

Suffrutescent herbs or shrubs to 1.5 m tall; bark gray-brown, smooth. Leaf blades elliptic to somewhat oblanceolate, 2-10 cm long, 1.6-4.5 cm wide, acute to sometimes acuminate at apex with tip 3-5 mm long, cuneate to attenuate at base, coriaceous and usually thickly so; secondary veins pinnate, 3-5 pairs, plane, without domatia; margins flat; petioles 5-15 mm long; stipules 15-34 mm long, 8-14 mm wide. Flowers solitary; peduncles 1-4 mm long; bracts lacking or 1-3 × 1-2 mm; calyx limb lacking or divided to base, the lobes 4, 5-10 mm long, 1-4 mm wide, ligulate to oblanceolate, acute; corolla salverform, white, the tube 45-75 mm long, the lobes 4, 15-25 mm long, 10-24 mm wide, elliptic, rounded; anthers 4, 7-8 mm long, subsessile, with tips positioned 5-8 mm below top of corolla tube; ovary 3-10 mm long; styles 13-15 mm long; stigmas 8-12 mm long, linear, positioned below middle of corolla tube. Capsules 30-75 mm long including a beak 1-3 mm long, 5-11 mm diam., without stipes, smooth; seeds 1.5-4 × ca. 0.5-1 mm, with filaments 6-13 mm long. Figure 11A-C.

Habitat, phenology, and distribution (Fig. 12). Southern Mexico to northern Guatemala and northern to central Costa Rica, in wet forests at 700-2700 m. Collected in flower December to June, in fruit in January, March, and May.

This species differs from Hillia tetrandra and H. maxonii in its acute or shortly acuminate, usually very thickly coriaceous leaf blades. It may represent an acute-leaved variant of H. maxonii. Aside from geographic range, no features separate the plants of Mexico and Guatemala described as H. macrocarpa from those of Costa Rica, and this name is placed in synonymy here. The resultant apparently disjunct range of this species is similar to that of H. panamensis and some species of Psychotria (Hamilton, 1989). The report of H. triflora from southern Mexico (Taylor, 1989) was a misidentification of H. loranthoides.
Representative specimens examined. COSTA RICA. Alajuela: La Palma de San Ramón, Brenes 3839 (CR, F), 3847 (CR, F), 5439 (CR, F, NY), 6137 (CR, F), Lent 1692 (CR, F). Cartago: El Retiro, Santa Cruz de Turrialba, Valerio 1359 (CR). Puntarenas: San Luis River valley 1.5 km upstream from San Luis village, Haber & Hammel 1787 (CR, MO). GUATEMALA. Baja Verapaz: Sierra de las Minas ca. 5 km S of Purulha, 1600 m, Williams et al. 41950 (F). Huehuetenango: km 332 of the Panamerican Hwy. 5 km E of the Mexican border at La Mesilla, Ilits & Lind C202 (WIS). Quetzaltenango: Quezaltenango, 2666 m, Vaught 305 (US). MEXICO. Chiapas: municipio La Trinitaria, 10 km ENE of Dos Lagos above Santa Elena, 1170 m, Breedlove & Almeda 57488 (CAS, NY). Oxaca: vicinity of Concordia, Montecristo, 1100 m, Makrinus 727 (US).

9. **Hillia tetrandra** Swartz, Prodr. 58. 1788.
   TYPE: Jamaica. Coldspring, O. Swartz s.n. (holotype, S not seen; isotype, BM not seen, photo NY).

**Hillia tuxtlensis** Sessé & Mocino ex DC., Prodr. 4: 351. 1830, nom. inval., pro syn.

Suffrutescent herbs or shrubs to 4 m tall; bark gray-brown, smooth. Leaf blades obovate to elliptic, 3-7.5(-10) cm long, 1-3(-4.5) cm wide, obtuse to usually rounded at apex, attenuate at base, subcoriaceous to coriaceous; secondary veins pinnate.
3–5(–6) pairs, plane, without domatia; margins flat; petioles 1–11 mm long; stipules 8–30 mm long, 5–20 mm wide. Flowers solitary; peduncles 1–5(–10) mm long; bracts lacking or 3–4 × 1–2 mm; pedicels 0–3 mm long; calyx limb lacking or divided to base, the lobes 4, 7–19 mm long, often unequal, 1–3(–5) mm wide, oblanceolate to ligulate, rounded; corollas salverform, white, the tube 25–78 mm long, the lobes 4, 10–27 mm long, 8–22 mm wide, elliptic to broadly elliptic, broadly rounded; anthers 4, subsessile, 4.5–5 mm long, with tips positioned 2–3 mm below top of corolla tube; ovary 5–10 mm long; styles 8–18 mm long; stigmas 7–11 mm long, 2–3 mm wide, linear to sublinear, positioned below middle of corolla tube. Capsules 25–80 mm long including a beak 1–3 mm long, 5–9 mm diam., not stipitate, with ca. 8 rounded to winged longitudinal ridges to 1 mm high; seeds 2.5–3.5 × 1.5–1.7 mm, with filaments 8–17 mm long. Figure 13A–E; Standley & Williams (1975: fig. 14).

to attenuate at base, coriaceous to usually thickly so; secondary veins pinnate, 4–5 pairs, plane, without domatia; margins flat; petioles 3–8 (15) mm long; stipules 12–32 mm long, 8–10 mm wide. Flowers solitary; peduncles 1–2 (4) mm long; bracts lacking or 1–3 × 1–2 mm; calyx limb lacking or divided to base, the lobes 4, 5–6 mm long, 0.5–2 mm wide, ligulate, acute; corollas salverform, white, the tube 42–55 mm long, the lobes 4, 15–27 mm long, 10–17 mm wide, elliptic, rounded; anthers 4, ca. 5 mm long, subsessile, with tips positioned ca. 3 mm below top of corolla tube; ovary 3–10 mm long; style ca. 15 mm long; stigmas ca. 7 mm long, linear, positioned below middle of corolla tube. Capsules 29–60 mm long including beak 1–3 mm long, 5–9 mm diam., not stipitate, smooth to slightly ridged longitudinally; seeds 2–4 × 0.5–1 mm, with filaments 6–13 mm long. Figure 13F, G.

Habitat, phenology, and distribution (Fig. 15). Central Nicaragua to Ecuador, in wet forests at 0–2400 m: montane regions, Nicaragua to Panama, to mangrove formations and along rivers, Panama to Ecuador. Collected in flower April, May, July to September, and December, in fruit January to March, May to July, November, and December.

This species is characterized by its coriaceous leaf blades that are obverse to rounded at the apex and smooth to slightly ridged capsules. Plants from Costa Rica and Ecuador are apparently disjunct by several hundred miles from those of central Panama.
ama and are found in coastal formations rather than wet ridge forests. In Panama plants have been collected in both habitats. No morphological differences between the Central and South American plants are evident. 

**Cosmibuena macrocarpa** (Benth.) Walp. occupies a similar geographic range and set of habitats.

**Hillia maxonii** is similar to *H. tetrandra*, and these species have sometimes been combined (Dwyer, 1980). The distinctions between them are discussed under the treatment of the latter species. **Hillia maxonii** is also similar to *H. palmana* of southern Central America; this latter species has consistently smaller flowers and usually smaller leaves.


**Hillia chiapensis** subsp. *grandifolia* Dwyer, Ann. Missouri Bot. Gard. 67: 216. 1980. **Type:** Panama. Veraguas: 6-7 km W of Santa Fe on new road past agriculture school, 2900 ft. [950 m], M. Nee 9698 (holotype, MO).

Suffrutescent herbs or shrubs to 5 m tall; bark gray-brown, smooth. Leaf blades elliptic to oblanceolate, 2-7 cm long, 1.5-3.5 cm wide, obtuse to rounded or rarely truncate at apex, cuneate to attenuate at base, coriaceous; secondary veins pinnate, 3-4 pairs, plane, without domatia; margins flat; petioles 3-8 mm long; stipules 12-20 mm long, 8-10 mm wide. Flowers solitary; peduncles 1-2 mm long; bracts lacking or 1-3 × 1-2 mm; calyx limb lacking or divided to base, the lobes 4, 4-6 mm long, 1-2 mm wide, ligulate, acute to rounded; corollas salverform, white, the tube 35-40 mm long, the lobes 4, 8-12 mm long, 6-12 mm wide, elliptic to suborbicular, rounded; anthers 4, ca. 5 mm long, subsessile, with tips positioned 2-3 mm below top of corolla tube; ovary 3-5 mm long; style ca. 15 mm long; stigmas ca. 7 mm long, linear, positioned below middle of corolla tube. Capsules 3-6 cm long including beak 1-3 mm long, 5-8 mm diam., not stipitate, smooth; seeds 2-4 × 0.5-1 mm, with filaments 6-13 mm long. Figure 11D, E.

**Habitat, phenology, and distribution (Fig. 16).** Central Nicaragua to central Panama, in wet forests at 675-2500 m. Collected in flower December to October, most frequently May to June, in fruit December to February, May, and July to October.

This species is distinguished by its medium-sized leaf blades that are usually obtuse to rounded at the apex and small flowers. It is similar to *Hillia maxonii* and *H. panamensis*; the distinctions among these three species are discussed in the treatments of the last two species.

**Representative specimens examined.** COSTA RICA. Alajuela: Fila Volcán Viejo, San Carlos, Gómez-Laurito 11095 (CR). Cartago: Vulcán Irauzú, SW slopes near Guayabillos, Cygodonitis 465 (F). Guanacaste: between the laguna del Arenal and el Alto de La Carpintera, cerca de Tilarán, Brenes 12644 (F, US). Heredia: entre Finca La Georgina y Vara Blanca, Jiménez 2075 (CR, F, NY). Limón: Reserva Indígena Talamanca, camino a Sokí entre la quebrada Amubri, margen izquierda del rio Lari, 9°29'40"N, 82°03'40"W, 200 m, Chacón 18 (MO). Puntarenas: Monteverde area, 10°20'N, 84°50'W, W. Haber 760 (MO), 1156 (MO), 4564 (MO), 6174 (MO), Haber & Bello 3671 (CR, MO), 4263 (CAS, CR, MO), 4267 (CR, MO), 4530 (MO). San José: near Altos de Tablazo ca. 7 km SSE of Higuito, ca. 9 km SSE of Los Remates, 12°36'N, 85°45'W, Moreno 24936 (MO). Granada: lado NO del volcan Momotombo, Finca San Joaquín, 11°50'N, 85°55'W, Moreno & Hickey 8510 (MO). Jinotega: ca. 1.5 km from Hwy. 3 on road to Aranjuez, 13°02'N, 85°55'W, Stevens 5947 (MO). Matagalpa: ridge along road between La Danta and La Laguna, 11°30'N, 85°43'W, Stevens 9616 (MO). PANAMA. Bocas del Toro: trail from Boquete to Cerro Pate Macho, 8°49'N, 82°24'W, McPherson & Merello 8328 (MO). Chiriqui: vicinity of Fortuna Dam, 8°40'N, 79°50'W, McPherson 10577 (MO). Darién: E slope of
Suffrutescent herbs or shrubs to 4 m tall; bark gray-brown, smooth. Leaf blades elliptic to narrowly elliptic, 6–15 mm long, 3–10 mm wide, rounded to obtuse at apex, cuneate to attenuate at base, subcoriaceous to coriaceous; secondary veins pinnate, ca. 2 pairs, smooth, without domatia; margins flat; petioles 1–2 mm long; stipules 4–5 mm long, 1–1.5 mm wide. Flowers solitary; peduncles ca. 1 mm long; bracts lacking; calyx limb usually lacking or divided to base, the lobes 4, 6–7 mm long, 1–3 mm wide, ligulate, rounded; corollas white, salverform, the tube 24–35 mm long, the lobes 4, 8–10 mm long, 3–5 mm wide, lanceolate, acute; anthers 4, 1–2 mm long, subsessile, with tips positioned 1–2 mm below top of corolla tube; ovary 2–3 mm long; style 7–12 mm long; stigmas 5–10 mm long, linear, positioned below middle of corolla tube. Capsules 2–4 cm long including beak 1–2 mm long, ca. 3 mm diam., not stipitate, smooth or usually with ca. 10 longitudinal ridges; seeds 1–2 × 0.5 mm, with filaments 6–13 mm long. Figure 11F–I; Dwyer (1980: fig. 48, as Hillia chiriquisensis).

Habitat, phenoology, and distribution (Fig. 12). Southern Mexico to Guatemala and Belize, and southern Nicaragua to western Panama, in wet forests at 20–2300 m. Collected in flower December, January, and June through August, in fruit November to April, August, and September.

This species is distinguished by its lanceolate acute corolla lobes and relatively small, usually narrow leaf blades, stipules, and capsules. The plants of southern Mexico and Guatemala are apparently disjunct from those of southern Central America, but no morphological differences are apparent and they appear to occupy similar habitats. Therefore Hillia chiapensis is here placed in synonymy. Similar apparently disjunct geographic ranges are seen in H. loranthoides and species of Psychotria (Hamilton, 1989).

Hillia panamensis is similar to H. palmana; the latter species has elliptic rounded corolla lobes 6–12 mm wide, and usually larger, proportionally broader leaf blades, stipules, and capsules.

Several sterile and fruiting specimens from relatively low elevations in Nicaragua and Costa Rica are provisionally included here, although they have relatively broad leaves and ridged capsules.


A subgeneribus ceteris Hilliae corollis infundibularibus 5–9-labiis viridibus flavovirentibus vel colore atque purpureo suffusis et stigmatibus subcapitatis supra antheras positis differt.

Calyx limb lacking, very reduced, or with 5–9 well-developed lobes; corollas membranaceous to carnose, funnelform, green to yellow-green or flushed with dull dark purple, the lobes 5–9, triangular to suborbicular; stamens attached above middle or near top of corolla tube, the anthers...
subsessile or with filaments well developed; stigmas subcapitate, positioned above anthers; capsules usually stipitate.

Seven species throughout northern and central South America, one extending north to Costa Rica.


This species is distinguished by its reduced calyx limb and bright pale green to yellow-green, broadly funnelform corollas. It is similar to *Hillia illustris* and *H. psammophila* of South America; the distinctions among these are discussed in the treatments of the other two species. Vegetatively *H. grayumii* resembles *H. triflora* var. *triflora*, with which it is sympatric, and these species can be difficult to separate in fruit.

*Hillia grayumii* appears to be uncommon and ephemeral. It was first discovered in a well-studied area of the La Selva Biological Station, where it apparently grew to flowering size rapidly, but within two years was no longer found in the vicinity (Hamel, pers. comm.; Grayum, pers. comm.). Representative specimens examined. COSTA RICA. Alajuela: Monteverde Biological Reserve, Rio Peñas Blancas, 10°19′N, 84°43′W, *Haber & Cruz* 8464 (CR). Cartago: on Casa de Tajas ridge above Río Gato, 9°47′N, 83°41′W, Lent 3703 (F, NY). Limon: shores of Caño Pereira, 10°45′-47′N, 83°36′-37′W, Stevens et al. 25120 (CR, MO).


Suffrutescent vines, climbing by adventitious roots; bark smooth. Leaf blades elliptic to lance-elliptic, 4.5–6.5 cm long, 2–3 cm wide, acuminate at apex with tip 4–10 mm long, acute at base, coriaceous; secondary veins pinnate, 3–4 pairs, plane, without domatia; margins flat; petioles 6–11 mm long; stipules not seen. Flowers solitary; peduncles 4–5 mm long; bracts not seen; calyx limb divided to base, the lobes 6, ca. 18 mm long, 3.5 mm wide, triangular to narrowly elliptic, rounded; corollas funnelform, yellow-green, the tube ca. 6 cm long, the lobes 6, ca. 1 cm long, ca. 15 mm wide, rounded; anthers 6, sessile, 7–8 mm long, with tips positioned ca. 5 mm below top of corolla tube; ovary ca. 7 mm long; stigmas ca. 2 mm long, subcapitate, positioned immediately above anthers. Capsules not seen. Steyermark (1963: fig. 74).

Habitat, phenology, and distribution (Fig. 8). South-central Venezuela, in wet forests at 1100 m. Collected in flower in April.

This species is distinguished by its relatively small leaves and anthers situated just below the top of the corolla tube. The original and subsequent descriptions of this species (Steyermark, 1963, 1974) describe the filaments as ca. 15 mm long, but the anthers are sessile and the filaments adnate to the corolla for ca. 45 mm. *Hillia psammophila* is similar to *H. illustris*; the distinctions between them are discussed in the treatmen of the latter species. *Hillia psammophila* is also similar to *H. grayumii* of Costa Rica and may be closely related; *H. grayumii* differs in its larger leaf blades, 9–16 cm long, and its anthers positioned just below the top of the corolla tube.


*Hillia tubaeformis* Cham., Linnaea 9: 260. 1834. TYPE:
Hillia illustris (Veil.) K. Schum. — A. Habit with flower. — B. Leaf. — C. Capsule. — D. Seed. — E. Stipule (floral). A, E, from Dusen 15539 (MO); B, from Vásquez & Jaramillo 4130 (MO); C, D, from Encarnación 26178 (MO). A–C to same scale, D to three times this scale, E to twice the first scale.

Brazil. Brazilia aequinoctialis, Sello 5988 (holotype, B destroyed, photos F, GH, NY; isotype, F).


Suffrutescent herbs, shrubs, or small trees to 8 m tall; bark gray-brown to red-brown, smooth, sometimes peeling. Leaf blades elliptic, 8.5–15 cm long, 3–8 cm wide, acute to usually acuminate at apex with tip 5–10 (–15) mm long, acute to cuneate at base, thickly coriaceous; secondary veins pinnae, 4–7 pairs, plane or with midrib sometimes prominently abaxially, without domatia; margins flat; petioles 6–13 mm long; stipules subtending leaves 23–33 mm long, 7–10 mm wide, those subtending flowers 26–60 mm long, 6–18 mm wide. Flowers solitary (–3); peduncles 1–5 mm long; bracts not seen; calyx limb divided to base, the lobes 6, 9–35 mm long, often unequal by ca. 1 mm, 1.5–2 (–4) mm wide, narrowly triangular, acute; corolla funnelform to broadly so, bright green to yellow-green, the tube 48–61 mm long, the lobes 6, 8–16 mm long, elliptic, obtuse to rounded; anthers 6, subossisile, 10–11 mm long, with tips positioned at or 1–2 mm above top of corolla tube; ovary 6–10 mm long with stipe 1–5 mm long; stigmas ca. 2 mm long, subcapitate, positioned immediately above anthers. Capsules with peduncles 2–10 mm long, (50–)85–115 mm long including beak 1–5 mm long, 8–15 mm diam., stipe 5–10 mm long, smooth or usually with ca. 10 low longitudinal ridges; seeds 2–4 × 0.5–2 mm, with filaments 14–22 mm long. Figure 17; Robbrecht (1988: fig. 6b, as Hillia tibiflora).

Habitat, phenology, and distribution (Fig. 15). Sporadic throughout tropical South America, in wet forests at 70–800 m, frequently along rivers. Collected in flower December, January, May to July, and September, in fruit January to March and May to November.

This species is distinguished by its relatively large, acute to acuminate leaf blades with pinnate venation, and stipitate capsules. Both vegetative and reproductive parts vary rather widely in size, as in several other species of Hillia.

Hillia illustris is similar to H. ulei, but the latter species is distinguished by its usually shorter, proportionally broader leaf blades with subpalmate venation. Hillia illustris also resembles H. grayumii, which has capsules that are not stipitate, a very reduced calyx limb, and filaments ca. 10 mm long, and H. psammophila, which has smaller leaf blades, filaments ca. 15 mm long, and anthers positioned below the top of the corolla tube.
There appears to be no morphological difference between plants of Trinidad and the mainland, and *Hillia trinitensis* is not maintained here. *Hillia goudotii*, based on a single specimen, differs from typical *H. illustris* only in having flowers borne in a cyme of three rather than solitary. A similar variation in flower number is seen in *H. saldanhae*, and the reverse variation, with flowers usually three but rarely one or two, is found in *H. triflora*. Therefore *Hillia goudotii* is not maintained here.

Some authors (e.g., Robbrecht, 1988) have corrected the spelling of *H. tubaefera* (tube-shaped) to "tubiflora" (tube-shaped), but Chamisso based his description on a flowering specimen, and most likely intended to apply the first, more appropriate epithet.

### Representative specimens examined.

**BOLIVIA.**

**ECUADOR.**

**PERU. Loreto**: prope Yurimaguas, Aug 1902, *E. Ule* 6305 (holotype, B destroyed, photos F, GH, MO, NY; isotype, F). *Steyermark* (1972) cited *Ule* 6303 as the type collection, but this seems to be an error.


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Suffrutescent herbs or shrubs to 2 m tall; bark gray-brown, smooth. Leaf blades elliptic to broadly elliptic, 2–6.5(–7.5) cm long, 1.3–4 cm wide, acute to usually acuminate at apex with tip 3–5 mm long, rounded to cuneate at base, thickly coriaceous; secondary veins subpalmate, 5–7 pairs, plane or with midrib sometimes prominent abaxially, without domatia; margins flat; petioles 4–11 mm long; stipules 5–17 mm long, 1.5–8 mm wide. Flowers solitary; peduncles 1.5–2 mm long; bracts lacking or 2–3 × 0.5–1.5 mm; calyx limb divided to base, the lobes 7–10, 8–15 mm long, often unequal by 1–3 mm, 1–2 mm wide, narrowly ligulate to triangular, acute to rounded; corollas broadly funnelform, bright green to yellow-green, the tube 28–39 mm long, lobes 7–10, 6–7 mm long, rounded; anthers 8, subsessile, 6–8 mm long, with tips positioned at top of corolla tube; ovary 5–10 mm long, stigmas 8–10 mm long, stigmas ca. 2 mm long, subcapitate, positioned immediately above anthers. Capsules with peduncles 1.5–3 mm long, 6–10.2 cm long including bead 1–5 mm long, 8–10 mm diam., stigmas 8–15 mm long, smooth; seeds 1–2 × 0.5–1 mm, with filaments 11–24 mm long. Figure 18.

**Habitat, phenoology, and distribution** (Fig. 6). Sporadic throughout tropical South America and eastern Panama, in wet forests at 0–900 m, most frequently along rivers. Collected in flower March to May, July, and August, in fruit January, March to May, July to September, and November.

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