A REVISION OF THE GENUS HELIOCARPUS L.¹
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INTRODUCTION

_Heliocarpus_ has received considerable attention from plant systematists probably because of the perplexing variation found in the genus and because of the few constant characters of taxonomic value. Furthermore, in the herbarium, the specimens are either in fruit or in flower, never both; and when in flower are either hermaphrodite or pistillate. Thus, assigning them to any particular species becomes extremely difficult. Despite a recent taxonomic study of the genus,² there is still considerable confusion regarding many species both in the literature and in the herbarium. More than fifty species and varieties have been named thus far, and with the prevalent vagueness in the concept of speciation, there appears superficially to be but two alternatives: either to split the genus into innumerable indistinct and undefinable "species" or to lump them indiscriminately into few categories of scarcely greater reality.

In my study of the genus an attempt has been made to escape this dilemma by clarifying the concept of speciation. However, as this study has been confined entirely to herbarium specimens which represent only very small portions of the woody plants, no definite idea or suggestion as to the individual variations of single plants has been obtained. I have been fortunate enough in being able to study specimens from nearly all the major herbaria both in the United States and in Europe. The standard method of the herbarium taxonomist has been used for the interpretation of the species, and an attempt has been made to identify the fruiting specimens with the flowering ones. As far as possible, no intergrading forms have been considered as worthy of specific rank, and I have tried to group the "species" into fewer categories of perhaps greater biological reality, in the hope that they will be satisfactory both from a taxonomic and from a practical standpoint. The key has been so prepared that it should be usable for both the fruiting and the flowering specimens.

GENERIC RELATIONSHIPS

_Heliocarpus_ L.³ commonly is referred to the tribe Grewieae⁴ of the family Tiliaceae and usually is recognized by its characteristic fruits. The genus is distinct from the other genera of Grewieae except _Triumfetta_. There is no difficulty in distinguishing the two genera when both are in fruit, as the fruits are very dis-

¹ An investigation carried out at the Missouri Botanical Garden and submitted as a thesis in partial fulfillment of the requirements for the degree of Master of Arts in the Henry Shaw School of Botany of Washington University.
tinct. A very good description of the fruit of *Heliocarpus* was given by Linnaeus, who asked, in naming the genus, "Who could ever behold an almost rounded fruit, bordered with a halo of rays, without thinking of the sun as conceived by the painters?" In *Triumphetta* the fruit is a burr, with many bristles all over the surface.

It is slightly more difficult to differentiate between the two genera in the case of flowering specimens. Both have alternate, palmately reticulated leaves with long, slender petioles and stellate pubescence. The aspect of the specimens also is very similar and the superficial resemblance rather striking. The chief differentiating characters may be summarized as follows:

1. The inflorescence—In *Heliocarpus* usually terminal, and when axillary large and spreading; in *Triumphetta* generally axillary, rarely large and spreading.

2. The cymes—In *Heliocarpus* disposed in nodose clusters of about 12–20 flowers each; in *Triumphetta* generally not in nodose clusters, and if in nodose clusters usually 6- to 12-flowered.

3. The flowering peduncles—In *Heliocarpus* nearly always 3-flowered (rarely 2-flowered), and usually ebracteolate; in *Triumphetta* 1- or 2-flowered (rarely 3-flowered) and conspicuously bracteolate.

4. The mature floral buds—In *Heliocarpus* as long as 6–7 mm., the sepals appended or unappended at the tips, the petals valvate; in *Triumphetta* as long as 2–3 cm., the sepals always with apical appendages, the petals with twisted aestivation.

5. The number of stamens—In *Heliocarpus* usually 12–40; in *Triumphetta* usually more numerous.

6. The gonophore—Simple in *Heliocarpus*; in *Triumphetta* with a ciliate saucer-shaped margin (urceolus) surrounding the stamens.

7. The ovary—In *Heliocarpus* either borne upon a gynophore or sessile upon the gynophore, 2-celled, laterally compressed and ciliate about the margins; in *Triumphetta* always sessile upon the gonophore, 3- to 5-celled, not laterally compressed, and generally pubescent.

8. The style—In *Heliocarpus* not more than three to four times the length of the ovary, usually much shorter, always bifid at the tip with the stigma lobes spreading; in *Triumphetta* usually longer than three to four times the length of the ovary, simple throughout, the stigma flattened or capitate.

*Heliocarpus* can be divided into two major groups of species based on the presence or absence of a gynophore in flower or fruit; further, the presence of appendages at the tips of the sepals is a character which is correlated in the majority of species (except in *H. mexicanus* and *H. nodiflorus*) with the absence of the gynophore.

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GEOGRAPHICAL DISTRIBUTION

The geographical range of *Heliocarpus* embraces nearly the whole of the tropical Americas. With the exception of the predominantly South American *H. popayanensis*, the species are indigenous entirely to Mexico and Central America. The presence of some plants of *H. popayanensis* in Hawaii apparently is due to recent introduction for reforestation in the foothills. Possibly in the same category is the presence of some plants of *H. Donnell-Smithii* in Martinique.

The species can be divided into five groups with respect to their geographical distributions:

1. Northwestern Mexico—*H. attenuatus* and *H. Palmeri*.
2. Southwestern Mexico—*H. terebinthinaceus*, *H. pallidus*, and *H. occidentalis*.
4. Southeastern Mexico—*H. americanus*.
5. Southern Central America and South America—*H. popayanensis*.

The species of the sessile-fruited group are confined for the most part to the northern range of the distribution; while those of the stipitate-fruited group, where the fruits are borne upon bristly gynophores, are mostly in the middle and southern areas of distribution.

The northernmost limit of the genus is in subtropical Sonora and Chihuahua, Mexico, where the plants grow in canyon forests or oak flats; the southernmost limit is in central Argentina, where lower elevations along river banks are inhabited.

Except for shrubby plants (*H. occidentalis* and *H. pallidus*), which sometimes grow on barren hill slopes, the majority of the species, consisting of small trees, grow only in moist places at higher elevations, usually at about 1000 m. or more, in rain- or cloud-forests, along roadways or river banks in sheltered places, or on edges of forests (usually on cut-over lands in second growth, where they sometimes form a pure stand).

ECONOMIC VALUE

In so far as is known from collectors' notes and from the published accounts of Standley6 and Martinez7, the economic importance of *Heliocarpus* is primarily in its bark, which produces a very strong and durable fibre. The bark of the young branches yields a fibre from which a strong but coarse rope is made. It is used also for weaving mats and baskets. The principal component of the Mexican fabric *belem* is the cordage extracted from the barks. Resistant paper formerly was made from the wood in Mexico; in Brazil it is still so used to some extent. The wood of the trees is soft and light and is used for floats and bottle-stoppers. Because of its lightness it has been used for rafts. The bark is used for *mecates* in Guate-

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7 Plantas utiles de Mexico, p. 253. 1936.
mala, and a decoction is used in sickness of cattle, and sometimes is applied on sores. In Hawaii the trees have been planted on the foothills for reforestation.

VERNACULAR NAMES

H. americana: janote (Vera Cruz).
H. appendiculatus: burio, burio blanco, and burio colorado (Costa Rica); cajetan (Guatemala); balsa and pastano mula (Nicaragua); calagua (El Salvador); jonote, jonote blanco, jonote colorado (Vera Cruz); majao (Honduras).
H. attenuatus: samo baboso (Sinaloa).
H. Donnell-Smithii: bolol (Quintana Roo); jolocin (Tabasco); jonote (Vera Cruz); majao (Honduras); mobo, "broad-leaved mobo", and "mountain mobo" (British Honduras).
H. mexicana: antigua, cajeto, and majagua (Guatemala); mobo (British Honduras).
H. nodiflorus: "broad-leaf mobo" (British Honduras); cajeto (Guatemala); majao (Honduras).
H. occidentalis: pulmonilla, guasima, and panigua (Chiapas and Jalisco).
H. pallidus: guasima and tilia (Guerrero, Jalisco, and Mexico).
H. Palmeri: coche (Sinaloa); rama kowusamo, and palo chichu (Sonora).
H. popayanensis: balsa (Colombia); majagua (Venezuela); palo de balsa (Peru); sanpan (Ecuador).
H. terebinthinaceus: cuahualagwa or quanbalagwa (Morelos and Puebla); guasima, jolotzin, majorbua, and jonote (Morelos, Oaxaca, and Guerrero).

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Royal Botanic Gardens of Trinidad and Tobago, Port-of-Spain, Trinidad, B.W.I.
University of California, Berkeley, California.
University of Michigan, Ann Arbor, Michigan.
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Woody trees or shrubs; older branches cream to brown, nearly glabrate, the younger branches usually stellate-pubescent, dark brown, fibrous, with many mucilage canals. Leaves alternate, petiolate, stipulate, the stipules usually large, early deciduous, very rarely persistent, the blade 3-lobed to undivided, venation palmate and either 5- to 7-costate or 3-costate at the base, irregularly serrated, the basal serrations usually glandular, slightly to densely stellate-pubescent, acute to

Illustrations of taxonomic criteria of the genus Heliocarpus: 1, leaf of H. terebinthinaceus showing the 3-costate venation at the base; 2, leaf of H. appendiculatus showing the 5-costate venation at the base and the 2 leafy auricles at the basal sinus; 3, sessile fruit of H. occidentalis showing the separate tufts of stellate hairs; 4, stipitate fruit of H. Donnell-Smithii borne on a bristly gynophore; 5, floral bud of H. Palmeri showing the relatively large, reflexed, trigonal appendages on the tips of the sepals; 6, floral bud of H. appendiculatus (note the absence of apical appendages); fig. 7, 3-radiate flowering peduncle (cymule) of H. Palmeri with a pair of bracteoles.
acuminate, the base rounded or cordate. Inflorescence gynodioecious or hermaphrodite, usually terminal (axillary in some species), large and spreading, consisting of numerous aggregate dichasia, the main axis branching sympodially and at each node bearing a cluster (cyme) of some 12–20 flowers, the terminal branches with 5–7 cymes, usually more or less secund, each cyme consisting of reduced sympodially branched axes terminating in 3– (rarely 2-) flowered cymules. Flowers either hermaphrodite or pistillate, regular, hypogynous, 4- to 5-merous; the sepals valvate, usually stellate-pubescent without, glabrate within, sometimes with small appendages at the tips; the petals 4–5 in hermaphrodite flowers, absent in the pistillate, free, valvate, 1- to 3-nerved, shorter than the sepals, usually ciliate at the base, sometimes slightly so at the apex; the stamens 12–40 in hermaphrodite flowers, staminodial or absent in the pistillates, borne cyclically on the enlarged gonophore, with 2-lobed, 4-celled, introrse, longitudinally dehiscent anthers; the ovary wholly superior, sessile upon the gonophore or with a manifest gynophore, ellipsoid to orbicular, laterally compressed, ciliate and with shorter pubescence on the faces, 2-celled, falsely 4-celled at the base, each cell with 2 anatropous ovules, the style filiform, bifid at the tip with the stigma lobes spreading and simple or slightly 3-lobed. Fruit dry, indehiscent, 2-celled, 2-seeded, laterally compressed, ellipsoid to orbicular, slightly rugose, sessile or stipitate upon the accrescent gynophore, ciliate with 2 rows of plumose bristles decurrent upon the gynophore when present, the faces pubescent to glabrate; the seed compressed-ovoid or -pyriform, with a median funicular groove, endosperm oily.

Standard species: *Heliocarpus americanus* L.

KEY TO THE SPECIES

A. Fruit sessile; ovary sessile on the gonophore.

B. Leaves 3-lobed, veins 3-costate at the base; buds with or without appendages at the tips of the sepals.

C. Leaves with dense, coarse pubescence on both surfaces, cordate, 3-lobed, about 14 cm. long and 12 cm. wide; buds sometimes with small appendages at the tips of the sepals; fruit spherical, tomentose; southwestern Mexico .............................1. *H. terebinthinaceus*

CC. Leaves with pale, smooth tomentum beneath, glabrate above, the base rounded to slightly cordate, 3-lobed to obscurely so, about 10 cm. long and 8 cm. wide; buds with conspicuous, erect appendages at the tips of the sepals; fruit ovoid, glabrate; southwestern Mexico .................................2. *H. pallidus*

BB. Leaves not lobed, veins 5- to 7-costate at the base; buds with conspicuous appendages at the tips of the sepals.

C. Leaves cordate.

D. Leaves nearly glabrate on both surfaces, about 14 cm. long and 10 cm. wide, acuminate; appendages on the sepals trigonal, large and reflexed; stamens about 40; style about 4 times longer than the ovary; fruit spherical, with a distinct groove in the body, slightly tomentose; northern Mexico .................................3. *H. Palmeri*

DD. Leaves glabrescent above, tomentose beneath, small, about 8 cm. long and 5 cm. wide, caudate-acuminate; appendages on the sepals linear, erect; stamens 16–20; style about twice the length of the ovary; fruit ellipsoid, tomentose; northern Mexico .................................4. *H. attenuatus*

CC. Leaves rounded or cuneate at the base, glabrate or nearly so on both surfaces; appendages on the sepals short, erect; stamens about 40; style about twice the length of the ovary; fruit ovoid with short, separate tufts of stellate hairs; southwestern Mexico .................................5. *H. occidentalis*
AA. Fruit borne on a bristly gynophore; ovary borne on a gynophore upon the gonophore.

B. Inflorescences axillary, leafy; leaves not lobed, the base rounded, glabrate, slightly tomentose beneath; buds with conspicuous appendages at the tips of the sepals; stamens about 25–30; fruit ellipsoid, glabrous; southern central Mexico and Central America

BB. Inflorescences generally terminal, not leafy.

C. Leaves with two conspicuous auricles at the basal sinus, usually not lobed, the base rounded or subcordate, glabrate above, tomentose beneath; buds without appendages at the tips of the sepals; stamens about 30; fruit suborbicular, tomentose; southern central Mexico and Central America

CC. Leaves without conspicuous auricles at the basal sinus.

D. Leaves not lobed, rounded at the base, not longer than 14 cm. or wider than 10 cm.

E. Leaves very densely tomentose beneath, glabrate above; stamens about 20; style very briefly bifid; fruit orbicular, tomentose; southeastern Mexico

EE. Leaves glabrate on both surfaces; stamens about 12–16; style bifid about half its length; fruit ellipsoid, glabrate; southern central Mexico and Central America

DD. Leaves generally 3-lobed, cordate at the base, about 17 cm. long and over 14 cm. wide.

E. Leaves glabrate above, the lower surface puberulent with short, stellate and long, simple hairs, especially on the veins; buds without appendages at the tips of the sepals; stamens about 12; style briefly bifid, each stigma with 3 acute lobes; fruit ovoid, slightly tomentose to nearly glabrate; southern Central America and South America

EE. Leaves glabrate on both surfaces, veins not pubescent on the lower surface; buds sometimes with short appendages at the tips of the sepals; stamens about 24; style bifid about half its length, stigma-lobes simple, acute; fruit orbicular, slightly tomentose; southern Mexico and Central America


Small trees or shrubs 4–5 m. high; older branches cream to brownish, glabrate, slightly longitudinally ridged, irregularly punctate with white lenticels; younger branches and inflorescence axes rough, scurfy, ferruginous-tomentose with stellate hairs. Leaves 3-lobed, acuminate, about 13–15 cm. long and 10–12 cm. wide, 3-costate, the mid-costa arising independently of the lateral costae, and each lateral costa consisting of 2 or 3 veins united at the basal sinus, base cordate, irregularly and bluntly serrated, both surfaces light green or pale brownish with thick, matted, stellate pubescence, the veins more pubescent with both stellate and long simple hairs; petioles slender, about 8 cm. long, covered with ferruginous tomentum. Inflorescences gynodioecious; the hermaphrodite usually axillary, rarely terminal, large and leafy, usually about 20 cm. long and 15 cm. wide, sometimes about 25 cm. long and 20 cm. wide, the cymes of about 15–18 flowers, rather compact in nodose clusters, the flowering peduncles 3-radiate, about 2 mm. long, the pedicels about 2 mm. long, the buds obovoid, constricted towards the base, sometimes with small erect appendages on the tips of the sepals, the sepals 4, spatulate, about 4–5
Fig. 1. *H. terebinthinaceus*

mm. long, densely stellate-tomentose without, glabrate within, the petals 4, linear, 1-nerved, about 3–4 mm. long, the ovary ellipsoid, about 1.5 mm. long, sessile, with a style about 3 mm. long, bifid about one quarter of its length and with stigma lobes acute, spreading; the pistillate much smaller than the hermaphrodite, about 10–15 cm. long and 8–10 cm. wide, the cymes of about 18 flowers, very much crowded in compact nodose clusters, the flowering peduncles 3-radiate, very short, less than 1 mm. long, the pedicels about 1–2 mm. long, the buds obovoid, not appendaged at the tips of the sepals, the sepals 4, linear, about 2 mm. long, densely stellate-tomentose without, glabrate within, the petals none, the staminodes about 10–12, the ovary ellipsoid, minute, sessile, with a style about twice the length of the ovary, briefly bifid at the tip, and with the stigma lobes acute. Fruit suborbicular, 4–5 mm. in diameter, rather densely tomentose, sessile, the fringe of two rows of plumose bristles about 5–7 mm. long; the seed ovoid, about 2 mm. long, with a very slight groove in the middle.

Distribution: On the highlands of central Mexico, especially on open hill slopes, altitude above 1000 m. Flowers throughout September and October, and fruits from late October to December.

**Mexico:** Chiapas: Tuxtla Gutiérrez, Juzepczuk 1461. Guerrero: above Chilpancingo, Nelson 7046; Sierra Madre, alt. 1250 m., Langlássé 572. Jalisco: road to San Domingo mine, alt. 5160 ft., Etztatan, Barnes & Land 285; barranca, Guadalajara, alt. 4500 ft., Pringle 9693; Guadalajara, Pringle 1791. Mexico: Tejupilco, Temascaltepec,
This species is very distinct and can be recognized easily by its 3-lobed leaves with the characteristic venation, and also by its sessile fruits. Hochreutiner pointed out that Berlandier 1064, collected from Cuernavaca, which Rose cited for H. Nelsonii, is identical with the specimen which de Candolle, on the assumption of a 4-locular ovary, described as Grewia terebinthinaceus.

Rose differentiated his H. Nelsonii (type: Nelson 1243 & 1485), H. reticulatus (type: Pringle 1791) and H. microcarpus (type: Pringle 8710) primarily on the degree of pubescence on the fruits. This character is extremely variable. In matching the three types, it is noticeable that H. microcarpus has slightly smaller fruits and that the flowers have minute erect appendages. The size of the fruits varies slightly from plant to plant and sometimes on the same plant. Furthermore, the apical appendages on the sepals, when present, are extremely minute and not clearly seen. As they stood, it was difficult to tell the three species apart and there were many misdeterminations.


Small trees or shrubs about 2–4 m. high; older branches yellowish brown, glabrate, slightly rugose, punctate with few white lenticels; younger branches and inflorescence axes scurfy, slightly ferruginous-tomentose. Leaves small, younger ones generally not lobed or obscurely so, older ones 3-lobed, about 8–10 cm. long and 7–8 cm. broad, 3-costate, with the mid costa arising independently of the two lateral costae, and each lateral costa consisting of 2 or 3 veins united at the sinus, base usually cordate or subcordate, in younger leaves slightly rounded, acuminated, irregularly serrated, upper surface dark green, glabrate, lower surface whitish, densely stellate-tomentose with appressed hairs; petioles long and slender, 6–7 cm. long. Inflorescence hermaphrodite, usually axillary, large and spreading, leafy, about 14–20 cm. long and 12–20 cm. wide; the cymes of about 12–15 flowers borne loosely in nodose clusters, the flowering peduncles 3-radiate, about 2–3 cm. long, the pedicels about 4–5 mm. long, the buds obovoid, constricted at the base, with small linear, acute, erect appendages at the tips of the sepals, the sepals 4, linear, 4–6 mm. long, light green and slightly stellate-pubescent without, glabrate and yellowish within, the petals 4, linear, about 3–4 mm. long, the ovary ovoid, small, 0.5–1.0 mm. long, sessile, with a style about twice the length of the ovary, briefly bifid at the tip, and with the stigma lobes acute. Fruit ovoid, usually in compact clusters, very tomentose when immature, becoming glabrate at maturity, about 5 mm. long and 3 mm. wide, sessile, the fringe of two rows of plumose bristles about 4–5 mm. long; the seed obliquely ovoid, about 3 mm. long and 2 mm. wide, with a very deep groove in the middle.

Distribution: On the highlands of central and southwestern Mexico, especially on open hill slopes, altitude above 500 m. Flowers from October to November, and fruits in December and January. Usually leafless in January.


The types of the two species H. pallidus (E. Palmer 157) and H. velutinus (Pringle 8694) have leaves which apparently look distinct, those of H. pallidus being small, obscurely 3-lobed, with rounded base, and of H. velutinus relatively
small but definitely 3-lobed with subcordate base. It is apparent that the type of *H. pallidus* represents the immature and that of *H. velutinus* the mature state of the leaves. On the same branch (cf. *Hinton 5410* and *Mexia 1100*) the leaves at the base of the specimens may correspond to those of *H. velutinus* and those near the tip to *H. pallidus*.

The fruits on the type of *H. velutinus* are slightly larger and more glabrate than those on the type of *H. pallidus*. There are many intermediates between these two extremes, in specimens that answer to the above descriptions. Presumably the fruit, which is slightly tomentose when young, becomes nearly glabrate at maturity.


*H. polyandrus* S. Wats. loc. cit. 1886. (T.: E. Palmer 100).

*H. glaber* Brandegee, in *Bot.* 5:207. 1804. (T.: Brandegee s.n. in Herb. Calif.).

Diffusely spreading shrubs about 2–3 m. high; older branches dark brown, glabrate with few short tufts of stellate hairs mostly around the white lenticels; younger branches and inflorescence axes covered lightly with short stellate tomen-
Fig. 3. *H. Palmeri*

Map 3. Distribution of *H. Palmeri*
tum. Leaves broadly ovate, 12–14 cm. long and 8–10 cm. wide, not lobed, 5-costate, narrowly acuminate, base cordate or subcordate, thin, unequally and bluntly serrated, basal serrations glandular, upper surface dark green, nearly glabrate to glabrate, rough, with few short suppressed, scattered tufts of stellate hairs, sometimes slightly scabrous on the veins, lower surface lighter green, slightly more pubescent than the upper, nearly glabrate, generally coarse, with short suppressed stellate hairs, veins scabrous, prominent; petioles slender, 5–7 cm. long, covered very lightly with short suppressed yellowish stellate pubescence. Inflorescence hermaphrodite, terminal, rarely axillary, slightly leafy, about 14 cm. long and 12 cm. wide, rarely larger, the cymes of about 12 flowers rather loose, the flowering peduncles 3-radiate, about 2 mm. long, the pedicels 3–4 mm. long, the buds obovoid, constricted towards the base, with conspicuous appendages at the tips of the sepals, the sepals 5, spatulate, 5–6 mm. long, 3-nerved, with large, about 2 mm. long, reflexed, trigonal appendages at the tips, light green with short suppressed tufts of stellate hairs without, glabrate, yellow to yellowish brown within, the petals 5, linear, slightly shorter than the sepals, about 4 mm. long, 1- to 3-nerved, yellowish brown, the stamens about 40, with filaments about 4–5 mm. long, the ovary orbicular, 1–2 mm. long, sessile, with a slender style about 4 times the length of the ovary, briefly bifid at the tip, and with small acute stigma lobes. Fruit orbicular, sessile, densely stellate-pubescent, 5 mm. in diameter, with a distinct groove in the middle of the fruit body, the fringe dense, of 2–3 rows of plumose bristles shorter than the diameter of the fruit body, about 3 mm. long; the seed plump, ovoid, very slightly grooved, about 2 mm. long.

Distribution: On shady canyon slopes or oak flats in northwestern Mexico, altitude about 500 m. Flowers in September–October and fruits in late October–December.

MEXICO: CHIHUAHUA: Hacienda San Miguel, near Batopilas, E. Palmer 97, 100, 101; Guerro, Río Mayo, Gentry 2440, 2009; La Mesa, Gentry 6607; Almaden, Le Sueur 1404. SINALOA: Cerro Colorado, alt. 2000 ft., Gentry 5060; vicinity of Culican, Brandegee s. n. (type of H. glaber). SONORA: Canyon Sapopa, Río Mayo, Gentry 1644, 1709.

A very distinct species with nearly glabrous leaves and sessile fruits characteristically grooved in the middle and with flowers bearing relatively large trigonal apical appendages on the sepals.

The leaves in the type of H. Palmeri (E. Palmer 191) are slightly more pubescent than those of H. polyandrus (E. Palmer 100), but in both they are nearly glabrous and the variation is only one of slight degree. S. Watson mentioned that in H. Palmeri the number of stamens is about 20, but I have not been able to find any specimen that answers to the description of H. Palmeri with 20 stamens, either in the specimens cited by S. Watson or in others.


Small shrubs about 2–3 m. high; older branches dark brown, rather slender, slightly pubescent, smooth, irregularly punctate with few white lenticels; younger branches and inflorescence axes softly tomentose with relatively long, light yellowish brown, stellate hairs, smooth. Leaves ovate to very obscurely 3-lobed, 5-costate at the base and gradually tapering to the cuneate-acuminate tip, base cordate or subcordate, irregularly and bluntly serrated, upper surface slightly pubescent, coarse, with many suppressed stellate hairs, scabrous on the veins, lower surface densely stellate-pubescent especially on the veins. Inflorescence hermaphrodite, usually axillary, small, leafy, about 8 cm. long and 10 cm. wide, rarely larger, the cymes of about 16–18 flowers borne loosely in nodose clusters, the flowering peduncles mostly 3-radiate, rarely 2-radiate, about 5–6 cm. long, usually subtended by two short bracteoles, the pedicels 2–3 mm. long, the buds obovoid, very slightly constricted towards the base, with short appendages on the tips of the sepals, the sepals 3 or 4, linear, 4–5 mm. long, 1- to 3-nerved, the short, erect appendages on the tips 1 mm. long, light green with fine tomentum without, glabrate, yellowish brown within, the petals 3 or 4, linear, shorter than the sepals, 2–3 mm. long, the stamens about 16–20, with the filaments as long as the petals, the ovary ovoid, 1.0–1.5 mm. long, sessile, with a style about twice the length of the ovary, bifid about one quarter of its length and with the stigma lobes acute, spreading. Fruit ovoid, sessile, densely tomentose, 3 mm. long and 2 mm. wide, the fringe of two rows of slender plumose bristles, 6–7 mm. long; the seed ovoid, 1–2 mm. long.

Distribution: Confined entirely to northwestern Mexico, apparently rare, usually growing at altitudes of about 300–500 m. Flowers from August to September and fruits from October to December.

This is a very distinct species, with the caudate-acuminate leaves the smallest known for the genus. It does not resemble any other species in its vegetative characters. The leaves of the type of *H. viridis* (*Rose, Standley & Russell 12828*) are small but not caudate-acuminate. The type is from a relatively young plant and rather poorly preserved. I have not been able to find any other specimen which matches the type, and I am doubtful about the type itself. Except for its small wrinkled leaves, there is nothing which would prevent its identification with *H. attenuatus* (type: E. Palmer 09).


Small trees or shrubs about 5–6 m. high; older branches generally glabrate, cream to brownish, slightly rugose, irregularly punctate with white lenticels; younger branches and inflorescence axes covered with rather dense tomentum of short yellowish stellate hairs. Leaves broadly ovate, sometimes rather obscurely 3-lobed, 10–13 cm. long and 8–11 cm. wide, 5- to 7-costate at the base, narrowly acuminate, base rounded or cuneate, rarely subcordate, somewhat regularly and doubly serrated, upper surface generally dark green, glabrate, coarse, with suppressed stellate hairs, veins and veinlets more pubescent with short tufts of yellowish stellate hairs, lower surface slightly more pubescent than the upper, becoming
Fig. 5. *H. occidentalis*

nearly glabrate when mature, yellowish green, the veins and veinlets covered with dense tufts of yellow stellate hairs; petiole about 6 cm. long, slender, covered lightly with yellow stellate hairs. Inflorescences hermaphrodite, usually axillary, rarely terminal, rather leafy, about 14 cm. long and 10 cm. wide, sometimes much smaller, the cymes of about 12 flowers, rather loose in nodose clusters, the flowering peduncles 3-radiate, about 2 mm. long, subtended by two small bracteoles, the pedicels 2–3 mm. long, the buds obovoid, slightly constricted towards the base, with conspicuous appendages at the tips of the sepals, the sepals 5, rarely 4, linear-spatulate, 4–5 mm. long, 3- to 5-nerved, with small, about 1 mm. long, erect, linear appendages at the tips, light green with short stellate hairs without, glabrate, cream or light brown within, the petals 5, rarely 4, linear, nearly as long as the sepals, 1- to 3-nerved, the stamens about 40, with the filaments about 4–5 mm. long, the ovary ovoid, 1.0–1.5 mm. long, sessile, with a short style about twice the length of the ovary, briefly bifid at the tips and with small acute stigma lobes. Fruit orbicular, sessile, punctate with short separate tufts of stellate hairs, about 3 mm. in diameter, the fringe of relatively stout plumose bristles about 8–9 mm. long; the seed ovoid, about 2 mm. long.

Distribution: Plants of central Mexico, growing on hill slopes and chaparrals, between 500 and 1000 m. Flowering in September and October and fruiting from October to December.


The fruits of this species are very characteristic, being nearly orbicular, with short separate tufts of stellate hairs. The small erect sepal appendages and the glabrate leaves make this species an easy one to identify. *H. laevis* (type: Rose 2860) which has been identified with many other species actually is conspecific with this.

Triumfetta mexicana Turcz. in loc. cit. 31:1:230. 1858.
H. yucatenensis Millsp. in herb.

Small trees or shrubs 5–6 m. high; older branches dark brown, glabrate, slightly rugose, punctate irregularly with minute white lenticels; younger branches and inflorescence axes very lightly scurfy-pubescent, with small clusters of simple and stellate hairs, nearly glabrate. Leaves broadly ovate to ovate-lanceolate, the more mature ones broadly ovate, the younger ones around the inflorescence usually ovate-lanceolate, 5-costate at the base, not lobed, 12–14 cm. long and 6–10 cm. wide, acute to acuminate, base rounded or slightly obtuse, irregularly and bluntly serrated, the basal serrations glandular, upper surface dark green, glabrate with few suppressed stellate hairs, lower surface more pubescent with fine, weak, crisped, stellate
Fig. 6. *H. mexicanus*

Map 6. Distribution of *H. mexicanus*
hairs, becoming nearly glabrate at maturity. Inflorescences gynodioecious, axillary, large and very leafy; the hermaphrodite large and spreading, very leafy, about 20 cm. long and 15 cm. wide, the cymes of about 20 flowers, rather loose, the flowering peduncle mostly 3-radiate, about 2–3 mm. long, usually subtended by a pair of small blunt bracteoles, the pedicel about 6–8 mm. long, the buds obovoid, slightly constricted in the middle towards the base, rusty brown, with small appendages at the tips of the sepals, the sepals usually 5, rarely 4, spatulate, about 5–6 mm. long, 1–2 mm. wide, rusty brown and glabrate without, lighter brown and glabrate within, with linear, about 1.5 mm. long, erect appendages on the tips, the petals 5, rarely 4, linear, 1-nerved, 3–4 mm. long, the stamens 24–30, with the filaments as long as the petals, the ovary ellipsoid, 1–2 mm. long, borne on a very short gynophore, with a style about 3 times the length of the ovary, briefly bifid, and with acute, slightly spreading stigma lobes; the pistillate nearly as large as the hermaphrodite, the cymes of about 20 flowers, greatly condensed and crowded in nodose clusters, the flowering peduncles 3-radiate, short, less than 1 mm. long, the pedicels about 1 mm. long, the buds about 2–3 mm. long, appendaged at the tips of the sepals, the sepals 5, linear, about 3 mm. long, appendaged at the tips, rusty brown and glabrate without and within, the petals none, the staminodes about 20–30, the ovary ovoid, less than 1 mm. long, borne on a very short gynophore, with a short style, briefly bifid and with acute stigma lobes. The fruit ellipsoid, glabrate, surface red-glandular, about 6–8 mm. long and 3 mm. wide, with few ridges, borne on a bristly gynophore 2–8 mm. long, the fringe usually of one row of plumose bristles 6–8 mm. long; the seed pyriform, blunt-pointed, about 3–4 mm. long.

Distribution: Plants of southeastern Mexico and northern Central America, growing along roadways, river banks, or on hill slopes; in thickets of bushy slopes or on hill tops in open places. Flowers from September to October and sometimes as late as December, and fruits from November to February.

**Mexico:** Campeche: Tuxpena, Lundell 050, 1102. Oaxaca: locality not mentioned, Ghiesbrecht 51. **Vera Cruz:** Zacuapan, Linden 898; Cordillera, Galeotti 4154; Zacuapan and vicinity, Purpus 2227; Mirador, Liebmnn 523; Mirador, Linden 858; rocky barranca near Gauchio, Viejo, Purpus 15074a. **Yucatán:** Pocoboch, Chac tolo, Gaumer 1315; San Anselmo, Gaumer 1234; Calotmul, Gaumer 2302; Chichankanab, Gaumer 2275; Xnocao, Gaumer 23488, 24177.

**British Honduras:** El Cayo District, Vaca, Gentle 2273; Jacinto Hills, alt. 600 ft., Schipp S-589.

**Guatemala:** Alta Verapaz: southwest of Lanquin, alt. 600–1000 m., Steyermark 44076. Chimaltenango: along Rio Guacalate, southwest of Chimaltenango, alt. about 1700 m., Standley 80064, 81067; Chimaltenango, Johnston 1106, 1322. Chiquimula: Volcán Ipala, near Amatillo, alt. 900–1510 m., Steyermark 30377. **Guatemala:** exact locality lacking, Aguilar 81; alt. 1485 m., Morales 1122. Jutiapa: Volcán Suchitlan, northwest of Asuncion Mita, alt. 600–2050 m., Steyermark 31912. **Sacatepéquez:** near Pastores, alt. 1560–1650 m., Standley 59888; near Antigua, alt. 1500–1600 m., Standley 64273. **Santa Rosa:** above Cerro Redondo, Steyermark 52218; near Cuilapilla, alt. about 900 m., Standley 78068; Chupadero, alt. 5000 pp., Heyde & Lux 3950. **Data Incomplete:** Heyde 381.

**Honduras:** El Paraíso: Guinope, alt. 1430 m., Rodriguez 1679.
El Salvador: vicinity of San Salvador, Renson 61; vicinity of San Salvador, alt. 650–850 m., Standley 19060.
Costa Rica: San José: Río Torres, alt. 1100 m., Touduz 7451; bords de Río Torres près San Francisco de Guadalupe, alt. 1100 m., Touduz 8453.

This species has been described by most authors as having sessile fruits. Actually the fruits are borne on a gynophore the length of which varies from 2 to 8 mm. Many species have been named because of the extreme variability of the length of the gynophore. The correlation of the flowering with the fruiting specimens has been greatly confused.

*H. mexicanus* (type: Galeotti 4154) can be recognized easily by its brown glabrate fruits borne either on a very short or on a slightly longer gynophore. In flower, this is one of the easiest species to identify because of the large erect appendages on the tips of the sepals and the nearly glabrate ovate-lanceolate leaves, as well as by the leafy axillary inflorescence.

This species actually is a link between the sessile-fruited and the stipitate groups. It has the characteristics of both the groups.


Trees 12–14 m. high; older branches dark brown, scurfy, ferruginous-tomentose with both simple and stellate hairs, rarely glabrate, ridged, punctate irregularly with small, white lenticels; younger branches and inflorescence axes covered with thick, scurfy, ferruginous tomentum. Leaves broadly ovate, sometimes obscurely 3-lobed, 14–16 cm. long and 12–14 cm. wide, 5- to 7-costate at the base, acuminate, base subcordate or rounded, with two conspicuous leafy auricles at the basal sinus, each about 5–7 mm. wide and 4–5 mm. long, unequally and bluntly serrated, the basal serrations glandular, upper surface dark green, glabrate, with few suppressed, compact tufts of stellate hairs, lower surface whitish, with dense stellate tomentum, petioles relatively stout, about 6–8 cm. long, covered with dense scurfy, ferruginous tomentum. Inflorescences hermaphrodite, usually terminal, rarely axillary, slightly leafy, about 15 cm. long and 12–14 cm. wide, the cymes of about 16–18 flowers, rather loose, the flowering peduncles 3-radiate, about 2–3 mm. long, the pedicels 3–4 mm. long, the buds obovoid, slightly constricted in the middle, rather large for the genus, about 6 mm. long, not appended at the tips of the sepals, the sepals 4, linear, 6–7 mm. long, light green with short separate tufts of stellate hairs without, glabrate, yellow-brown within, the petals 4, spatulate, 3-nerved, 3–4 mm. long, the stamens about 30, with filaments about 4–5 mm. long, the ovary ellipsoid, 1–2 mm. long, borne upon a gynophore about the length of the ovary itself, with a style about twice the length of the ovary, bifid about half its length and with small, acute, spreading stigma lobes. The fruit suborbicular, about 5 mm. long and 3–4 mm. wide, densely tomentose, borne upon a gynophore about 5–8 mm. long, with 2–3 pairs of plumose bristles, the fringe of 1 or 2 rows of plumose bristles about 6–8 mm. long; the seed pyriform with a shallow groove, slightly stellate-pubescent, about 2–3 mm. long.
Fig. 7. *H. appendiculatus*

Map 7. Distribution of *H. appendiculatus*
Distribution: Plants of central Mexico and Central America: a species of relatively wide distribution, usually growing along river banks or roadways in secondary growth subjected to seasonal floods; at times forming a pure stand in moist places, usually in heavy red clay loam, at various altitudes but most abundant above 1000 m. Flowers from December to about the middle of March and fruits persistent up to about the middle of June.

Mexico: San Luis Potosi: near Tancanhuitz, Nelson 4383; Tabasco: locality lacking, alt. 300 m., Linden 1600; Teapas, Linden 2065, *Vera Cruz*: Fortuno, Coatzaacoalcos River, alt. 30–50 m., L. Williams 8273, 8288, 8280, 8400, 8526, 8527; Rio Seco prope Cordova, Woronow 2063; Mirador, Linden 460; near Jalapa, Rose & Hough 4314.

Guatemala: Alta Verapaz: Pansamala, alt. 3800 pp., J. D. Smith 1723; ½ miles west of Cubilquitz, alt. 250–300 m., Steyermark 48087; trail from Senahu to Actala, Maxon & Hay 3305, 3306, 3322; Cubilquitz, alt. 350 m., Thureckheim 7828. Huehuetenango: between Maxbal and Xoxlac, Sierra de los Cuchumatanes, alt. 1500–1600 m., Steyermark 48087; Cerro Chiblac, between Finca San Rafael and Ixcan, Sierra de los Cuchumatanes, alt. 1200–2000 m., Steyermark 49100.

Honduras: Atlantida: Lancetilla Valley, near Tela, alt. 20–600 m., Standley 54006.

Nicaragua: Segovia: region of Braggman’s Bluff, Englesing 136, 140; Chontales, alt. 600 m., Levy 483; Chontales, Tate 31 (384).

Costa Rica: Cartago: Rubber Plant Investigation Station, Turrialba, Aguilera 97100.

Guanacaste: upper slopes of Cerro San Jose de Libano, alt. 500–900 m., Dodge, Hankele & Thomas 6370; San Jose: vicinity of El General, alt. 700 m., Skutch 3282; vicinity of El General, alt. 670 m., Skutch 4226. Data incomplete: Rowlee & Rowlee 212; Tibarica, alt. 980 m., Solis R. 534; Santiago, Brenes 655.

An extremely easy species to identify due to the presence of two conspicuous auricles at the basal sinus of the relatively large leaf. The fruits are suborbicular and tomentose.


Small trees 3–5 m. high; older branches light brown, glabrate, smooth, irregularly punctate with many small white lenticels; younger branches and inflorescence axes lightly tomentose with both stellate and simple hairs. Leaves ovate, not lobed, 10–12 cm. long and 6–8 cm. wide, 5-costate at the base, acuminate, base rounded or obtuse, never cordate, irregularly and bluntly serrated, upper surface dark green, glabrate with few highly suppressed stellate hairs, lower surface whitish, very densely tomentose with both long stellate and simple hairs; petioles relatively stout, about 4 cm. long, very densely tomentose. Inflorescences hermaphrodite, terminal, about 15 cm. long and 12 cm. wide, sometimes very slightly leafy, the cymes of about 18–20 flowers, densely crowded in nodose clusters, the flowering peduncles 3-radiate, short, about 1 mm. long, the pedicels about 1–2 mm. long, the buds obovoid, slightly constricted towards the base, without appendages at the tips of the sepals, the sepals 4, spatulate, 4–5 mm. long, light green and densely tomentose without, glabrate, yellow to yellow-brown within, the petals 4, linear, 1-nerved,
about 2–3 mm. long, the edges slightly ciliate, the stamens about 20, with the filaments about 3 mm. long, the ovary ovoid, about 1 mm. long, borne on a short gynophore, with a style about 2–3 times the length of the ovary, bifid about one quarter of its length and with acute, spreading stigma lobes. Fruit ovoid, densely tomentose, becoming slightly less so with age, about 3–4 mm. long and 2–3 mm. wide, borne on a long bristly gynophore about 5–8 mm. long, with 2–3 pairs of plumose bristles, the fringe of two rows of plumose bristles about 4–6 mm. long; the seed ovoid, about 1.5 mm. long and 1.0 mm. wide, with a distinct groove in the middle, slightly stellate-pubescent.

Fig. 8. *H. americanus*  
Map 8. Distribution of *H. americanus*

**Distribution:** Plants of central and southeastern Mexico, growing at altitudes between 400–1200 m. Flowers in January and February and the fruits are persistent up to the middle of May.

**Mexico:** Oaxaca: locality not mentioned, Galeotti 4162, 4162b. Puebla: Huazachinango, convalles torrentis, alt. 1100 m., Fröderström & Hulten 860. Vera Cruz: Zacuapan and vicinity, Purpus 2226, 2387; Zacuapan, Purpus 8275; Mirador, Liebmanna 475; Orizaba, Botteri 340, 341, 882, 888, 922; Vallee de Cordova, Bourgeau 1819, 1974; Mirador, alt. 400 m., Linden 857; Cordova, J. G. Smith 284; near Jalapa, Rose & Hough 4304; Estacion El Fortin, Orizaba, Consatti 1604; near Orizaba, alt. 4000 ft., Pringle 0100; Sanborn, Orcutt 3068; circa Cordoba, Woronow 2947; Rio Seco prope Cordoba, Woronow 3034; Cordoba, Greenman 101; barranca of Chevastl near Huatusco, Rozynski 782. Data incomplete: Sumiebrat 882.

The identity of *H. americanus* is based on the interpretations by E. G. Baker and T. A. Sprague. This species has very characteristic ovate-lanceolate leaves, which are densely tomentose only on the lower surface.


Small trees about 10 m. high; older branches glabrous, smooth, yellow to yellowish brown, irregularly punctate with white lenticels; younger branches and inflorescence axes slightly pubescent with short stellate and simple hairs. Leaves broadly ovate, 12-14 cm. long and 8-10 cm. wide, not lobed, 5-costate at the base, shortly acuminate, base rounded or obtuse, irregularly serrated, lower serrations glandular, upper surface dark green, essentially glabrous with short greatly suppressed stellate hairs, lower surface lighter green, slightly more pubescent than the upper, nearly glabrate, with short stellate pubescence; petioles glabrous, smooth, 6-8 cm. long. Inflorescences gynodioecious, usually terminal, rarely axillary; the hermaphrodite large and spreading, about 18 cm. long and 15 cm. wide, the cymes of about 20 flowers, rather loose, the flowering peduncle mostly 3-radiate, rarely 2-radiate, 2 mm. long, the pedicels 4-5 mm. long, the buds obovoid, slightly constricted in the middle, not appended at the tips of the sepals, the sepals 4, linear, 4-6 mm. long and 1-2 mm. wide, light green with stellate pubescence without, glabrate, yellow to yellowish brown within, the petals 4, linear-spatulate, 3-nerved, slightly shorter than the sepals, about 4 mm. long, the stamens 12-16, with filaments about as long as the petals, the ovary ellipsoid, about 1-2 mm. long, borne upon a gynophore nearly as long or very slightly shorter than the ovary itself, with a style 3-4 mm. long, bifid about one quarter of its length and with stigma lobes acute, spreading; the pistillate greatly condensed and crowded, about 5 cm. long and 5 cm. wide, the cymes of about 20 flowers, crowded in nodose clusters, the flowering peduncles very short, 3-radiate, bearing 2 small bracteoles, the pedicels 1-2 mm. long, the buds about 2-3 mm. long, not appended at the tips of the sepals, the sepals 4, linear, 2-3 mm. long, light green and slightly pubescent without, generally brownish and glabrate within, the petals none, the staminodes none, the ovary suborbicular, about 1 mm. long, borne upon a very short gynophore shorter than the length of the ovary, with a style nearly twice the length of the ovary, very briefly bifid, the stigma lobes acute. The fruit ellipsoid, nearly glabrate at maturity, slightly rugose, 5 mm. long and 3 mm. wide, borne on a gynophore 8-12 mm. long, bearing 2-4 pairs of plumose bristles, the fringe of two rows of plumose bristles 5-7 mm. long; the seed obliquely ovoid, 2-3 mm. long and about 2 mm. wide, with a distinct groove in the middle.

Distribution: Plants of southern Mexico and Central America. This species is of rather wide continental distribution but its presence in Martinique is difficult to explain, unless through introduction. It is abundant on the edges of forest, in secondary growth, and on mountain slopes at altitudes from 100 to 1500 m. Flowers from December to February, and the fruits are persistent up to June.
Fig. 9. *H. Donnell-Smithii*

Map 9. Distribution of *H. Donnell-Smithii*
This species is characterized by its ellipsoid, nearly glabrate fruits borne on a long bristly gynophore, and by its ovate leaves, which are nearly blabrous to glabrate.


*H. diclinus* Hochr. loc. cit. 117. 1914. (T.: **H. H. Smith 1008**).

*H. bolivianus* Hochr. loc. cit. 118. 1914. (T.: **Bang 1491**).

*H. stipulatus* Hochr. loc. cit. 121. 1914. (T.: **Poeţiţig 2102**).

*H. Roset* Hochr. loc. cit. 119. 1914. (T.: **Bang 2305**).


*H. australis* E. E. Wats. loc. cit. 124. 1923. (T.: **Hassler 557**).

*H. rudis* E. E. Wats. loc. cit. 126. 1923. (T.: **Pettij 3082**).

*H. subtetiolus* Sprague, in Bot. Gaz. 61:257. 1923. (T.: **Fendler 1277B**).

Trees usually about 8–10 m. high or more; older branches glabrate, slightly rugose, cream to brown, irregularly punctate with few, rather small, white lenticels; younger branches and sometimes a few of the older branches covered lightly with ferruginous tomentum of both stellate and long coarse simple hairs. Leaves usually 3-lobed with acuminate apices, but sometimes only obscurely so, about 16–20 cm. long and 14–18 cm. wide, base markedly cordate on mature leaves, younger leaves usually with rounded bases, irregularly serrated, upper surface generally dark green, glabrate with short ferruginous stellate tomentum, especially on the veins and veinlets, lower surface light green, slightly more pubescent than the upper, the
pubescence varying from densely stellate to thinly suppressed stellate, the principal veins usually with simple hairs about 2 mm. long; petioles 6–8 cm. long, usually densely covered with both stellate and simple hairs. Inflorescences gynodioecious, usually terminal; the hermaphrodite about 12 cm. long and 14 cm. wide, the cymes of about 12–16 flowers, the flowering peduncles 3-radiate, about 1–2 mm. long, the pedicels about 2–3 mm. long, the buds obovoid, slightly constricted towards the base, without appendages at the tips of the sepals, the sepals 4, spatulate, generally 3-nerved, about 5 mm. long, light green and densely tomentose without, glabrate and yellowish brown within, the petals 4, spatulate, about 3–4 mm. long, slightly ciliate, the stamens about 12–16, with the filaments about 3–4 mm. long, the ovary suborbicular, laterally compressed, about 1.0–1.25 mm. long, borne on a gynophore about 0.75 mm. long, with a style about twice the length of the ovary, bifid about one quarter of its length and with the stigma lobes spreading, each with 3 acute lobes; the pistillate rather large, much larger than the hermaphrodite, about 14 cm. long and 20 cm. wide, the cymes of 12–16 flowers, rather condensed in nodose clusters, the flowering peduncles 3-radiate, less than 1 mm. long, the pedicels about 1 mm. long, the buds about 3 mm. long, the sepals 4, linear, about 3 mm. long, light green, stellate-tomentose without, glabrate, cream to light brown within, the petals none, the staminodes about 12, the ovary suborbicular, about 1 mm. long, borne on a short gynophore, with a style about twice the length of the ovary, bifid about one quarter of its length and with spreading stigma lobes, each with 3 acute lobes. The fruit ellipsoid to ovoid, with many short tufts of stellate hairs, slightly pubescent, about 5–6 mm. long and 2–3 mm. wide, borne on a bristly gynophore about 1.0–1.5 mm. long with 2–3 pairs of plumose bristles, the fringe of two rows of plumose bristles about 8–12 mm. long; the seed ovoid, about 2 mm. long, with a shallow depression in the middle.

Distribution: A species which extends from Costa Rica to northern Argentina. It is primarily South American and is the only species known there. In southern Central America and northern South America it is found in highlands above 1000 m. altitude, while in Paraguay and Argentina it is usually at lower elevations. *H. popayanensis* frequents steep slopes in forested river valleys, thickets, or in sunny bushy slopes, usually in second growth in cut-over forests. It is abundant in rain or cloud forests or on the edges of forests at stream sides. Flowers in its northern
range from December to January and in its southern range from May to June. Fruits persistent in the north until about the middle of March and in the south to about the end of September.

Costa Rica: Alajuela: hills west of Zapate, San Carlos, alt. 1550 m., A. Smith NY12063; Zacro, upper continental divide, alt. 1800 m., A. Smith HI1558. Heredia: Vera Blanca de Sapiqui, near slope of Central Cordillera, between Poas and Barba volcanoes, alt. 1680 m., Skutch 3346. San José: La Palma de San Ramon, Brench 6360; Carpintera, alt. 5700 ft., Stork 1158. Data incomplete: Charco, Goicochea, alt. 1400 m., Jimenez 993.

Panama: Canal Zone: Cerro Gordo, near Culebra, alt. 50–290 m., Pittier 2305; Barro Colorado Island, Frost 218; Canal Zone and vicinity, C.16, back of Curundu, Harvey 5258; Barro Colorado Island, Shattuck 662, 754; near lab., Barro Colorado Island,

TRINIDAD: St. Ann's Cascade, Broadway 6560; Santa Cruz, Simmonds 281; Lady Chancellor Road, St. Ann's, Broadway 9200; Knagg's Hill, R. O. Williams 12671; St. Cruz, collector unknown 649, 650.

COLOMBIA: ANTOquia: vicinity of Medellin, Toro 206. BOYACA: 130 m. n. of Bogota, El Umbo, alt. 3700 ft., Lawrince 500. CAUCA: El Tambo in silva, alt. 1700 m., Sneidern 434; highlands of Popayan, alt. 1400–2000 m., Lehmann 5502; Rio Toribio region, alt. 100–1200 m., Espiña & Giacometto 20801; cerca de Popayan, matorrales in Rio Blanco, alt. 1800 m., Arbelaez & Cuatrecasas 5798. MAGDALENA: Santa Marta, alt. 2000 ft., H. H. Smith 1008; Pita, André 467. NARINO: frontera Colombo-ecuatoriana, selva higrosfila del Rio San Miguel, junto a la de los cadare del Rio Conejo, alt. 300 m., Cuatrecasas 10025. NORTE DE SANTANDER: Cordillera Oriental, region of the Sarare, quebrada de la China (in the Hoya del Cubugon), Santa Librada in El Reposo, alt. 800 m., Cuatrecasas 13262, 13340; Cordillera Oriental, region of the Sarare, Hoya del Rio Chitaga entre Chorro Colorado y Bata, alt. 1500 m., Cuatrecasas, Schultes & Smith 12237; Cordillera Oriental, region of the Sarare, La Cabuya, alt. 1300 m., Cuatrecasas, Schultes & Smith 12590; Cordillera Oriental, region of the Sarare, entre el Alto del Loro y el Alto de Santa Ines, bosques, alt. 1800–2000 m., Cuatrecasas, Schultes & Smith 12471.

VENezUELA: distrito federal: Caracas, alt. 3000 pp., Funck & Schlim 150; Caratea, alt. 930 m., L. Williams 9057. MERIDA: prope dominion Tovar, Fendler 1277, 1277B. MIRANDA: La Malva, near Las Mostazas, Allart 273; La Malva, cerca de las Mostazas, Pittier 273; in valley from El Valle to Cua, Pittier 11075; in matorrales a lo largo de la carretera de los Teques, alt. 1200 m., L. Williams 10602. YARACUY: Hacienda Iboa near San Pablo, Pittier 12605. DATA INCOMPLETE: Las Trincheras, Warming 313; al sur de Rio Claro, alt. 1360, Saer 778.

BRAZIL: ACRE: near mouth of Rio Macauhan (tributary of Rio Yaco), lat. 9.20' S., and long. 69. W., Krukoff 5261.

ECUADOR: AZUAY: along Rio Patul between Hacienda Yubay and Hacienda San José de Caimocan, in region of Sanaguin, alt. 850 m., Steyermark 52754; Hacienda Yubay, at Sanaguin, on south side of Rio Patul, alt. 850 m., Steyermark 52604; Rio Norcay between Rio Gamolotol and Rio Norcay, alt. 1095–1370 m., Steyermark 52878. CHIMBORAZO: Chimbo, alt. 1000 m., Rimbach 288. DATA INCOMPLETE: vicinity of Ventura, Rose & Rose 25518.


BOLIVIA: COCHABAMBA: Incachaca—S. Antonio, alt. 1500 m., Webermann 2126. LA PAZ: Calapampa, Corico, Bang 2305; Mapiri, Bang 1491; Guanai-Tipuni, Bang 1455; Guanai, alt. 2000 ft., Rugby 1402; Beni River, Rugby 1403; Moryungs, Region von Coripata, Hacienda "El Choro", Buchbien 8125; Province of S. Yungas, basin of Rio Bopí, San Bartoloma (near Calisaya), alt. 750–900 m., Krukoff 10429, 10283, 10409. SANTA CRUZ: Legunillas, Cordillera of Tecahusai, alt. 1600 m., Cardenas 2830.

ARGENTINA: CATAMARCA: Del Alto, Bataguas, alt. 1250 m., Venturi 7074. MISIONES: vicinity of Puerto Aguirre, alt. 100 m., Curran 9, 17; vicinity of Puerto Leon, alt. 75–100 m., Curran 700, 718. TUCUMAN: Famailla, San Pablo, alt. 600 m., Venturi 1002, 1002C;
Fanailla, San Rafael, Venturi 9205; locality not mentioned, Hauman 9206.
Hawaii: Oahu, planted in foothills for reforestation, Degener 10843.

The plants of this species have leaves whose diversity of shape and size is unparalleled in the whole genus. A general tendency is for the plants in the central range of the species to have leaves more definitely and acutely 3-lobed than those towards either the northern or the southern limits, where the leaves frequently may be quite undivided. The pubescence varies from slightly tomentose to nearly glabrate. The constant characters throughout its wide distribution are the hirsute indumentum on the lower nerves, the sepals without appendages, the 3-parted stigma lobes, and the fruits, which are ellipsoid to ovoid and slightly tomentose.


Fig. 11. H. nodiflorus

Trees about 10–18 m. high; older branches glabrate, longitudinally ridged, light brown, punctate irregularly with few white lenticels; younger branches and inflorescence axes scurfy, slightly ferruginous-pubescent with both simple and stellate hairs. Leaves 3-lobed, sometimes obscurely so, generally medianly oblique, large, 16–18 cm. long and 15–18 cm. wide, 5- to 7-costate at the base, acute to
acuminate, base usually cordate, sometimes slightly rounded, rather regularly and doubly serrated, lower serrations slightly glandular, upper surface dark green, glabrate, with few tufts of short stellate hairs in the nerve axes, lower surface light green, slightly more pubescent than the upper, especially in the nerve axes; petioles large and stout, about 10 cm. long, lightly ferruginous-stellate-pubescent, scurfy; stipules sometimes persistent. Inflorescences gynodioecious, usually terminal, large and spreading; the hermaphrodite about 15 cm. long and 18 cm. wide, the cymes of about 15–20 flowers borne in compact nodose clusters, the flowering peduncles 3-radiate, about 2 mm. long, the pedicels 1–3 mm. long; the buds obovoid, slightly constricted in the middle towards the base, sometimes with small acute appendages on the tips of the sepals, the sepals 4, spatulate, 4–5 mm. long, light green with stellate tomentum without, glabrate and yellowish brown within, the petals 4, linear, 1-nerved, about 4 mm. long, the stamens about 20–24, with the filaments about 4 mm. long, the ovary ovoid, slightly compressed, about 1.5 mm. long, borne on a short gynophore less than 1 mm. long, with a style about 3–4 mm. long, bifid about half its length at anthesis and with the stigma lobes acute and spreading; the
pistillate about as large as the hermaphrodite, the cymes of about 20 flowers, rather compressed and crowded in nodose clusters, the flowering peduncles 3-radiate, less than 1 mm. long, the pedicels about 1–2 cm. long, the buds about 2–3 mm. long, usually not appended at the tips of the sepals, the sepals 4, linear, about 2–3 mm. long, light green and stellate-pubescent without, glabrate and yellowish brown within, the petals none, the staminodes about 12–16 or none, the ovary ovoid, small, about 1 mm. long, slightly compressed, borne on a short gynophore, with a style slightly longer than the ovary, briefly bifid and with the stigma lobes acute. Fruit orbicular, slightly tomentose with short separate tufts of stellate hairs, about 5–6 mm. in diameter, borne on a bristly gynophore 10–15 mm. long, bearing 2–3 pairs of plumose bristles, the fringe of 1 or 2 rows of plumose bristles 6–8 mm. long; the seed obliquely ovoid, about 2–3 mm. long, with a distinct groove in the middle.

Distribution: A species primarily of Central America, extending into southeastern Mexico. It is common in clearings and in wet thickets, nearly always in secondary growth besides rivers or in sheltered valleys, usually at altitudes from 1000 to 2500 m. Flowers from January to February, the fruits persisting until about the middle of April.

British Honduras: Gracie Rock, Sibun River, Gentle 1787; Stann Creek Valley, 17 miles, Gentle 3202, 3203, 3204; Stann Creek Valley, Big Eddy Creek, Gentle 3470; Little Coquericot, Belize River, Lundell 4177.


Honduras: atlantida: Lancetilla Valley, near Tela, alt. 20–600 m., Standley 55854, 55701, 55703, 50640.

Nicaragua: granada: Mombacho, Oersted 14820.


It is unfortunate that the type of H. nodiflorus (Heyde & Lux 4329) has flowers with small apical appendages. The appendages in this species actually are rarely present, and if present are extremely small. This species is characterized by its large leaves, the largest known for the genus, which are nearly glabrous on both the surfaces. The fruit is like that of H. Donnell-Smithii, but is more spheroid, slightly more tomentose, and larger in size. It can be distinguished from H. popayanensis by its large orbicular fruits, as well as by its glabrous leaves.
Italicized numerals refer to collector's numbers, s. n. (sine numero) to unnumbered collections; parenthetical numerals refer to the numerals of taxonomic entities conserved in this revision.

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