the holotype, H. Pittier & A. Tonduz 9173. C drawn from L.D. Gomez *et al.* 20415. D–F drawn from B. Hammel 13717. G drawn from J. Gomez-Laurito 9538.



long, 0.6–1.2 mm wide, apically acute to rounded, midrib slightly raised above and below, secondary veins not visible, prominently punctate, scattered minutely furfuraceous lepidote, the margin entire, flat; floral bracts 0.5–2.2 mm long, 0.3–1.1 mm wide, otherwise as the inflorescence bracts; pedicels cylindrical, 0.6–1.2(–1.6) mm long, scattered minutely furfuraceous lepidote, early glabrescent. *Flowers* 5-merous, white or rarely pink; calyx lobes almost free, chartaceous, narrowly lanceolate to narrowly oblong, 2.3–4.7 mm long, 0.9–1.1 mm wide, symmetrical, apically very narrowly acute to subulate, densely and prominently black punctate and punctate-lineate, glabrous, the margin irregular, erose, hyaline, sparsely glandular-ciliolate; corolla lobes membranaceous, 5–6.5 mm long, the tube 0.2–0.5 mm long, the lobes lanceolate 4.5–6.3 mm long, 2–2.8 mm wide at base, apically acute, reflexed in anthesis, prominently pellucid punctate, the margins hyaline, entire, glabrous; stamens 3.5–5 mm long; filaments connate throughout their length into a chartaceous elobate tube, the tube 0.3–0.8 mm long, adnate to the corolla basally, epunctate, glabrous; anthers connate by their sutures, at least at first, lanceolate, 3–4.5 mm long, 0.7–1.1 mm wide at base, sessile on staminal tube, apically apiculate, basally cordate, longitudinally dehiscent by narrow, sublatrose slits, the connective densely and prominently black punctate; pistil obturbinate 5.3–7 mm long; ovary 1.2–1.5 mm long, glabrous; style 3.8–4.4(–5.8) mm long, erect, inconspicuously pellucid punctate, glabrous; stigma punctiform; placenta ellipsoid, 0.4–0.7 mm long, 0.2–0.5 mm in diam., apically apiculate; ovules 13–17, pluriseriate. *Fruit* obovoid to globose, 4.8–5.8 mm long, 3.8–4.5 mm in diam., densely and prominently punctate, the style base persistent.

*Distribution*.—Limón, Costa Rica and Bocas del Toro, Panama, from 25–500 m elevation.

*Ecology and conservation status*.—Known only from primary lowland tropical moist forests, collected from the understory along ridgetops, *Hymenandra stenophylla* should be considered threatened.

*Etymology*.—The epithet 'stenophylla' comes from the Greek "stenos" meaning narrow, and 'phyllus' referring to the leaves. It describes the very narrow leaf blades of the taxon.

Specimens examined. COSTA RICA. Limón: Talamanca Valley, without elev., 1927 (ster.), *G. Cooper* 12 (US); 7 km SW of Bribri, 100–250 m, 4 May 1983 (fl), *L. Gómez et al.* 20415 (LL, MO); Sitio de exploración petrolera, Suretka, Talamanca, 250 m, 6 Jul 1983 (fr), *J. Gómez-Laurito* 9538 (F); Headwaters of Quebrada Mata de Limón, central fork, and hills between central and W forks, Finca Anai, Sixaola region, 09° 35' N, 82° 39' W, 25–40 m, 19 Nov 1984 (fr), *M. Grayum et al.* 4486 (MO, NY); Hitoy Cerere Reserve and vicinity in Valle la Estrella, S of Finca Concepción, from station to top of ridge Miramaror Los Jabillos, 09° 42' N, 83° 02' W, 140–500 m, 1 Aug 1985 (fr), *B. Hammel & M. Grayum* 14342 (MO); Reserve Biol. Hitoy-Cerere, near the station, Valle de la Estrella, 09° 40' 30" N, 83° 01' 30" W, 100 m, 20 Sep 1991 (fr), *A. Moreno* 7 (MO); Forests de Tsâki, Talamanca, 200 m,



Apr 1895 (fl) *A. Tonduz* 9586 (G 3-sheets, US). PANAMA. Bocas del Toro: Along oil pipeline road between continental divide and Chiriquí Grande, second bridge over Río Guabo, along dirt acces[s] road, 08° 50–55' N, 82° 9–15' W, 120–200 m, 1–2 May 1985 (fl), *B. Hammel* 13717 (MO); Filo Almirante along trail to Riscó Abajo, 3 km SW of town of Almirante, 100–200 m, 3 Jan 1975 (fr), *M. Nee & B. Hansen* 14099 (MO); Vicinity San San River, Davao Farm, United Fruit Co., Almirante, 26 Aug 1940 (fr), *R. Seibert* 1572 (MO, US).

*Hymenandra stenophylla* appears to be most closely related to *H. calycosa* by virtue of its oblong or narrowly oblong to narrowly lanceolate calyx lobes. However, the erose and sparsely glandular-ciliate calyx lobe margins, the calyx lobes smaller than the corolla lobes, and generally smaller flowers, easily separate the two species.

Populations corresponding to the type of *Ardisia oblanceolata* are notable only for the slightly larger and more prominent punctations on the leaves and slightly shorter pedicels. It is otherwise identical to *Hymenandra stenophylla*.

2. *Hymenandra calycosa* (Hemsl.) Pipoly & Ricketson, comb. nov. (Fig. 1A, 3). *Ardisia calycosa* Hemsl., Biol. Centr.-Amer., Bot. 2:292. 1882. *Chontalesia calycosa* (Hemsl.) Lundell, *Wrightia* 7:42. 1982. TYPE. NICARAGUA. CHONTALES: Chontales, without elev., 1867–1868 (fl), *R. Tate* 239 {454} (HOLOTYPE: K; ISOTYPES: BM, P n.v.).

*Shrub or tree* 1–4 m tall. *Trunk and vegetative shoots* terete, 4–7 mm in diam., minutely and densely furfuraceous lepidote at first, early glabrescent; *reproductive shoots* as in vegetative ones but 1–4 mm in diam., minutely scattered furfuraceous lepidote. *Vegetative shoot leaf blades* coriaceous, narrowly elliptic, 7.5–20.3 cm long, 2.8–5.2 cm wide, apically long-acuminate, the acumens 0.5–2.2 cm long, gradually tapering to the cuneate base, decurrent to petiole base, midrib slightly raised above, prominently raised below, secondary veins 7–21 pairs, slightly depressed or not visible above, prominently raised below, prominently punctate, glabrous above, minutely scattered furfuraceous lepidote below, early glabrescent, the margins crenate; petioles marginate, 0.2–0.8 cm long, glabrous above, minutely scattered furfuraceous lepidote below, early glabrescent; *reproductive shoot leaf blades* as in vegetative ones but 7.2–15.7 cm long, 1.6–4.1 cm wide, secondary veins 7–20 pairs; petioles like the vegetative ones but 0.3–0.9 cm long. *Inflorescence* terminal, pinnately or bipinnately paniculate, 4.5–14 cm long, pyramidal, secondary branches 2.7–4.3 cm long, minutely scattered furfuraceous lepidote, early glabrescent, terminating in 3–7-flowered corymbs; inflorescence bracts early caducous, membranaceous, oblong, 5.5–9 mm long, 0.7–1.1 mm wide, apically acute, basally sessile, midrib slightly raised above and below, secondary veins not visible, prominently punctate, mostly glabrous above, densely minutely furfuraceous lepidote below, the margins entire, flat; floral bracts similar to inflorescence bracts but lanceolate to narrowly elliptic 2.8–4.1 mm long, 0.4–1.2 mm wide; pedicels cylindrical, 7–15





FIG. 3. *Hymenandra calycosa* (Hemsl.) Pipoly & Ricketson. A. Reproductive shoot. B. Detail of abaxial leaf surface. C. Detail of inflorescence. D. Detail of flower. E. Detail of stamens, showing abaxial (left) and adaxial (right) surfaces. F. ovules. G. Fruit. A–B drawn from BM isoelectotype, R. Tate 239 {454}. C–F drawn from M. Chinchilla 93. G drawn from R. Villalobos 37.



mm long, minutely scattered furfuraceous lepidote, early glabrescent. *Flowers* 5-merous, 6.9–8 mm long; calyx lobes almost free, coriaceous, narrowly lanceolate to lorate, 4.2–9.7 mm long, 1.2–2.1 mm wide, symmetrical, apically acute to rounded, prominently punctate, appearing prominently because of the prominently brown punctations, scattered lepidote outside at the base, the margins entire; corolla lobes basally connate, membranaceous, the tube 1.5–1.8 mm long, elliptic, the lobes 5.4–6.2 mm long, 2.2–2.4 mm wide at the middle, apically acute to acuminate, reflexed in anthesis, prominently pellucide punctate, the margins hyaline, entire, glabrous; stamens 4.8–5.1 mm long; filaments connate into a chartaceous elobate tube, the tube 0.4–0.5 mm long, adnate to the corolla basally, epunctate, glabrous; anthers connate by their sutures, at least at first, lanceolate, 4.5–4.7 mm long, 1.2–1.5 mm wide at the base, sessile on the staminal tube, apically apiculate, basally cordate, longitudinally dehiscent by narrow, sublatrose slit, the connective conspicuously raised, pellucid punctate; pistil obturbinate 6.5–7.2 mm long; ovary 1.2–1.4 mm long, glabrous; style 5.3–5.8 mm long, erect, epunctate, glabrous; stigma punctiform; placenta ellipsoid, 0.6–0.8 mm in diam., apically apiculate; ovules 11–19, pluriseriate. *Fruit* elliptic, 6.2–7 mm long, 5.2–5.8 mm in diam., nearly epunctate, the style base persistent.

*Distribution.*—Jinotega, Chontales, Zelaya and Río San Juan, Nicaragua and Alajuela and Guanacaste, Costa Rica. It grows from (10–)450–1,100 m elevation.

*Ecology and conservation status.*—This species normally occurs in premontane wet forests, especially along ridgetops. The locations where the species has been found are actually premontane even though their absolute elevations are at times quite low. This phenomenon is due to the relative flatness of the Atlantic Slope in Nicaragua, where even elfin forest has been found under 1,000 m elevation. With increasing habitat destruction, and its consequent desertification, *Hymenandra calycosa* should be considered a threatened species.

*Etymology.*—The specific epithet refers to the calyx, which is always longer than the corolla and is accrescent in fruit.

Specimens examined. **NICARAGUA.** Chontales: Cerro Oluma, on ridge top of Cordillera Amerisque, 750 m, 4 Jan 1984 (fr), A. Gentry *et al.* 43939 (DUKE, MO, NY); Cerro Oluma, ca 3 km SW de Ciudad Cuapa, 12° 18' N, 85° 20' W, 700–740 m, 3 Jan 1984 (fl), A. Grijalva *et al.* 3393 (M); Cerro El Portillo, ca. 3 km al NE de Ciudad Cuapa, 758 m, 1 Mar 1984 (fl, fr), A. Grijalva y D. Bradford 3652 (MO). Jinotega: Kilambé, Cerro San Pedro, 13° 36' N, 85° 39' W, ca. 600–800 m, 25 Mar 1981 (fl), P. Moreno 7532 (MO, NY); Las Brisas, Comarca Kilambe, 13° 35–36' N, 85° 39' O, 930 m, 13 Jul 1980 (fl), J. Sandino 159 (MO, NY). Río San Juan: Boca de Sábalo, trail to Buena Vista, 11° 03' N, 84° 27' W, ca. 70 m, 24 Mar 1985 (fl, fr), P. Moreno 25630 (MO); Sábalo, 1 km al N de Río San Juan, 11° 02' N, 84° 27' W, ca. 100 m, 9–10 Jul 1985 (fr), P. Moreno 26053 (MO); Bocas de Sábalo, 11° 03' N, 84° 27' W, 70–100 m, 14 Mar 1987 (ster.), P. Moreno 26753 (MO). Zelaya: Río Punta Gorda, Atlanta, desembocadura del Caño el Guineo, 11° 33' N, 84°



02' W, ca. 10 m, 11 Nov 1981 (fr), *P. Moreno & J. Sandino* 12853 (MO). **COSTA RICA.** **Alajuela:** Ca. 3 km NNE of Bijagua along the new road to Upala, 10° 45' N, 85° 03' W, 450 m, 7–8 Nov 1975 (fr), *W. Burger & R. Baker* 9869 (F); E slopes of Volcán Miravalles, W of Bijagua, near the Río Zapote, 10° 44' N, 85° 05' W, ca. 600 m, 11–12 Feb 1982 (fl), *W. Burger et al.* 11687 (F, LL, NY); Cataratas (Los Angeles) de San Ramon, without elev., 17 Apr 1925 (fl), *A. Brenes* 21243 (NY); San Carlos Cantón, Betania de Cutris, 150 m, 26 Feb 1983 (fl), *A. Carvajal* U. 392 (DUKE, LL, MO, NY); El Silencio de Tilarán, without elev., 31 May 1932 (fl, fr), *A. Brenes* 15655 (F, NY); Upala Cantón, P.N. Guanacaste, Cordillera de Guanacaste, Estación San Ramón, Dos Ríos, 10° 52' 50" N, 85° 24' 05" W, 550 m, 3 Apr 1995 (fl), *M. Chinchilla* 93 (MO), 100 (MO); Along road between Canas & Upala 4 km NNE of Bijagua on slopes leading into Río Zapote, ca. 400 m, 24 Jun 1976 (fl), *T. Croat* 36246 (LL, MO, NY); Upala Cantón, P.N. Guanacaste, Cordillera de Guanacaste, Estación San Ramón, bosque en el sendero El Argentino, 10° 52' 40" N, 85° 24' 15" W, 550 m, 22 Mar 1994 (fl), *D. García* 312 (MO); Santa María National Park, road down Caribbean slope 1 km E of summit of road, 4 km W of E side of park, 4 km E of colored house at junction of road to Hacienda Santa María, 10° 37' N, 85° 17' W, ca. 600 m, 7 Feb 1978 (fl), *R. Liesner* 5066 (LL, MO, NY); 2 km N of Santa Rosa, 15 km N of Boca Arenal on Quesada-Muelle San Carls-Los Chiles road, 10° 38' N, 84° 31' W, ca. 100 m, 28 Apr 1983 (fl), *R. Liesner et al.* 15041 (MO); Upala Cantón, P.N. Guanacaste, Cordillera de Guanacaste, Estación San Ramón, sendero El Argentino, camino al Volcán Cacao, 10° 53' 50" N, 85° 24' 29" W, 850 m, 27 Feb 1996 (fl), *J. Morales* 5305 (MO); Moravia de Cutris-San Carlos, without elev., without date (ster.), *L. Poredat et al.* 3681 (F); Cantón San Carlos, Cuenca de Pocosal, Escaleras, 20 km después de Pavón, Finca Elky María, 10° 52' 30" N, 84° 30' 25" W, 100 m, 16 Mar 1997 (fl), *A. Rodríguez & N. Zamora* 2067 (CR, F, INB, MO); Villa Quesada, 850 m, 21 Feb 1939 (fl), *A. Smith* 1630 (F, GH, MICH, NY), 1726 (F, MICH), 2609 (F, MO); On the slope of Volcán Rincón de la Vieja, along the road N from Liberia, ca. 5 km from the park, 400–700 m, 1 Mar 1985 (fl), *C. Taylor* 4551 (DUKE, LL-frag. of DUKE); 2 km N of Bijagua along roadside and on trail to San Miguel or 7 km N of Río Naranjo, 400–500 m, 8 Jul 1976 (fl), *J. Utley & K. Utley* 5318 (DUKE). **Alajuela-Guanacaste Border:** Border region on the slopes of Volcán Miravalles, along road N of Bagaces, from Guayabo to Aguas Claras, 400–600 m, 2 Mar 1985 (fl, fr), *C. Taylor & C. Skotak* 4630 (DUKE). **Guanacaste:** La Cruz Cantón, Parque Nacional Guanacaste, Cordillera de Guanacaste, Estación Pitilla, Sederlo los Memos, 10° 59' 26" N, 85° 25' 40" W, 740 m, 15 Apr 1995 (fl, fr), *E. Alfaro* 169 (MO); Liberia Cantón, Parque Nacional Guanacaste, Cordillera de Guanacaste, Nueva Zelandia, Estación San Ramón, 10° 52' 50" N, 85° 24' 05" W, 550 m, 23 Mar 1994 (fl, fr), *D. García* 112 (MO); Tilarán, ridge above town ca. 2.5 mi, without elev., 6 Oct 1971 (fr), *A. Gentry* 2011 (LL, MO); Ridge to N of Río Las Flores, ca. 1 km E of Río Tenorio, Hacienda Montezuma, 10° 40.5' N, 85° 04.5' W, 475–500 m, 24 Jan 1985 (fr), *M. Grayum & G. Herrera* 4852 (MO); Forest along Río San Juan, lower W Pacific slopes of Volcán Tenorio, Hacienda Montezuma, 10° 40.5' N, 85° 03' W, 600–700 m, 25 Jan 1985 (fl), *M. Grayum et al.* 4969 (LL, MO); El Dos de Tilarán, 4 km N, Cerro La Chirripa, Atlantic slope, 10° 25' N, 84° 50' W, 1,000 m, 12 Apr 1986 (fl, fr), *W. Haber et al.* 4430 (MO), 4432 (LL), 4447 (MO); La Chirripa ridge, 4 km NE El Dos de Tilarán, continental divide, 10° 25' N, 84° 53' W, 1,000 m, 8 May 1986 (fl), *W. Haber et al.* 4752 (MO), 4759 (MO), 4848 (MO); Tilarán, Río Chiquito de Quebrada Grande, Zona Monteverde, Finca López, Vertiente Atlántica, 10° 25' N, 84° 53' W, 700–900 m, 6 Jun 1987 (fl), *W. Haber & E. Bello* C. 7433 (MO); Parque Nacional Guanacaste, Estación Pitilla, camino al E de la Estación, 11° 02' N, 85° 25.3' W, 600 m, 24 May 1989 (fl, fr), *B. Hammel et al.* 17370 (BRIT, MO); Santa Cecilia, La Cruz, Estación pitilla, Faldas Cerro Orosilito, 10° 57' N, 83° 28' W, 700 m, 14 Jun



1989 (fl), *Q. Jiménez et al.* 709 (BRIT, MO); Santa Elena to Tilarán road, ca. 24 km from Santa Elena, ca. 1,000 m, 17 Feb 1984 (fl, fr) *Khan et al.* 1141 (BM 2-sheets); Liberia Cantón, Parque Nacional Guanacaste, Cordillera de Guanacaste, Estación Cacao, El Cañon, 10° 55' 43" N, 85° 28' 10" W, 1,100 m, 10 Feb 1995 (fr), *M. Lobo* 47 (MO); Estación pitilla, La Cruz, Parque Nacional Guanacaste, 10° 59' 26" N, 85° 25' 40" W, 700–1,000 m, 7 Nov 1990 (fr), *C. Moraga* 214 (MO); Liberia Cantón, Parque Nacional Guanacaste, Cordillera de Guanacaste, Nueva Zelandia, Estación San Ramón, sendero al Volcán Cacao, 10° 53' 50" N, 85° 29' 29" W, 850–950 m, 23 Mar 1994 (fl), *J. Morales et al.* 2544 (MO); Forest at top of divide, 4 km NW of Tilarán, without elev., 27 Feb 1972 (fl), *P. Opler* 580 (F); Liberia Cantón, Parque Nacional Guanacaste, Cordillera de Guanacaste, Estación Cacao, Sendero Nayo, 10° 55' 43" N, 85° 28' 10" W, 1,000 m, 9 Feb 1995 (fl), *A. Picado et al.* 51 (MO); Hacienda Tenorio, without elev., 17 Feb 1956 (fl), *B. Schubert* 1079 (A, F); El Silencio, near Tilarán, ca. 450 m, 13 Jan 1926 (fl), *P. Standley & J. Valerio* 45539 (US), 45545 (US); La Tejona, N of Tilarán, 600–700 m, 25 Jan 1926 (fr), *P. Standley & J. Valerio* 45862 (US); Quebrada Serena, SE of Tilarán, ca. 700 m, 27 Jan 1926 (fl), *P. Standley & J. Valerio* 46181 (US), 46221 (US); El Silencio, 800 m, 15 Aug 1923 (fr), *J. Valerio* 147 (F); Liberia Cantón, Parque Nacional Guanacaste, Cordillera de Guanacaste, Estación Cacao, Cerro Cacao, 10° 55' 43" N, 85° 28' 10" W, 1,100 m, 8 Feb 1995 (fl, fr), *R. Villalobos* 37 (MO).

*Hymenandra calycosa* is closely related to *H. stenophylla*, but is very easily recognized by the calyx lobes entire, longer than the corolla and accrescent in fruit, larger corollas and crenate leaf margins.

**3. *Hymenandra sordida* (Lundell) Pipoly & Ricketson, comb. nov. (Figs. 1H, 4).** *Auriculardisia sordida* Lundell, *Wrightia* 7:272. 1984. *Ardisia sordida* (Lundell) Lundell, *Phytologia* 61:66. 1986, nomen. invalidum. *Ardisia sordida* (Lundell) J.F. Morales, *Phytologia* 83:111. 1997 [1998]. TYPE. COSTA RICA. ALAJUELA: Finca Los Ensayos, ca. 11 mi. NW of Zarcero, ca. 850 m, 15 Aug 1977 (fl), *T. Croat* 43538 (HOLOTYPE: LL; ISOTYPES: CR n.v., MO).

*Subshrubs* 0.4–1 m tall. *Vegetative shoots* unknown; *reproductive shoots* terete, 4–7 mm in diam., densely appressed furfuraceous lepidote. *Vegetative shoot leaves* unknown; *reproductive shoot leaf blades* chartaceous, elliptic to oblanceolate, 16–29.5 cm long, 4.5–10.8 cm wide, apically acuminate, the acumen 0.5–1.8 cm long, basally attenuate, the midrib depressed above, prominently raised below, the secondary veins 35–70 pairs, slightly depressed or not visible above, prominently raised below, abaxially densely appressed furfuraceous lepidote along and near the midrib, adaxially glabrous, the margin entire, inrolled; petioles marginate, 0.5–2.1 cm long, glabrous above, densely appressed furfuraceous lepidote below. *Inflorescence* terminal, pinnately or bipinnately paniculate, 4.2–10.5 cm long, a columnar panicle of 7–14-flowered corymbs, appearing racemose in fruit, secondary branches 0.5–2.3 cm long, the rachis densely appressed furfuraceous lepidote, glabrescent; inflorescence bracts early caducous, membranaceous, lanceolate, 1.4–2.8 cm long, 2.2–4.4 mm wide, sessile, midrib slightly raised above and below, secondary veins obscure to not visible above and below, scattered furfuraceous lepidote to mostly glabrous below, densely appressed furfuraceous lepidote below,



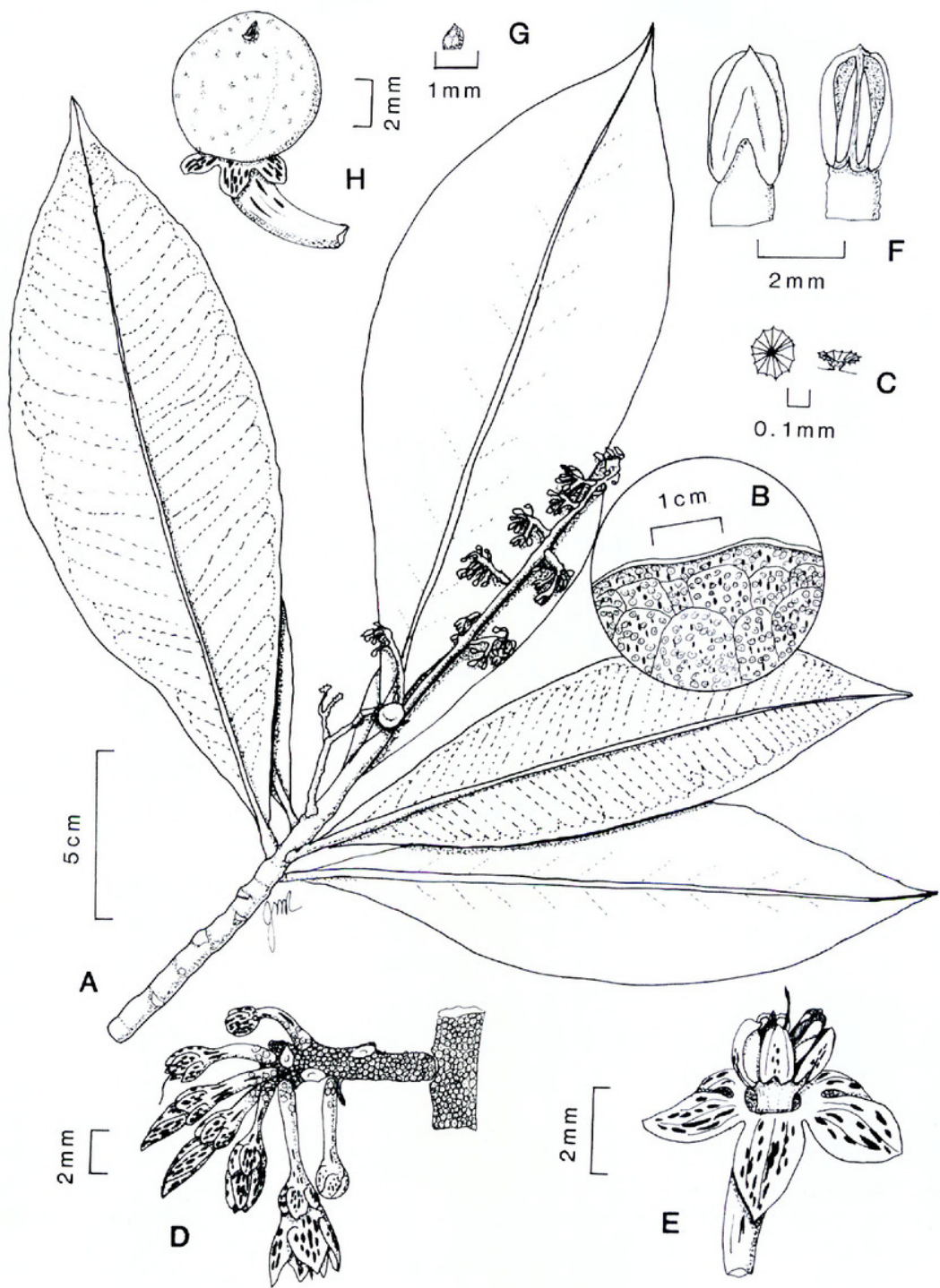


FIG. 4. *Hymenandra sordida* (Lundell) Pipoly & Ricketson. A. Reproductive shoot. B. Detail of abaxial leaf surface. C. Lepidote scale from above and from the side. D. Detail of inflorescence. E. Detail of flower. F. Detail of stamens, showing abaxial (left) and adaxial (right) surfaces. G. ovules. H. Fruit. A–D & G drawn from holotype, *T. Croat* 43538. E–F drawn from *B. Hammel et al.* 14078. H drawn from *A. Molina R. et al.* 17525.



the margins entire, ciliolate; floral bracts 1.1–1.7 mm long, 0.3–0.5 mm wide, otherwise as in the inflorescence bracts; pedicels cylindrical, 5.5–8.7 mm long, scattered to densely appressed furfuraceous lepidote, glabrescent with age, persistent. *Flowers* pendent, 5-merous, reddish-violet; calyx lobes almost free, chartaceous, suborbicular, 1.9–2.2 mm long, the lobes 1.2–1.5 mm long, 1–1.2 mm wide, asymmetric, apically rounded, subapically notched, conspicuously black punctate medially, sparsely furfuraceous lepidote, glabrescent, the margin irregular, somewhat erose, hyaline, densely glandular-cilioate, glabrescent; corolla lobes connate basally, membranaceous, lanceolate, 3.2–3.7 mm long, the lobes 2.3–2.5 mm long, 1.2–1.3 mm wide near the base, apically acute, reflexed in anthesis, conspicuously, black-punctate, the margin erose, hyaline, entire, glabrous; stamens 2.4–2.5 mm long; filaments connate into a chartaceous elobate tube, the tube 1.0–1.1 mm long, adnate to the corolla basally, epunctate, glabrous; anthers connate by their sutures, at least at first, ovate, 1.4–1.7 mm long, 0.7–0.9 mm wide at base, sessile on the staminal tube, apically apiculate, basally cordate, longitudinally dehiscent by narrow, sublatrose slits, the connective conspicuously reddish punctate; pistil obturbinate, 2.8–3.8 mm long; ovary 0.5–0.6 mm long, glabrous; style 2.3–3.2 mm long, erect, inconspicuously black punctate, glabrous; stigma punctiform; placenta ellipsoid, 0.1–0.3 mm long, 0.1–0.15 mm in diam., apically apiculate; ovules 6–9, pluriseriate. *Fruit* depressed-globose, 6–6.5 mm long, 6.5–7.5 mm in diam, inconspicuously black punctate, the style base persistent.

*Distribution*.—Alajuela and Guanacaste Provinces, Costa Rica, from 500–1,200 m elevation.

*Ecology and conservation status*.—*Hymenandra sordida* is a ridgetop species, known only from primary and mildly disturbed cloud forests, and should thus be considered threatened.

*Etymology*.—The epithet comes from the Latin word '*sordidus*', meaning dirty, soiled or ugly.

Specimens examined. **COSTA RICA**. Alajuela: Reserva Biológica Monteverde Río Peñas Blancas, Laguna Poco Sol, 10° 21' N, 84° 40' W, 500–800 m, 6 Aug 1989 (fl), *E. Bello C. 1059* (MO); San Carlos, San Miguel de San Isidro, 600 m, 29 Jun 1985 (fl), *W. Haber & E. Bello C. 1714* (MO); Peñas Blancas river valley NE of San Carlos, along road from Jabillos, 10° 22' N, 84° 38' W, 650 m, 29 Jun 1985 (fl), *B. Hammel et al. 14078* (MO); Cantón de Upala, Bijagua, Finca Montezuma, Ladera Sur de Cerro Montezuma, 10° 41' 10" N, 85° 03' 40" W, 600 m, 18 Jul 1993 (fl), *G. Herrera 6279* (F, K, MO); 15 km NW of Arenal by air, 2 km NW of Nuevo Arenal on road to Tilarán, then 3 km NE on road to San Rafael de Guatuso, then 2 km W on road to Finca Cote, 10° 34.5' N, 84° 54' W, 700 m, 30 Apr 1983 (fl), *R. Liesner et al. 15108* (MO); Near La Laguna, 6–8 km S of Villa Quesada, 1,200 m, 19 Feb 1966 (fr), *A. Molina R. et al. 17525* (F). **Guanacaste**: Parque Nacional Guanacaste, La Cruz, 9 km al S de Santa Cecilia Estación Pitilla, 10° 59' 26" N, 85° 25' 40" W, 700 m, 13 Sep 1990 (fl), *C. Chávez 71* (MO); Parque Nacional Guanacaste, Estación Pitilla y Sendero



El Mismo, 10° 59' 26" N, 85° 25' 40" W, 700 m, 15 Jun 1991 (fl, fr), *P. Ríos* 374 (INB, MO); Parque Nacional Guanacaste, Cordillera de Guanacaste, Estación Pitilla, Santa Cecilia, 9 km S, 10° 59' 00" N, 85° 25' 40" W, 700 m, 20 Aug 1993 (fl), *V. Ramírez et al.* 62 (BRIT, CR, INB, MO); N slopes of the Volcán Orosí along lower reaches of broad ridge running to the N, 650 m, 18 Jan 1968 (fr), *R. Wilbur & D. Stone* 9745 (LL).

*Hymenandra sordida* appears to be most closely related to *H. squamata* but may be immediately distinguished by the columnar shape of the panicle, and the larger sepals with merely erose (not erose-fimbriate) margins.

#### 4. *Hymenandra squamata* (Lundell) Pipoly & Ricketson, comb. nov. (Figs.

11, 5). *Auricularia squamata* Lundell, *Phytologia* 56:19. 1984. *Ardisia squamata* (Lundell) Lundell, *Phytologia* 61:67. 1986, nomen. invalidum. *Ardisia squamata* (Lundell) J.F. Morales, *Phytologia* 83:111. 1997 [1998]. TYPE. COSTA RICA. HEREDIA: Original forest near the Río Puerto Viejo, ca. 2 km upstream from the confluence with Río Sarapiquí, formerly "Finca La Selva" of L.R. Holdridge, 10° 26' N, 84° 00' W, 100 m, 14–17 Jun 1968 (fl), *W. Burger & R. Stolze* 5853 (HOLOTYPE: F; ISOTYPES: CR n.v., DUKE, F, LL, MO).

*Subshrubs* 0.2–1 m tall. *Trunk and vegetative shoots* terete, 3–5 mm in diam., densely appressed furfuraceous lepidote, glabrescent; *reproductive shoots* 1–2.5 mm diam., densely and minutely appressed furfuraceous lepidote, persistent. *Vegetative shoot leaf blades* membranaceous, elliptic, 7.4–22.4 cm long, (1.2–)3.5–6.9 cm wide, apically short to long-acuminate, the acumen 0.9–1.9 cm long, basally attenuate, midrib depressed above, prominently raised below, secondary veins 18–26 pairs, slightly depressed or not visible above, prominently raised below, densely appressed furfuraceous lepidote along and near the midrib below, appearing velutinous, glabrous above, the margin entire, inrolled; petioles marginate, 0.4–1.1 cm long, glabrous above, densely appressed furfuraceous lepidote below; *reproductive shoot leaf blades* similar to the vegetative ones but (3–)9.0–13.5 cm long, (0.9–)2.2–3.5 cm wide, the acumen 0.6–1.1 cm long, basally obtuse; petioles like those of the vegetative but 0.2–0.6 cm long. *Inflorescence* terminal, pinnately or bipinnately paniculate, 1.4–5.2 cm long, pyramidal, secondary branches 0.6–1.8 cm long, the rachis densely appressed furfuraceous lepidote, glabrescent, terminating in 5–14-flowered corymbs; inflorescence bracts early caducous, membranaceous, lanceolate, 5.7–8.1(–20.2) mm long, 2.4–3.9 mm wide, apically acute, sessile, midrib slightly raised above and below, secondary veins obscure to not visible above and below, scattered furfuraceous lepidote to mostly glabrous below, densely appressed furfuraceous lepidote below, the margins entire, ciliolate; floral bracts like the inflorescence ones but reduced in size, 0.9–2.4 mm long, 0.2–0.8 mm wide, apically subulate; pedicels cylindrical, 4.1–6.9 mm long, scattered, appressed furfuraceous lepidote, usually persistent with age, persistent. *Flowers* 5-merous, reddish-violet; calyx chartaceous, suborbicular, 2–2.2 mm long, the tube 1–1.1 mm long, the



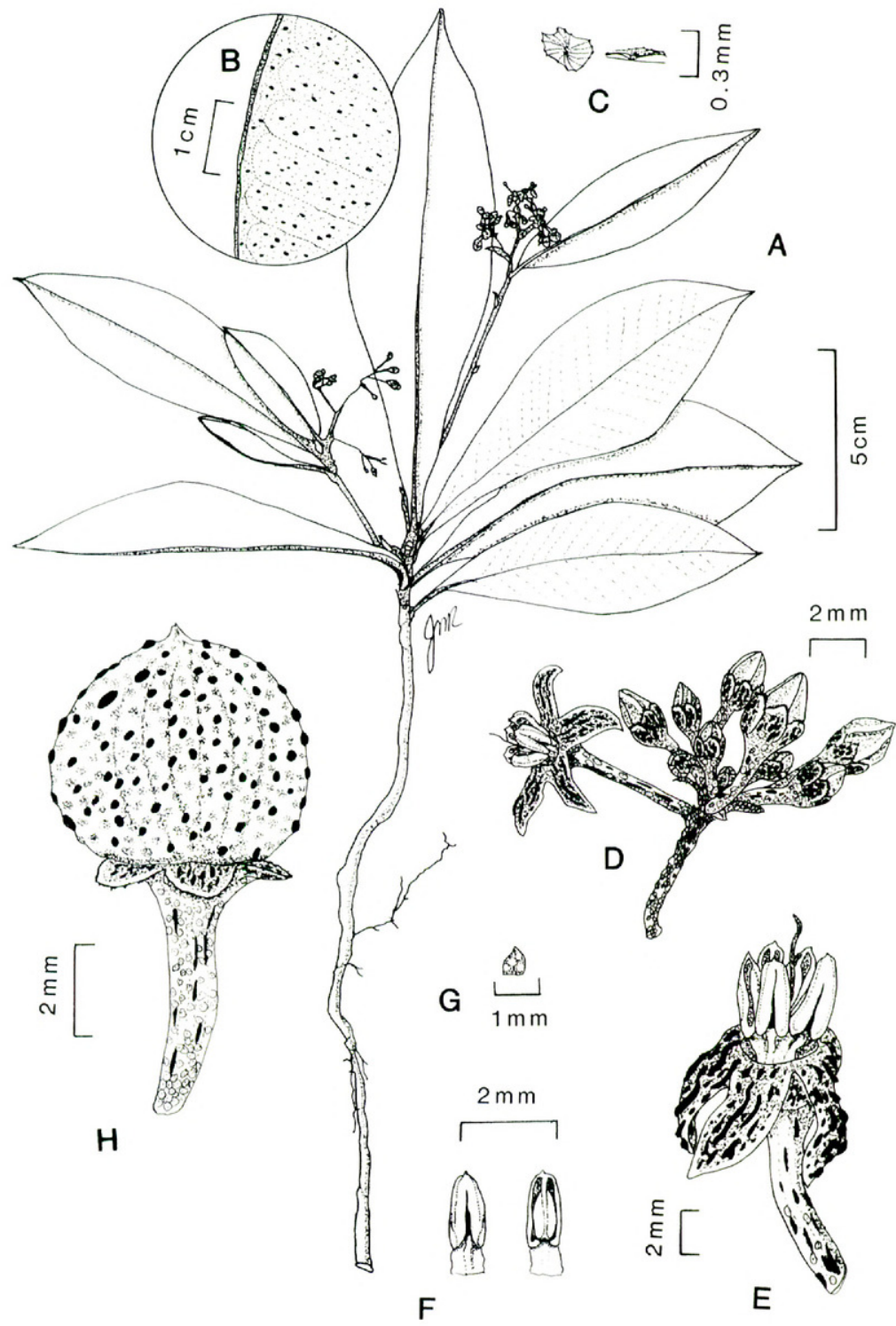


FIG. 5. *Hymenandra squamata* (Lundell) Pipoly & Ricketson. A. Reproductive shoot. B. Detail of abaxial leaf surface. C. Lepidote scale from above and from the side. D. Detail of inflorescence. E. Detail of flower. F. Detail of stamens, showing abaxial (left) and adaxial (right) surfaces. G. ovules. H. Fruit. A–G drawn from MO isotype, W. Burger & R. Stolze 5853. G drawn from M. Grayum & G. Herrera 7857.



lobes almost free 1–1.2 mm long, 0.9–1.1 mm wide, asymmetric, apically rounded, subapically notched, prominently black punctate medially, sparsely furfuraceous lepidote, glabrescent, the margin irregular, minutely erose-fimbriate, hyaline, densely glandular-cilioate; corolla membranaceous, 4.2–4.4 mm long, the tube 1–1.2 mm long, the lobes connate basally, lanceolate 3–3.2 mm long, 1.2–1.3 mm wide near the base, apically acute, reflexed in anthesis, prominently black punctate, the margin erose, hyaline, glabrous; stamens 2.6–3 mm long; the filaments connate into a chartaceous elobate tube, the tube 1–1.2 mm long, adnate to the corolla basally, epunctate, glabrous; anthers connate by their sutures, at least at first, ovate, 1.6–1.8 mm long, 0.8–0.9 mm wide at base, sessile on the staminal tube, apically apiculate, basally cordate, longitudinally dehiscent by narrow, sublatrorse slits, the connective prominently reddish punctate; pistil obturbinate, 2.1–3.4 mm long; ovary 0.5–0.7 mm long, glabrous; style (1.6–)2.5–2.7 mm long, erect, inconspicuously black punctate, glabrous; stigma punctiform; placenta ellipsoid, 0.1–0.3 mm long, 0.1–0.15 mm in diam., apically apiculate; ovules 7–10, pluriseriate. *Fruit* depressed-globose, 4.5–6 mm long, 5.5–6.8 mm in diam., conspicuously black punctate, the style base persistent.

*Distribution*.—Provinces of Heredia, Limón and San José, Costa Rica, at 90–1,400 m elevation.

*Ecology and conservation status*.—*Hymenandra squamata* is known only from the swamp forests of the Atlantic drainage in Costa Rica. It occurs just above the high water level. Because these forests yield high volumes of timber, the species should be considered under threat.

*Etymology*.—The epithet comes from the Latin "*squamatus*" which means "provided with scales," referring to the scales of the shoots and leaf blades.

Specimens examined. **COSTA RICA**. Heredia: Between Río Peje and Río Sardinalito, Atlantic slope of Volcán Barva, 10° 17' N, 84° 04.5' W, 800–1,000 m, 7 Apr 1986 (fr), M. Grayum & R. Chazdón 6853 (MO); Finca La Selva, the OTS Field Station on the Río Puerto Viejo just E of its junction with the Río Sarapaquí, along E River Road near Holdridge Trail, ca. 100 m, 15 May 1978 (fl), M. Grayum 1303 (DUKE); Finca la Selva, Puerto Viejo de Sarapiquí, along Quebrada El Taconazo, Between Quebrada El Sura and W boundary Trail, without elev., 15 Aug 1979 (fr), M. Grayum 2371 (DUKE); Parque Nacional Braulio Carrillo, 10° 15.5' N, 84° 05' W, 1,200–1,400 m, 13 Nov 1986 (fr), M. Grayum & G. Herrera 7857 (MO); Finca la Selva, Puerto Viejo de Sarapaquí along Quebrada El Santo, Hartshorn Trail, ca. 100 m, 17 May 1980 (fl), B. Hammel 8693 (DUKE), 22 May 1980 (fl), B. Hammel 8762 (DUKE); La Selva, on Río Puerto Viejo just E of its junction with Río Sarapaquí, Central Trail, 1,500 m S of edge of Trail, 100 m, 7 Jul 1981 (fr), B. Hammel 10962 (DUKE); La Selva, just E of junction of Río Puerto Viejo and Río Sarapiquí, ca. 100 m, 20 May 1982 (fl), B. Hammel 12372 (DUKE, LL), 7 Jun 1982 (fl), B. Hammel & J. Trainer 12757 (DUKE, LL); Finca La Selva, El Swampo, 600 m, 16 Jun 1984 (fl), B. Jacobs 2377 (DUKE); La Selva, Sendero El Peje, ca. 2,800 m line E-W, ca. 100 m, 18 May 1985 (fl), B. Jacobs 3113 (DUKE); 9 km SE of San Ramón, 10° 16' N, 84° 05' W, 1,000 m, Sep 1985 (fr), B. Loiselle 144 (MO); La Selva, near Puerto Viejo, along line B, 90 m, 29 May 1971



(fl), *P. Opler* 188 (F), along line A, 4 Aug 1971 (ster.), *P. Opler* 332 (F); Finca la Selva, Puerto Viejo, 1,600 Line Trail, without elev., 6 Jul 1979 (fr), *J. Sperry* 790 (DUKE); Finca La Selva, Río Puerto Viejo just E of its junction with the Río Sarapiquí, S Research Trail, 19 May 1984 (fl), *R. Wilbur & B. Jacobs* 34720 (DUKE), along S bounday of new property from the SE corner to the Sarapiquí Trail at about 4,000 m on grid system, ca. 100 m, 19 May 1984 (fl), *R. Wilbur & B. Jacobs* 34747 (DUKE); La Selva, Jaguar Trail from Quebrada El Sura to the 3,000 m line, ca. 100 m, 14 Jul 1986 (fl, fr), *R. Wilbur* 39948 (DUKE); La Selva, S Experimental Trail at the 700 m point on line; 100 m, 25 Jul 1986 (fr), *R. Wilbur* 40442 (DUKE); La Selva, slopes just arising out of the swamp at about 200 m on the El Swampo Trail, ca. 100 m, 29 May 1995 (fl, fr), *R. Wilbur* 64246 (DUKE). **Limón:** Siquirres, Las Brisas de Pacuarito, 500 m, 17 Abr 1985 (fl), *L. Gómez et al.* 23383 (BRIT, NY); Ridge E of Río Pacuare, ca. 15 km S of Pacuarito, in vicinity of community of Las Brisas, 10° 00' N, 83° 30' W, 200–500 m, 27 Jun 1988 (fl), *B. Hammel & M. Chavarría* 17073 (MO). **San José:** Parque Nacional Braulio Carrillo, Carrillo station, 300–600 m, 31 May–5 Jun 1980 (fl), *C. Todzia* 1302 (TEX).

*Hymenandra squamata* is very closely related to *H. sordida*, but easily separated from it by the smaller, minutely erose-fimbriate calyx lobes, the pyramidal panicle and the dense furfuraceous lepidote tomentum, appearing velutinous.

##### 5. *Hymenandra wilburiana* (Lundell) Pipoly & Ricketson, comb. nov. (Figs.

1D, 6). *Auriculardisia wilburiana* Lundell, Phytologia 63:76. 1987. *Ardisia wilburiana* (Lundell) Lundell, Phytologia 63:463. 1987. TYPE. COSTA RICA. HEREDIA: Finca La Selva, the OTS Field Station on the Río Puerto Viejo just E of junction with the Río Sarapiquí, Paso Perdido Trail, ca. 3,200 m line (EW), ca. 100 m, 16 Jul 1984 (fl), *B. Jacobs* 2917 (HOLOTYPE: LL; ISOTYPES: DUKE, MO).

*Auriculardisia sarapiquiensis* Lundell, Phytologia 63:74. 1987, SYN. NOV. *Ardisia sarapiquiensis* (Lundell) Lundell, Phytologia 63:463. 1987. TYPE. COSTA RICA. HEREDIA: Finca La Selva, the OTS Field Station on the Río Puerto Viejo just E of its junction with the Río Sarapiquí, in forest on ridge at SW corner of new property, ca. 100 m, 20 Jul 1982 (fl), *B. Hammel & J. Trainer* 13262 (HOLOTYPE: LL; ISOTYPE: DUKE).

*Tree* 1–7 m tall, trunk to 3 cm in diam. *Vegetative shoots* terete, 4–6 mm in diam., minutely scattered furfuraceous lepidote below, densely furfuraceous apically at least when young; *reproductive shoots* similar to vegetative ones but 1.5–3.5 mm in diam. *Vegetative shoot leaf blades* coriaceous, elliptic to oblong, 5.5–22.2 cm long, 1.3–7.8 cm wide, apically acuminate, the acumen 2–3 cm long, basally acute, midrib slightly raised above, prominently raised below, the secondary veins 11–19 pairs, slightly depressed or not visible above, prominently raised below, minutely scattered furfuraceous lepidote along the midrib below and on the blade below, glabrescent with age, the margin entire, flat; petioles marginate, 0.5–2.2 cm long, glabrous above, scattered and minutely furfuraceous lepidote below; *reproductive shoot leaf blades* as in the vegetative except 7.2–17.3 cm long, 2.1–4.7 cm wide, secondary veins 9–15 pairs; petioles as in vegetative ones but 0.3–1.3 cm long. *Inflorescence* terminal, pendent, pinnately or bipinnately paniculate, 7–16.5 cm long, pyramidal, secondary branches 4–6.5 cm long, the rachis





FIG. 6. *Hymenandra wilburiana* (Lundell) Pipoly & Ricketson. A. Reproductive shoot. B. Detail of abaxial leaf surface. C. Detail of inflorescence. D. Detail of flower. E. Detail of stamens, showing adaxial (left) surfaces. F. Detail of stamens, showing abaxial (right) surfaces. G. Detail of flower, showing sepal and pistil. H. Ovules. I. Fruit. A–B drawn from holotype, B. Jacobs 2917. C–H drawn from holotype of *Auriculardisia sarapiquiensis* Lundell, B. Hammel & J. Trainer 13262. I drawn from R. Robles 1571.



minutely scattered furfuraceous lepidote, glabrescent, terminating in 6–12-flowered corymbs; inflorescence and floral bracts unknown (presumably early caducous); pedicels cylindrical, 6.8–13.2 mm long, scattered furfuraceous lepidote, persistent. *Flowers* 5-merous, white; calyx lobes essentially free, chartaceous, suborbicular, 1.4–1.8 mm long, 1.6–2 mm wide, asymmetric, notched below the apex, apically obtuse, prominently black punctate medially, sparsely furfuraceous lepidote, the margin irregular, minutely erose, hyaline, densely glandular-cilioate; corolla lobes basally free, membranaceous, lanceolate, 5.5–6.5 mm long, 1.4–1.6 mm wide near the base, apically acute, reflexed in anthesis, prominently pellucid punctate without, sparsely so medially within, the margin erose, hyaline, glabrous; stamens 6–6.5 mm long; filaments connate into a chartaceous elobate tube, the tube 1.4–1.9 mm long, adnate to the corolla basally, epunctate, glabrous; anthers connate by their sutures, at least at first, lanceolate, 5.5–5.8 mm long, 1.9–2.2 mm wide at base, sessile on the staminal tube, apically apiculate, basally cordate, longitudinally dehiscent by narrow, sublatrose slits, the connective conspicuously brown or pellucid punctate; pistil obturbinate, 5.7–6.5 mm long; ovary 1.5–1.8 mm long, glabrous; style 4.2–4.7 mm long, erect, inconspicuously pellucid punctate, glabrous; stigma punctiform; placenta ellipsoid, 0.4–0.5 mm long, 0.2–0.3 mm in diam., apically apiculate; ovules 16–20, pluriseriate. *Fruit* subglobose, 7–8 mm long, 6–6.5 mm in diam., at times with noticeable longitudinal costae, densely and prominently punctate, the style base persistent.

*Distribution.*—Río San Juan, Nicaragua to Heredia and Limón, Costa Rica, from 0–700 m elevation.

*Ecology and conservation status.*—*Hymenandra wilburiana* is a ridgetop species in the lowland to premontane wet forest transition areas. It has a rather restricted distribution, but not enough is known of its population dynamics to determine its conservation status.

*Etymology.*—The species is named for Dr. Robert L. Wilbur, professor of botany at Duke University, expert in Mesoamerican Ericaceae and long-time student of the flora of the La Selva OTS station in Costa Rica.

Specimens examined. **NICARAGUA.** Río San Juan: Near Caño Chontaeno, 20 km NE of El Castillo, 200 m, 18–21 Apr 1978 (fr), *D. Neill & P. Vincelli* 3506 (MO, NY). **COSTA RICA.** Heredia: Sarapiquí Cantón, trail between Canta Rana Camp and Río Peje, Magsasay, 400 m, 14 Jan 1983 (fr), *I. Chacón* 80 (MO); Finca la Selva, on Río Puerto Viejo just E of its junction with Río Sarapiquí. Fila Río Peje, along the line at 3,600–2,200 m, 100 m, 21–22 Apr 1983 (fr), *I. Chacón* 717 (DUKE); N of Puerto Viejo, 10 km down road, then 7–8 km W, without elev., 2 Feb 1983 (fr), *N. Garwood et al.* 936 (MO); Finca El Bejuco, S base of Cerros Sardinal, Chilamate de Sarapiquí, 10° 27' N, 84° 04' W, 70–100 m, 2 Jun 1985 (fr), *M. Grayum & B. Jacobs* 5352 (BRIT, LL, MO); Sarapiquí Cantón, Parque Nacional Braulio Carrillo, Estación Magsasay, 10° 23' 03" N, 84° 03' 00" W, 200 m, *B. Hammel et al.* 17829 (BRIT, F, MO); Finca La Selva, Sendero El Peje, 3,200 m–1,600 m on line along



ridge, ca. 100 m, 28 May 1985 (fr), *B. Jacobs* 3189 (DUKE); Sarapiquí Cantón, Horquetas, Estación El Plástico, 15 km de Horquetas, Sendero el Tigre, 10° 17' 03" N, 84° 02' 47" W, 700 m, 11 Jan 1994 (fr), *J. Sánchez et al.* 308 (F, K); Sarapiquí Cantón, Zona Protectora La Selva, 6 km by road from Río Peje crossing, 5 km SSE of Magsasay, E from basecamp to ridge above Río Peje, then S, 10° 21' N, 84° 03–04' W, 300–500 m, 14 Jan 1983 (fr), *G. Schatz & M. Grayum* 599 (DUKE); 500 m, 19 Jan 1983 (fr), *G. Schatz & M. Grayum* 653 (DUKE, LL). Limón: SW-most ridge of Cerro Coronel, NW-facing slope, just S of the Río Colorado, 10° 40' N, 83° 39' 30" W, 10–80 m, 17–18 Sep 1986 (fl), *G. Davidse & G. Herrera* 31379 (MO); Parque Nacional Tortuguero, Estación Agua Fría, ca. 7 km al SE Cerro Azules, 10° 27' N, 83° 34' W, 70 m, 21 Jan 1988 (fr), *R. Robles* 1571 (MO, US); Parque Nacional Tortuguero, Estación Agua Fría, ca. 12 km al NE, on other side of Río Pueblo Nuevo, over the Lomas de Sierpe, 10° 26' N, 83° 32' W, 80–100 m, 2 Mar 1988 (fr), *R. Robles* 1666 (MO); Cerro Coronel, E of Río Zapote, 10° 40' N, 83° 40' W, 10–100 m, 24 Jan 1986 (fr), *W. Stevens* 23977 (MO); Cerro Coronel, E of Laguna Danto, 10° 41' N, 83° 38' W, 20–170 m, 15–20 Sep 1986 (fl), *W. Stevens & O. Montiel* 24432 (MO); Cerro Coronel, along ridge from E of Laguna Danto SW toward hills E of Río Zapote, 10° 40–41' N, 83° 38–39' W, 30–170 m, 17 Mar 1987 (fr), *W. Stevens et al.* 24972 (MO).

*Hymenandra wilburiana* is most closely related to *H. pittieri* but may be distinguished by the much shorter perianth and androecial parts, smaller leaves and much thinner stems.

Populations corresponding to the type of *Auriculardisia sarapiquiensis* are notable only for their slightly smaller inflorescence and slightly smaller leaves. The types of *Hymenandra wilburiana* and *Auriculardisia sarapiquiensis* were both collected at the Finca La Selva OTS Station.

**6. *Hymenandra pittieri* (Mez) Pipoly & Ricketson, comb. nov. (Figs. 1C, 7).** *Ardisia pittieri* Mez, Bull. Herb. Boissier, Ser. 2, 3:236. 1903. *Auriculardisia pittieri* (Mez) Lundell, Phytologia 49:345. 1981. TYPE. COSTA RICA. CARTAGO: Las Vueltas, Tucurrique, 635–700 m, May 1899 (fr), *A. Tonduz* 13369 (LECTOTYPE here designated: US (US # 1339917, LL Neg. # 1971-83); ISOLECTOTYPES: G 4-sheets, P 4-sheets, US (US # 1339916, LL Neg. # 1971-83)).

*Ardisia cutteri* Standl., J. Wash. Acad. Sci. 17:52. 1927, SYN. NOV. *Auriculardisia cutteri* (Standl.) Lundell, Wrightia 7:267. 1984. TYPE. COSTA RICA. CARTAGO: vicinity of Pejivalle, ca. 900 m, 7 Feb 1926 (fr), *P. Standley & J. Valerio* 47122 (HOLOTYPE: US, (US Neg. # 2368, LL Neg. # 1971-31)).

*Ardisia coclensis* Lundell, Ann. Missouri Bot. Gard. 28:453. 1941, SYN. NOV. *Auriculardisia coclensis* (Lundell) Lundell, Phytologia 49:343. 1981. TYPE. PANAMA. COCLÉ: vicinity of El Valle de Antón, ca. 600 m, without date (fl), *P. Allen* 2056 (HOLOTYPE: MICH, (LL Neg. # 1971-4)). [Ulicate].

*Tree* (0.9–)2–5(–8) m tall, 2–8 cm in diam. *Vegetative shoots* terete, 7–24 mm in diam., minutely scattered furfuraceous lepidote, glabrescent; *reproductive shoots* as in the vegetative but 2–9 mm in diam. *Vegetative shoot leaf blades* coriaceous, obovate to oblanceolate, 33.7–72.2 cm long, 5.3–16.5 cm wide, apically acute to rounded, gradually tapering to a cuneate base, decurrent to near the petiole base, midrib slightly raised above, prominently raised below, secondary veins 24–41 pairs, prominently raised above and



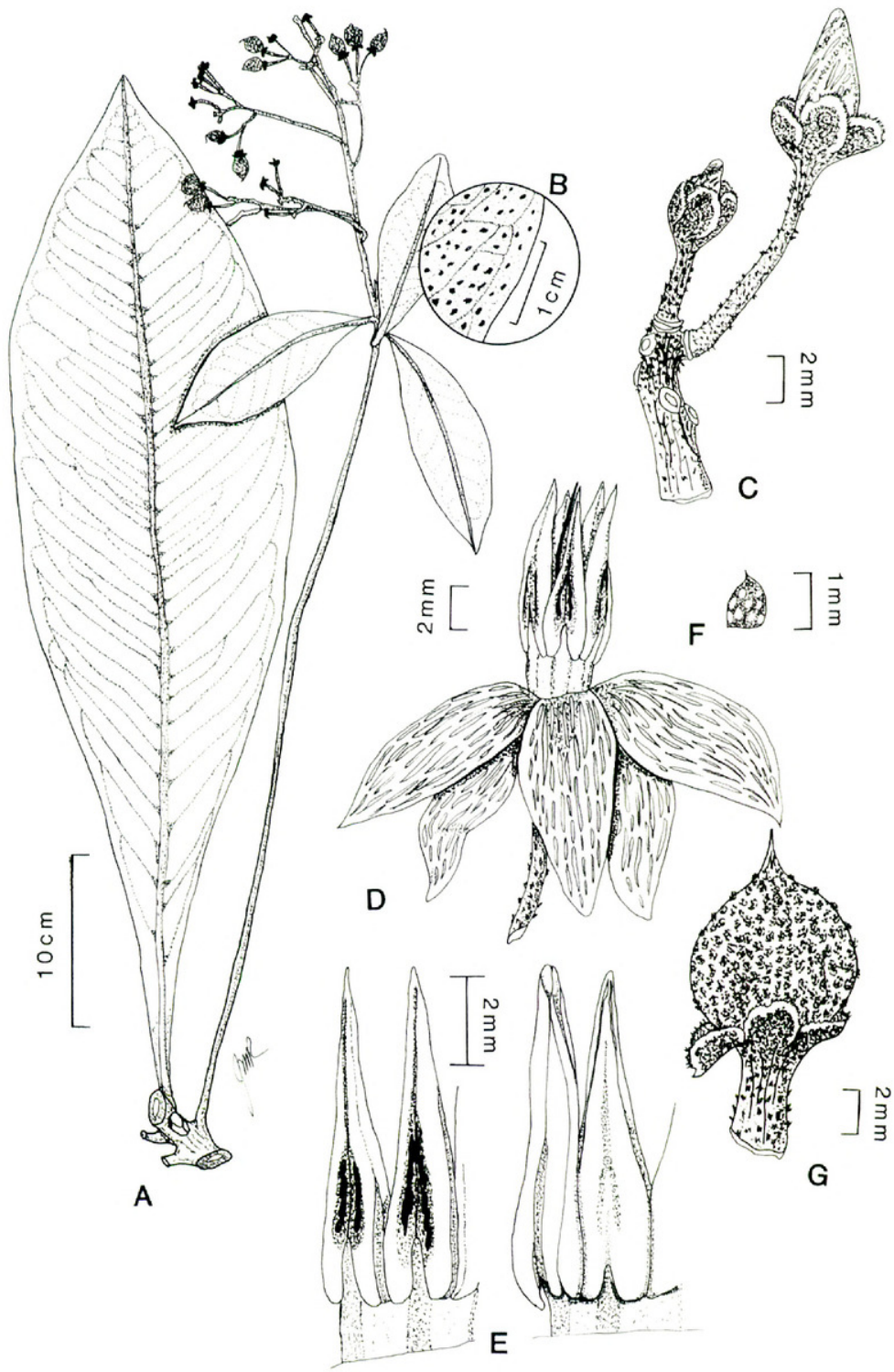


FIG. 7. *Hymenandra pittieri* (Mez) Pipoly & Ricketson. A. Reproductive shoot. B. Detail of abaxial leaf surface. C. Detail of inflorescence. D. Detail of flower. E. Detail of stamen, showing abaxial (left) and adaxial (right) surface. F. Ovules. G. Fruit. A–B drawn from G. de Nevers 7203. C, F–G drawn from P lectotype, A. Tonduz 13369. D–E drawn from J. Morales & Y. Salazar 1195.



below, prominently punctate above and below, glabrous above, minutely scattered furfuraceous lepidote below, glabrescent, the margin regular, entire, flat; petioles marginate 1.8–4.7 cm long, glabrous above, minutely scattered furfuraceous-lepidote below; *reproductive shoot leaf blades* similar to the vegetative but 3.9–34.3 cm long, 1.2–11.8 cm wide, secondary veins 20–36 pairs, basally tapering to a rounded base appearing auriculate; petioles similar to the vegetative ones but 0.4–1.1 cm long. *Inflorescence* subterminal, pinnately or bipinnately paniculate, (7–)12–30(–36) cm long, pyramidal, secondary branches 3.5–12.5 cm long, the rachis densely and minutely furfuraceous tomentose, terminating in 8–13-flowered corymbs; inflorescence bracts early caducous, membranaceous, oblong, 7–13.5 mm long, 3.4–4.6 mm wide, apically acute to rounded, basally sessile, midrib slightly raised above and below, secondary veins not visible, prominently punctate, densely and minutely furfuraceous tomentose, the margin entire, flat; floral bracts 1.7–2.8 mm long, 1.1–2.1 mm wide, otherwise as in the inflorescences bracts; pedicels cylindrical, 7.5–14 mm long, densely and minutely furfuraceous tomentose. *Flowers* 5-merous, pink; calyx lobes almost free, chartaceous, suborbicular, 2.2–2.8 mm long, 2–2.4 mm wide, asymmetrical, subapically notched, apically obtuse to broadly rounded, prominently punctate, densely and minutely furfuraceous tomentose, the margin, irregular, minutely erose, hyaline, sparsely glandular-ciliolate; corolla lobes basally free, chartaceous, ovate to lanceolate, 9–10.5 mm long, 4–4.7 mm wide, apically acute, reflexed in anthesis, prominently pellucid punctate on both surfaces, the margin hyaline, entire, glabrous; stamens 8.7–9.5 mm long; filaments connate into a coriaceous elobate tube, the tube 1.2–1.5 mm long, free from the corolla basally, epunctate, glabrous; anthers connate by their sutures, at least at first, lanceolate, 7.5–8 mm long, 1.4–1.7 mm wide at base, sessile on the staminal tube, apically acute, at times with a minute emarginate tip, basally cordate, longitudinally dehiscent by narrow, sublatrose slits, the connective inconspicuously pellucid to black punctate; pistil 6.8–8.4 mm long; ovary 1.8–2.2 mm long, glabrous; style 5–6.2 mm long, erect, inconspicuously punctate, glabrous; stigma punctiform; placenta ellipsoid, 0.9–1.1 mm long, 0.8–0.9 mm in diam., apically apiculate; ovules 14–16, pluriseriate. *Fruit* globose, 0.7–1.6 cm in diam., densely and prominently black punctate, the style base persistent, the exocarp thick, juicy, bright red.

*Distribution*.—Limón, Cartago, San José and Puntarenas, Costa Rica and Coclé, Colon and San Blas, Panama, from 50–1,300 m elevation.

*Ecology and conservation status*.—*Hymenandra pittieri* is an understory tree along ridgetops in lowland and premontane wet forest. Throughout its range, this species is locally common and is not threatened at this time.

*Etymology*.—This species is named for Dr. Henri Pittier, early explorer in



Central America but also known for his work in South America and particularly, for establishing the Herbario Nacional de Venezuela.

Specimens examined. **COSTA RICA.** Cartago: Along Camino Raíz de Hule, SE of Platanillo (Tsipirí), 1,200–1,400 m, 1 Jul 1976 (fl), *T. Croat* 36703 (LL, MO); 24 km NE of Turrialba on hwy. to Limón, then E at Tres Equis on jeep road 1.5 km, 09° 58' N, 83° 34' W, 450–525 m, 10 May 1983 (fl), *R. Liesner et al.* 15348 (MO); Pavones, Turrialba, 650 m, 18 May 1972 (fl), *L. Poveda* 106 (MO). **Limón:** Near the Río Catarata (Río Sand Box) in the hills between Bri Bri on the Río Sixaola and the Caribbean coastal plain, 09° 37' N, 82° 49' W, 50–100 m, 28–29 Nov 1975 (fr), *R. Baker & W. Burger* 126 (F). **Puntarenas:** Cantón de Osa, Refugio Nacional Golfo Dulce, Península de Osa, Bahía Chal, entrance to Chocuaco, 08° 43' 00" N, 83° 34' 50" W, 200–350 m, 2 Nov 1994 (fr), *R. Aguilar et al.* 3663 (MO); Region between Río Esquinas & Palmar Sur de Osa, sea level, 30 Jan 1951 (fr), *P. Allen* 5828 (F), 75 m, 2 Feb 1951 (fr), *P. Allen* 5828A [sic] (F), 60 m, 18 Feb 1953 (fl), *P. Allen* 6726 (F); Cantón de Coto Brus, P.I. La Amistad, Cordillera de Talamanca, Las Cruces, 08° 47' 20" N, 82° 58' 30" W, 1,200–1,300 m, 30 Jun 1995 (fr), *L. Angulo* 394 (MO); Forested slopes E of Las Cruces and 5–6 km S of San Vito on and around the property of Mr. Robert Wilson, 8° 47' N, 82° 58' W, 1,100–1,200 m, 15–16 Jan 1967 (fr), *W. Burger & G. Matta* U. 4406 (F); Original forest ca. 10 km SE of Palmar Norte along the Interamerican Hwy., to Panama, 08° 54' N, 83° 02' W, 20 m, 26 Jan 1967 (fl), *W. Burger & G. Matta* U. 4644 (F, G); Cantón de Osa, Rincón, Fila Casa Loma, 08° 43' N, 83° 32' W, 50–400 m, 22 Jul 1990 (fr), *A. Chacón* 934 (MO); Quebradas Pastora, Arepa y Pintadora, Fila Esquinas-Osa, without elev., Nov 1983 (fr), *I. Chacón & G. Herrera* 1758 (MO); Along Río Jaba S of San Vito de Coto Brus, 08° 47' N, 82° 58' W, 1,150 m, 1 Jul 1984 (fr), *M. Grayum et al.* 3369 (MO); Refugio Nacional Golfito, both slopes of Fila Gamba and along crest of same, to ca. 0.7 km N of Golfito-Villa Briceno road, 08° 40.5' N, 83° 12' W, 160–260 m, 11 Dec 1988 (fr), *M. Grayum & G. Herrera* 9200 (MO); Palmar Norte to Chacarita, along Interamerican Hwy., ca. 2 km N of Chacarita, 08° 48' N, 83° 18' W, 50 m, 25 May 1986 (fr), *B. Hammel et al.* 15186 (MO); Alto La Palmera, Carretera Panamericana, 950 m, 28 Feb 1966 (fr), *A. Jiménez* (DUKE, F); Cantón de Osa, Rancho Quemado, sector E, Sierpe, 08° 40' 20" N, 83° 35' 15" W, 500 m, 6 Nov 1991 (fr), *J. Marín et al.* 257 (MO); Finca las Cruces, along road to stream below OTS field station, without elev., 10 May 1973 (fl), *B. McAlpin* 2250 (DUKE); Cantón de Osa, Camino a la toma de agua, Rancho Quemado Rincón, 08° 42' N, 83° 34' W, 200 m, 9 Dec 1990 (fr), *F. Quesada* 320 (MO); Wilson's finca, 6 km S of San Vito de Java, 4,000 ft [1,219 m], 16 Aug 1967 (fr), *P. Raven* 21829 (F 2-sheets, MO); Golfito, Parque Nacional Esquinas, margins of Quebrada Gamba, 08° 40' 30" N, 83° 12' 20" W, 70 m, 29 Sep 1995 (fr), *J. Sánchez* 565 (CR, F). **San José:** Cantón de Pérez Zeledón, Tinamaste, Swiss farm, 09° 17' 40" N, 83° 46' 00" W, 1,000 m, 12 Jun 1997 (fr), *D. Argüello M. et al.* 11 (CR, F, MO, NY); Valley of the Río Hondura, below La Palma, NE of San Jeronimo, 10° 3' N, 83° 58' W, 1,000 m, 15 May 1968 (fl), *W. Burger & R. Stolze* 3738 (F, MO); El General Valley, vicinity of San Isidro El General, Alto San Juan, road to Dominical, 900 m, 28 Feb 1966 (fl, fr), *A. Molina R. et al.* 18090 (F 2-sheets, NY, US); Z.P. La Cangreja, Santa Rosa de Puriscal, faldas de la Fila La Cangreja, 09° 42' 28" N, 84° 23' 38" W, 500 m, 8 Mar 1993 (fl), *J. Morales & Y. Salazar* 1195 (MO); Cantón de Acosta, Fila Bustamante, by Fila San Jerónimo, headwaters of Quebrada Colorado, 09° 43' 20" N, 84° 16' 45" W, 1,040 m, 29 May 1994 (fr), *J. Morales & V. Ureña* 2852 (INB-2 sheets, MO 2-sheets); Cantón de Amadrib, Fila Bustamante, Zoncuano, falda Sur de Fila Zoncuano, ca. del Río Parritilla, 09° 42' 02" N, 84° 13' 37" W, 700–900 m, 4 Jun 1995 (fr), *J. Morales* 4354 (MO); Zapatón de Puriscal, 400 m, 1 Aug 1986 (fr), *N. Zamora & Q. Jiménez* 1268 (MO). **PANAMA.** Coclé: Hills N of El Valle de Antón, 1,000 m, 23 Jun 1940 (fr), *P.*



*Allen* 2176 (F); Loma del Tigre, region N of El Valle de Antón, 1,000 m, 16 Nov 1946 (fl), *P. Allen* 3806 (G, MO, NY); 7 km from Llano Grande on road to Coclesito near continental divide, 1,200 ft [366 m], Jul 1979 (fr), *T. Antonio* 1364 (MO); On the Atlantic side, ca. 5 hr. walk from sawmill at El Cope, along slopes above Norte Río Blanco near small village of Caño Sucio, 400–500 ft [122–152 m], 2 Feb 1980 (fr), *T. Antonio* 3627 (LL, MO), 3632 (MO); Area of El Valle, 2 km E of La Mesa, N slope of Cerro Gaital, 08° 38' N, 80° 07' W, 800 m, 16 Nov 1983 (fr), *H. Churchill* 3867 (LL, MO, NY); 3876 (MO); Near continental divide along lumber road ca. 1.5 mi N of El Cope, ca. 900 m, 19 Jan 1978 (fr), *T. Croat* 44581 (BRIT, MO); Hills above El Valle de Antón, without elev., 13 Aug 1972 (fr), *W. D'Arcy & J. D'Arcy* 6749 (MO); Road from Penonome to Coclesito, 9 km N of Llano Grande, on tributary on Río Caseaja, without elev., 11 Oct 1978 (fr), *W. D'Arcy & B. Hammel* 12292 (LL, MO); Area between Caño Blanco del Norte, Caño Sucio and Chorro del Río Tife, 08° 43' 06" N, 80° 36' 30"–38' 00" W, 200–400 m, 3 Feb 1983 (fr), *G. Davidse & C. Hamilton* 23484 (MO); Hills N of El Valle de Antón, ca. 800 m, 17 Jan 1973 (fl, fr), *R. Dressler* 4254 (MO); Near Aserradero El Copé, N of El Copé, E of sawmill, 700–800 m, 2 Nov 1980 (fl, fr), *R. Dressler* 5962 (FLAS 2-sheets, MO); Slopes of Cerro Pilón near El Valle, 700–900 m, 10 Jun 1967 (fr), *J. Duke* 12197 (MO); Summit of Cerro Pilón, above El Valle de Antón, 2,700 ft [823 m], 28 Mar 1969 (fr), *J. Dwyer et al.* 4476 (LL, MO); Cerro Pilón, bottom of slope, ca. 2,500 ft [762 m], 19 Jan 1968 (fr), *J. Dwyer* 8351 (MO), 13 Jul 1968 (fr), *J. Dwyer & B. Lallathin* 8690 (F, MO), 14 Jul 1968 (ster.), 8690A (MO); Adjacent to chicken farm, La Mesa, above El Valle, without elev., 3 Jan 1974 (fr), *J. Dwyer* 11869 (MO); 7 km N of el Copa de Veraguas, near Rivera sawmill, Alto Calvario, 900–1,300 m, 11 Jan 1977 (fl), *J. Folsom* 1242 (BRIT, LL, MO); New Works at Rivera sawmill, Alto Calvario, 600–800 m, 12 May 1977 (fr), *J. Folsom* 3163 (MO); Area around Rivera sawmill, 7 km N of El Cope, Atlantic slope, N side of summit, Alto Calvario, 700–850 m, 3 Oct 1977 (fr), *J. Folsom et al.* 5741 (MO); Vicinity of La Mesa, N of El Valle, 1,000 m, 23 Dec 1972 (fr), *A. Gentry* 6854 (LL); Hills above El Valle, ca. 1,000 m, 24 Dec 1972 (fl), *A. Gentry* 6872 (LL, MO); Near continental divide along lumber road, 8.4 km above El Cope, 1 km beyond sawmill, 900 m, 19 Jan 1978 (fr), *B. Hammel* 958 (LL, MO); 7 km N of Llano Grande on road to Coclesito, 1,700 ft [518 m], 8 Mar 1978 (fr), *B. Hammel* 1928 (MO); La Mesa region N of Cerro Gaital vicinity of El Valle, 2,400 ft [732 m], 2 Jul 1978 (fr), *B. Hammel* 3898 (MO); Continental divide N of Penonome on road to Coclesito, 1,600 ft [488 m], 25–26 Jul 1978 (fr), *B. Hammel* 4054 (MO); S of Cascajal along Continental Divide, 8° 45' N, 80° 25' W, 800–900 m, 7 Nov 1981 (fr), *S. Knapp* 1965 (MO); Cerro Pilón, 2,700 ft [823 m], Jul 1968 (fr), *B. Lallathin* 35A (MO); Along road ca. 8 mi N of El Valle de Antón, without elev., 3 Aug 1970 (fr), *J. Luteyn & H. Kennedy* 1704 (DUKE, GH, LL, MO); Vicinity of la Mesa, beyond El Valle, N slopes of Cerro Gaital, 8° 37' N, 80° 07' W, 850 m, 14 Jul 1987 (fr), *G. McPherson* 11270 (MO); Ca. 3 km NE of El Valle, along farmers road, without elev., 2 Nov 1974 (fl, fr), *S. Mori & J. Kallunki* 2978 (LL, MO); Continental Divide above El Copé, 8° 38' N, 80° 39' W, 650–750 m, 27 Nov 1985 (fl), *G. de Nevers et al.* 6398 (LL, MO); Foot of Cerro Pilón, above El Valle de Antón, 2,000 ft [610 m], 27 Mar 1969 (fr), *D. Porter et al.* 4422 (MO), 28 Mar 1969 (fr), *D. Porter et al.* 4597 (LL, MO); La Mesa, 2 km NW of Cerro Pilón, 800 m, 22 Jul 1976 (fr), *G. Sullivan* 553 (MO); Between Río Blanco and Caña Susio 1 hr. hike to the W, Río Blanco is ca. 5 hr. hike N down from Continental Divide above El Copé and El Petroso sawmill, 8° 38' N, 80° 36' W, 350–400 ft [107–122 m], 13 Dec 1980 (fr), *K. Sytsma et al.* 2453 (LL, MO); Ca. 1 km E of Quebrada Amarillo in La Mesa, 2.5 km N of El Valle, 8° 37' N, 80° 07' W, 2,600 ft [792 m], 14 Feb 1981 (fr), *K. Sytsma & W. D'Arcy* 3565 (LL, MO). Colón: Santa Rita lumber road, ca. 15 km E of Colón, without elev., 5 Oct 1969 (fl, fr), *R. Dressler & W. Lewis* 3725 (LL, MO); Santa Rita Ridge, logging area 19 km in from Transisthmian Hwy., with-



out elev., 28 Jan 1968 (fr), *J. Dwyer* 8551 (F, MO); Río Escandaloso near the abandoned Manganese mine, 500 ft [152 m], 26 Apr 1978 (fr), *B. Hammel* 2662 (LL, MO); S approach to Cerro Bruja from Río Escandaloso, ridge top, without elev., 20 May 1978 (fr), *B. Hammel* 3220 (MO); On Santa Rita Ridge Trail, beyond end of Santa Rita Ridge Road (Panamanian Hwy. R2OD), 17–35 km from Boyd-Roosevelt Hwy, 400–800 m, 21 May 1975 (fr), *S. Mori & M. Crosby* 6313 (LL, MO); Santa Rita Ridge, km 13.8, 9° 20' N, 79° 45' W, 350 m, 24 Feb 1986 (fr), *G. de Nevers* 7203 (LL, MO). **San Blas:** Río Cangandi, pueblo Cangandi, camino de caballos al S del pueblo, 9° 27' N, 79° 07' O, 40 m, 17 May 1987 (fr), *H. Herrera & P. Perez* 98 (MO); campamento Nusagandi, en la Carretera El Llano-Carti, a 19.1 km de la Carretera Panamericana, Cuadrante Nusagandi y Sendero Nusagandi, 9° 12' N, 78° 16' W, 350 m, 19 Mar 1993 (fr), *R. Paredes* 944 (BRIT, F, MO, PMA, STRI).

*Hymenandra pittieri* is most closely related to *H. wilburiana*, but is a much more robust plant, with larger sepals, stems and androecial parts.

Populations corresponding to the type of *Ardisia cutteri* are notable according to Standley for their large leaves and fruits. The subsessile leaf bases appearing auriculate have also been used to recognize it. However, we have now found that the subsessile leaves are restricted to the flowering shoots of *Hymenandra pittieri*, so the confusion is the result of an incomplete specimen rather than due to biological difference. Lundell (1971) stated that *Ardisia coclensis* may have affinity to *A. pittieri*, but he only knew it from the brief description by Standley (1938).

**7. *Hymenandra callejasii* (Pipoly) Pipoly & Ricketson, comb. nov. (Figs. 1E, 8).** *Ardisia callejasii* Pipoly, Novon 2:389. 1992. TYPE. COLOMBIA. ANTIOQUIA: Municipio de Mutatá, N of Hacienda El Darién, right margin of Río Chontadural, without elev., 28 Jul 1978 (fl, fr), *R. Fonnegra G. & E. Renteria A.* 953 (HOLOTYPE: HUA; ISOTYPES: COL, MEDEL, MO).

*Tree* to 7 m tall. *Vegetative shoots* terete, 7–10 mm in diam., densely and minutely furfuraceous lepidote; *reproductive shoots* unknown. *Vegetative shoot leaf blades* coriaceous, oblanceolate, (25–)31–45.5 cm long, (5–)7–12.2 cm wide, apically long-attenuate, the acumen 1.8–3.5 cm long, gradually tapering to a cuneate base, decurrent to petiole base, midrib slightly raised above, prominently raised below, secondary veins 16–20 pairs, slightly depressed or not visible above, prominently raised below, glabrescent, the margin regular, entire, flat; petioles marginate (0.6–)1–1.2 cm long, glabrous above, densely and minutely furfuraceous lepidote below; *reproductive shoot leaves* unknown. *Inflorescence* subterminal, pinnately or bipinnately paniculate, (7.5–)12.5–24.5 cm long, pyramidal, secondary branches 3–12 cm long, the rachis minutely densely furfuraceous lepidote, glabrescent, terminating in 7–12-flowered corymbs; inflorescence bracts unknown (presumably early caducous); floral bracts early caducous, membranaceous, ovate to oblong, 2.3–2.5 mm long, 1.2–1.4 mm wide, apically acute to rounded, sessile bases, midrib slightly raised above and below, secondary veins not visible, prominently punctate, scattered and minutely furfuraceous lepidote, the margins erose,



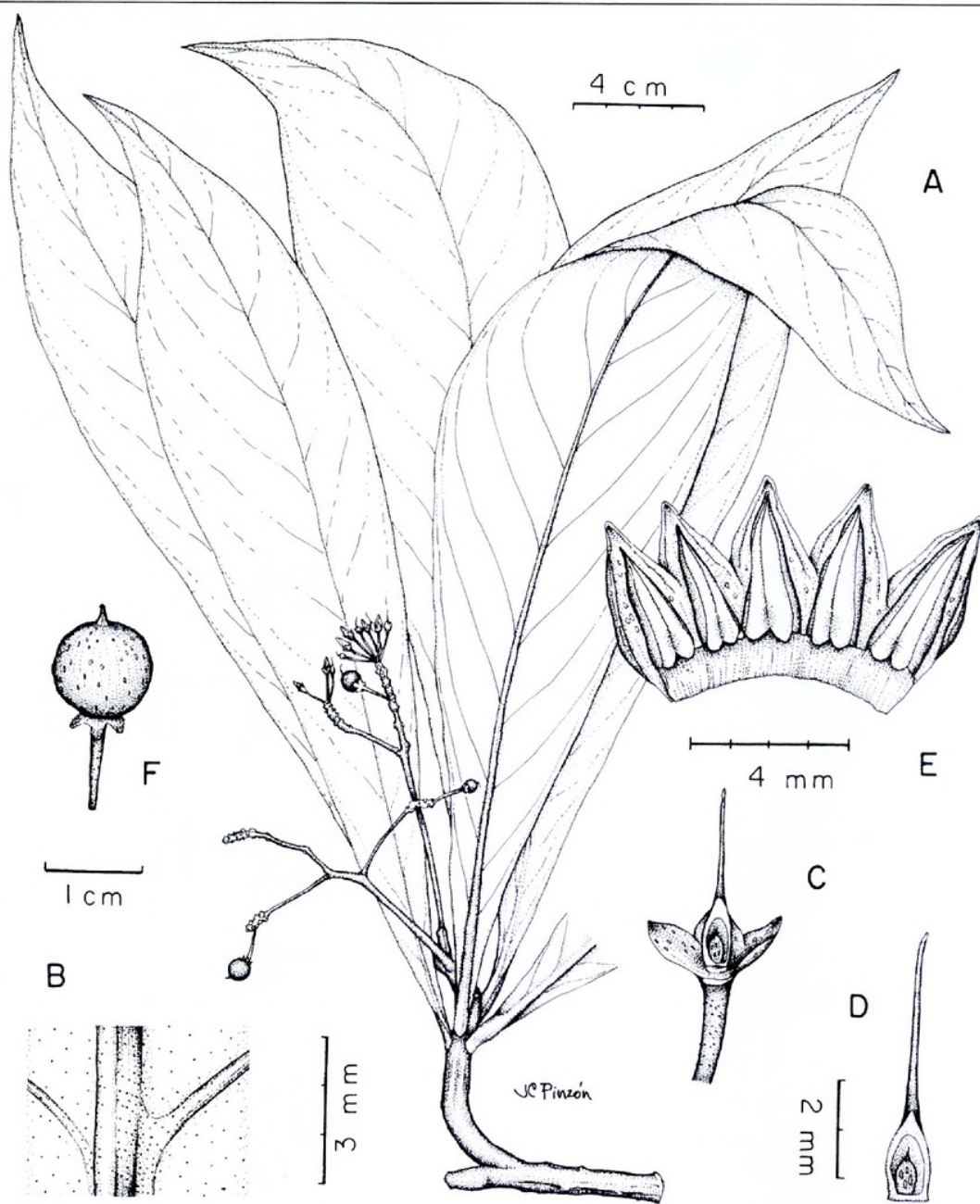


FIG. 8. *Hymenandra callejasii* (Pipoly) Pipoly & Ricketson. A. Reproductive shoot. B. Detail of abaxial leaf surface. C. Longisection of pistil and calyx, showing ovate calyx lobes, elongate style, and punctiform stigma. D. Longisection of pistil, showing apiculate placenta with pluriseriate ovules. E. Detail of flower, showing corolla lobes and stamens. F. Fruit. A–F drawn from holotype, R. Fonnegra G. & E. Renteria A 953. Original drawing from Pipoly (1992).

hyaline, entire, flat; pedicels cylindrical, 0.7–1.8 cm long, densely furfuraceous lepidote, persistent. *Flowers* 5-merous, pink; calyx lobes almost free, chartaceous, ovate, 2–2.8 mm long, 1–1.3 mm wide, symmetrical, apically obtuse, prominently punctate medially, densely and minutely furfuraceous



lepidote, the margin irregular, erose, hyaline, sparsely glandular-cilioate; corolla lobes basally connivent, coriaceous, ovate, 5.3–5.9 mm long, apically acute, highly reflexed in anthesis, medially thickened, prominently pellucid punctate without, somewhat so medially within, the margin hyaline, entire, glabrous; stamens 4.9–5.4 mm long; filaments connate into a coriaceous elobate tube 1.2–1.3 mm long, epunctate, glabrous; anthers free, lanceolate, 3.5–4.2 mm long, 1.3–1.6 mm wide, sessile on the staminal tube, apically attenuate, basally cordate, longitudinally dehiscent by narrow, sublatrose slits, the connective inconspicuously pellucid punctate; pistil ellipsoid; ovary 1.5–1.7 mm long, glabrous; style 3.8–4 mm long, erect, inconspicuously pellucid punctate, glabrous; stigma punctiform; placenta ellipsoid, 0.8–1 mm long, 0.3–0.4 mm in diam., apically apiculate; ovules 12–15, pluriseriate. *Fruit* globose, 8–10 mm in diam., densely and prominently black punctate, the style base persistent.

*Distribution*.—Endemic to the Colombian Chocó Floristic Province, in the Municipio de Mutatá, Department of Antioquia, from 80–180 m elevation.

*Ecology and conservation status*.—This species is locally common on one farm, in lowland pluvial forest, but has not been found elsewhere. Therefore it should be considered threatened. The lowland pluvial forests of the Colombian Chocó are some of the wettest in the tropics, receiving annual precipitation well in excess of 8,000 mm per year.

*Etymology*.—The species was named in honor of Ricardo Callejas Posada, head of the graduate program in biology at the Universidad de Antioquia, Medellín, Colombia. Ricardo is the pre-eminent authority on the phylogeny and systematics of the Piperaceae on a worldwide basis.

Specimens examined. **COLOMBIA**. **Antioquia**: Corregimiento Longani, del Río Longani, 2 kms. N de Mutatá, 7° 20' N, 76° 30' O, 80–100 m, 19 Nov 1987 (fl), *R. Callejas et al.* 5683 (NY); Municipio Mutatá, margin of Río León (Bucabá), Villa Arteaga, Las Caucheras, hill above water tap, 100–180 m, 2 Oct 1961 (bud), *J. Cuatrecasas* 26156 (US); Hacienda El Darién, right bank of Río Chontadural, 20 Jun 1979 (fr), *R. Fonnegra et al.* 1228 (COL, HUA, MO), (fl) 1249 (COL, HUA, MO), 13 Sep 1979 (fr), *R. Fonnegra et al.* 1343 (COL, HUA, MO).

*Hymenandra callejasii* is rather isolated within the genus; its inflorescence is rather unusual, as is the fact that no leaves have been seen on reproductive shoots. Further field study will be necessary to document the entire life history of *Hymenandra callejasii*.

8. *Hymenandra acutissima* (Cuatrec.) Pipoly & Ricketson, comb. nov. (Figs. 1G, 9). *Parathesis acutissima* Cuatrec., Revista Acad. Colomb. Ci. Exact 8:324. 1951. *Ardisia acutissima* (Cuatrec.) Lundell, Wrightia 4:53. 1968. TYPE. COLOMBIA. VALLE [DE CAUCA]: Costa del Pacífico, Río Cajambre, Barco, 5–80 m, 28 Abr 1944 (fr), *J. Cuatrecasas* 17219 (HOLOTYPE: F; ISOTYPES: LL, US).

*Tree* 2–6 m tall. *Vegetative shoots* terete, 7.5–9.5 mm in diam., sparsely



and minutely furfuraceous lepidote, glabrescent; *reproductive shoots* as in the vegetative ones but 2.5–3.5 mm in diam. *Vegetative shoot leaf blades* coriaceous, ovate to lanceolate, 15.4–27.2 cm long, 9.3–10 cm wide, apically acute to long-attenuate, the acumen when present 0.5–1.5 cm long, basally acute to cuneate, midrib slightly depressed above, prominently raised below, secondary veins 18–36 pairs, slightly depressed or not visible above, raised below, glabrous throughout, the margin entire, flat; canaliculate, 2.1–2.3 cm long, minutely appressed furfuraceous lepidote, glabrescent; *reproductive shoot leaf blades* as in the vegetative ones except 15.5–17.8 cm long, 5.6–6.8 cm wide, the secondary veins 18–32; petioles as in the vegetative ones but 2.1–2.5 cm long. *Inflorescence* terminal, pinnately or bipinnately paniculate, 9–16.5 cm long, obpyramidal, secondary branches 5–5.5 cm long, rachis glabrous throughout, terminating in 6–12-flowered corymbs; inflorescence and floral bracts unknown (presumably early caducous); pedicels cylindrical, 0.9–1 cm long, glabrous, persistent. *Flowers* 5-merous; calyx lobes almost free, chartaceous, oblate, 1–1.1 mm long, 1.4–1.6 mm wide, symmetrical, apically obtuse, prominently black punctate medially, glabrous, the margin irregular, erose-fimbriate along entire length, hyaline, sparsely glandular-ciliolate; corolla, stamens and pistil unknown. *Fruit* globose, 8–12 mm in diam., densely and prominently black punctate, the style base persistent.

*Distribution*.—From the central Chocó Floristic Province of Colombia, from 5–80 m elevation.

*Ecology and conservation status*.—This species occurs in coastal forests along rivers, an area frequently colonized by squatters. Therefore, the species should be considered threatened.

*Etymology*.—The epithet is the superlative form of the Latin word, “*acutus*,” referring to the apically acute to long-attenuate leaf apices.

Specimens examined. COLOMBIA. Chocó: Río San Juan Basin, Río Bicordó, above Noanamá; river margin; 04° 42' N, 76° 55' W, without elev., 6 Apr 1979 (fr), E. Forero *et al.* 4713 (COL, MO).

*Hymenandra acutissima* is most closely related to the vicariant *H. crosbyi*, but easily recognized because of its much longer sepals, terminal inflorescence and much larger fruit.

9. *Hymenandra crosbyi* (Lundell) Pipoly & Ricketson, comb. nov. (Figs. 1F, 10). *Ardisia crosbyi* Lundell, *Wrightia* 6:73. 1979. *Itacorea crosbyi* (Lundell) Lundell, *Phytologia* 49:348. 1981. TYPE. PANAMA. COLÓN: On trail at end of Santa Rita Ridge Road, 18–30 km from Boyd–Roosevelt Highway, 600–800 m, 30 May 1975 (fr), S. Mori & M. Crosby 6423 (HOLOTYPE: LL (F Neg. # 55657); ISOTYPE: MO (LL Neg. # 1979-1)).

*Ardisia calvarioana* Lundell, *Wrightia* 6:66. 1979, SYN NOV. *Itacorea calvarioana* (Lundell) Lundell, *Phytologia* 49:347. 1981. TYPE. PANAMA. COCLÉ: Around Rivera Sawmill



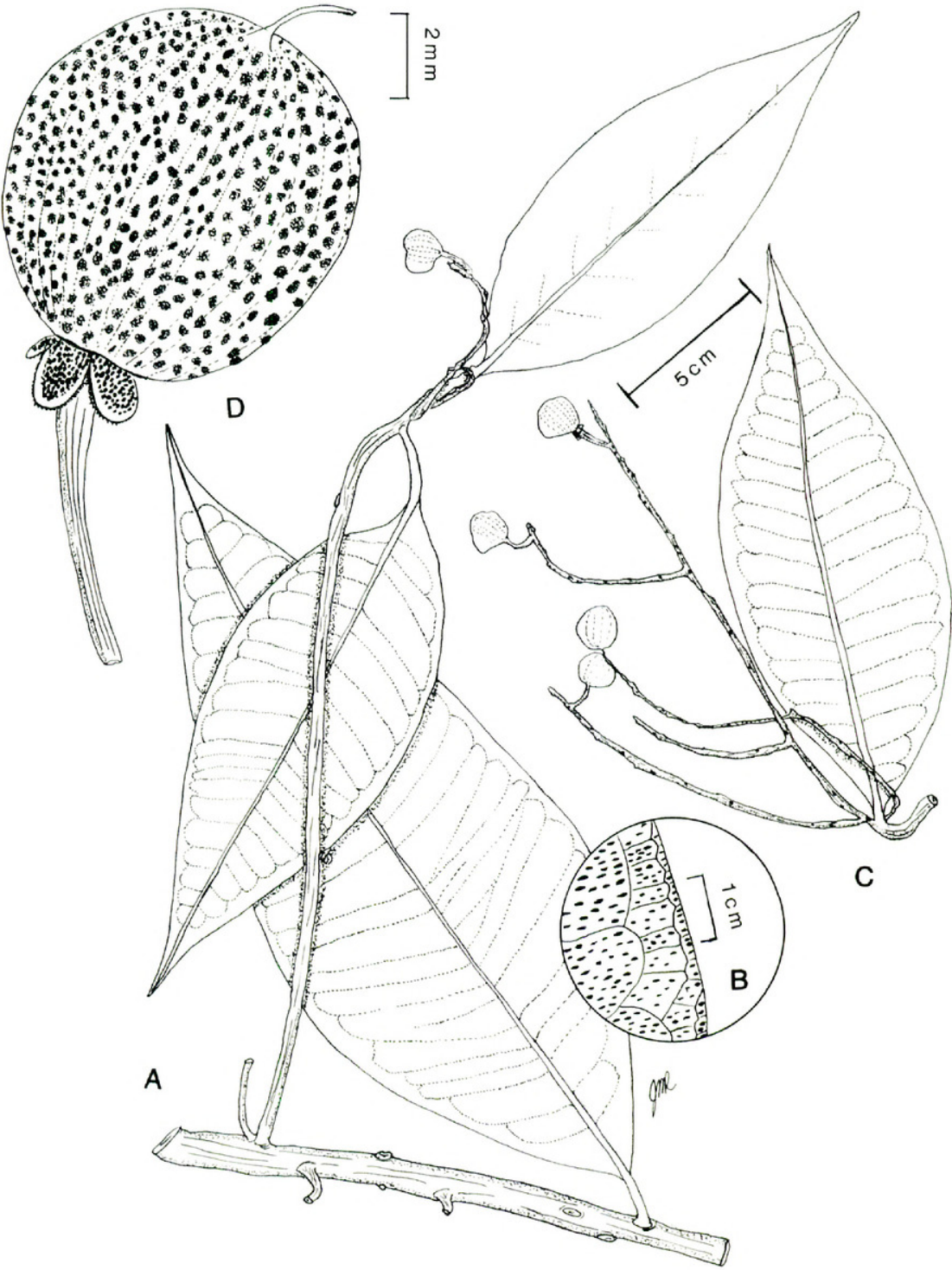


FIG. 9. *Hymenandra acutissima* (Cuatrec.) Pipoly & Ricketson. A. Reproductive shoot. B. Detail of abaxial leaf surface. C. Inflorescence. D. Fruit. A–B & D drawn from holotype, *J. Cuatrecasas* 17219. C drawn from isotype, *J. Cuatrecasas* 17219.



near to Alto Calvario, 7 km N El Cope, New Works, trout stream, 700–850 m, 20 Oct 1977 (fr), J. Folsom & R. Page 5970 (HOLOTYPE: MO; ISOTYPE: LL).

*Tree* 1–3 m, 1–3 cm in diam. *Vegetative shoots* terete, 3–5 mm in diam., densely and minutely furfuraceous lepidote when young, glabrescent; *reproductive shoots* as in the vegetative ones but 1.5–3 mm in diam. *Vegetative shoot leaf blades* chartaceous, ovate or lanceolate to elliptic, 11.5–22 cm long, 3.2–7.6 cm wide, apically long-attenuate, the acumen 1.2–2.4 cm long, basally obtuse to rounded, only slightly decurrent, midrib slightly raised above, prominently raised below, secondary veins 12–30 pairs, slightly depressed above, or not visible above, prominently raised below, prominently pellucid to black punctate above and below, glabrous above, scattered and minutely furfuraceous lepidote below, the margin entire, flat; petioles marginate, 1.7–5.4 cm long, glabrous above, scattered and minutely furfuraceous lepidote below; *reproductive shoot leaf blades* as in the vegetative ones except 5.5–15.7 cm long, 1.7–5.2 cm wide, secondary veins 10–26 pairs; petioles like the vegetative ones except 1.6–3.9 cm long. *Inflorescence* subterminal, pinnately or bipinnately paniculate, 2.7–8.8 cm long, obpyramidal, secondary branches 1.3–3.5 cm long, rachis sparsely and minutely furfuraceous lepidote, early glabrescent, terminating in 4–6-flowered corymbs; inflorescence bracts membranaceous, lanceolate to elliptic, 1.4–2.4 mm long, 0.4–0.7 mm wide, apically acute, pellucid to black punctate medially, scattered and minutely furfuraceous lepidote below, the margin entire; floral bracts like the inflorescence bracts but 0.8–2.1 mm long, 0.4–0.8 mm wide; pedicels cylindrical, 0.8–12.2 cm long, scattered and minutely furfuraceous lepidote, glabrescent, persistent. *Flowers* 5(–6)-merous; calyx lobes (in fruit) almost free, chartaceous, ovate, 0.9–1.6 mm long, 0.9–1.2 mm wide, symmetrical, apically acute, conspicuously pellucid to black punctate, scattered and minutely furfuraceous lepidote, glabrescent, the margin irregular, erose, hyaline, glandular-cilioate; corolla 3.5–3.7 mm long, membranaceous, lanceolate, the tube 0.3–0.5 mm long, the lobes (in young bud) basally connate, 3.1–3.3 mm long, 1.2–1.4 mm wide at base, apically acute, prominently pellucid punctate, somewhat so medially within, the margins erose, hyaline, glabrous; stamens (in young bud) 2.6–2.7 mm long; filaments connate into a membranaceous elobate tube, the tube 0.3–0.5 mm long, adnate to the corolla basally, epunctate, glabrous; anthers connate by their sutures, at least at first, lanceolate, 2.2–2.5 mm long, 0.4–0.6 mm wide at base, sessile on staminal tube, apically apiculate, basally cordate, longitudinally dehiscent by narrow, sublatrose slits, the connective prominently pellucid punctate; pistil 3–3.2 mm long; ovary 0.7–0.9 mm long, glabrous; style 2.1–2.5 mm long, erect, inconspicuously pellucid punctate, glabrous; stigma punctiform; ovules 22–24, pluriseriate. *Fruit* globose, 4.5–6.5 mm in diam., prominently raised pellucid to black punctate, glabrous, the style base persistent.





FIG. 10. *Hymenandra crosbyi* (Lundell) Pipoly & Ricketson. A. Reproductive shoot. B. Detail of abaxial leaf surface. C. Detail of inflorescence. D. Detail of calyx and pedicel. E. Fruit. A–B & D drawn from the holotype, S. Mori & M. Crosby 6423. C drawn from G. de Nevers 6757. E drawn from K. Sytsma et al. 4279.



*Distribution*.—Restricted to the Caribbean slope, in the provinces of Coclé, Colón and San Blas, Panama, from 100–850 m elevation.

*Ecology and conservation status*.—*Hymenandra crosbyi* occurs at the natural ecotone of premontane and cloud forest. Its conservation status cannot be determined owing to a lack of populational data.

*Etymology*.—The species is named for Dr. Marshall Crosby of the Missouri Botanical Garden, who collected the type specimen.

Specimens examined. **PANAMA**. Coclé: Coclecito Road, elevational transection from 1 mile beyond the divide to the ridge top, 08° 42' N, 80° 28' W, 300–500 m, 12 Jan 1986 (fr), *G. de Nevers et al.* 6757 (LL, MO). Colón: Upper Río Piedras headwaters, along trail from end of Santa Rita Ridge Road, ca. 11 km SW of Cerro Braja, 09° 25' N, 79° 35' W, 600–700 m, 2 May 1981 (fr), *K. Sytsma et al.* 4220 (LL, MO); Ridge between Río Piedras and Río Gatun waterbeds, along trail from end of Santa Rita Ridge road, ca. 5–8 km SW of Cerro Bruja, 09° 27' N, 79° 36' W, 700–800 m, 2 May 1981 (fr), *K. Sytsma et al.* 4279 (LL, MO). San Blas: El Llano-Carti Road, 17.4 km from Interamerican Hwy., 09° 19' N, 78° 55' W, 350 m, 27 Sep 1984 (fr), *G. de Nevers et al.* 3941 (MO); Trail along Continental Divide, 5–10 km W of El Llano-Carti Road, 350 m, 10 Jan 1985 (fr), *G. de Nevers & H. Herrera* 4490 (MO); Río Nergala, 9° 22' N, 79° 07' W, 100–300 m, 12 Jan 1985 (fl), *G. de Nevers & H. Herrera* 4531 (MO).

*Hymenandra crosbyi* is most closely related to the vicariant *H. acutissima*, but may be recognized by the shorter and obtuse sepals, the subterminal inflorescence, shorter secondary branches, and smaller fruit.

#### ACKNOWLEDGMENTS

We thank the Missouri Botanical Garden and the Flora Mesoamericana Project for funding that allowed J. Ricketson (MO) to travel to Fort Worth and for J. Pipoly to travel to MO. We have enjoyed the continuing support of the staff of the C.L. Lundell Herbarium (LL), housed at the University of Texas at Austin. Without access to that critical collection, assembled by C.L. Lundell over a period of nearly 60 years, the present study would not have been possible. We also thank the curators of the herbaria cited for loans of specimens. We are grateful to the staff of TEX/LL, especially Billie L. Turner, Tom Wendt, Carol Todzia, Beryl Simpson, and José Panero, for their cooperation and hospitality. We are also grateful to those who have been so instrumental in assisting us in our work, including Gerrit and Jeany Davidse, Linda Oestry, Mary Bard, and Catherine Mayo (MO), and Barney Lipscomb and Lindsay Woodruff (BRIT). Illustrations were prepared by the junior author except for *H. callejasii*, drawn by Juan Pinzón (COL). Reviews of the manuscript by Tom Wendt (TEX), and Melissa Luckow (BH) greatly improved the presentation of the paper.



## REFERENCES

- CANDOLLE, A. DE 1834. A review of the natural order Myrsineae. Trans. Linn. Soc. London 17:95–138.
- \_\_\_\_\_. 1841. Deuxieme memoire sur les Myrsinacees. Ann. Sci. Nat., Bot., ser. 2, 16:65–97.
- C. CHEN, C. AND J. PIPOLY. 1996. Myrsinaceae. In: Wu Zheng-yi and P. Raven, eds. Fl. China 15:34–38. Science Press, Beijing and Missouri Botanical Garden, St. Louis, MO. USA.
- CONRAN, J. 1995. Family distributions in the Liliiflorae and their biogeographical implications. J. Biogeography 22:1023–1034.
- DOBSON, J. 1996. A paleogeographic link between Australia and eastern North America: a New England connection? J. Biogeog. 23:609–617.
- FURTADO, C.X. 1958. Some new or noteworthy species of Malaysia. Gard. Bull. Sing. 17:279–311.
- GENTRY, A. 1983. *Alstonia* (Apocynaceae): Another paleotropical genus in Central America. Ann. Missouri Bot. Gard. 70: 206–207.
- HALLÉ, F., R.A. OLDEMAN & P. B. TOMLINSON. 1978. Tropical trees and forests. An architectural analysis. Springer-Verlag. New York.
- HICKEY, L. 1984. A revised classification of the architecture of dicotyledonous leaves. Pp. 25–39. In: C.R. Metcalfe & L. Chalk (editors). Anatomy of the Dicotyledons. Vol. 1. Syshootatic anatomy of leaf and shoot, with a brief history of the subject. Clarendon Press. Oxford, U.K.
- LAVIN, M. & M. LUCKOW. 1993. Origins and relationships of tropical North America in the context of the Boreotropics Hypothesis. Amer. J. Bot. 80:1–14.
- LINDLEY, J. 1848. Illustrated dictionary of botanical terms. Excerpt from illustrated dictionary of botanical terms by John Lindley. [Reprint, With an Introduction by Alice Eastwood, Stanford University, School of Earth Sciences, 1964].
- LUNDELL, C.L. 1966. Myrsinaceae. In: P.C. Standley & L.O. Williams, eds. Flora of Guatemala, Part VIII Number 1. Fieldiana, Bot. 24 (8/2):135–200.
- \_\_\_\_\_. 1971. Flora of Panama, Part VIII. Family 150. Myrsinaceae. Ann. Missouri Bot. Gard. 58:285–353.
- \_\_\_\_\_. 1981. Neotropical Myrsinaceae–VI. Phytologia 49:341–354.
- \_\_\_\_\_. 1982. Neotropical Myrsinaceae–VII. Wrightia 7:38–50.
- METCALFE, C.R. 1984. Some basic types of cells and tissues. Pp. 54–62. In: C.R. Metcalfe and L. Chalk, eds. Anatomy of the Dicotyledons. Vol. 1. Syshootatic anatomy of leaf and shoot, with a brief history of the subject. Clarendon Press. Oxford, U.K.
- MEZ, C. 1902. Myrsinaceae. In: A. Engler, ed. Das Pflanzenreich IV. 236(Heft 9):1–437.
- NAYAR, M.P. & G.S. GIRI. 1975 [1976]. A synopsis of the genus *Hymenandra* A. DC. (Myrsinaceae) and a new species from Burma. J. Bom. Nat. Hist. Soc. 72:818–821.
- PIPOLY, J. 1987. A systematic revision of the genus *Cybianthus* subgenus *Grammadenia* (Myrsinaceae). Mem. New York Bot. Gard. 43:1–76.
- \_\_\_\_\_. 1992a. The genus *Cybianthus* subgenus *Conomorpha* (Myrsinaceae) in Guayana. Ann. Missouri Bot. Gard. 79:908–957.
- \_\_\_\_\_. 1992b. *Ardisia callejasii* (Myrsinaceae): A new species from the Antioquian Chocó of Colombia. Novon 2:389–391.
- PIPOLY, J. AND J. RICKETSON. 1998. A revision of the genus *Ardisia* subgenus *Graphardisia* (Myrsinaceae). Sida 18:433–472.
- RICKETSON, J. AND J. PIPOLY. 1997. A. synopsis of the genus *Gentlea* (Myrsinaceae) and a key to the genera of Myrsinaceae in Mesoamericana. Sida 17:697–707.
- STÄHL, B. 1996. The relationships of *Heberdenia bahamensis* and *H. penduliflora* (Myrsinaceae). Bot. J. Linn. Soc. 122:315–333.



- STANDLEY, P.C. 1938. Flora of Costa Rica: Myrsinaceae. Publ. Field Mus. Nat. Hist., Bot. Ser. 18:884–900.
- STONE, B.C. 1991 [1992]. New and noteworthy Malesian Myrsinaceae, VI. Revision of the genus *Hymenandra* A. DC. Gard. Bull. Sing. 43:1–17.
- TIFFNEY, B. 1985a. Perspectives on the origin of the floristic similarity between eastern Asia and eastern North America. J. Arn. Arb. 66:73–94.
- . 1985b. The Eocene North Atlantic land bridge: its importance in Tertiary and modern phytogeography of the northern hemisphere. J. Arn. Arb. 66:243–273.
- THEOBALD, W.L., J. KRAHULIK & R.C. ROLLINS. 1984. Trichome description and classification. Pp. 40–53. In: C.R. Metcalfe & L. Chalk, eds. Anatomy of the Dicotyledons. Vol. 1. Syshootatic anatomy of leaf and shoot, with a brief history of the subject. Clarendon Press, Oxford, U.K.
- WENDT, T. 1988. *Chiangioidendron* (Flacourtiaceae: Pangieae), a new genus from southeastern Mexico representing a new tribe for the New World flora. Syst. Bot. 13:435–441.
- . 1989. Las selvas de Uxpanapa, Veracruz-Oaxaca, Mexico: Evidencia de refugios florísticos cenozoicos. Anal. Inst. Biol. UNAM, Ser. Bot. 58:29–54.
- . 1993. Composition, floristic affinities and origins of the canopy tree flora of the Mexican Atlantic slope rain forests. Pp. 595–680. In: T. Ramawoorthy, R. Bye, A. Lot and J. Fa, eds. Biological Diversity of Mexico: Origins and Diversity. Oxford University Press, NY.
- WOLFE, J. 1975. Some aspects of plant geography of the northern hemisphere during the late Cretaceous and Tertiary. Ann. Missouri Bot. Gard. 74:264–279.
- ZONA, S. 1990. A monograph of *Sabal* (Arecaceae: Coryphoideae). Aliso 12:583–666.

NUMERICAL LIST OF *HYMENANDRA* TAXA

1. *H. stenophylla* (Donn. Sm.) Pipoly & Ricketson
2. *H. calycosa* (Hemsl.) Pipoly & Ricketson
3. *H. sordida* (Lundell) Pipoly & Ricketson
4. *H. squamata* (Lundell) Pipoly & Ricketson
5. *H. wilburiana* (Lundell) Pipoly & Ricketson
6. *H. pittieri* (Mez) Pipoly & Ricketson
7. *H. callejasii* (Pipoly) Pipoly & Ricketson
8. *H. acutissima* (Cuatrec.) Pipoly & Ricketson
9. *H. crosbyi* (Lundell) Pipoly & Ricketson

## LIST OF EXSICCATAE

Figures in parentheses refer to the numbers from the numerical list of taxa. Collection numbers in **boldface** type indicate type specimens.

Aguilar, R., et al., 3663 (6); Alfaro, E., 169 (2); Allen, P., **2056** (6); 2176 (6); 3806 (6); 5828 (6); 5828A (6); 6726 (6); Angulo, L., 394 (6); Antonio, T., 1364 (6); 3627 (6); 3632 (6); Argüello M., D. et al., 11 (6).

Baker, R. & W. Burger, 126 (6); Bello C., E., 1059 (3); Brenes, A., 15655 (2); 21243 (2); Burger, W. & R. Baker, 9869 (2); Burger, W. & G. Matta U., 4406 (6); 4644 (6); Burger, W. & R. Stolze, 3738 (6); 5853 (4); Burger, W. et al., 11687 (2).

Callejas, R. et al., 5683 (7); Carvajal U., A., 392 (2); Chacón, A., 934 (6); Chacón, I., 80 (5); 717 (5); Chacón, I. & G. Herrera, 1758 (6); Chávez, C., 71 (3); Chinchilla, M., 93 (2); 100 (2); Churchill, H., 3867 (6); 3876 (6); Cooper, G., 12 (1); 370 (1); Croat, T., 36246 (2); 36703 (6); 43538 (3); 44581 (6); Cuatrecasas, J., 17219 (8); 26156 (7).



D'Arcy, W. & J. D'Arcy, 6749 (6); D'Arcy, W. & B. Hammel, 12292 (6); Davidse, G. & C. Hamilton, 23484 (6); Davidse, G. & G. Herrera, 31379 (5); Dressler, R., 4254 (6); 5962 (6); Dressler, R. & W. Lewis, 3725 (6); Duke, J., 12197 (6); Dwyer, J., 8351 (6); 8551 (6); 11869 (6); Dwyer, J. & B. Lallathin, 8690 (6); 8690A (6); Dwyer, J. et al., 4476 (6).

Folsom, J., 1242 (6); 3163 (6); Folsom, J. & R. Page, 5970 (9); Folsom, J. et al., 5741 (6); Fonnegra et al., 953 (7); 1228 (7); 1249 (7); 1343 (7).

García, D., 112 (2); 312 (2); Garwood, N. et al., 936 (5); Gentry, A., 2011 (2); 6854 (6); 6872 (6); Gentry, A. et al., 43939 (2); Gómez, L. et al., 20415 (1); 23383 (4); Gómez-Laurito, J., 9538 (1); Grayum, M., 2371 (4); Grayum, M. & R. Chazdon, 6853 (4); Grayum, M. & G. Herrera, 4852 (2); 7857 (4); 9200 (6); Grayum, M. & B. Jacobs, 5352 (5); Grayum, M. et al., 3369 (6); 4486 (1); 4969 (2); Grijalva, A. & D. Bradford, 3652 (2); Grijalva, A. et al., 3393 (2).

Haber, W. & E. Bello C., 1714 (3); 7433 (2); Haber, W. et al., 4430 (2); 4432 (2); 4447 (2); 4752 (2); 4759 (2); 4848 (2); Hammel, B., 958 (6); 1928 (6); 2662 (6); 3220 (6); 3898 (6); 4054 (6); 8693 (4); 8762 (4); 10962 (4); 2372 (4); 13717 (1); Hammel, B. & M. Chavarria, 17073 (4); Hammel, B. & M. Grayum 14342 (1); Hammel, B. & J. Trainer, 12757 (4); 13262 (5); Hammel, B. et al., 14078 (3); 15186 (6); 17370 (2); 17829 (5); Herrera, G., 6279 (3); Herrera, H. & P. Perez, 98 (6).

Jacobs, B., 2377 (4); 2917 (5); 3113 (4); 3189 (5); Jiménez, A., 3738 (6); Jiménez, Q. et al., 709 (2).

Khan et al., F. 1141 (2); Knapp, S., 1965 (6).

Lallathin, B., 35A (6); Liesner, R., 5066 (2); Liesner, R. et al., 15041 (2); 15108 (3); 15348 (6); Lobo, M., 47 (2); Loiselle, B., 144 (4); Luteyn, J. & H. Kennedy, 1704 (6).

Marín, J. et al., 257 (6); McAlpin, B., 2250 (6); McPherson, G., 11270 (6); Molina R., A. et al., 17525 (3); 18090 (6); Moraga, C., 214 (2); Morales, J., 4354 (6); 5305 (2); Morales, J. & Y. Salazar, 1195 (6); Morales, J. & V. Ureña 2852 (6); Morales, J. et al., 2544 (2); Moreno, A., 7 (1); Moreno, P., 7532 (2); (2); 26053 (2); 26753 (2); Moreno, P. & J. Sandino, 12853 (2); Mori, S. & M. Crosby, 6313 (6); 6423 (9); Mori, S. & J. Kallunki, 2978 (6).

Nee, M. & B. Hansen, 14099 (1); Neill, D. & P. Vincelli, 3506 (5); Nevers, G. de, 7203 (6); Nevers, G. de & H. Herrera, 4490 (9); 4531 (9); Nevers, G. de et al., 3941 (9); 6398 (6); 6757 (9).

Opler, P., 188 (4); 332 (4); 580 (2).

Paredes, R., 944 (6); Picado, A. et al., 51 (2); Pittier, H. & A. Tonduz, 9173 (1); Poredat, L. et al., 3681 (2); Porter, D. et al., 4422 (6); 4597 (6); Poveda, L., 106 (6).

Quesada, E., 320 (6).

Ramírez, V. et al., 62 (3); Raven, P., 21829 (6); Ríos, P. 374 (3); Robles, R., 1571 (5); 1666 (5); Rodríguez, A. & N. Zamora, 2067 (2).

Sánchez, J. et al., 308 (5); Sandino, J., 159 (2); Schatz, G. & M. Grayum, 653 (5); 1303 (4); Schubert, B., 1079 (2); Seibert, R., 1572 (1); Smith, A., 1630 (2); Sperry, J. 790 (4); 1726 (2); 2609 (2); Standley, P. & J. Valerio 44588 (2); 45539 (2); 45545 (2); 45862 (2); 46181 (2); 46221 (2); 47122 (6); Stevens, W., 23977 (5); Stevens, W. & O. Montiel, 24432 (5); Stevens, W. et al., 24972 (5); Sullivan, G., 553 (6); Sytsma, K. & W. D'Arcy, 3565 (6); Sytsma, K. et al., 2453 (6); 4220 (9); 4279 (9).

Tate, R., 239 [454] (2); Taylor, C., 4551 (2); Todzia, C., 1302 (4); Taylor, C. & C. Skotak 4630 (3); Tonduz, A., 9586 (1); 13369 (6).

Utley, J. & K., 5318 (2)

Valerio, J., 147 (2); Villalobos, R., 37 (2).

Wilbur, R., 39948 (4); 40442 (4); 64246 (4); Wilbur, R. & B. Jacobs 34720 (4); 34727 (4); Wilbur, R. & D. Stone, 9745 (3).

Zamora, N. & Q. Jiménez, 1268 (6).





Pipoly, John J. and Ricketson, Jon M. 1999. "DISCOVERY OF THE INDO-MALESIAN GENUS HYMENANDRA (MYRSINACEAE) IN THE NEOTROPICS, AND ITS BOREOTROPICAL IMPLICATIONS." *SIDA, contributions to botany* 18, 701–746.

**View This Item Online:** <https://www.biodiversitylibrary.org/item/34589>

**Permalink:** <https://www.biodiversitylibrary.org/partpdf/163215>

**Holding Institution**

Missouri Botanical Garden, Peter H. Raven Library

**Sponsored by**

Missouri Botanical Garden

**Copyright & Reuse**

Copyright Status: In copyright. Digitized with the permission of the rights holder.

License: <http://creativecommons.org/licenses/by-nc-sa/3.0/>

Rights: <https://biodiversitylibrary.org/permissions>

This document was created from content at the **Biodiversity Heritage Library**, the world's largest open access digital library for biodiversity literature and archives. Visit BHL at <https://www.biodiversitylibrary.org>.