

A REVISION OF THE GENUS *ARDISIA* SUBGENUS *GRAPHARDISIA* (MYRSINACEAE)

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ABSTRACT

A taxonomic revision of *Ardisia* subgenus *Graphardisia* is presented, including an emended description of the subgenus, a key to the species and subspecies, along with updated descriptions and new illustrations for each taxon. Six taxa are recognized, including three new combinations: *Ardisia opegrapha* subsp. *paquitensis* (Lundell) Pipoly & Ricketson, *A. opegrapha* subsp. *wagneri* (Mez) Pipoly & Ricketson, and *A. bartlettii* subsp. *lilacina* (Lundell) Pipoly & Ricketson. Four binomials, *Ardisia weberbaueri*, *A. opegrapha*, *A. wagneri* and *A. albovirens*, are lectotypified and twenty-one are newly relegated to synonymy. *Ardisia nigrovirens* J. F. Macbr. is relegated to synonymy under *A. albovirens* Mez, and both are excluded from subgenus *Graphardisia*.

RESUMEN

Se presenta una revisión taxonómica del género *Ardisia* subgénero *Graphardisia*. Se provee una descripción actualizada del subgénero junto con una clave para identificar las especies y subespecies, descripciones actualizadas y nuevas ilustraciones para cada taxon. Se reconoce seis taxa, incluyendo tres combinaciones nuevas: *Ardisia opegrapha* subsp. *paquitensis* (Lundell) Pipoly & Ricketson, *A. opegrapha* subsp. *wagneri* (Mez) Pipoly & Ricketson, y *A. bartlettii* subsp. *lilacina* (Lundell) Pipoly & Ricketson. Se lectotipifican cuatro binomiales: *Ardisia weberbaueri*, *A. opegrapha*, *A. wagneri* y *A. albovirens* y se relega veintiuno a la sinonimia. También, *Ardisia nigrovirens* se relega bajo sinonimia de *A. albovirens*, y ambas se excluyen del subgénero *Graphardisia*.

INTRODUCTION

The pantropical genus *Ardisia* Sw. is the largest within the Myrsinaceae, containing perhaps as many as 500 species (Chen & Pipoly 1996). The genus has been separated from all others in the Myrsinaceae by the free filaments and pluriseriate ovules (Mez 1902). While only a few groups within *Ardisia sensu latissimo* have been segregated as separate genera in the Paleotropics

(*Sadiria* Mez (1902), *Afrardisia* Mez (1902), *Tetrardisia* Mez (1902), *Hymenandra* A. DC. (1834), *Parardisia* Nayar & Giri (1986)), there has been an enormous increase in separation of species groups from *Ardisia* to new genera in the Neotropics, starting with those who recognize Aublet's (1775), *Icacorea* (against which *Ardisia* is conserved), followed by Alphonse de Candolle (1841), Ducke (1930), and finally Cyrus Lundell (1963, 1964, 1981a, 1981b, 1981c, 1981d, 1982). Lundell's contribution was clearly the most extensive, consisting of the segregation of *Amatlanianthus* Lundell, *Auricularia* Lundell, *Chontalesia* Lundell, *Yunckeria* Lundell (= *Ctenardisia* Ducke), *Gentlea* Lundell, *Graphardisia* (Mez) Lundell, *Ibarrea* Lundell, *Oerstedianthus* Lundell, *Synardisia* (Mez) Lundell, *Valerioanthus* (Mez) Lundell, and *Zunilia* Lundell. Because the group is comprised of over 800 names, it will be some time before each species has been reviewed and the entire group is revised. In the meantime, we suggest using the key to the Mesoamerican genera we published (Ricketson & Pipoly 1997) to identify specimens to generic level (*Ardisia* versus *Synardisia*, *Ctenardisia* or *Gentlea*). For groups within *Ardisia*, the use of *Flora of Guatemala* (Lundell 1966a) and *Flora of Panama* (Lundell 1971) will permit rough identification, at least to species groups, until our review of the entire complex is complete. While most of the taxa described in the remaining segregated groups are best placed in *Ardisia*, it appears that some currently placed in *Icacorea* and *Chontalesia* may prove to be problematic. Treatment of those taxa is now underway (Pipoly & Ricketson, in prep.).

Ardisia subgenus *Graphardisia* Mez (1902) was described in the *Das Pflanzenreich* treatment of the Myrsinaceae and was comprised of only two species. *Ardisia opegrapha* Oerst. and *A. wagneri* Mez. Mez considered subgenus *Graphardisia* allied to *Ardisia* subg. *Synardisia* Mez [= *Synardisia* (Mez) Lundell] by its imbricate or contorted (but not valvate) corolla lobes and the included (rather than exserted) stamens. Subgenus *Graphardisia* was separated from subg. *Synardisia* by the rotate (not infundibuliform) corolla, with lobes connate to only 1/3 (not 3/4) their length. He also considered *Ardisia* subg. *Graphardisia* closely related to *A.* subg. *Ardisia*, because of the often persistent inflorescence bracts and floral bud shape, and contrasted these two subgenera with *A.* subg. *Icacorea* (Aubl.) Mez, known for its very inconspicuous inflorescence bracts.

Lundell (1966b) treated subgenus *Graphardisia*, but later raised *Graphardisia* to generic rank (Lundell 1981c). He (Lundell 1981c) stated that it was most closely related to *Oerstedianthus* Lundell, because both groups of species have linear-lanceolate anthers deshiscent by apical pores. *Oerstedianthus* (Lundell 1981c) is comprised of a group including *Ardisia nigrescens* Oerst., *A. tuerckheimii* Donn. Sm., and eight other taxa, formerly placed by Mez (1902) in subgenus *Icacorea*, but segregated from *Icacorea* by Lundell because of its glandular trichomes of the branchlets, inflorescence and perianth parts. Lundell

(1981c) separated *Graphardisia* from *Oerstedianthus* by the following key:

- "1. Filaments strictly glabrous; stems and inflorescence glabrous; punctuation of all parts dense and blackish; bracts and bractlets usually foliaceous and often persistent; sepals and petals large, accrescent, usually blackened, usually ribbed or with dense elevated black glands.*Graphardisia*
- 1. Filaments pubescent with gland-tipped hairs; stems and inflorescence rarely glabrous, usually puberulent, hirtellous or densely hirsute-tomentose; bractlets and sepals small, not accrescent; sepals not ribbed with glands.*Oerstedianthus*"

Upon examination of the six taxa we recognize in *Ardisia* subgenus *Graphardisia*, 4 taxa (comprising two species in our classification) have either stalked glandular papillae or sessile glandular granules on the filaments near the base, thus invalidating the first part of Lundell's lead couplet. While members of the *Oerstedianthus* species group have anthers very similar to that of *A.* subg. *Graphardisia*, the unique glandular tomentum, and small, corymbose inflorescences are much different than the panicles of corymbs, and essentially glabrous plants of subgenus *Graphardisia*. Our studies indicate that *Ardisia* subg. *Graphardisia* is most closely related to *A.* subg. *Icacorea* based on its well-developed panicles with flowers in terminal corymbs; apiculate, subapically poricidal, concolorous anthers, and style two to three times longer than the ovary. The two subgenera may be separated by the following key:

- 1. Branchlets and inflorescence rachises glabrous or rarely, sparsely glandular-granulose; leaf blades, inflorescence and floral bracts, and perianth densely and prominently black or red punctate and/or punctate-lineate; sepals accrescent, usually clasping the developing fruit.....*Ardisia* subg. *Graphardisia*
- 1. Branchlets and inflorescence rachis furfuraceous-lepidote; leaf blades rarely conspicuously but never prominently punctate-lineate, the inflorescence and floral bracts mostly orange, rarely black, punctate, the perianth mostly orange, rarely black punctate; sepals not accrescent, never clasping the developing fruit.*Ardisia* subg. *Icacorea*

While preparing a treatment of *Ardisia* subg. *Graphardisia* as part of the Myrsinaceae for *Flora Mesoamericana*, we treated the entire subgenus so that it might serve as a precursor to our treatment of the tribe Ardisieae for *Flora Neotropica*, that is now in preparation. The revision here presented provides a nomenclator for *Ardisia* subg. *Graphardisia*, that is beyond the format limitations of the *Flora Mesoamericana*.

NOTES ON KEYS, TAXONOMIC CONCEPTS, 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 stem diameters, inflorescence rachises, pedicels, leaf and fruit shape and size were taken from dried herbarium specimens.

Our concept of subspecies follows that of Pipoly (1987) who defined subspecies as: "groups of populations within a single lineage of ancestor-descendant populations that show variation by unique combinations of plesiomorphies, or homoplastic apomorphies, correlated with biogeography and/or ecology. This rank is primarily used to convey information regarding variation in the life histories of these populations and character state differences hypothesized to be the result of this variation. The subspecific rank in no way attempts to predict speciation events."

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

TAXONOMIC TREATMENT

Ardisia subgenus **Graphardisia** Mez in Engl., Pflanzenr. IV. 236 (Heft 9):78. 1902; Lundell, Wrightia 3:192–198. 1966. *Graphardisia* (Mez) Lundell, Phytologia 48:139. 1981; Lundell, Phytologia 59:429–433. 1986. TYPE: *Ardisia opegrapha* Oerst. (LECTOTYPE, here designated).

Mez (1902) included both *Ardisia opegrapha* as well as *A. wagneri* in his new subgenus. Subsequently, Lundell (1966b) did not designate a lectotype. Therefore, we have chosen *A. opegrapha* because it most closely fits the original circumscription of the subgenus.

Subshrubs to *trees*. *Branchlets* mostly terete, glabrous or rarely, glandular-granulose. *Leaves* petiolate; blades membranaceous to subcoriaceous, densely and prominently black (rarely pellucid-) punctate and punctate-lineate, the margins entire to crenulate, rarely sharply and irregularly dentate. *Inflorescence* terminal, uni- to tripinnately paniculate, pyramidal to obpyramidal rarely globose, the ultimate branches corymbose, at times in high anthotactic spirals and thus appearing umbellate, the rachis often densely and prominently black punctate and punctate-lineate; inflorescence and floral bracts foliaceous, mostly persistent, resembling the vegetative leaves but acropetally reduced in size. *Flowers* white, pink, lavender or purple, densely and prominently black punctate and punctate-lineate; calyx with sepals free or nearly free, large, accrescent and clasping fruits at maturity; corolla rotate, the lobes imbricate in bud, basally short-connate and sparsely to densely yellow glandular-

granulose within, densely and prominently black punctate-lineate, stamens inserted at corolla tube base, the filaments basally connate to form an inconspicuous tube, the tube free from the corolla tube, the apically free portions of the filaments glandular-granulose or glandular-papillate, less than half the length of the anthers, the anthers ovoid-lanceoloid, linear or lanceoloid, prominently apiculate, dehiscent by subapical pores; ovary globose, the style slender, equalling the sepals, 2–3 times longer than the ovary, the placenta apiculate, the ovules pluriseriate, biseriate, or apparently uniseriate (few in number and in a very high anthotactic spiral). *Fruit* globose or oblongoid, densely punctate and punctate-lineate, basally surrounded by persistent, clasping sepals.

Distribution.—A small distinctive subgenus of three species with five subspecies found from Nicaragua to Bolivia and adjacent Brazil.

Ecology.—Members of the subgenus occur in diverse vegetation types, including wet and pluvial lowland, premontane, montane, and cloud forests.

The subgenus is defined by: 1) glabrous branchlets and inflorescence rachises; 2) dense and prominently raised black, or rarely, reddish-black, punctations or punctate-lineations on all leaf and floral parts; 3) sepals often accrescent and usually clasping the developing fruit; 5) linear-lanceolate, concolorous, apiculate anthers with subapically poricidal dehiscence; and 6) style 2–3 times longer than the ovary. Species of the subgenus are often used for home decoration and for use in Christian churches for religious holidays (Pipoly, pers. obs.).

KEY TO TAXA OF *ARDISIA* SUBGENUS *GRAPHARDISIA*

1. Stoloniferous subshrubs mostly less than 1(–2) m tall; leaf blade margins sharply and irregularly dentate; corolla tube and filaments yellow glandular-granulose; Ecuador to Bolivia and adjacent Brazil.1. *A. weberbaueri*
1. Shrubs to small trees (0.5–)2–6(–10) m tall without stolons; leaf blade margins entire, undulate or crenulate; corolla tube yellow glandular-granulose; filaments glabrous or sessile to stalked glandular-papillate; Nicaragua to Colombia.
 2. Sepals membranaceous, oblong, 4.2–8 mm long, apically broadly rounded to obtuse, hyaline throughout, the margins entire; filaments sessile to stalked- glandular-papillate.2. *A. opegrapha*
 3. Inflorescence obpyramidal; leaf blades oblanceolate or rarely obovate, 3.5–7.5(–8) cm wide, 3 or more times longer than wide.
 4. Floral bracts caducous; stamens 5.2–6.5 mm long; filaments 2.5–3 mm long; sepals 5–8 mm long. ...2a. *A. opegrapha* subsp. *opegrapha*
 4. Floral bracts persistent; stamens 3.8–5 mm long; filaments 1.5–2 mm long; sepals 4.2–5.2 mm long.2b. *A. opegrapha* subsp. *wagneri*
 3. Inflorescence globose; leaf blades elliptic to broadly elliptic (7.5–)8–14.5 cm wide, 2–2.5 times longer than wide.
 -2c. *A. opegrapha* subsp. *paquitensis*

- 2. Sepals chartaceous, ovate, 1.5–2.5 mm long, apically acute, opaque except at margin, the margins subentire to erose; filaments glabrous.3. *A. bartlettii*
- 5. Sepals 1.5–1.8 mm long; petal lobes 6–6.5 mm long; stamens 3.5–4.8 mm long; style base tapering; tall wet forests.3a. *A. bartlettii* subsp. *bartlettii*
- 5. Sepals 2–2.5 mm long; petal lobes 7–8 mm long; stamens 4.5–5.7 mm long; style base stylopodic; strand vegetation and beach forests.3b. *A. bartlettii* subsp. *lilacina*

1. *Ardisia weberbaueri* Mez, (Figs. 1D, 2), Repert. Spec. Nov. Regni Veg. 3:97. 1906. *Graphardisia weberbaueri* (Mez) Lundell, Wrightia 7:46. 1982. TYPE: PERU. JUNÍN: Prov. Tarma, near La Merced in Chanchamoyo Valley, without elev., Dec 1902 (fl), *A. Weberbauer 1809* (HOLOTYPE: B-dest.; LECTOTYPE, here designated: F).

The holotype of *Ardisia weberbaueri* was destroyed in Berlin (B) in 1943 during WWII. According to *Index Herbariorum* (Holmgren et al. 1990), other institutions housing duplicate *A. Weberbauer* collections are: F, MOL, USM and WRS�. Through the kindness of Carlos Reynel (MOL), Asunción Cano (USM), and Krzysztof Swierkosz (WRS�), thorough searches were conducted at their respective institutions, all failing to locate isotypes of *A. Weberbauer 1809*. A fragment of the holotype, including a mature flower and leaf fragment, was taken from B in 1926, and is available at F (a “clastotype”—see Pipoly 1983), and is here selected as the lectotype.

*Ardisia vigo*i Lundell, Wrightia 6:94. 1979. SYN. NOV. *Graphardisia vigo*i (Lundell) Lundell, Phytologia 48:140. 1981. TYPE: PERU. SAN MARTÍN: Prov. Mariscal Cáceres, Dtto. Tocache Nuevo, Río de la Plata, NE of Tocache, 500–600 m, 5 May 1975 (fl, fr), *J. Schunke Vigo 8384* (HOLOTYPE: LL-TEX; ISOTYPE: MO).

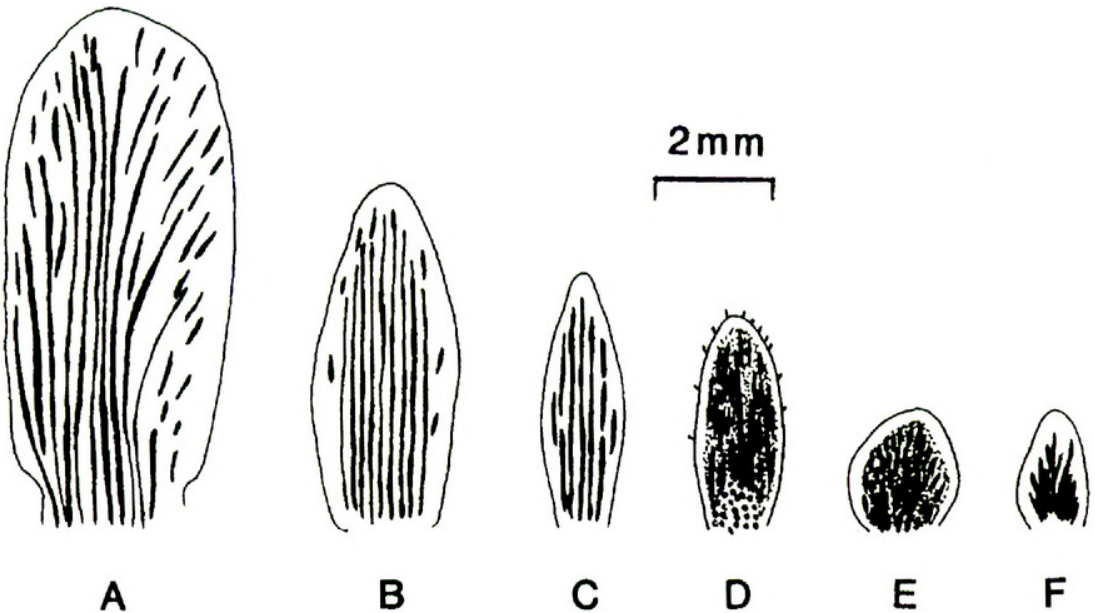


FIG. 1. Comparison of sepal size, shape and punctations among the taxa of *Ardisia* subgen. *Graphardisia*. See individual taxon descriptions for details. A. *Ardisia opegrapha* subsp. *opegrapha*, drawn from *G. Webster 16867*. B. *Ardisia opegrapha* subsp. *wagneri*, drawn from *L.D. Gomez 24093*. C. *Ardisia opegrapha* subsp. *paquitensis*, drawn from *Araquistain 3007*. D. *Ardisia weberbaueri*, drawn from *R. Vasquez 5924*. E. *Ardisia bartlettii* subsp. *bartlettii*, drawn from *H. Bartlett & T. Lasser 16720*. F. *Ardisia bartlettii* subsp. *lilacina*, drawn from *J. Dwyer 4354*.

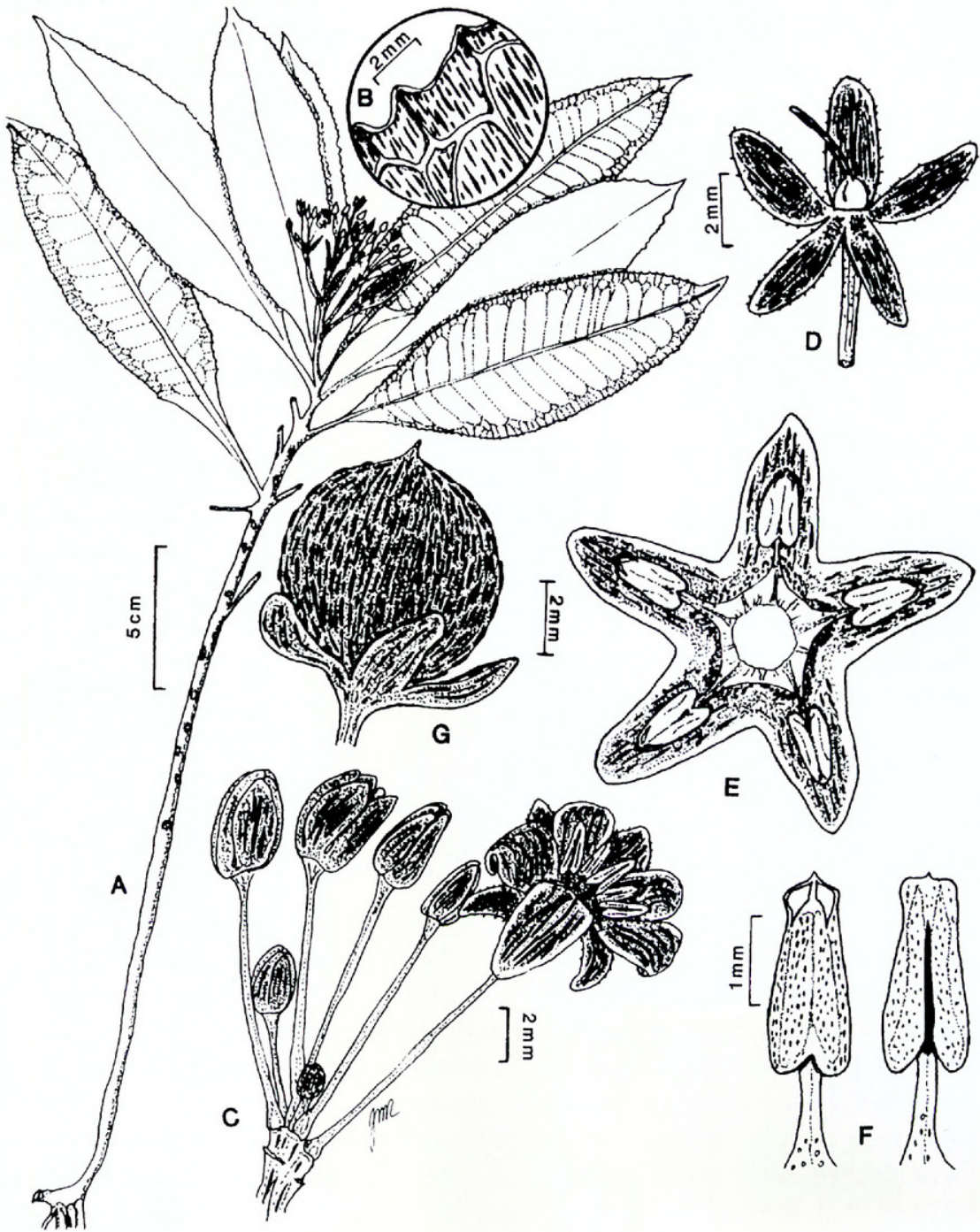


FIG. 2. *Ardisia weberbaueri* Mez. A. Habit, flowering branch. B. Detail of abaxial leaf surface. C. Detail of inflorescence. D. Detail of flower, showing calyx and pistil. E. Detail of flower, showing corolla and stamens. F. Detail of stamen, showing adaxial and abaxial surfaces. G. Fruit. A-G drawn from R. Vasquez 5924.

Stoloniferous *subshrubs* to *shrubs*, 0.75–1.0(–2.0) m tall. *Branchlets* slender, terete, 2–4 mm in diam., glabrous to scattered glandular-granulose. *Leaves* alternate; blades membranaceous to chartaceous, oblong to elliptic, 8.2–19.4 cm long, 1.9–6.6 cm wide apically acuminate, the acumen 5–9 mm long, basally acute to acuminate, decurrent on the petiole, the midrib impressed above, prominently raised below, the secondary veins 22–26 pairs, obscure above, prominent below, conspicuously punctate and punctate-lineate, glabrous, the margins irregularly dentate, the teeth 0.4–0.8 mm long, mostly flat; petioles slender, canaliculate, 0.7–2.1 cm long, glabrous. *Inflorescence* terminal, 2.5–7 cm long, 2.5–8 cm wide, usually shorter than the leaves, the rachis conspicuously punctate and punctate-lineate, glabrous to sparsely scattered glandular-granulose; peduncle 2–5 mm long; inflorescence branch bracts foliaceous, membranaceous, oblong or elliptic, 1.4–2.5 cm long, 0.5–0.8 cm wide, apically acute to rounded, the midrib impressed above, prominently raised below, the secondary veins obscure above and below, conspicuously punctate and punctate-lineate, glabrous, the margins entire to undulate; petioles 0.8–1.2 mm long, glabrous; inflorescence branches 2–9 mm long, conspicuously punctate and punctate-lineate, glabrous to scattered glandular-granulose, bearing terminal corymbs; floral bracts resembling secondary inflorescence branch bracts, but 7.2–8.1 mm long, 1.7–2.2 mm wide, sessile or nearly so; pedicels 11.6–13.5 mm long, slender, mostly accrescent in fruit, glabrous to scattered glandular-granulose. *Flowers* 5-merous (occasionally with sepals 6–7), membranaceous, 4.5–5.5 mm long; calyx with sepals free, oblong, 3.2–4.2 mm long, 1.4–1.6 mm wide, apically broadly obtuse to rounded, densely and prominently punctate and punctate-lineate, glabrous, except densely glandular-granulose within basally, the margins hyaline, subentire, glandular-ciliolate; corolla rotate, 4.3–5.3 mm long, the tube 0.4–0.5 mm long, densely yellow glandular-granulose within apically above staminal tube and below corolla tube and lobe junction, the lobes ovate, 4.1–4.8 mm long, 2.3–2.5 mm wide, apically rounded to obtuse, prominently punctate and punctate-lineate, glabrous, the margins entire; stamens 3.2–3.8 mm long, connate by their bases and adnate to corolla to form a tube 0.4–0.5 mm long, the free portion 2.8–3.3 mm long, the filaments 1.2–1.4 mm long, 0.5–0.7 mm wide at base, conspicuously punctate, glabrous except scattered sessile glandular-papillate basally, the anthers linear-lanceoloid, 2.0–2.2 mm long, 0.9–1.0 mm wide at base, apically apiculate, basally sagittate, dehiscent by subapical pores, the connective prominently black punctate dorsally; pistil obturbinate, the ovary glabrous, the style 1.9–2.7 mm long, slender, tapering, punctate, glabrous, the ovules 13–14, pluriseriate. *Fruit* globose, 6.1–6.8 mm in diam., densely and prominently punctate and punctate-lineate, the style base persistent, glabrous.

Distribution.—*Ardisia weberbaueri* is endemic to the junction of the Andes

and Western Amazonia, from Napo and Pastaza Provinces, Ecuador, southward through the Departments of Loreto, San Martín, Junín and Madre de Dios, Peru, to the Departments of Beni, La Paz and Santa Cruz, Bolivia and the adjacent state of Acre, Brazil. It grows from 180–1,100 m in elevation. This is the first report of the species for Ecuador.

Ecology and conservation status.—*Ardisia weberbaueri* is restricted to tall, lowland and premontane tropical moist and wet forests, where it is an understory subshrub, growing in loose detritus in sheltered areas near rocks and tree buttresses. While it is certainly not common, at this time, there are no data to suggest the species is threatened.

Etymology.—*Ardisia weberbaueri* is named in honor of August Weberbauer (1871–1948), a German botanist and phytogeographer who collected in Peru from 1901–1905 and again from 1908–1948 (Stafleu & Cowan 1988). During the 1920s, he was sponsored by the Field Museum of Natural History (F), under J. Francis MacBride's *Flora of Peru* project. Many of Weberbauer's collections are type specimens today. *Ardisia weberbaueri*'s taxonomic synonym, *Ardisia vigoi* Lundell, was named in honor of José Schunke Vigo, who had a long collaborative history with the Missouri Botanical Garden (MO), Field Museum of Natural History (F) and Peruvian Herbaria's revived *Flora of Peru* project. José is the son of Carlos Schunke, who was guide and field assistant to J. Francis MacBride of the Field Museum and G.S. Bryan of the University of Wisconsin, during their 1923 botanical expedition to Peru (Dahlgren 1936). Unfortunately, Lundell (1979), confused José's second surname (maternal) with his legal (paternal) one, hence the epithet "vigoi" instead of "schunkei."

Additional specimens examined. **ECUADOR.** **Napo:** Laguna de Yuturí, along both sides of Río Yuturí, 00° 36' S, 76° 01' W, 220 m, 26 Feb 1990 (fr), *J. Jaramillo & A. Grijalva 11402* (K); Cantón Orellana, Yasuní National Park, Maxus road and pipeline under construction, km 3 of NPF-Puerto Maxus branch, 04° 01' 00" S, 76° 25' 00" W, 250 m, 10 Jun 1994 (fr), *N. Pitman & M. Aulestia 232* (BRIT, F, MO). **Pastaza:** Cantón Pastaza, "Masaramu" Oil well, of UNOCAL, 40 km NNE of Montalvo, 00° 44' S, 76° 52' W, 400 m, 1–16 May 1990 (fr), *E. Gudiño 355* (BRIT, MO, QCNE). **PERU.** **Huánuco:** Prov. Pachitea, Region Pucallpa, W part, "Sirá Mountains," and adjacent lowland; 20–24 km SE of Puerto Inca, Crest of mountain range going W to E from "Campamento Oro," to "Campamento Sirá" 09° 28' S, 74° 47' W, 600 m, 20 Dec 1987 (fr), *B. Wallnöfer 16-201287* (BRIT, MO, USM, W), 700 m, 8 Apr 1988 (fr), *B. Wallnöfer 18-8488* (BRIT, MO, W). **Junín:** Prov. Chanchamayo, Chanchamayo, without elev., 22 Oct 1863 (fl), *J. Isern 2234* (F, MA). **Loreto:** Prov. Maynas, Allpahuayo, Estación IIAP, without elev., 13 Nov 1984 (fl), *R. Vásquez et al. 5924* (MO); Prov. Maynas, Iquitos, Estación Experimental IIAP, Allpahuayo, 21 km al S de Iquitos, 4° 10' S, 73° 30' W, 180 m, 19 Sep 1990 (ster.), *J. Pipoly et al. 12168* (MO). **Madre de Dios:** Prov. Manu, Manu, Parque Nacional Manu, Cocha Juárez, Río Manu, 400 m, 3–5 May 1987 (fr), *P. Núñez et al. 8053* (MO). **San Martín:** Prov. Huallaga, Chazute, Río Huallaga, 260 m, Mar 1935 (fl), *G. Klug 3978* (F, GH, MO); Prov. Mariscal Cáceres, Quebrada Huicte, Río Huallaga, 590 m, 26 May 1964 (fr), *J. Schunke V. 6449* (MO); Dpto. Tocache Nuevo, Quebrada de Huaquisha, right

bank of Río Huallaga, without elev., 17 May 1970 (fr), *J. Schunke* V. 3983 (F), 8 Jun 1970 (fr), *J. Schunke* V. 4039 (F); Puerto Pizana, right bank of Río Huallaga, without elev., 3 Sep 1971 (fr), *J. Schunke* V. 4983 (F, MO); Quebrada de Cachiyacu de Lopuna, Progreso Hwy., 500–850 m, 21 Jul 1974 (fl, fr), *J. Schunke* V. 7647 (MO); Quebrada Paraíso, 5 km below Tocache, 400 m, 27 Nov 1974 (fl, fr), *J. Schunke* V. 8133 (MO). **BOLIVIA.** Beni: Prov. Ballivián, lower slopes of Serranía Pilon Lajas, 14.3 km N of the bridge over the Río Quiquibey, 15° 19' S, 67° 03' W, 700 m, 10 Jun 1985 (fr), *J. Solomon* 13940 (MO); Misión Fátima, S of San Borja, near Río Maniquí, on affluent of Río Chimané, behind the Misión, 240 m, 20 May 1988 (fr), *S. Beck* 16323 (MO); E slopes, 21 km from Yucumo, 15° 17' S, 67° 04' O, 1,035 m, 17 May 1989 (fr), *D. Smith et al.* 13188 (MO). **La Paz:** Prov. Nor Yungas, Alto Madidi, ridge top ca. 7 km NE of camp, 13° 35' S, 68° 46' W, 300 m, 27 May 1990 (fr), *A. Gentry & S. Estensoro* 70712 (MO); Alto Beni, trail from bridge toward San Antonio, 570 m, 3 Jan 1988 (fr), *R. Seidel & M. Schulte* 2316 (MO); Prov. Sud Yungas, Alto Beni, Sapecho Concession, Yungas, 15° 30' S, 67° 20' W, 550 m, 3 Apr 1989 (fr), *R. Seidel et al.* 2671 (MO), 3 Feb 1990, *R. Seidel & V. Baptista* 2824 (MO). **Santa Cruz:** Prov. Ichilo, Parque Nacional Amboró, 3 km SW of Estancia San Rafael de Amboró, 17 km by air, SSE of Buena Vista, forest near Río Surutu, 17° 36' S, 63° 37' W, 350 m, 29 Jul 1987 (fr), *M. Nee et al.* 35424 (MO, TEX); ca. 15 km (SE) up the Río Pitasama from the Río Surutú, 17° 44' S, 63° 40' W, 700 m, 28 Aug 1985 (fr), *J. Solomon* 14104 (MO). **BRAZIL.** Acre: Rio Acre, Seringal, São Francisco, without elev., Oct 1911 (fl), *E. Ule* 9641 (K).

Ardisia weberbaueri appears to be most closely related to *A. bartlettii*, based on its sepals that are opaque except along the margin, relatively small inflorescences with early caducous floral bracts, and non-entire margined leaf blades. However, *Ardisia weberbaueri* may be easily separated from *A. bartlettii* by its diminutive, stoloniferous habit, sharp and irregular teeth of the leaf blades, and the glandular-granulose filaments.

Detailed study of the lectotype of *A. weberbaueri* and the type of *A. vigoi* revealed no quantitative or qualitative difference between the two respective type specimens.

2. *Ardisia opegrapha* Oerst.

Shrubs or small trees (0.6–)2–10 m tall. *Branchlets* (2–)3–5(–7) mm in diam., glabrous throughout. *Leaves* alternate or pseudovercillate; blades membranaceous, elliptic, broadly elliptic, oblanceolate, or obovate, 10–30 cm long, 3.5–14.5 cm wide, apically acuminate, base acute or attenuate, decurrent on the petiole; midvein impressed above, prominently raised below, the secondary veins prominulous above, inconspicuous below, densely and conspicuously punctate and punctate-lineate, glabrous, the margins entire or irregular; petioles canaliculate and usually marginate, 0.2–3.5 cm long, glabrous. *Inflorescence* terminal, a bipinnate, radially symmetrical (globose) or obpyramidal panicle of corymbs, 2–12 cm long, 2–15 cm wide, usually shorter than the leaves; peduncle obsolete to 3.5 cm long, conspicuously punctate and punctate-lineate, glabrous, inflorescence branch bracts membranaceous, widely ovate, 7.2–26 mm long, 1.4–8 mm wide, apically broadly

rounded, densely and prominently punctate and punctate-lineate, glabrous, caducous or persistent in fruit, the margins entire; floral bracts as in secondary branch bracts except oblong, 3.7–12 mm long, 0.8–5.5 mm wide; pedicels 6–23 mm long, slender, conspicuously punctate and punctate lineate, sparsely glandular-glandulose. *Flowers* 5-merous, membranaceous, 7.5–10 mm long; calyx with sepals free, linear, oblong or broadly elliptic, 4.2–8 mm long, 2.2–3.1 mm wide; apically rounded, emarginate, densely and prominently punctate and punctate-lineate, very sparsely glandular-granulose without, densely glandular-granulose at base within, the margins entire, sparsely glandular-ciliolate or not; corolla rotate, 6.5–9.5 mm long, the tube 0.3–0.7 mm densely yellow glandular-granulose within apically above staminal tube as well as below corolla tube and lobe junction, the lobes ovate to elliptic, 6.5–9 mm long, 3.8–5.7 mm wide, apically rounded, densely and prominently punctate and punctate-lineate, glabrous, the margins entire; stamens 3.8–6.5 mm long, the staminal tube 0.3–0.8 mm long, the filaments 1–3 mm long, 0.5–0.8 mm wide, epunctate, scattered glandular-papillate, the anthers linear-lanceoloid, 2.3–3.6 mm long, 0.9–1.1 mm wide at base, apiculate, basally sagittate, concolorous, dehiscent by subapical pores, the connective inconspicuously punctate dorsally; pistil obturbinate, the ovary glabrous, the style 3.5–5 mm long, slender, punctate and punctate-lineate, glabrous, the ovules 11–13, pluriseriate. *Fruit* globose, 4.2–8 mm in diam., densely and prominently punctate, glabrous.

Ardisia opegrapha, as here circumscribed, includes three newly recognized subspecies for which combinations are made herewith.

2a. *Ardisia opegrapha* Oersted subsp. *opegrapha* (Figs. 1A, 3). *Ardisia opegrapha* Oerst., Vidensk. Meddel. Dansk Naturhist. Fören Kjøbenhavn 1861:126. 1861. *Graphardisia opegrapha* (Oerst.) Lundell, Phytologia 48:140. 1981. TYPE: COSTA RICA. ALAJUELA: Aguacate, without elev., Nov 1847 (fl), *A. Oersted* 29A (LECTOTYPE, here designated: C, (F Neg. # 22954); ISOLECTOTYPE: F).

In the Botanical Museum, University of Copenhagen Herbarium (C), there are two different collections that were cited in the protologue by Oersted, two duplicates of *A.S. Oersted* 29 from Jaris, and one of *A. Oersted* 29A from Aguacate, of which only *A. Oersted* 29A is duplicated in the Field Museum of Natural History (F). The collection from Jaris was made in November 1846, and that from Aguacate in November 1847. In Oersted's original description he states "Crescit in montibus costaricensibus Aguacate et Jaris (1500–2000'), ubi florentem et fructificantem Novembri legi," without further specifying the location. Mez (1902) and subsequent authors have not designated a lectotype. We here select the collection from Aguacate at C as the lectotype because it contains the greatest number of dissections in the original fragment packet, indicating it was a more critical element in the description of the species.

Ardisia oliveri Mast., Gard. Chron., n.s., 8:680, fig. 132. 1877. SYN. NOV. non Bot. Mag., 104[ser. 3, vol. 34]:t. 6357. 1878. *Graphardisia oliveri* (Mast.) Lundell, Phytologia 54:285. 1983. TYPE: COSTA RICA. PROV. UNKNOWN: From Messrs. Veitch & Sons Nursery, Jul 1876 (fl), *A. Endres* s.n. (HOLOTYPE: K, (LL-TEX Neg. # 71-146); ISOTYPES:

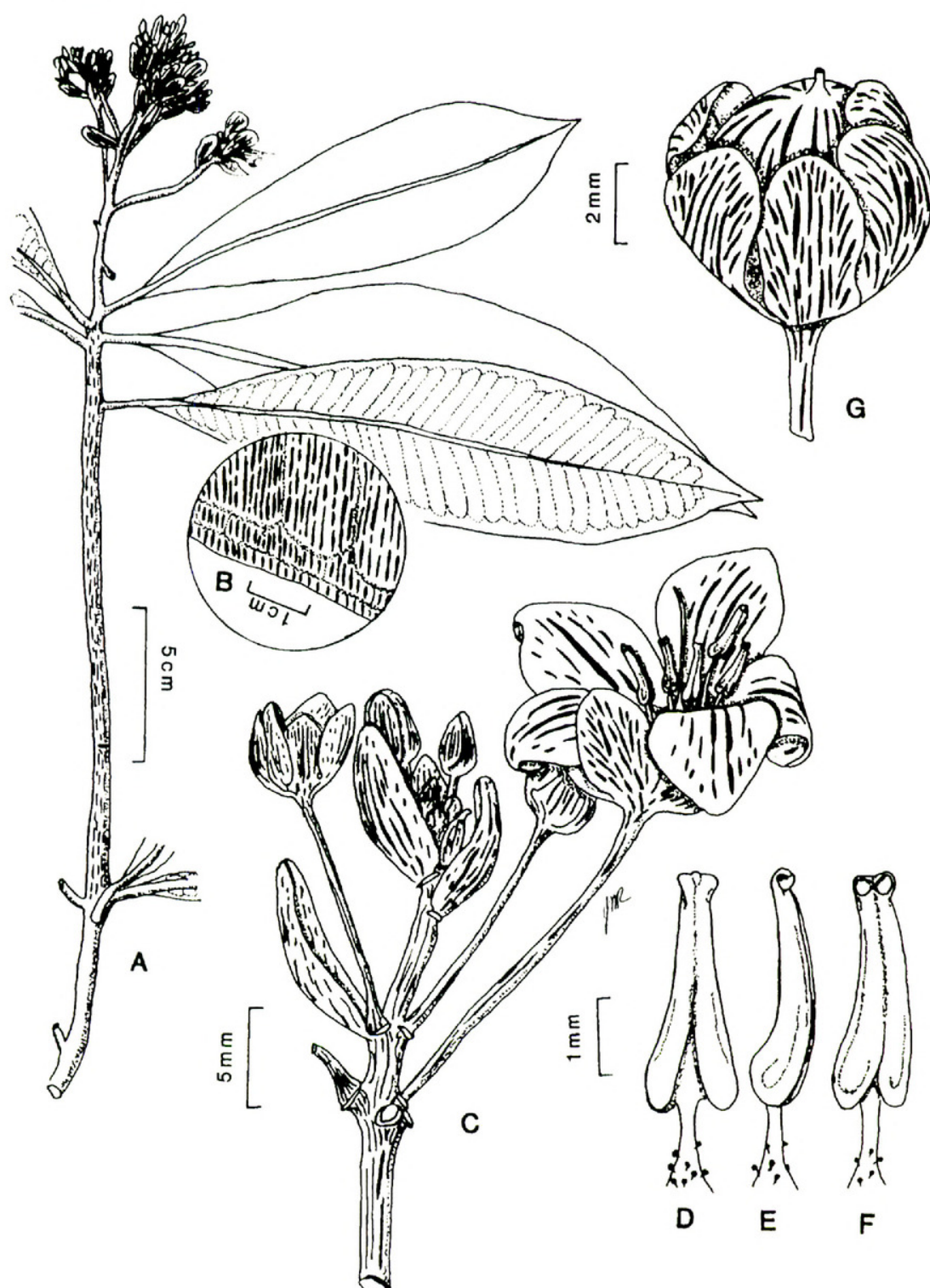


FIG. 3. *Ardisia opegrapha* Oersted subsp. *opegrapha*. A. Habit, flowering branch. B. Detail of abaxial leaf surface. C. Detail of inflorescence. D. Detail of stamen, showing adaxial surface. E. Detail of stamen, showing lateral surface. F. Detail of stamen, showing abaxial surface. G. Fruit. A, B drawn from lectotype. C–F drawn from *G. Webster 16516*. G drawn from *R. Mendoza 26*.

W 3-sheets).

- Ardisia seibertii* Standl., Ann. Missouri Bot. Gard. 24:198. 1937. SYN. NOV. *Graphardisia seibertii* (Standl.) Lundell, Phytologia 48:140. 1981. TYPE: PANAMA. COCLÉ: El Valle de Antón and vicinity, 500–700 m, 23–27 Jul 1935 (fl, fr), *R.J. Seibert 456* (HOLOTYPE: F, (F Neg. # 68250); ISOTYPES: A, K, MO (LL-TEX Neg. # 71-102)).
- Ardisia skutchii* C. V. Morton, J. Wash. Acad. Sci. 27:309. 1937. SYN. NOV. *Graphardisia skutchii* (Morton) Lundell, Phytologia 59:432. 1986. TYPE: COSTA RICA. SAN JOSÉ: Vicinity of El General, 1,070 m, Jun 1936 (fl), *A.F. Skutch 2660* (HOLOTYPE: US (CM Neg. # 49641, LL-TEX Neg. # 71-104, US Neg. # 2386); ISOTYPE: MO (LL-TEX Neg. # 71-104)).
- Ardisia subcoriacea* Lundell, Wrightia 3:193. 1966. SYN. NOV. *Graphardisia subcoriacea* (Lundell) Lundell, Phytologia 48:140. 1981. TYPE: PANAMA. COCLÉ: El Valle de Anton, vicinity of La Mesa, ca. 1,000 m, 22 Jun 1941 (fl), *P.H. Allen 2571* (HOLOTYPE: US, (LL-TEX Neg. # 71-111); ISOTYPES: A, F (F Neg. # 68253)).
- Ardisia picturata* Lundell, Wrightia 4:164. 1971. SYN. NOV. *Graphardisia picturata* (Lundell) Lundell, Phytologia 48:140. 1981. TYPE: PANAMA. PANAMÁ: Cerro Campana area, above Su Lin Motel, ca. 3,000 ft [904 m], 11 Aug 1967 (fr), *J. D. Dwyer & J.H. Kirkbride Jr. 7818* (HOLOTYPE: LL-TEX n.v.; ISOTYPES: K n.v., LL-TEX, MO, NY, UC n.v., US).
- Graphardisia coibana* Lundell, Phytologia 59:429. 1986. SYN. NOV. *Ardisia coibana* (Lundell) Lundell, Phytologia 61:63. 1986, nomen invalidum. TYPE: PANAMA. VERAGUAS: Playa Rosario, N tip of Coiba Island, without elev., 26 Aug 1970 (fr), *R. Foster 1600* (HOLOTYPE: LL-TEX; ISOTYPES: DUKE n.v., F (F Neg. # 68357), MO).
- Graphardisia nicaraguensis* Lundell, Phytologia 59:429. 1986. SYN. NOV. *Ardisia esquipulasana* Lundell, Phytologia 61:63. 1986, nomen novum invalidum, non *Ardisia nicaraguensis* Oerst., Vidensk. Meddel. Dansk Naturhist. Fören Kjøbenhavn 1861:123. 1861. TYPE: NICARAGUA. ZELAYA: Montaña Esquipulas, 130 m, 22 Nov 1951 (fr), *P.J. Shank & A. Molina R. 4719* (HOLOTYPE: F (F Neg. # 68356); ISOTYPE: US).
- Graphardisia obtusata* Lundell, Phytologia 59:430. 1986. SYN. NOV. *Ardisia obtusata* (Lundell) Lundell, Phytologia 61:66. 1986, nomen invalidum. TYPE: PANAMA. DARIÉN: Río Tuquesa, at middle Tuquesa Mining Company camp called Charco Peje, ca. 250 m, 8 Jul 1975 (fr), *S. Mori 7034* (HOLOTYPE: LL-TEX; ISOTYPE: MO).
- Graphardisia oxyphylla* Lundell, Phytologia 59:430. 1986. SYN. NOV. *Ardisia riomontana* Lundell, Phytologia 61:66. 1986, nomen novum invalidum, non *Ardisia oxyphylla* Wall., Numer. List 2291. 1830. TYPE: PANAMA. CHIRIQUÍ: 2.5 km from Questa Piedra along Río Monte Road, at stream, without elev., 27 Jun 1977 (fl), *J.P. Folsom 3975* (HOLOTYPE: LL-TEX; ISOTYPES: CR n.v., MEXU n.v., MO, NY, PMA n.v.).
- Graphardisia ustupoana* Lundell, Phytologia 59:432. 1986. SYN. NOV. *Ardisia ustupoana* (Lundell) Lundell, Phytologia 61:68. 1986, nomen novum invalidum. TYPE: PANAMA. SAN BLAS: through cultivation on mainland in front of Ustupo, overhanging river, without elev., 9 Nov 1975 (fr), *W.G. D'Arcy 9535* (HOLOTYPE: LL-TEX; ISOTYPES: BRIT, MO).
- Graphardisia murphyae* Lundell, Phytologia 63:77. 1987. SYN. NOV. *Ardisia murphyae* (Lundell) Lundell, Phytologia 63:463. 1987. TYPE: COSTA RICA. PUNTARENAS: N of La Lucha road to Progreso, 1,200 m, 23 May 1984 (fl), *H. Murphy 1248* (HOLOTYPE: DUKE, n.v., LL-TEX fragment of holotype).
- Graphardisia serenoana* [seranoana] Lundell, Phytologia 59:431. 1986. SYN. NOV. *Ardisia serenoana* (Lundell) Lundell, Phytologia 61:66. 1986, nomen invalidum. TYPE: PANAMA. CHIRIQUÍ: road from Volcán to Río Sereno [Serano], road that turns E 7.2 km from Río Sereno, 3.2 km along side road, without elev., 29 Jun 1977 (fl), *J.P. Folsom 4029* (HOLOTYPE: LL-TEX; ISOTYPES: MEXU n.v., MO, PMA n.v.).

Shrubs or small trees (1–)2–10 m tall, 2–5 cm in diam. *Branchlets* 3–5 mm in diam. *Leaves* with blades elliptic to lanceolate, broadly elliptic or oblanceolate, 12–25 cm long, 3.5–7.5 cm wide; petioles canaliculate, usually marginate, 0.2–1.5 cm long. *Inflorescence* obpyramidal, bipinnately paniculate, 2–12 cm long, 4–15 cm wide; peduncle 0.5–1.5 cm long; inflorescence branch bracts widely ovate, 16–18 mm long, 14–16 mm wide, caducous; floral bracts 7–12 mm long, 3–5.5 mm wide, oblong, caducous; pedicels 10–23 mm long. *Flowers* 9–10 mm long; sepals linear, oblong to broadly elliptic, 5–8 mm long, 2.2–2.5 mm wide; corolla 8–9.5 mm long, the tube 0.4–0.6 mm long, the lobes oblong to broadly elliptic 7.6–8.9 mm long, 4.5–5.5 mm wide; stamens 5.2–6.5 mm long, the staminal tube 0.4–0.7 mm long, the filaments 2.5–3 mm long, 0.6–0.8 mm wide, the anthers 2.7–3 mm long, 0.9–1 mm wide at base; ovary with style 4–5 mm long, the ovules 12-many. *Fruit* 5–8 mm in diam.

Distribution.—Nicaragua (Jinotega, Matagalpa, Zelaya, Río San Juan), Costa Rica (Alajuela, Puntarenas, San José), Panama (Chiriquí, Veraguas, Herrera, Los Santos, Coclé, Panamá, San Blas, Darién) and Colombia (Chocó); sea level–2,500 m elevation. It is notable that the subspecies principally inhabits areas facing the Pacific coast of Central and adjacent South America.

Ecology and conservation status.—*Ardisia opegrapha* subsp. *opegrapha* inhabits a wide range of habitats, including beach thickets; gallery forests in deciduous woodlands and dry oak forests; moist, wet, lower montane, montane, cloud and elfin forests. Because it is mostly found at forest margins, and along watercourses, subsp. *opegrapha* may be found in primary and disturbed or remnant sites.

Etymology.—The epithet 'opegrapha' comes from the Greek, 'opsis', resembling, and *graphe*, meaning drawing, picture or writing. This refers to the densely and prominently punctate and punctate-lineate vegetative and floral parts.

Additional specimens examined. **NICARAGUA**. **Jinotega**: Cerro San Pedro, Comarca Kilambé, 13° 36' N, 85° 38–39' W, 820 m, 21 Jul 1980 (fl), *J. Sandino* 192 (MO). **Matagalpa**: Las Brisas, 15 km W of Waslala, road to El Tuma, 13° 15' N, 85° 28' W, 250–300 m, 23 Dec 1982 (fr), *P. Moreno* 19225 (MO). **Río San Juan**: Buenos Aires, 1 km al N of Caserío Sábalo, along Río Sábalo, 11° 02' N, 84° 28' W, 70 m, 10 Sep 1985 (fr), *P. Moreno* 26297 (MO); between Río Santa Cruz and Caño Santa Crucita, La Palma, 11° 02–04' N, 84° 24–26' W, 40–60 m, 30 Nov–2 Dec 1984 (fr), *W. Stevens et al.* 23470 (MO). **Zelaya**: El Achioté, 11° 47' N, 84° 26' W, 200 m, 25 Aug 1982 (fr), *M. Araquistain* 3130 (MO); San Antonio, 200 m, 29 Aug 1982 (fr), *A. Laguna* 27 (MO); along Río El Zapote, W of Nueva Guinea, 11° 42' N, 84° 26' W, 130 m, 21 Aug 1983 (fr), *J. Miller & J. Sandino* 1257 (MO); 4.4 km N of base camp, base camp 3.6 km SE of Cerro San Isidro, Río Kama, Río Escondido, 12° 05–15' N, 83° 45'–84° 20' W, sea level–65 m, 16 Mar 1966 (fr), *G. Proctor et al.* 27151 (NY, LL-TEX); 5 km SE de La Providencia, along Caño Chiquito, without elev., 21 Aug 1983 (fr), *J. Sandino* 4534 (MO); Comarca de El Cabo, 40–45 km SW of Waspám, 10–100 m, 21 Jan 1970 (fr), *F. Seymour* 3783 (MO); Esquipulas and Alemán,

Río Alemán drainage, 150 m, 27–29 Nov 1951 (fr), *P. Shank & A. Molina* R. 4783 (F, LL-TEX, MO). **COSTA RICA. Alajuela:** toward center of Cerro de San Isidro, San Ramón, 1,150 m, 10 Jul 1925 (fl), *A. Brenes* 4313 (F, LL-TEX); between Santiago and San José de San Ramón, without elev., 17 Oct 1928 (fr), *A. Brenes* 6349 (F); San Miguel de San Ramón, without elev., 21 Jul 1934 (fl), *A. Brenes* 19242 (F); Río Grande, San Isidro, San Ramón-Alajuela, 1,000 m, 10 Jun 1982 (fr), *A. Carvajal* 269 (LL-TEX, MO); 3 km E of San Ramón, 1,025 m, 22 Jun 1969 (fl), *R. Lent* 1765 (F); Los Angeles de Las Gania, 1,100 m, 21 Dic 1936 (fl), *F. Solís* R. 495 (LL-TEX, MO). **Puntarenas:** Cantón Coto Brus, Las Cruces Botanical Garden, Cordillera de Talamanca, 08° 47' 10" N, 82° 58' 30" W, 1,200–1,300 m, 30 Jun 1995 (fr), *L. Angulo* 388 (BRIT, MO); "Hort. Eisgmb, Clt. Lauche," without elev., 1895 (fl), *C. Beck s.n.* (W); Cerro Pando, ridges above the Río Cotón and the Río Negro, near La Lucha, Río Cotón, 08° 55' N, 82° 45' W, 1,000–1,800 m, 19–21 Feb 1982 (fr), *K. Barringer & L. Diego* G. 1652 (F); Puerto Quepos, along stream in shady woods on W side of National Park, 16 mi E of town, without elev., 28 Feb 1982 (fr), *J. Churchill* 82022 (F); foothills of the Cordillera de Talamanca, directly N of Las Alturas, 08° 57' N, 82° 50' W, 1,400–1,500 m, 28 Aug 1983 (fr), *G. Davidse* 24159 (MO); Fila El Tigre, SE of Las Alturas, 08° 56' N, 82° 51' W, 1,350–1,450 m, 29 Aug 1983 (fr), *G. Davidse* 24176 (MO); Foothills of Cordillera de Talamanca, forested valley of the Río Cotón between Sitio Cotón (Cotoncito), and Sitio Tablas, 08° 57' N, 82° 46' W, 1,500–1,600 m, 2 Sep 1983 (fl), *G. Davidse* 24428 (MO); Parque Bolívar, without elev., 10 Jul 1945 (fl), *J. Echeverría* 4147 (F); La Tigra-Las Mellizas, 1,280 m, Aug 1983 (fl, fr), *L. Gómez et al.* 21982 (LL-TEX, MO); Cantón Coto Brus, NE slopes of Fila de Cal, between San Vito de Coto Brus and Ciudad Neily, 08° 41' N, 82° 56' 50" W, 500–620 m, 12 Jul 1985 (fr), *M. Grayum & B. Hammel* 5638 (MO); Alturas de Coto Brus, ca. 20 km NE of San Vito, 1–3 km S of Las Alturas, 08° 56' N, 82° 50' W, 1,300–1,400 m, 13 Jul 1985 (fl), *B. Hammel & M. Grayum* 14201 (MO); Las Cruces Botanical Garden, San Vito, jungle trail, 08° 47' 08" N, 82° 57' 29" W, 1,250 m, 4 Jul 1994 (fl), *W. Kress & T. Prinzie* 4572 (MO, US); Amistad Biosphere Reserve, near Las Alturas de Cotón Biological Station, 08° 57' 00.3" N, 82° 49' 56.8" W, 1,455–2,100 m, 8 Jul 1994 (fl), *W. Kress & T. Flores* 4266 (MO, US); 1,475–1,750 m, 8 Jul 1994 (fl), *W. Kress & T. Prinzie* 4582 (BRIT, MO, US); above La Tigra, Talamanca Range, near Panamanian border, 1,600–1,800 m, 20 Mar 1982 (fr), *D. Hazlett* 5064 (F); between Sitio Tigra and Sitio Las Tablas picnic area, near Cerro Chivo, S of Cotón river, 1,600–1,800 m, 17 Jul 1983 (fl), *D. Hazlett* 5229 (F); beside Río Bella Vista near Las Alturas, 08° 56' N, 82° 51' W, 1,300 m, 8 Jul 1972 (fl), *R. Lent* 2693 (F, MO); Cañas Gordas, 1,100 m, Feb 1897 (fr), *H. Pittier* 11190 (LL-TEX); 1 mi S of San Vito de Java, 3,500 ft [1,067 m], 18 Aug 1967 (fr), *P. Raven* 21889 (F, MO); Piedra Blanca de Villa Colón, 1,200 m, 17 Abr 1935 (fl), *M. Valerio* 1268 (F); 7.5 km NE of Sabalito, 08° 51' N, 82° 53' W, 1,021 m, 7 Jul 1977 (fl), *G. Webster* 21876 (F); Finca Loma Linda, SW of Cañas Gordas, 08° 44' N, 82° 56' W, 3,600 ft [1,097 m], 17 Jul 1977 (fl), *G. Webster* 21937 (F); 4 km S of Las Alturas, 1,400 m, 15 Jul 1977 (fl), *R. Wilbur et al.* 22713 (MO). **San José:** forest along Quebrada de los Micos, ca. 8.5 km by road, W of Ciudad Colón, 09° 55' 50" N, 83° 17' 50" W, 600 m, 16 Jan 1986 (fr), *M. Grayum & P. Sleeper* 6103 (MO); Zona Protectora La Cangreja, along Río Negro, ca. 1.5 km E of Santa Rosa de Puriscal, 09° 42' N, 84° 23' 05" W, 320 m, 14 May 1987 (fl), *M. Grayum et al.* 8325 (MO); between Pedernal and Candelaria, 900 m, 29 May 1966 (fl), *A. Jiménez* 3966 (F, MO); road from Santiago to Parrita, 600 m, 24 Sep 1967 (fr), *R. Lent* 1321 (F, NY); Zona Protectora La Cangreja, Santa Rosa de Puriscal, en las márgenes del Río Negro, 09° 42' 24" N, 84° 23' 35" W, 400 m, 10 Aug 1992 (fr), *J. Morales* 318 (BRIT, MO); "Cultivé, Jardin Monte Alegre á San José", without elev., without date (fl), *H. Pittier* 2298 (BR); vicinity of El General, 1,190 m, Nov 1936 (fl, fr), *A. Skutch* 2890 (GH, MO), 670 m, Jun 1939 (fl), *A. Skutch* 4371 (A, F, K, LL-TEX, MO); Cantón Turrubares, flank of Cerro

Pelón, Zona Protectora Cerros de Turrubares, 09° 48' 50" N, 84° 28' 00" W, 1,500 m, 7 Nov 1990 (fr), *R. Zúñiga et al.* 392 (BRIT, MO). **PANAMA.** Chiriquí: Cerro Colorado, mining road 15.6 mi above bridge over Río San Félix, 1,330 m, 21 Nov 1979 (fr), *T. Antonio* 2573 (LL-TEX, MO); Cerro Colorado, 8.5 km from Escopeta, along stream, 800–1,000 m, 17 Aug 1977 (fr), *J. Folsom* 4925 (LL-TEX, MO). Coclé: vicinity of El Valle, 800–1,000 m, 22 Dec 1936 (fl), *P. Allen* 72 (LL-TEX, MO); vicinity of El Valle, 800–1,000 m, 5 Sep 1938 (fl, fr), *P. Allen* 786 (LL-TEX, MO); N rim of El Valle, without elev., 4 Jun 1939 (fl), *P. Allen & A. Alston* 1846 (MO); El Valle de Antón, 750 m, 2 Jul 1941 (fl), *P. Allen* 2577 (A, LL-TEX, MO), 1,000 m, 16 Jun 1946 (fl), *P. Allen* 3535 (BM, MO); El Valle de Antón, N hills, without elev., 29 Jun 1946 (fl), *P. Allen* 3561 (F-3-sheets, G, LL-TEX -2 sheets, MO, MU); El Valle, without elev., 20 Jun 1966 (fl) *K. Blum et al.* 2382 (MO); 5 km W of El Valle on dirt road to top of grassy ridge, 3,000 ft [914 m], 26 Feb 1978 (fl), *B. Hammel* 1764 (LL-TEX, MO); hills NE of El Valle de Antón, 2,000 ft [610 m], 27–29 May 1967 (fl), *W. Lewis et al.* 1803 (LL-TEX, MO); El Valle, on mountain slope near hotel, without elev., 30 Nov 1975 (fl), *R. Mendoza* 26 (MO); ca. 15–20 km NE of La Pintada towards Toábre, largest peak in vicinity, 600–1,000 ft [183–305 m], 15 Feb 1981 (fl), *K. Sytsma & W. D'Arcy* 3610 (MO); border Coclé-Panamá Prov., N slopes of Cerro Guacamayo, SE of El Valle, 08° 36' N, 80° 07' W, 1,800 ft [549 m], 3 Jul 1971 (fl), *G. Webster* 16867 (MO); between Las Margaritas and El Valle, without elev., 15 Jul–8 Aug 1938 (fl), *R. Woodson et al.* 1239 (A, LL-TEX, MO), 1746 (MO). **Herrera:** hill above Chepo de Las Minas, 700 m, 19 Dec 1977 (fr), *J. Folsom et al.* 6991 (LL-TEX, MO); W of Las Minas, on Montosa de Chepo, vicinity of Chepo, 07° 42' N, 80° 51' W, 900 m, 20 May 1987 (fl), *G. McPherson* 10933 (MO, PMA). **Los Santos:** Río Guanico Valley, 07° 18' N, 80° 30' W, 600 m, 25 May 1986 (fl), *G. McPherson* 9248 (BRIT, LL-TEX, MO, PMA); above Guanico River, on hills W of river, 07° 20' N, 80° 30' W, 550–650 m, 5 Jan 1989 (fr), *G. McPherson* 13513 (BRIT, MO, PMA). **Panamá:** Camino de Plantación, 09° 04' N, 79° 39' W, 80 m, 1 Jun 1995 (ster.), *S. Aguilar & A. Castillo* 2116 (F); Summit of Cerro Campana, 800–1,000 m, 1 Sep 1940 (fl), *P. Allen* 2226 (F, LL-TEX); Cerro Campana, trail Campana to Chica, 600–800 m, 10 Aug 1941 (fl), *P. Allen* 2661 (LL-TEX); Interpretation Trail, 1 km E of INRENARE Forest Ranger Camp, 8° 40' N, 79° 55' W, 800–900 m, 2 Aug 1989 (fl), *M. Correa et al.* 5139 (BRIT, MO, PMA); Cerro Campana above Su Lin Motel, without elev., 25 May 1971 (fl), *T. Croat* 14746 (MO); Cerro Campana at turnoff to FSU cabin, without elev., 20 Jul 1974 (fl), *T. Croat* 25189 (MO); Cerro Campana, 2,500 ft [762 m], 17 Aug 1982 (fr), *W. D'Arcy & C. Hamilton* 14976 (LL-TEX, MO); Cerro Campana, upper slopes in National Park, 207 m, 13 May 1980 (fl), *D. LeDoux* 2630 (MO); Cerro Campana, beyond Su-Lin, 2,700–3,000 ft [823–914 m], 8 Sep 1966 (ster.), *J. Duke* 8650A (MO); Cerro Azul, 1 mi below Goofy Lake, 2,000 ft [610 m], 21 Jul 1972 (fl), *A. Gentry & J. Dwyer* 5512 (F, MO); Cerro Campana, slopes S of radio tower, 2,500 ft [762 m], 1 Jul 1978 (fl), *B. Hammel* 3761 (LL-TEX, MO); between peaks of Cerro Trinidad, saddle on SE slope, without elev., 5 May 1968 (fl), *J. Kirkbride & J. Duke* 1642 (MO); Cerro Campana, without elev., 10 Dec 1967 (fl), *W. Lewis et al.* 3038 (LL-TEX, MO); Altos de Campana, 285 m from Motel Su Lin, 951 m, 25 Jun 1977 (fl), *R. Méndez* 45 (MO), without elev., 25 Jun 1977 (fl), *R. Méndez* 47 (MO), 3,045 ft [928 m], 3 Dic 1977 (fr), *R. Méndez* 80 (F, MO); Cerro Campana, 2,800 ft [853 m], 29 Aug 1965 (fl), *S. McDaniel* 6912 (MO); W of Inter-American Hwy. near Capira, Cerro Campana, 08° 40' N, 79° 50' W, 900 m, 11 Nov 1985 (fl, fr), *G. McPherson* 7458 (BRIT, F, LL-TEX, MEXU, MO, PMA, US); Parque Nacional Altos de Campana, Interpretation Trail, 1 km E of forest INRENARE forest ranger cabin, Tree No. S2158, 08° 40' N, 79° 55' W, 800–900 m, 8 Jul 1988 (fl), *M. Ruíz et al.* 165 (BRIT, PMA), 30 Sep 1988 (fr), *M. Ruíz et al.* 210 (BRIT, PMA), 2 Aug 1989 (fl), *M. Ruíz et al.* 5139 (BRIT, PMA), 23 Aug 1990 (fl), *M. Ruíz et al.* 7320 (BRIT, PMA), 23 May 1991 (fl), *M. Ruíz et al.* 7800 (BRIT,

PMA), 13 Jun 1991 *M. Ruiz et al.* 7865 (BRIT, PMA); Goofy Lake, SW facing slope, 500 m, 5 Jul 1976 (fl), *G. Sullivan* 58 (MO); Cerro Campana, 08° 40' N, 79° 55' W, 2,700–2,800 ft [823–853 m], 11–12 Jun 1971 (fl), *G. Webster & G. Breckon* 16516 (MO, TEX). **Veraguas:** Vicinity Santa Fé, forested slopes of Cerro Tute, 2,500 ft [762 m], 25 Mar 1947 (fl), *P. Allen* 4404 (F, G, MO); vicinity of Escuela Agricultura Alto Piedra, near Santa Fé, along trail to top of Cerro Tute, 3,600–4,000 ft [1,097–1,219 m], 29 Jun 1980 (fl), *T. Antonio* 4961 (LL-TEX, MO); Islas Contreras, Isla Uva, 08° 48' N, 81° 45' W, 50 m, 18 Jul 1984 (fr), *H. Churchill* 5687 (LL-TEX, MO); along road on Pacific slope 1–3 km above Escuela Agrícola Alto Piedra, 700–800 m, 26 Jul 1974 (fl), *T. Croat* 25995 (LL-TEX, MO); between Santa Fé and Escuela Agrícola Alto de Piedras, without elev., 29 Aug 1974 (fr), *T. Croat* 27350 (LL-TEX, MO); 0.2 mi beyond fork in road at Escuela Agrícola Alto de Piedra on road to Río Calovebora, 750 m, 3 Apr 1976 (fl, fr), *T. Croat & J. Folsom* 33865 (LL-TEX, MO); above Santa Fé beyond Escuela Agrícola Inter-Americana, 1.8 mi beyond fork in road on Pacific slope, on side of Cerro Tute, without elev., 5 Apr 1976 (fr), *T. Croat* 34205 (LL-TEX, MO); along road between Santa Fé and Río Calovebora, 1.8 mi beyond Escuela Agrícola Alto de Piedra, 735 m, 5 Apr 1976 (fr), *T. Croat & J. Folsom* 34267 (MO); vicinity of Santa Fé, along dirt road past Escuela Circo Alto de Piedra, formerly Escuela Agrícola Alto de Piedra, to Río Luis, along Río Primero Brazo, first stream below school, on Atlantic Coast, 08° 33' N, 81° 08' W, 490 m, 28 Jun 1987 (fl), *T. Croat* 66873 (BRIT, LL-TEX, MO, PMA); Parque Nacional, Cerro Tute, vicinity of Santa Fé, along road between Alto Piedra, on slopes of Cerro Tute, 800–1,030 m, 15 Jul 1994 (fl), *T. Croat & G. Zhu* 76926 (MO); 7 km NW on road to Santa Fé, without elev., 5 Dec 1975 (fr), *W. D'Arcy* 10274 (MO); SW side of Cerro Tute, La Cuchilla, 2,500 m, 10 Sep 1982 (fl), *W. D'Arcy* 15019 (MO); Isla de Coiba, without elev., 18 Aug 1961 (fl, fr), *J. Dwyer* 1612 (F); along beach of Isla de Coiba, without elev., 28 Jul 1962 (fr), *J. Dwyer* 2363 (MEXU, NY); traditional campsite, 1 km past Ag School, forest slope to the rear, road from Santa Fé, 1,000–1,200 m, 5 Feb 1977 (fr), *J. Folsom & L. Collins* 1613 (MO); shoulder of Cerro Tuti, without elev., 25 May 1977 (fl), *J. Folsom et al.* 3375 (MO); Cerro Tute ridge up from former Escuela Agrícola, Santa Fé, 08° 35' N, 81° 05' W, 800–1,100 m, 15 Jul 1983 (fl), *C. Hamilton & K. Krager* 3973 (LL-TEX, MO); trail on ridge to summit of Cerro Tute, Cordillera de Tute, 1 km past Escuela Agrícola Altos de Piedras, W of Santa Fé, 08° 36' N, 81° 06' W, 750–950 m, 15 Dec 1981 (fl), *S. Knapp & K. Sytsma* 2498 (LL-TEX, MO); (fr), *S. Knapp & K. Sytsma* 2518 (LL-TEX, MO); above Escuela Agrícola Alto de Piedra, just W of Santa Fé, 3,200 ft [975 m], 7 Jun 1973 (fl), *J. Luteyn* 4012 (LL-TEX); N of Santa Fé, on property of Escuela Agrícola Alto de Piedra, woods near cattle shelter at Girasol, 16 Oct 1974 (fl), *S. Mori & J. Kallunki* 2520 (LL-TEX, MO); Cerro Tute, ca. 10 km NW of Santa Fé, on lower slopes, 750–1,000 m, 19 Jun 1975 (fl), *S. Mori* 6738 (LL-TEX, MO), 2 Aug 1975 (fl), *S. Mori et al.* 7545 (LL-TEX, MO); Cerro Tute, along ridge-trail towards summit, 08° 30' N, 81° 07' W, 1,000–1,250 m, 21 Mar 1987 (fr), *G. McPherson* 10744 (MO); vicinity of Cerro Tute-Arizona, along trail to summit beyond Altos de Piedra, above Santa Fé, 08° 30' N, 81° 10' W, 850–1,100 m, 27 Jul 1988 (fl), *G. McPherson* 12797 (BRIT, F, LL-TEX, MO, PMA); along trail to summit of Cerro Tute, ca. 3 km above Escuela Agricultura Alto Piedra near Santa Fé, 2600–2800 ft [792–853 m], 4 Jan 1981 (fr), *K. Sytsma & T. Antonio* 2997 (BRIT, MO). **COLOMBIA.** **Chocó:** Quebrada Changamé to the mouth of the Río Jurubidá, 06° 05' N, 77° 10' W, sea level–100 m, 5 May 1990 (fl), *C. Barbosa* 6412 (BRIT, MO); trail between Curiche and Alto de Curiche, 10–1,000 m, 22 Jun 1968 (fl, fr), *J. Duke* 15799 (MO, OS).

It is notable that *Ardisia coibana* (Lundell) Lundell, *A. esquipulasana* Lundell, *A. obtusata* (Lundell) Lundell, *A. riomontana* Lundell, and *A. ustupoana* (Lundell) Lundell, are all invalid names because Lundell (1986) made the

transfers “to obviate the incentive of workers to undertake such unnecessary reductions [of *Icacorea* (Aubl.) Mez, *Auriculardisia* Lundell, *Gentlea* Lundell, *Graphardisia* (Mez) Lundell, *Oerstedianthus* Lundell, *Ibarrea* Lundell, *Amatlanianthus* Lundell, and *Zunilia* Lundell] to subgenera.” Therefore, according to ICBN 34.1, we feel that the names are invalidly published because both clauses, “(a) when it is not accepted by the author in the original publication, and (b) when it is merely proposed in anticipation of the future acceptance of the group concerned, or of a particular circumscription, position or rank of the group,” are clearly fulfilled. However, this is not the case for *Ardisia murphyae* (Lundell) Lundell because the transfer (Lundell 1987) was effected with no commentary on the part of the author. We have not validated Lundell’s combinations in *Ardisia* here because we consider these names taxonomic synonyms and to do so would require that we recognize them as distinct taxa.

Ardisia opegrapha subsp. *opegrapha* exhibits great quantitative variation among relative size of its organs within individuals and among populations within its somewhat restricted geographic range. Repeated sampling from one individual at Parque Nacional Altos de Campana, Panama (M. Ruíz *et al.* 165, 210, 5139, 7320, 7800, 7865) over a three year period revealed that relative size of leaves to inflorescence is highly variable even within the same individual. Given that the inflorescences are terminal, the branches are pseudoverticillate and growth is rhythmic, *Ardisia opegrapha* exhibits Scarrone’s Model (Hallé *et al.* 1978). Repeated collections would amount to a pruning experiment and while the tree grew from 1.5 m tall when first collected in July of 1988 (M. Ruíz *et al.* 165) and reached a height of three meters in June of 1991 (M. Ruíz *et al.* 7865), some of the radical size difference among the leaves on the specimens may be consequent to reiteration phenomena previously discussed by Pipoly (1992, 1998). Unfortunately, no data is available to determine whether successive specimens were taken from normal sympodial (by substitution) branches of the tree, or from reiterative (bayonet type) shoots as a direct result of pruning effected during specimen collection. Morphological variation among populations is much greater than that observed within individuals, and this plasticity has led to overdescription, because species circumscription has been reliant on relative size of inflorescences to leaves, bracts to pedicels, relative crowding of the flowers in the corymbs, length of floral parts, and plant height. The rationale for relegating 12 species to synonymy is explained below; relative terms (larger, smaller, thinner, and thicker) refer to comparisons with populations with features of the type of *Ardisia opegrapha*.

Ardisia oliveri was collected from populations whose inflorescences are larger than average, large relative to the leaves, and whose flowers were in full anthesis. *Ardisia seibertii* also has inflorescences that are large relative

to the size of the leaves; the inflorescence branches bear pedicels in high anthotactic spirals, giving the impression that the flowers are in umbels rather than true corymbs. The type of *Ardisia skutchii* is notable only for its sepals that are slightly shorter and wider than the average, short petioles and flowers white with only a slight pink tinge. *Ardisia subcoriacea* was described because it has relatively smaller, subcoriaceous leaves, petioles not marginate to the base, smaller flowers, elliptic sepals with hyaline margins and short stamens. *Graphardisia coibana*, whose type is a fruiting collection, was separated by its thick leaves with abruptly caudate-acuminate apices and long-attenuate bases. However, both of these features lie well within the range of quantitative variation for the subspecies.

Ardisia picturata's type represents populations with extremely thin leaves, but otherwise identical to "typical" subspecies *opegrapha*. It is interesting to note that the type (Dwyer & Kirkbride 7818) is a specimen that amply demonstrates the range of variation in size and shape of the leaves within the taxon; the LL-TEX isotype has small nearly elliptic leaves, while the isotypes at MO and NY have leaves nearly twice as large as the LL-TEX sheet, and are elliptic to widely oblanceolate (essentially obovate). Clearly, there is no practical way to separate the *A. picturata* morphotype. Other taxa segregated principally because of thin leaves include *Graphardisia nicaraguensis* and *G. obtusata*, both of which are otherwise notable for their oblanceolate and oblong leaves, the former with obovate or elliptic sepals and the latter with narrowly obtuse sepal apices. Recognition of these various taxa amounts to describing plants different in overall aspect rather than unique characters.

Other examples of minor variations used to separate species include the sparsely ciliolate sepals found on the type of *Graphardisia ustupoana*, and the pellucid rather than black punctate leaves found on the type of *Graphardisia murphyae*. In addition, *Graphardisia oxyphylla* has reddish instead of black punctate-lineate sepals, relatively thick petioles and flower size at the smaller end of the continuum for the subspecies. The description of *Graphardisia seranoana* was based primarily on its subsessile anthers, but reexamination of the type reveals that the measurements were taken from very young floral buds. The duplicate collection at MO contained more mature buds, and open floral remnants with stamens well within the size range of variation found in subsp. *opegrapha*. Therefore the mistake was owing to the holotype specimen's condition rather than to a biological characteristic.

Ardisia opegrapha is most closely related to *A. bartlettii* based on its yellow glandular-granulose corolla tube, but can easily be separated from it by the membranaceous, oblong apically broadly rounded to obtuse sepals with entire margins, and sessile- to stalked glandular-papillate filaments. Among the subspecies of *Ardisia opegrapha*, subspecies *opegrapha* is most

easily recognized by a combination of the obpyramidal inflorescence, caducous floral bracts and floral parts larger than the other two subspecies. It appears to be more closely related to subsp. *wagneri* than it is to subsp. *paquitensis* because of the obpyramidal inflorescence shape and leaves 3 or more times longer than wide.

2b. *Ardisia opegrapha* Oerst. subsp. *wagneri* (Mez) Pipoly & Ricketson, comb. et stat. nov. (Figs. 1B, 4). *Ardisia wagneri* Mez, Pflanzenr. IV. 236 (Heft 9):79. 1902. *Graphardisia wagneri* (Mez) Lundell, Phytologia 48:141. 1981. TYPE: PANAMA. CHIRIQUÍ: Volcán de Chiriquí [Volcán de Barú], without elev., without date (fr), *M. Wagner 623* (LECTOTYPE, here designated: GOET).

Mez (1902) listed collections from Volcán Barú, including *M. Wagner 623* and *F. Lehmann s.n.*, and cited herbaria at GOET, M, and W, without reference as to which specimen was deposited where. Searches of the collections at M and W failed to discover any material of either *M. Wagner 623* or *F. Lehmann s.n.* A misidentified collection of *Lehmann s.n.* was located at W, bearing a determination by Mez in 1901 as *Ardisia opegrapha*. Therefore, we assume it does not fit Mez's original concept of *A. wagneri*. The Wagner collection at GOET most closely fits the description of *A. wagneri* and we therefore designate it as the lectotype.

Ardisia bracteolata Lundell, Wrightia 6:65. 1979. SYN. NOV. *Graphardisia bracteolata* (Lundell) Lundell, Phytologia 48:140. 1981. TYPE: NICARAGUA. ZELAYA: 6.3 km S of bridge at Colonia Yolaina on road to Colonia Manantiales of Nueva Guinea, primary tall, evergreen forest on steep areas above stream, 200–300 m, 13–14 Feb 1978 (fr), *P.C. Vincelli 252* (HOLOTYPE: MO; ISOTYPE: NY).

Ardisia zelayensis Lundell, Wrightia 6:95. 1979. SYN. NOV. *Graphardisia zelayensis* (Lundell) Lundell, Phytologia 48:141. 1981. TYPE: NICARAGUA. ZELAYA: near Río Okwamwás, 12 km E of Rosita, without elev., 15 Jun 1978 (fl), *D. Neill 4478* (HOLOTYPE: MO (F Neg. # 55686)).

Graphardisia hyalina Lundell, Wrightia 7:273. 1984. SYN. NOV. *Ardisia neohyalina* Lundell, Phytologia 61:65. 1986, nomen novum invalidum, non *Ardisia hyalina* Lundell, Wrightia 3:99. 1964. TYPE: COSTA RICA. ALAJUELA: Finca Los Ensayos, ca. 11 mi NW of Zarcero, primary forest and perimeter, ca. 850 m, 15 Aug 1977 (fl), *T. Croat 43565* (HOLOTYPE: LL-TEX; ISOTYPE: MO).

Graphardisia purpurea Lundell, Phytologia 59:431. 1986. SYN. NOV. *Ardisia ebingeri* Lundell, Phytologia 61:63. 1986, nomen novum invalidum, non *Ardisia purpurea* Reinw. in Blume, Bijdr. 13:684. 1826. TYPE: PANAMA. CHIRIQUÍ: Boquete, 6 mi N of Concepción, second growth forest, without elev., 4 Aug 1960 (fr), *J.E. Ebinger 751* (HOLOTYPE: US; ISOTYPE: MO).

Shrubs to small trees (0.5–)2–6 m tall, 2–5 cm in diam. *Branchlets* 2–4 mm in diam. *Leaves* with blades elliptic or oblanceolate 10–23 cm long, 4–7.5(–8) cm wide; petioles canaliculate, 0.7–2 cm long. *Inflorescence* obpyramidal, a pinnate panicle of corymbs, 2–8.5 cm long, 4–15 cm wide; peduncle obsolete to 3.5 cm long; inflorescence branch bracts numerous, oblong, 10–26 mm long, 3.5–8 mm wide, persistent; floral bracts linear to oblong, 6–9.2 mm long, 1–3.1 mm wide, persistent; pedicels 6–23 mm long. *Flowers* 8–9.2 mm long; sepals oblong or widely oblong, 4.2–5.2 mm

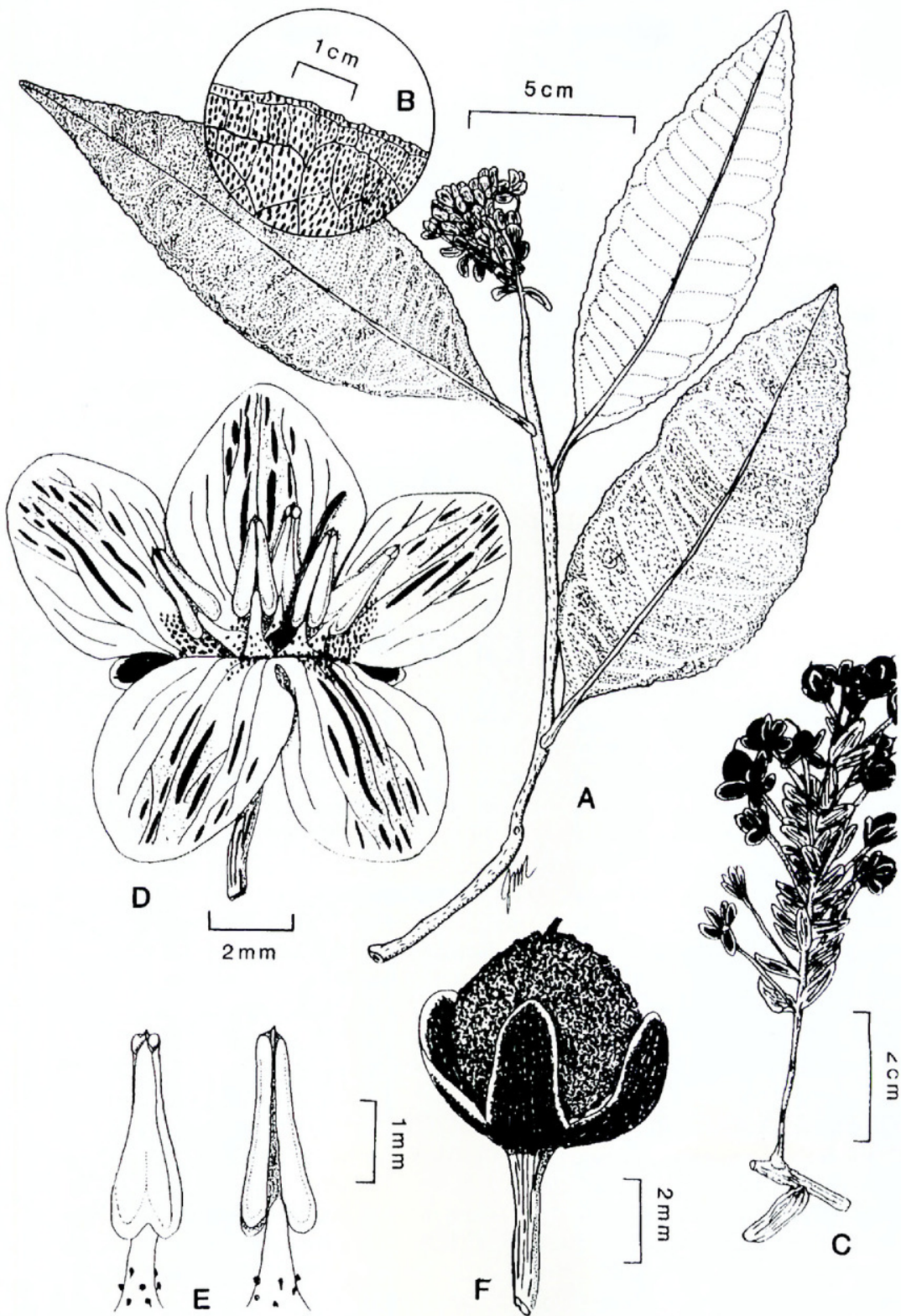


FIG. 4. *Ardisia opegrapha* Oersted subsp. *wagneri* (Mez) Pipoly & Ricketson. A. Habit, flowering branch. B. Detail of abaxial leaf surface. C. Detail of inflorescence. D. Detail of flower, showing corolla and stamens. E. Detail of stamen, showing adaxial and abaxial surfaces. F. Fruit. A, B, drawn from lectotype. C, F drawn from *P. Moreno & W. Robleto 20745*. D–E, drawn from *F. Araya et al. 306*.

long, 2.2–3.1 mm wide; corolla 7.1–9 mm long, the tube 0.3–0.5 mm, the lobes ovate, 7.0–8.5 mm long, 3.8–4.5 mm wide; stamens 3.8–5 mm long, the staminal tube 0.3–0.6 mm long, the filaments (0.5–)1.5–2 mm long, 0.5–0.7 mm wide, the anthers 2.3–3.2 mm long, 0.9–1.1 mm wide at base; ovary with style 3.5–5 mm long; ovules 12–13, pluriseriate. *Fruit* 4.2–5.5 mm in diam.

Distribution.—Central America, primarily in areas with drainage toward the Caribbean, subsp. *paquitensis* is found from Nicaragua (Jinotega, Matagalpa, Chontales, Zelaya and Río San Juan) southward through Costa Rica (Guanacaste, Alajuela, Heredia, Puntarenas and Limón) to Panama (Chiriquí and Bocas del Toro) from sea level–1450 m elevation.

Ecology and conservation status.—Primary, remnant and secondary forests in lower montane, premontane, evergreen tropical wet forests and cloud forests.

Etymology.—The specific epithet commemorates Moritz Friedrich Wagner (1813–1887), Bavarian botanist and zoologist, who traveled to Panama and Ecuador between 1857–1860.

Additional specimens examined. **NICARAGUA. Chontales:** Santo Domingo, 500–1000 m, 13 Jan 1970 (fl, fr), *J. Atwood 3346* (MO); Cerro Oluma, near top of Cordillera Amerisque, 12° 18' N, 85° 24' W, 840 m, 3 Jan 1984 (fr), *A. Gentry et al. 43897* (MO); 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. 3380B* (MO); Cerro Las Nubes, El Tamagás and Loma San Gregorio, ca. 2 km N of Santo Domingo, 600 m, 20 Jan 1984 (fr), *A. Grijalva & D. Ríos 3493* (MO); 4 km NNW of Cuapa, ridgetops and summits of Cerro Oluma, 12° 18' N, 85° 23' 30" W, 700–775 m, 23 Sep 1983 (fl), *M. Nee 28425* (MO). **Jinotega:** Comarca Santa Cruz, el Calvario, al SW del Cerro Kilambé, 13° 34' N, 85° 40' W, 900–1,000 m, 27 Mar 1981 (fr), *P. Moreno 7730* (MO); Las Brisas, Comarca Kilambé, 13° 35–36' N, 85° 39' W, 930 m, 13 Jul 1980 (fl), *J. Sandino 160* (MO); Cerro San Pedro, Comarca Kilambé, 13° 30' N, 85° 38–39' W, 820 m, 21 Jul 1980 (fl), *J. Sandino 186* (MO). **Matagalpa:** 78 km from Matagalpa, along Matagalpa-Siuna Hwy, La Gloria, 13° 15' N, 85° 35' W, 600 m, 13 Sep 1982 (fr), *P. Moreno 17227* (MO); El Comején, 1 km W of Hwy. to Waslala, 13° 15' N, 85° 34' W, 600 m, 23 Feb 1983 (fr), *P. Moreno 20597* (MO). **Río San Juan:** Along Río Sábalo, 11° 03' N, 84° 28' W, 40 m, 07–08 Jul 1984 (fl), *P. Moreno & W. Robleto 25981* (MO); La Lupe near Río Santa Cruz, 11° 08' N, 84° 22' W, without elev., 7 Oct 1990 (fr), *J. Salick 7860* (MO). **Zelaya:** Nueva Guinea, 11° 46' N, 84° 26' 30" W, 200 m, 11 Ago 1982 (fl), *M. Araquistain 3007* (MO); Nueva Guinea, Colonia Yolaina, 11° 40' N, 84° 22' 30" W, without elev., 13 Ago 1982 (fl), *M. Araquistain 3087* (MO); El Achiote, 11° 47' N, 84° 26' W, 200 m, 25 Ago 1982 (fl), *M. Araquistain 3132* (MO); Cerro El Naranjo, ca. 15 km SW of Waní, without elev., 14 Sep 1982 (fl), *A. Grijalva & P. Moreno 1134* (MO), (fr), *A. Grijalva & P. Moreno 1153* (MO); Río Punta Gorda, Atlanta, La Richard, Loma San Jorge, 11° 31' N, 84° 04' W, 150–160 m, 13 Nov 1981 (fr), *P. Moreno & J. Sandino 13039* (MO); Río Punta Gorda, Atlanta, al SE de La Richard, 11° 32' N, 84° 05' W, 30 m, 14 Nov 1981 (fr), *P. Moreno & J. Sandino 13100* (MO); Comarca Waslala, 6.5 km al SE de Waslala, 13° 16' N, 85° 24' W, 520–560 m, 14 Sep 1982 (fr), *P. Moreno 17273* (MO); El Naranjo, a 50 km de Siuna, along Matagalpa-Siuna Hwy., 10 km al W de la cuesta El Guayabo, 13° 34' N, 85° 10' W, 300 m, 14 Sep 1982 (fr), *P. Moreno 17312* (MO); La Posolera, 5 km al W de Waslala, carretera El Tuma a Waslala, 13° 17' N, 85° 24'

W, 700 m, 22 Dic 1982 (fr), *P. Moreno* 19119 (MO); El Guásimo, camino a El Dos, NE de Siuna, 13° 48' N, 84° 39' W, 360–380 m, 25 Feb 1983 (fr), *P. Moreno & W. Robleto* 20745 (MO); Mpio. de Siuna, Waní, without elev., 27 Ago 1982 (fr), *F. Ortiz* 49 (MO); Mpio. de Siuna, Comarca Santa Rosa, without elev., 6 Sep 1982 (fr), *F. Ortiz* 112 (MO); Mpio. de Siuna, Comarca Danlí, 100–130 m, 31 Sep 1982 (fl), *F. Ortiz* 201 (MO); Mpio. de Siuna, Waspado, 100–120 m, 6 Oct 1982 (fr), *F. Ortiz* 281 (MO); Mpio. de Siuna, El Torno, 120 m, 10 Oct 1982 (fr), *F. Ortiz* 324 (MO); Sector Mina Nueva América, 13° 45' N, 84° 30' W, 500 m, 22 Sep 1984 (fr), *F. Ortiz* 2130 (MO); Bonanza, on ground of Neptune Mining Co, 14° 02' N, 84° 35' W, 350–450 m, 26 Feb 1979 (fr), *J. Pipoly* 3516 (MO); Laguna Santa Rosita on road from Bonanza to El Salto Grande, 14° 03' N, 84° 37' W, 140–160 m, 27 Feb 1979 (fl), *J. Pipoly* 3670 (MO); Finca Waylawás, 13° 39' N, 84° 48' W, 80 m, 12 Mar 1979 (fl), *J. Pipoly* 4420 (MO); Risco de Oro, 40 m, 22 Mar 1979 (fl), *J. Pipoly* 5010 (MO); Estación Experimental El Recreo, 12° 09' N, 84° 17' W, 15 m, 10 Jan 1985 (fr), *D. Ríos* 232 (MO); 1 km S de Colonia Verdún, en Nueva Guinea, 11° 38' N, 84° 26' W, 200–250 m, 17 Jul 1982 (fl), *J. Sandino* 3260 (MO); Cerro El Escobín, 4 km de Colonia Serrano, 11° 33–34' N, 84° 21–22' W, 120–130 m, 30 Jul 1982 (fl), *J. Sandino* 3369 (MO); 1 km de Colonia Serrano, Río Serrano, 11° 34' N, 84° 21–22' W, 70–80 m, 31 Jul 1982 (fl), *J. Sandino* 3427 (MO); Toro Bayo and Esquipulas, drainage of Ríos Jícaro and Esquipulas, 130 m, 20 Nov 1951 (fr), *P. Shank & A. Molina* R. 4610 (F); Esquipulas Mountains, 130 m, 22 Nov 1951 (fr), *P. Shank & A. Molina* R. 4696 (F); Esquipulas Mountains and Alemán, Río Alemán Drainage Basin, 150 m, 27–29 Nov 1951 (fr), *P. Shank & A. Molina* R. 4766 (F), (ster.), *P. Shank & A. Molina* R. 4850 (F); Ríos Punta Gorda, Alemán, and Zapote Drainage Basins, 30 m, 5 Dic 1951 (fl), *P. Shank & A. Molina* R. 4966 (F); Estación Experimental El Recreo, ca. 1.5 km SE of the station, 100 m, 10 Ene 1985 (fr), *D. Soza et al.* 378 (MO). along new road from Río Blanco to Río Copalar, ca. 31 km E of Río Blanco, 12° 50–55' N, 85° 00–05' W, 200–400 m, 13 Feb 1979 (fl), *W. Stevens* 12153 (MO, NY); along road from Bonanza to Constanza, 13° 58'–14° 01' N, 84° 37–40' W, 160–360 m, 21 Feb 1979 (fl), *W. Stevens* 12493 (MO); along road between El Empalme and Limbaika, ca. 1.5 km SE of Palmera, 13° 35' N, 84° 20' W, 60 m, 24 Feb 1979 (fr), *W. Stevens* 12836 (MO); along Río Waspúk ca. 1 km upstream from confluence of Río Pis-Pís, 14° 15' N, 84° 36' W, 75–100 m, 1 Mar 1979 (fr), *W. Stevens* 13083 (MO). **Without Department:** 1867 (fl), *B. Seeman* s.n. (BM). **COSTA RICA.** Alajuela: Cantón San Ramón, R.F. San Ramón, Cordillera de Tilarán, trail to Volcán Muerto, 10° 12' 55" N, 84° 36' 25" W, 1,100–1,200 m, 11 May 1993 (fl), *F. Araya et al.* 306 (BRIT, MO, NY); Reserva Biológica Monteverde Río Peñas Blancas, Parcela de Manuel Rojas, 850 m, 8 Aug 1988 (fl), *E. Bello* 291 (MO); Cantón Upala, ca. 3 km NNE of Bijagua along new road to Upala, 10° 45' N, 85° 03' W, 450 m, 7–8 Nov 1975 (fr), *W. Burger & R. Baker* 9847 (F); E slopes of Volcan Miravalles, W of Bijagua, near the Río Zapote, 10° 44' N, 85° 05' W, 600 m, 11–12 Feb 1982 (fr), *W. Burger et al.* 11684 (BM, F, LL-TEX); along road between Canas (Guanacaste) and Upala, near Río Zapote, 1.8–2.7 km S of Río Canalete, 100 m, 25 Jun 1976 (fl), *T. Croat* 36349 (BRIT, MO); along Hwy. 15, between Naranjo and Aguas Zarcas, 8 km NE of Quesada, 600 m, 3 Feb 1979 (fr), *T. Croat* 46928 (MO); without further locality, without elev., without date (fl), *E. Friedrichsthal* 1296 (W); Cantón Upala, P.N. Guanacaste, Cordillera de Guanacaste, Estación San Ramón, La Campana, Dos Ríos, 10° 52' 50" N, 85° 24' 05" W, 550 m, 23 Mar 1994 (fl), *T. García* 203 (BRIT, MO); Laguna de Río Cuarto, Sarapiquí, 400 m, 5 Nov 1984 (fr), *J. Gómez-Laurito* 10215 (F); along creek in Florencia San Carlos, 250 m, 30 Jun 1985 (fl), *W. Haber et al.* 1770 (MO); Cantón San Ramón, Valley of Río La Esperanza, 4 km SW of La Tigra, Finca Araya Ledezma, Bosque Eterno de Los Niños, 10° 18' N, 84° 37' W, 500–600 m, 3 Jul 1992 (fl), *W. Haber et al.* 11260 (MO); Cantón Upala, Dos Ríos, 5 km S of Brasília, right bank of Río Pizote to Minga House, 10° 55' N, 85° 20' W, 500 m, 31 Oct 1987 (fr), *G. Herrera*

1060 (MO); Cantón San Carlos, along Río Rafael, near La Marina, Llanura de San Carlos, 550 m, 21 Feb 1966 (fr), *A. Molina et al.* 17708 (F); Parque Nacional Rincón de la Vieja Colonia Blanca, farm in Quebrada Rancho Grande, 10° 46' 55" N, 85° 15' 10" W, 500 m, 14 Jul 1991 (fl), *G. Rivera* 1452 (MO); S slope of Volcan Arenal, above Río Agua Caliente, without elev., 21 Feb 1989 (fr), *G. Russell et al.* 870 (MO, US); 9.8 km N of Río Naranjo on road to Upala, local name for area is El Macho, 440 m, 8 Nov 1975 (fr), *J. Utley & K. Utley* 3273 (F); ca. 2 km S of the town of Canalete along road to Upala, 100 m, 12 Nov 1975 (fr), *J. Utley & K. Utley* 3305 (F); Cantón Aguas Zarcas, Atlantic rain forest area on Hacienda la Marina, Río San Rafael, 450–500 m, 8 Feb 1965 (fr), *L. Williams et al.* 29120 (F). **Guanacaste:** Cantón Tilarán, bosque entre La Laguna del Arenal y el Alto de La Carpintera, 700 m, 26 Jun 1930 (fl), *A. Brenes* 12653 (F); Z.P. Tenorio, Cordillera de Guanacaste, Estación Tenorio, 10° 36' 40" N, 84° 59' 45" W, 1,050 m, 10 Aug 1992 (fl), *G. Carballo* 436 (MO); Rancho Harold, región del Volcán Cacao, 700–1,200 m, 30 Jul 1986 (fl), *J. Chacón & A. Chacón* 2153 (MO); La Cruz de Abangares, 1,400 m, 15 Jul 1985 (fl), *W. Haber & E. Bello C.* 1995 (MO), *W. Haber* 2000 (MO), 2079 (MO); 2 km SW of La Cruz, on J. Wolfe Farm, 1,400 m, 28 Aug 1985 (fl), *W. Haber* 2439 (MO), 2440 (LL-TEX), 2441 (MO), 2442 (MO); La Cruz de Abangares, 1,360 m, 4 Sep 1985 (fl), *W. Haber & J. Wolfe* 2513 (BRIT, LL-TEX, MO), 1,400 m, 10 Sep 1985 (fl), *W. Haber & E. Bello C.* 2667 (BRIT, LL-TEX, MO), 2691 (LL-TEX), 2693 (MO), 24 Sep 1985 (fl), *W. Haber & E. Bello C.* 2888 (LL-TEX, MO); Cantón Tilarán, Río Chiquito Zona Monteverde, Finca de Campos, Vertiente Atlántica, 10° 25' N, 84° 53' W, 1,100 m, 7 Jun 1987 (fl), *W. Haber & E. Bello C.* 7439 (MO), 7454 (MO, US); Cantón Liberia, Parque Rincón de La Vieja, del Mirador siguiendo la Fila al Volcán Santa María, 10° 46' N, 85° 49' W, 1,100–1,300 m, 27 Nov 1987 (fl, fr), *G. Herrera* 1435 (MO); Parque Nacional Guanacaste Estación Pitilla, Finca La Pasmompa, 11° 02' N, 85° 24' W, 300 m, 17 Jun 1989 (fl), *II INBIO* 53 (BRIT, MO); Silencio-Tilarán, without elev., 31 May 1932 (fl), *W. Kupper* 1529 (M); Cantón Liberia, Parque Nacional Guanacaste, Cordillera de Guanacaste, Estación Cacao, trail to Fran's House, 10° 55' 43" N, 85° 28' 10" W, 1,100 m, 8 Feb 1995 (fr), *M. Lobo* 25 (BRIT, MO); Sendero Nacho y La Esperanza, 10° 59' 26" N, 85° 25' 40" W, 700 m, 22 Jul 1991 (fl), *P. Ríos* 385 (MO); Hacienda Tenorio, without elev., 17 Feb 1956 (fl, fr), *B. Schubert* 1086 (A); ca. 3 km N of Río Naranjo, near the continental divide and ca. 100 m S of the Guanacaste–Alajuela border, 10° 42' N, 85° 04' W, 500 m, 5 Jan 1975 (fl), *J. Taylor* 18094 (F). **Heredia:** Carrillo Estación Magsasay, Sarapiquí, 10° 24' 18" N, 84° 03' 30" W, 200 m, 5 Jul 1990 (fl), *D. Acevedo et al.* 128 (MO); 5 Jul 1990 (fl), *G. Carballo* 151 (BRIT, MO); N of Puerto Viejo, 12 km to ferry, over ferry, 6 km along road, 100 m, 3 Feb 1983 (fr), *N. Garwood et al.* 961 (BM); Cantón Sarapiquí, Parque Nacional Braulio Carrillo, Estación Carrillo, Quebrada Sandijuela, 500 m, 25 Jul 1984 (fl), *L. Gómez et al.* 22966 (F, LL-TEX, MO); Finca La Selva, the OTS field station on the Río Puerto Viejo just E of its junction with the Río Sarapiquí, along West River Road, near point, without elev., 16 Aug 1979 (fl), *M. Grayum* 2403 (MO); edge of trail on point, 100 m, 8 Apr 1982 (fl), *B. Hammel* 11619 (F), 100 m, 23 Apr 1982 (fl), *B. Hammel* 11825 (F, LL-TEX); Cantón Sarapiquí, Finca La Selva, Puerto Viejo, forest along Quebrada Leonél, 10° 26' N, 84° 01' W, without elev., 11 Jul 1973 (fl), *G. Hartshorn* 1254 (BRIT, F, MO); La Selva, ca. 1,650 m along Holdridge Trail, at creek crossing, tributary of Quebrada El Pantana, 100 m, 15 Jul 1984 (fl), *B. Jacobs* 2871 (MO); La Selva, 775 m line, West River Road, 100 m, 22 Oct 1982 (fr), *T. McDowell* 562 (MO); E of 1120 West River Road, between Río Puerto Viejo and Hunters Cocoa grove, 100 m, 1 Dec 1982 (fr), *T. McDowell* 1007 (MO); Finca La Selva, ca. 4 km SE of Puerto Viejo, 10° 28' N, 84° 00' W, 50 m, 21 Jul 1976 (fl, fr), *J. Solomon* 5328 (F, MO). **Limón:** Cantón Pococi, R.N.F.S. Barra del Colorado, Llanura de Tortuguero, Sardinas, 15–20 m, 12 Dec 1992 (fl, fr), *F. Araya* 147 (MO); La Concepción, Llanuras de Santa Clara, 250 m, Apr 1896 (fl), *J. Donnell Smith* 6677 (LL-TEX); Vicinity of U.S. Department

of Agriculture Rubber Experiment Station, Los Diamantes, on Río St. Clara, 1.6 km E of Guapiles, 200 m, 9 Jul 1949 (fl), *R. Holm* & *H. Iltis* 315 (G, GH); Cantón Powel, La Granja, Finca Vieja, 260 m, 26 Jul 1936 (fl), *F. Solís* R. 416 (F, MO). **Puntarenas:** Monteverde, Altos del Río San Luis, División al Río Lagarto, Santa Elena, 10° 16' N, 84° 50' W, 1,000 m, 18 Jul 1989 (fl), *E. Bello* C. 1032 (MO); Reserva Biológica Monteverde, Altos de Santa Elena, 10° 19' N, 84° 49' W, 1,400 m, 6 Aug 1991 (fl), *E. Bello* C. 2929 (INB, MO); Monteverde, lower community, 1,350–1,400 m, 1 Mar 1985 (fr), *W. Haber* 1427 (MO), 1428 (LL-TEX); Monteverde, Pacific slope forest, 1,450 m, 8 Aug 1985 (fl), *W. Haber* 2187 (MO), 2188 (LL-TEX), 2189 (MO), 2190, 2191, 2192, 2193, 2194, 2195, 2196, 2197, 2198, 2199 (MO); Monteverde community, 1,450 m, 18 Aug 1985 (fl), *W. Haber* 2276 (MO), 2315, 2316 (LL-TEX); 2317 (MO), 2318, 2319, 2320, 2321, 2322, 2323, 2324, 2325, 2326, 2327, 2329, 2331 (MO); Monteverde community, Pacific slope, 10° 20' N, 84° 50' W, 1,400 m, 9 Jun 1986 (fl), *W. Haber* & *E. Bello* C. 5031, 5039, 5055, 5063 (MO), 16 Sep 1986 (fl), *W. Haber* & *E. Bello* C. 5641 (MO). **Province unknown:** without date, (fl), *E. Friedrichsthal* s.n. (W), (fl), *F. Lehmann* s.n. (W). **PANAMA.** **Bocas del Toro:** Water Valley, Vicinity of Chiriquí Lagoon, without elev., 9 Sep 1940 (fl), *H. von Wedel* 661 (LL-TEX, MO), 23 Sep 1940 (fl), *H. von Wedel* 932 (MO), 9 Oct 1940 (fl), *H. von Wedel* 1109 (MO), 5 Nov 1940 (fr), *H. von Wedel* 1536 (LL-TEX, MO), 26 Nov 1940 (fr), *H. von Wedel* 1769 (MO). **Chiriquí:** Without further locality, without elev., 1858 (fl), *M. Wagner* 246 (M (F Neg. # 20056)); Vicinity of San Bartolomé, Península de Burica, sea level–50 m, 28 Jul–01 Aug 1940 (fl), *R. Woodson* & *R. Schery* 906 (LL-TEX, MO).

As with the other two subspecies of *Ardisia opegrapha*, marked but continuous quantitative variation in relative sizes of parts and persistence of floral bracts has caused much overdescription. The type of *Ardisia bracteolata*, a fruiting collection, is notable only for its thin, narrowly oblong sepals that are at times emarginate apically, often varying within the same specimen. *Ardisia zelayensis* was described owing to its relatively large sepals with obtuse apices, and the leaves with acute apices and cuneate bases. Populations represented by the type of *Graphardisia hyalina* vary from all others of the subspecies because their anthers have more rounded bases and more narrow apices. The diminutive size of the inflorescence, its rachis and pedicels, together with the extremely slender pedicels of populations from which the type of *Graphardisia purpurea* was collected probably led to its description.

The numerous, persistent floral bracts distinguish subsp. *wagneri* from subsp. *opegrapha* and subsp. *paquitensis*. In late fruit, the bracts sometimes fall, but even then, this subspecies can easily be recognized by the crowded pedicel scars.

2c. *Ardisia opegrapha* Oerst. subsp. *paquitensis* (Lundell) Pipoly & Ricketson, comb et stat. nov. (Figs. 1C, 5). *Ardisia paquitensis* Lundell, Phytologia 2:4. 1941. *Graphardisia paquitensis* (Lundell) Lundell, Phytologia 48:140. 1981. TYPE: COSTA RICA. SAN JOSÉ: San José, low hills above Río Paquita, 5–50 m, 15 Aug. 1936 (fl, fr), *C. W. Dodge* & *V. F. Goerger* 9885 (HOLOTYPE: F, (F Neg. # 68245, LL-TEX Neg. # 1971-81); ISOTYPE: MO, (LL-TEX Neg. # 1971-81)).

Shrubs or *small trees* (0.6–)1–6 m tall. *Branchlets* 4–6(–7) mm in diam. *Leaves* with blades elliptic to broadly elliptic 20.5–30 cm long, (7.5–)8–

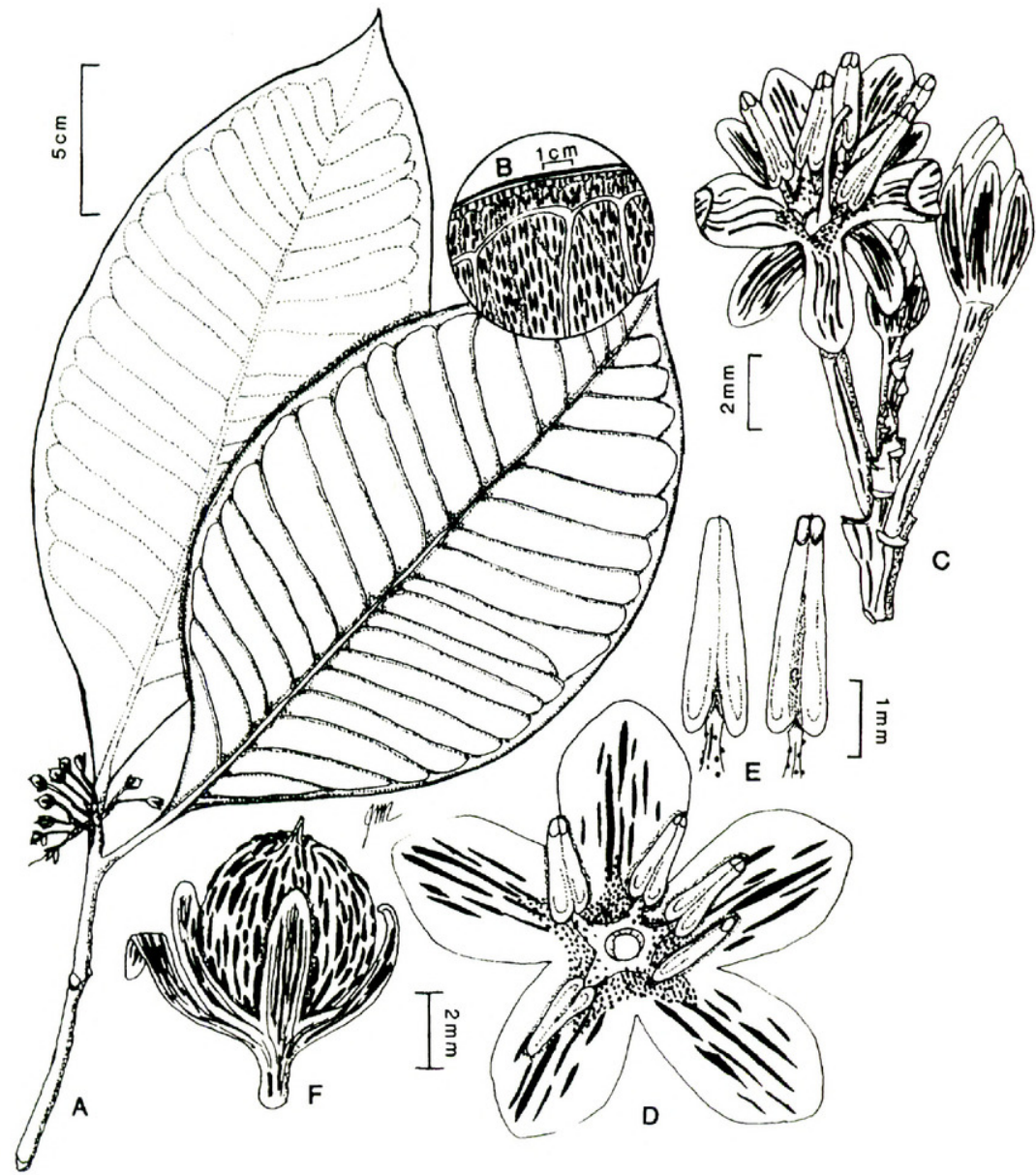


FIG. 5. *Ardisia opegrapha* Oersted subsp. *paquitensis* (Lundell) Pipoly & Ricketson. A. Habit, flowering branch. B. Detail of abaxial leaf surface. C. Detail of inflorescence. D. Detail of flower, showing corolla and stamens. E. Detail of stamen, showing adaxial and abaxial surfaces. F. Fruit. A, C–E drawn from holotype. B, F drawn from isotype.

14.5 cm wide; petioles marginate, (1.5–)2–3(–3.5) cm long. *Inflorescence* globose, a panicle of compound corymbs, (2.5–)3–5 (–7) cm long; peduncle obsolete to 0.5(–1) cm long; inflorescence branch bracts 7.2–15.5 mm long, 2.6–6.5 mm wide, caducous; floral bracts 3.7–4.8 mm long, 0.8–1.3 mm wide, caducous; pedicels 8.5–13 mm long. *Flowers* 7.5–10 mm long; sepals oblong, 4.5–7 mm long, 2.5–3 mm wide; corolla 7–9.5 mm long, the tube 0.6–0.7 mm long, the lobes widely ovate to oblong, 6.5–9 mm long, 4.6–5.7 mm wide; stamens 4–5.2 mm long, the staminal tube 0.6–0.8 mm long, the filaments 1–2.5 mm long, 0.5–0.7 mm wide, the anthers 3.3–3.6 mm long, 0.9–1.1 mm wide at base; ovary with style 4–4.2 mm long, the ovules 11–12, pluriseriate. *Fruit* 4.5–5(–7) mm in diam.

Distribution.—Endemic to Costa Rica, in the Provinces of Limón, Cartago, San José and Puntarenas (especially common in the Cantons of Osa and Golfito); sea level–1,400 m elevation.

Ecology and conservation status.—Subspecies *paquitensis* occurs in primary and secondary tropical wet forests as a locally infrequent component of the understory. Because of its restricted distribution, it should be considered threatened.

Etymology.—The specific epithet 'paquitensis' refers to the type locality, along the Río Paquita, Province of San José, Costa Rica.

Additional specimens examined. **COSTA RICA. Cartago:** above Tuíz, road to Moravia Chirripó, without elev., 1 Oct 1982 (fr), *D. Hazlett 5101* (F, LL-TEX). **Limón:** Reserva Indígena Talamanca Sukut, mouth of Río Sukut at Río Urén path to SE, toward Purisquí, 09° 24' 15" N, 82° 58' 10" W, 350–550 m, 6 Jul 1989 (fl), *B. Hammel et al. 17551* (BRIT, MO). **Puntarenas:** Cantón Osa, Reserva Forestal Golfo Dulce Aguabuena, 08° 41' 50" N, 83° 30' 43" W, 40–50 m, 2 Aug 1991 (fl), *R. Aguilar 178* (MO); Cantón Golfito, Parque Nacional Corcovado, Península de Osa, Estación Sirena, Sendero Ollas, 08° 28' 50" N, 83° 35' 30" W, 10 m, 13 Jun 1994 (fl), *R. Aguilar 3411* (BRIT, MO); Cantón Osa, vicinity of Palmar Norte, along Río Grande de Terraba, sea level, 2 Jul 1949 (fl), *P. Allen 5317* (A, F 3-sheets, GH, MO); vicinity Palmar Norte de Osa, 30 m, 6 Sep 1950 (fl), *P. Allen 5657* (F); Parque Nacional Corcovado, Península de Osa, Sendero Mirador, 08° 33' 10" N, 83° 30' 40" W, 200 m, 30 Aug 1995 (fr), *L. Angulo 487* (MO); Reserva Biología Carara Estación Quebrada Bonita, 09° 46' N, 84° 36' W, 30 m, 26 Jun 1990 (fl), *E. Bello C. & E. Rojas 2283* (BRIT, MO); near airport, 4 mi W of Rincón de Osa, 08° 42' N, 83° 31' W, 30 m, 4–7 Jun 1968 (fl), *W. Burger & R. Stolze 5463* (F); Cantón Golfito, along hwy from Río Claro (on Panamerican Hwy.) to Golfito, 2.5 m SE of Golfito, 27.5 mi S of Río Claro, 08° 36' N, 83° 04' W, 60 m, 15 Sep 1987 (fr), *T. Croat 67621* (BRIT, LL-TEX, MO); Sirena, 08° 28' 00" N, 83° 35' 00" W, 1–200 m, 26 Jun 1991 (fl), *P. Delprete 5117* (TEX); Quebrada Benjamín, Palmar Norte, 08° 59' N, 83° 28' W, 50 m, 14 Jan 1993 (fr), *A. Gentry et al. 78808* (BRIT, MO); Quebrada Cunabré, Hitoy-Cerera, Baja Talamanca, 500–800 m, Jul 1984 (fl), *L. Gómez 24093* (MO); divide between Quebrada Benjamín and Quebrada Batambal, SW slope of Fila Retinto, NW of Palmar Norte, 08° 59' 00" N, 83° 28' 30" W, 300–400 m, 9 Jul 1990 (fl), *M. Grayum & R. Evans 9867* (MO); La Palma, Río Rincón headwaters, trail to Cerro de Oro, 08° 35' N, 83° 30' 40" W, 100 m, 30 Jul 1990 (fl), *G. Herrera 4070* (BRIT, MO); Playa Cacao, lower basin of Quebrada Nazareno, 08° 37' 50" N, 83° 11' 00" W, 70 m, 27 May 1994 (fl), *G. Herrera & G. Rivera 7081* (F);

between Palmar Norte and Puerto Cortéz, Osa Peninsula, 50 m, 6 Aug 1964 (fl), *A. Jiménez* 2239 (F); In Webb's forest, between Palmar Sur and Puerto Cortéz, 400 m, 23 Aug 1965 (fl), *A. Jiménez* 3462 (F); Estación Sirena, Naranjo Trail, 08° 27–30' N, 83° 33–38' W, sea level–150 m, 27 May 1988 (fl), *C. Kernan* 537 (MO); Monkey Woods, 08° 27–30' N, 83° 33–38' W, sea level, 16 Aug 1988 (fr), *C. Kernan & P. Phillips* 828 (MO); Estación Sirena, S of Río Sirena along Río Camaronal, 08° 28' N, 83° 35' W, sea level, 22 Nov 1981 (fr), *S. Knapp* 2177 (MO); Corcovado National Park, on hills 0–1 km W of the park headquarters at Sirena, 08° 29' N, 83° 36' W, sea level–200 m, 4 Jul 1977 (fl), *R. Liesner* 2832 (MO); Along trail and in forest between park headquarters to Sirena and Pavo, 08° 30' N, 83° 36' W, sea level–10 m, 5 Jul 1977 (fl), *R. Liesner & G. Vega* 2900 (MO); Puntarenas-San José border, Barú, 100 m, 16 Aug 1974 (fl), *P. Maas & J. Cramer* 1359 (F); Osa Peninsula, Coronado de Osa, 08° 32' 30" N, 83° 18' 30" W, 1–10 m, 24 Jun 1995 (fl), *M. Madrigal* 76 (MO); Cantón Osa, Fila Estero Guerra, Sierpe, 08° 34' 30" N, 83° 34' 30" W, 300 m, 27 Sep 1991 (fr), *J. Marín* 204 (MO); near the airport area, 4 mi W of Rincón de Osa, 100 ft [30 m], 8 Aug 1967 (fr), *P. Raven* 21627 (F, MO); along road to Pacific Ocean, W of Rincón de Osa, Osa Peninsula, near Mile 15, 100 ft [30 m], 8 Aug 1967 (fl), *P. Raven* 21681 (F, MO); Rincón de Osa, region N of airfield and ridges running NE, 100–300 m, 23 Jul 1974 (fl, fr), *J. Utley & K. Utley* 1194 (F); San Luís de Turrubales, 450 m, 20 Jul 1933 (fl), *M. Valerio* 651 (F). **San José:** Cantón Pérez Zeledón, along road between San Isidro General and Domincal, Fila Tinamastes, 09° 18' 24" N, 83° 46' 11" W, 990–1,100 m, 9 Sep 1996 (fl), *T. Croat & D. Hannon* 79101 (MO); Cantón Tarrazú, San Lorenzo, 09° 34' 20" N, 84° 03' 52" W, 1,400 m, 9 Jul 1997 (fr), *L. Gutiérrez et al.* 64 (MO); between La Lengua y La Víbora de Puriscal, 1,030 m, 23 Apr 1963 (fl), *A. Jiménez* 692 (F); El General Basin, 675–900 m, Jul 1945 (fl), *A. Skutch* 5201 (F, MO, NY).

Ardisia opegrapha subsp. *paquitensis* is distinctive because of its globose inflorescence, dwarfed by relatively large elliptic to broadly elliptic leaves.

3. *Ardisia bartlettii* Lundell

Shrubs or small *trees* (0.5–)2–10 m tall, 1–5 cm in diam. *Branchlets* slender, (1.5–)2–3(–3.5) mm in diam., glabrous throughout. *Leaves* with blades membranaceous to chartaceous, lanceolate elliptic or oblong 5.5–16 cm long, 1.8–7 cm wide, apically acute to acuminate, basally acute to acuminate, decurrent on the petiole, midrib impressed above, prominently raised below, the secondary veins prominulous above, inconspicuous below, densely and prominently punctate and punctate-lineate, glabrous, the margins entire, undulate to irregularly crenulate; petioles marginate to canaliculate, slender to stout, 0.2–1.1 cm long, glabrous. *Inflorescence* terminal, bipinnately paniculate, 2–6 cm long, 3.5–7 cm wide, the rachis glabrous, the branches terminating in corymbs; peduncle obsolete to 0.5 cm; secondary inflorescence bracts early caducous, membranaceous, oblong, (2.8–)5.5–11.2(–14.2) mm long, (1.3–)2.5–3.9(–5.4) mm wide, apically acute to obtuse, the midrib prominulous above and below, the secondary veins inconspicuous, densely and prominently black punctate, glabrous, the margins entire, sparsely glandular-ciliolate; floral bracts very early caducous, unknown, at times not leaving detectable scars axillant to pedicel (aborted at primordial stage ?); pedicels 6–15 mm long, slender, mostly accrescent, glandular-grandulose. *Flowers*

5-merous, chartaceous, 6.8–9.2 mm long; calyx with sepals free, broadly ovate, 1.5–2.5 mm long, 0.9–2 mm wide, apically acute, prominently punctate and punctate lineate, glandular-grandulose within, opaque except at margin, the margins erose to subentire, ciliolate; corolla rotate, 6.5–9.2 mm long, the tube 0.5–1.4 mm long, the lobes ovate, elliptic or lanceolate, 6–8 mm long, 1.6–5 mm wide, apically rounded, prominently punctate and punctate-lineate, yellow glandular-grandulose at base between corolla lobe and tube junction and above staminal tube within, glabrous otherwise; margins entire, ciliolate; stamens 3.5–5.7 mm long, the staminal tube 0.5–1.5 mm long, the filaments 0.5–1.5 mm long, 0.2–0.5 mm wide at base, punctate, glabrous, the anthers linear-lanceoloid, 2.5–3.5 mm long, 0.6–0.9 mm wide at base, apiculate, basally sagittate, dehiscent by subapical pores, the connective darkened; ovary glabrous, the style 4.5–5 mm long, slender, stylopodic at base or not stylopodic (tapered), punctate, glabrous, the ovules 13–16, pluriseriate. *Fruit* globose to oblong, 4–5.2 mm long, 4.2–5 mm wide, densely and prominently punctate, glabrous.

Because of its yellow glandular-granules within the corolla tube, *Ardisia bartlettii* is most closely related to *A. opegrapha*, but is easily separated from it by the chartaceous ovate, sepals 1.5–2.5 mm long, with acute apices, opaque except at margin, and the margins subentire to erose. The glabrous filaments are also distinctive. *Ardisia bartlettii* is comprised of two subspecies, separated by size of floral parts, tapering vs. stylopodic style base, and habitat.

3a. *Ardisia bartlettii* Lundell subsp. *bartlettii* (Figs. 1E, 6). *Ardisia bartlettii*

Lundell, Contr. Univ. Michigan Herb. 7:37. 1942. *Graphardisia bartlettii* (Lundell) Lundell, Phytologia 48:140. 1981. TYPE: PANAMA. CANAL ZONE: Barro Colorado Island, Gatún Lake, along William Morton Wheeler Trail, without elev., 8–10 Aug 1940 (fl, fr), *H.H. Bartlett & T. Lasser* 16720 (HOLOTYPE: MICH; ISOTYPES: LL-TEX, MO (LL-TEX Neg. # 1971-20)).

Ardisia romeroi Cuatrec., Revista. Acad. Colomb. Ci. Exact. 8:319. 1951. SYN. NOV. *Graphardisia romeroi* (Cuatrec.) Lundell, Wrightia 7:46. 1982. TYPE: COLOMBIA. BOLÍVAR: Camino de Monte Líbano a San Pedro, without elev., 28 May 1949 (fl), *R. Romero Castañeda* 1756 (HOLOTYPE: F (LL-TEX Neg. 1971-92)).

Ardisia lewisii Lundell, Wrightia 4:146. 1970. SYN. NOV. *Graphardisia lewisii* (Lundell) Lundell, Phytologia 48:140. 1981. TYPE: PANAMA. COLÓN: Santa Rita Ridge, ca. 5.5–6 mi E of Transisthmian Highway, without elev., 9 Apr 1969 (fl), *W.H. Lewis, D.M. Porter, L.H. Durkee & R.K. Baker* 5377 (HOLOTYPE: LL-TEX; ISOTYPES: LL-TEX, MO, MOCZ n.v., UC).

Ardisia tuirana Lundell, Wrightia 6:91. 1979. SYN. NOV. *Graphardisia tuirana* (Lundell) Lundell, Wrightia 7:46. 1982. TYPE: PANAMA. DARIÉN: Río Tuira and Río Paca, without elev., 21 Jun 1962 (fr), *J.A. Duke* 5025 (HOLOTYPE: LL-TEX; ISOTYPES: BRIT, GH, MO).

Ardisia sapoana Lundell, Phytologia 48:135. 1981. SYN. NOV. *Graphardisia sapoana* (Lundell) Lundell, Wrightia 7:46. 1982. TYPE: PANAMA. DARIÉN: Cerro Sapo, NE slope of summit, approach from Garachiné, knife edge ridge before ascent to top, 2,800 ft [853 m], 9 May 1979 (fl), *B. Hammel* 7297 (HOLOTYPE: LL-TEX; ISOTYPE: MO).



FIG. 6. *Ardisia bartlettii* Lundell subsp. *bartlettii*. A. Habit, flowering branch. B. Detail of abaxial leaf surface. C. Detail of inflorescence. D. Detail of flower, showing corolla and stamens. E. Detail of stamen, showing abaxial surface. F. Detail of stamen, showing lateral surface. G. Detail of stamen, showing adaxial surface. H. Fruit. A C, E–H drawn from holotype. D drawn from *T. Croat 15005*.

Shrubs (0.5–)2–10 m tall, 1–5 cm in diam. *Branchlets* slender, 1.5–3 mm in diam., glabrous throughout. *Leaves* with blades 5.5–12.5 cm long, 1.8–4.5 cm wide; petioles slender, canaliculate and slightly marginate, 0.2–1.1 cm long. *Inflorescence* 2–6 cm long, 4–6.5 cm wide; peduncle obsolete to 0.5 cm; secondary inflorescence bracts 5.5–14.2 mm long, 2.5–5.4 mm wide; pedicels 6–15 mm long, slender, accrescent, glandular-glandulose. *Flowers* 6.8–7.2 mm long; sepals 1.5–1.8 mm long, 0.9–1.1 mm wide; corolla 6.5–7.7 mm long, the tube 0.5–1.2 mm long, the lobes ovate or elliptic to lanceolate, 6–6.5 mm long, 1.6–4.1 mm wide; stamens 3.5–4.8 mm long; the staminal tube 0.5–1.3 mm long, the filaments 1–1.5 mm long, 0.4–0.5 mm wide at base, punctate, glabrous, the anthers 2.5–2.8 mm long, 0.6–0.8 mm wide at base; ovary glabrous, the style 4.5–4.8 mm long, slender, not stylopodic at base, punctate, glabrous, the ovules 15, pluriseriate. *Fruit* globose to oblong, 4.5–5.2 mm long, 4.2–4.5 mm wide, conspicuously punctate, glabrous.

Distribution.—Known only from eastern Panama (Coclé, Colón, Panamá, Darién, San Blas), and on the Caribbean coast of Colombia (Bolívar), growing at sea level–900 m elevation.

Ecology and conservation status.—*Ardisia bartlettii* subsp. *bartlettii* occurs along streams and rivers in wet and pluvial lowland, premontane and cloud forests. It appears to be relatively tolerant of disturbance, so we believe it is not threatened at this time.

Etymology.—The specific and subspecific epithet honors Harley Harris Bartlett (1886–1960), American botanist at the University of Michigan at Ann Arbor, who collected the type specimen.

Additional specimens examined. **PANAMA**. Coclé: Santa Rita Ridge, 5–10 mi from Transisthmian Hwy., sea level–100 m, 28 Jun 1984 (fl), W. D'Arcy et al. 15548 (BRIT, LL-TEX, MO, PMA); from Torti to Pilota del Toro, mountain overlooking Torti Arriba, without elev., 27 Aug 1977 (fr), J. Folsom & G. Alonzo de Monte 4973 (LL-TEX, MO), 5012 (MO); mountains above Torti Arriba, without elev., 2 Dec 1977 (fr), J. Folsom et al. 6576 (MO); 4–5 hours walk upriver from Torti Arriba, 200–300 m, 6 Dec 1977 (fr), J. Folsom et al. 6844 (MO); lowland area along the stream that passes through Torti, on the S side of the Pan-American Hwy., on Quipo slopes over river, without elev., 25 May 1980 (fl), J. Folsom et al. 7825 (F, TEX); Hill S of Guacuco, 8 km E of Ipetí, 08° 55' N, 78° 20' W, 600 m, 18 Sep 1982 (fr), C. Hamilton & W. D'Arcy 1387 (LL-TEX, MO); Pipeline road, N of Gamboa, upstream of the tenth bridge (Río Guacharo), beyond the big waterfall, 09° 10' N, 79° 45' W, 100 m, 4 Aug 1984 (fl), G. de Nevers & D. Hews 3627 (LL-TEX, MO); Pipeline Road near Gamboa, Río Mendoza, upstream of road, without elev., 09° 09' N, 79° 42' W, 7 Jul 1985 (fl), G. de Nevers 5963 (LL-TEX, MO, US). **Colón**: Trail from end of Santa Rita Ridge Road to Río Piedras, 1,400–1,600 ft [427–488 m], 23 Mar 1980 (fr), T. Antonio 3889 (LL-TEX, MO); Santa Rita Ridge, along road, ca. 1 mi from Boyd Roosevelt Hwy., without elev., 9 Jul 1971 (fl), T. Croat 15340 (MO); Santa Rita Lumber Road, ca. 15 km E of Colón, without elev., 20 Apr 1971 (fl), R. Dressler & N. Williams 3967 (MO); Santa Rita Ridge, 20.7 km from Transisthmian Hwy., 09° 23' N, 79° 40' W, 530 m, 22 Mar 1992 (ster.), R. Foster et al. 14038 (MO); ridge top 1–3 mi W of Portobello, without elev.,

7 Sep 1971 (fr), *A. Gentry 1758* (F, MO); Santa Rita Ridge, ca. 12 km from Transisthmian Hwy., without elev., 28 Jun 1978 (fr), *B. Hammel 3646* (MO); end of Santa Rita Ridge Road, 21 km from Transisthmian Hwy., 09° 25' N, 79° 37' W, 400–500 m, 22 May 1982 (fl), *S. Knapp & R. Schmalzel 5247* (LL-TEX, MO); 26–28 km from Transisthmian Hwy. on the Santa Rita Ridge Road, 09° 25' N, 79° 37' W, 250–400 m, 23 May 1982 (fl), *S. Knapp & R. Schmalzel 5268* (LL-TEX 2-sheets, MO); Santa Rita Ridge Road, 21–26 km from Transisthmian Hwy., 09° 25' N, 79° 37' W, 500–550 m, 4 Jul 1982 (fl, fr), *S. Knapp 5892* (LL-TEX, MO); Santa Rita Ridge, SE of Colón, along ridge road, 10–12 mi from Transisthmian Hwy., 09° 20' N, 79° 45' W, 550 m, 21 May 1986 (fl), *G. McPherson 9206* (MO); Santa Rita Ridge Road, ca. 6 km from Boyd Roosevelt Hwy., without elev., 26 Sep 1974 (fr), *S. Mori & J. Kallunki 2140* (LL-TEX, MO); Santa Rita Ridge road, 20–25 mi from Transisthmian Hwy., 09° 24' N, 79° 39' W, 100–1,200 m, 10 Oct 1980 (fr), *K. Sytsma 1523* (LL-TEX, MO); 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, 30 Apr 1981 (fl), *K. Sytsma et al. 4192* (LL-TEX, MO); along Santa Rita Ridge, road to Estación Calibar Lluvia el Agua Clara, 09° 22' N, 79° 42–45' W, 1,300 ft [396 m], 26 Jun 1971 (fl), *G. Webster & R. Dressler 16745* (MO). **Darién:** vicinity of Tortí, 38.6 mi E of Bayano Dam Bridge, trail from village to mountains near Río Tortí, 50–250 ft [15–76 m], 17 May 1980 (fl), *T. Antonio 4674* (LL-TEX, MO); Río Tuira 2 mi upstream from Boca del Cupa, 4 Aug 1962 (fr), *J. Duke 5381* (MO); vicinity of Las Piñas, without elev., 2 Mar 1967 (fr), *J. Duke 10612* (LL-TEX); S of Garachiné near Pacific coast above Casa Vieja, along boundary trail of Parque Nacional Darién, W flank, Serranía del Sapo, 07° 58' N, 78° 23' W, 50–150 m, 21 May 1991 (fl), *N. Hensold 1078* (F, MO); Casa Vieja hacia Cerro Sapo, 07° 58' N, 78° 23' W, 180–500 m, 23 May 1991 (fl), *H. Herrera, et al. 984* (BRIT, F, MO, PMA); S of Garachiné on W flank of Serranía del Sapo, above place called Casa Vieja, along boundary trail of Darién National Park, 07° 58' N, 78° 23' W, 300–500 m, 24 May 1991 (fl, fr), *G. McPherson 15369* (BRIT, MO). **Panamá:** Barro Colorado, Mojanga swamp near mouth of Río Chagres, 1 m, 11 Mar 1935 (fl), *P. Allen 865* (MO); road to Cerro Jefe, 900 m, 9 Jul 1976 (fl), *T. Antonio 1296* (BRIT, LL-TEX, MO); Barro Colorado Island, without elev., 1931 (fl), *S. Aviles 10* (MO); Barro Colorado, Snyder-Molina Trail, without elev., 29 Jun 1940 (fl), *M. Chrysler 4796* (F); near Gamboa, without elev., 26 Jun 1972 (fl); *A. Clewell & E. Tyson 3222* (MO); Barro Colorado, Drayton Trail, without elev., 22 May 1968 (fl), *T. Croat 5756* (BRIT, MO); Barro Colorado, Wheeler Trail, without elev., 19 Sep 1968 (fr), *T. Croat 6215* (BRIT 2-sheets, MO); Barro Colorado, Wheeler Trail, without elev., 11 Jun 1970 (fl, fr), *T. Croat 10845* (F, MO); Barro Colorado, Shannon Trail, without elev., 15 Jul 1970 (fl, fr), *T. Croat 11271* (MO); Barro Colorado, Wheeler Trail, without elev., 17 Sep 1970 (fl, fr), *T. Croat 12219* (MO); Barro Colorado, without elev., 20 May 1971 (fl), *T. Croat 14650* (MO); Barro Colorado, Lake Trail, without elev., 16 Jun 1971 (fl), *T. Croat 15005* (MO); Barro Colorado, Barbour Trail, without elev., 25 Jun 1971 (fl), *T. Croat 15105* (F, MO), between Fort Sherman and Fort San Lorenzo, without elev., 10 Jul 1971 (fl), *T. Croat 15414* (LL-TEX, MO); Cerro Jefe, 2,900 ft [884 m], 21 Jul 1972 (fl), *J. Dwyer & A. Gentry 10249* (F, MO); Barro Colorado, Snyder Molino Trail, along edge of trail, 300–600 m, 25 Jun 1960 (fl), *J. Ebinger 182* (BRIT, MO); along the border of Canal Zona-Colón Prov., from parallel in NW shore of Canal along road to Achioté, within 2 mi of Achioté, without elev., 23 Jun 1977 (fl), *J. Folsom 3880* (LL-TEX, MO); road leading around the shoulder of Cerro Jefe, turns to the right at 21.5 km from the Pan-American Hwy., around the first stream encountered, 800 m, 29 Sep 1977 (fl, fr), *J. Folsom et al. 5663* (MO); ca. 1 mi upstream from Frizzel's Finca Indio, on slope of Cerro Jefe, without elev., 9 Sep 1970 (fl), *R. Foster & H. Kennedy 1849* (LL-TEX); Barro Colorado Island, without elev., 9 Oct 1985 (fr), *N. Garwood & S. Arne 1595* (F), 1 Dec 1985 (fr), *N. Garwood 1687* (F), 28 Sep 1986 (fl, fr), *N. Garwood 1943*

(F), 18 Nov 1988 (fr), *N. Garwood* 2658 (F); Pipeline Road, without elev., 30 Sep 1971 (fl), *A. Gentry & R. Dressler* 1979 (MO), 6 mi N of Gamboa, without elev., 28 Dec 1971 (ster.), *A. Gentry* 3319 (MO); Cerro Jefe, region roadside along road to Altode Pacora, 2 km N of turnoff to Cerro Jefe radio tower, along small stream, 2,500–2,700 ft [762–823 m], 30 Sep 1978 (fl), *B. Hammel* 4854 (MO); Fort Sherman, Atlantic coastal forest, without elev., Jul 1965 (fl), *M. Hayden* 95 (MO); trail along Río Petitpie from road to Fort Sherman from Gatun Locks, without elev., 22 Oct 1974 (fr), *S. Mori & J. Kallunki* 2665 (MO), 12 Dec 1974 (fr), *S. Mori & J. Kallunki* 3661 (MO); ca. 12 km NW of Gamboa, without elev., 26 Aug 1975 (fr), *S. Mori* 7943 (LL-TEX, MO), 9 km NW of Gamboa, 150 m, 29 Oct 1973 (fr), *M. Nee* 7657 (LL-TEX, MO), 125 m, 28 Nov 1973 (fl), *M. Nee* 8435 (LL-TEX 2-sheets, MO); Along road S1, 4 km W of Gatun Dam, 190–200 m, 20 Dec 1973 (fl), *M. Nee* 8913 (MO 2-sheets); Barro Colorado, near A.V. Armour Trail, 5, on Hubbell Permanent Plot, without elev., 13 Nov 1981 (fl), *R. Schmalzel & M. Aide* 56 (MO), Sugar Mill, without elev., 20 Dec 1931 (fr), *O. Shattuck* 611 (F, MO), Standley No. 20, without elev., 31 Jul 1934 (fr), *O. Shattuck* 1098 (BRIT, F, MO); Gatun Lake, 120 m, 18–24 Nov 1925 (fr), *P. Standley* 41029 (LL-TEX), Barro Colorado, Zetele Trail, without elev., 6 Jul 1931 (fl), *D. Starry* 28 (F, MO); Peña Blanca Trail, without elev., Jul 1931 (fl), *D. Starry* 178 (F); Cerro Jefe, 850–900 m, 29 Oct 1980 (fr), *K. Sytsma* 1975 (BRIT, MO); Cerro Jefe, 1.5 mi down right turnoff, 6.7 mi past Goofy Lake, 700 m, 27 Dec 1980 (fl, fr), *K. Sytsma et al.* 2900 (MO); Cerro Jefe, 6 mi past Cerro Azul on road to Altos Pacora, 2,600 ft [792 m], 19 Feb 1981 (fr), *K. Sytsma & W. D'Arcy* 3690 (LL-TEX, MO); vicinity of Salamanca Hydrographic Station, Río Pequení, 80 m, 28–29 Jul 1938 (fl), *R. Woodson et al.* 1569 (F, MO). **San Blas:** Nusagandi, Campo de PEMASKY, ca. 20 km on El Llano-Carti Road, trails near station, 09° 18' N, 78° 59' W, 350 m, 1 May 1992 (fl, fr), *R. Foster et al.* 917 (MO); 3–4 hours up Río Mulatupo by foot, without elev., 17 Aug 1967 (fr), *J. Kirkbride* 216 (MO); Udirbí Reserve, waterfall trail along park boundary, 09° 18' N, 78° 58' W, 350–400 m, 21 Jul 1986 (fl), *J. McDonagh et al.* 244 (MO); El Llano-Carti Road, 24.5–25 km from Inter-American Hwy., near continental divide, 13 Apr 1975 (fl), *S. Mori & J. Kallunki* 5556 (MO), 17.4 km from Inter-American Hwy, 09° 19' N, 78° 55' W, 350 m, 27 Sep 1984 (fl, fr), *G. de Nevers* 3943 (BRIT, MO), km 16.7, trail W to waterfall 5 km from road, 09° 19' N, 78° 55' W, 350 m, 16 Jun 1985 (fl), *G. de Nevers & S. Charnley* 5899 (LL-TEX, MO, US); Cerro Habú, trail from Río Sidro, 09° 23' N, 78° 49' W, 800–1,400 ft [244–427 m], 18 Dec 1980 (fr), *K. Sytsma* 2650 (MO).

Cuatrecasas misinterpreted *Ardisia romeroi* as a member of subgenus *Icacorea*, largely because of the early caducous floral bracts and concolorous, poricidally dehiscent anthers. However, it closely matches the type of *Ardisia bartlettii* subsp. *bartlettii*. *Ardisia lewisii* is notable only for its inflorescence with pedicels in loose (low) anthotactic spirals. *Ardisia tuirana* was separated because of its somewhat less punctate, ovate sepals and sparse, finely stellate tomentum on the lower branches of the inflorescence. It is otherwise not significantly different from the type of the subspecies. Populations corresponding to the type of *Ardisia sapoana* vary from the subspecies type only by having sessile inflorescences with longer secondary inflorescence branch bracts, and longer corolla tubes.

Ardisia bartlettii subsp. *bartlettii* may be separated from subspecies *lilacina* by the shorter calyx and corolla, the generally shorter stamens and tapering style base.

3b. *Ardisia bartlettii* Lundell subsp. *lilacina* (Lundell) Pipoly & Ricketson, comb. et stat. nov. (Figs. 1F, 7). *Ardisia lilacina* Lundell, *Wrightia* 3:198. 1966. *Graphardisia lilacina* (Lundell) Lundell, *Phytologia* 48:140. 1981. TYPE: PANAMA. COLÓN: Porto Belo [Bello], beach, without elevation [ca. sea level], 13 Jul 1964 (fl), *J. Dwyer* 4354 (HOLOTYPE: MO).

Shrubs or small trees (0.5–)2–7 m tall, 1–4 cm in diam. *Branchlets* slender, 2–3.5 mm in diam., glabrous throughout. *Leaves* with blades 6–16 cm long, 3.5–7 cm wide; petioles stout, marginate, 0.4–1 cm. *Inflorescence* 2.5–4 cm long, 3.5–7 cm wide, sessile or nearly so; peduncle obsolete to 0.2 cm; secondary inflorescence bracts 2.8–11.2 mm long, 1.3–3.9 mm wide; pedicels 10–15 mm long, slender, glandular-glandulose. *Flowers* 8–9.2 mm long; sepals 2–2.5 mm long, 1.5–2 mm wide; corolla 7.5–9.2 mm long, the tube 0.5–1.4 mm long, the lobes ovate to elliptic, 7–8 mm long, 4.5–5 mm wide; stamens 4.5–5.7 mm, the staminal tube 0.5–1.5 mm long, the filaments 0.5–1 mm long, 0.2–0.3 mm wide at base, punctate, glabrous; the anthers 3–3.5 mm long, 0.7–0.9 mm wide at base; ovary glabrous, the style 4.5–5 mm long, slender, stylopodic at base, punctate, glabrous, the ovules 14–16, pluriseriate. *Fruit* globose, 4–5 mm in diameter, conspicuously punctate, glabrous.

Distribution.—Subspecies *lilacina* is restricted to the Caribbean coast of Panama (Colón, Panamá, San Blas), with one disjunct population in the Chocó, Colombia. We may also expect subsp. *lilacina* in lowland Antioquia and Valle Departments of Colombia, areas sorely lacking in collections. It grows from sea level–180 m elevation.

Ecology and conservation status.—This subspecies occurs in strand vegetation and beach forests. It is said to be locally uncommon, so it should be considered threatened.

Etymology.—The epithet 'lilacina' refers to the striking lilac color of the flowers.

Additional specimens examined. **PANAMA. Colón:** vicinity of Viento Frio, along the beach, sea level, 07–08 Aug 1911 (fl), *H. Pittier* 4114 (F); Río Indio de Fató, sea level, 24 Aug 1911 (fl), *H. Pittier* 4273 (F, LL-TEX, NY); 3 km SW of Río Guanche along road from Puerto Pilón to Portobelo, sea level, 20 May 1981 (fl), *K. Sytsma & L. Andersson* 4791 (LL-TEX, MO). **Panamá:** Río Providencia and ridge S of river, 5–170 m, 5 Dec 1973 (fl, fr), *A. Gentry & M. Nee* 8706 (LL-TEX, MO). **San Blas:** Río Cangandí, pueblo Cangandí, path to Quebrada Inadí, 09° 27' N, 79° 07' W, 50 m, 20 May 1987 (fl), *H. Herrera & P. Pérez* 127 (MO); Vertiente Pacífica de la Cordillera de San Blas, Cabecera del Río Piriadí, 09° 11' 05" N, 78° 16' W, 100–150 m, 14 Jun 1994 (fl), *H. Herrera* 1633 (BRIT, F, MO, PMA); Comarca de San Blas, tierra firme de Playón Chico, vicinity of the aqueduct trail, 09° 17' N, 78° 15' W, 30 m, 12 Sep 1994 (fr), *H. Herrera* 1839 (BRIT, MO, PMA); Playón Chico and vicinity San Blas, Yantuppu, coral island, without elev., 8 Jul 1975 (fl), *F. Stier* 193 (MO). **COLOMBIA. Chocó:** Mpio. Acandí, Vereda El Páramo, Quebrada Sardí, 08° 20' N, 77° 06' W, 180 m, 22 May 1989 (fl), *R. Fonnegra et al.* 2792 (HUA, MO), *F. Roldán et al.* 1190 (HUA, MO).

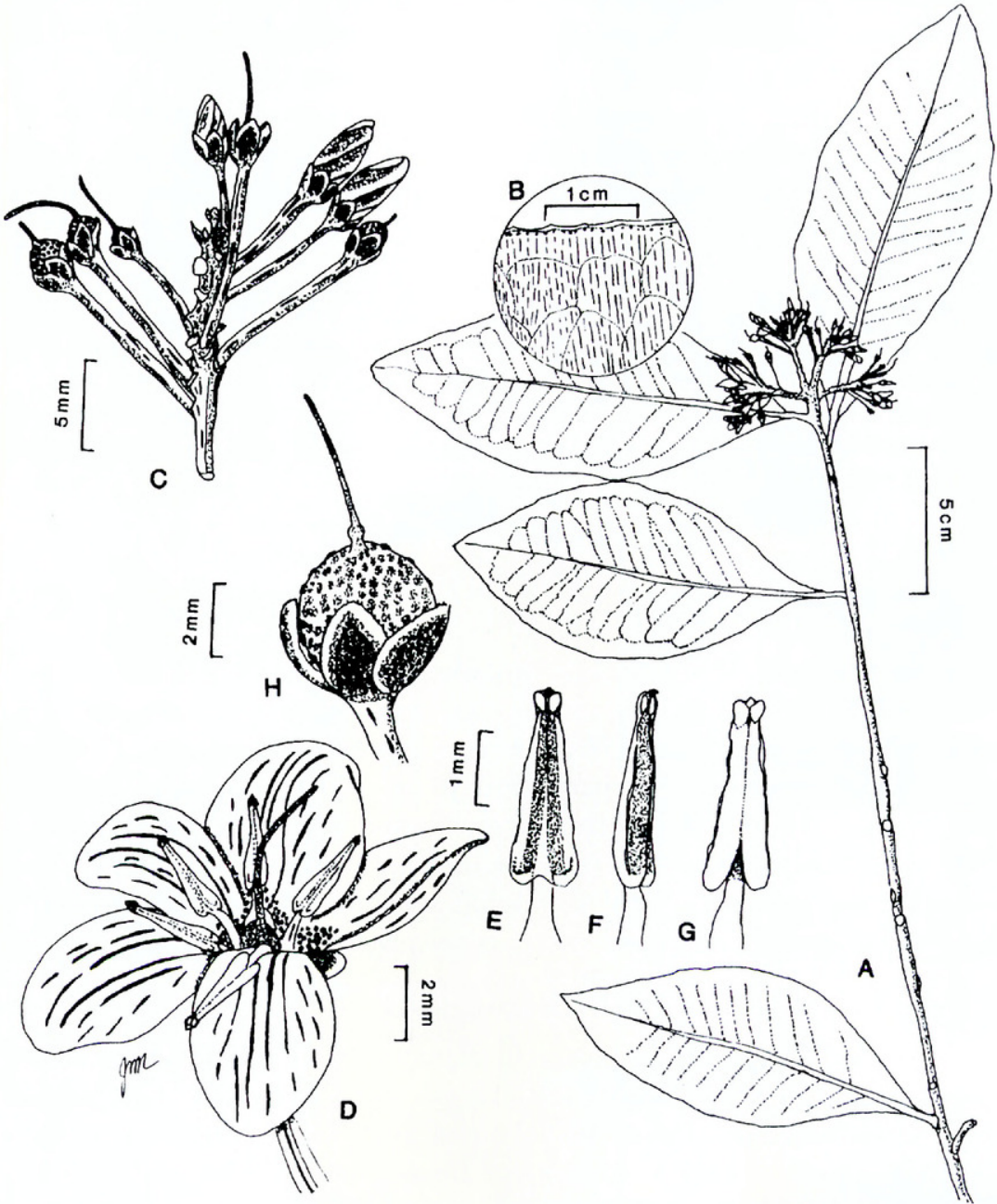


FIG. 7. *Ardisia bartlettii* Lundell subsp. *lilacina* (Lundell) Pipoly & Ricketson. A. Habit, flowering branch. B. Detail of abaxial leaf surface. C. Detail of inflorescence. D. Detail of flower. E. Detail of stamen, showing abaxial surface. F. Detail of stamen, showing lateral surface. G. Detail of stamen, showing adaxial surface. H. Fruit. A–G drawn from holotype. H drawn from *F. Stier* 193.

Ardisia bartlettii subsp. *lilacina* may easily be separated from subsp. *bartlettii* by its longer perianth parts, usually longer stamens and unique stylopodic (swollen) style base. While the stylopodic style base is unique within the subgenus, there is no corresponding unique feature for subspecies *bartlettii* to define it. Therefore, the two taxa are recognized at the subspecific level. In addition, it is restricted to strand and beach forests, while subsp. *bartlettii* is from tall wet forests.

EXCLUDED NAMES

Ardisia albovirens Mez, Repert. Spec. Nov. Regni Veg. 16:311. 1920. *Graphardisia albovirens* (Mez) Lundell, Wrightia 7:46. 1982. TYPE: BRAZIL. ACRE: Río Acre bei Xapury [Xapuri], without elev., Jan. 1911 (fl), *E. Ule* 9682 (HOLOTYPE: B-destroyed in 1943 (F Neg. # 4876); LECTOTYPE, here designated; K; photo of lectotype: LL-TEX Neg. # 71-157).

Ardisia nigrovirens J. F. Macbr., Candollea 5:397. 1934. SYN. NOV. *Graphardisia nigrovirens* (J. F. Macbr.) Lundell, Wrightia 7:46. 1982. TYPE: PERU. LORETO: Puerto Arturo, Yurimaguas, lower Río Huallaga, 155–210 m, 15 Nov 1929 (fr), *L. Williams* 5081 (HOLOTYPE: F (LL-TEX Neg. # 1971-74)).

Now that recent collections have provided us with material both in flower and fruit, it is clear that this species is not a member of subgenus *Graphardisia*, but rather, subgenus *Ardisia*. This species has ovate anthers with subapical pores opening into slits, has panicles with racemose branchlets, inflorescence and secondary inflorescence branch bracts that are subcoriaceous to coriaceous and cucullate, and coriaceous sepals that are quincuncial. We postulate that the rather large floral and secondary inflorescence branch bracts of the species may have led to its misplacement.

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NUMERICAL LIST OF TAXA

- | | |
|--|---|
| 1. <i>A. weberbaueri</i> Mez | 3. <i>A. bartlettii</i> Lundell |
| 2. <i>A. opegrapha</i> Oerst. | 3a. subsp. <i>bartlettii</i> |
| 2a. subsp. <i>opegrapha</i> | 3b. subsp. <i>lilacina</i> (Lundell) Pipoly & Ricketson |
| 2b. subsp. <i>wagneri</i> (Mez) Pipoly & Ricketson | |
| 2c. subsp. <i>paquitensis</i> (Lundell) Pipoly & Ricketson | |

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