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NEW SPECIES OF CLUSIACEAE FROM CENTRAL AMERICA WITH NOTES ON CLUSIA AND SYNONYMY IN THE TRIBE CLUSIEAE

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ABSTRACT. Two new species of Clusiaceae, *Clusia cylindrica* Hammel and *Tovomitopsis silvicola* Hammel, are described. Among Central American species of *Clusia* three main groups can be distinguished on the basis of leaf, floral, and pollen morphology. Each group is here characterized and a list of species included in each is provided along with a key to the species in the *Clusia minor* group. To clarify the circumscriptions of a number of species for the floras of La Selva and Nicaragua, taxonomic synonyms concerning species of *Clusia, Havetiopsis, Tovomita,* and *Tovomitopsis* are discussed.

Clusia and the related genera Chrysochlamys, Havetiopsis, Oedematopus, Ouapova, Tovomita, and Tovomitopsis form the entirely New World tribe Clusieae of the subfamily Clusioideae in the Clusiaceae. The Clusieae are distinguished within the subfamily by their terminal inflorescences and succulent capsular fruits (Engler, 1925; pers. obs.). An understanding of the taxonomy of this group has been plagued by the difficulties inherent in studying dioecious, succulent, arborescent, epiphytic, and diverse tropical taxa (Hammel & Grayum, 1982). The following new species and notes are the result of several years of fieldwork in Costa Rica and Panama and have been stimulated by preparation of the Clusiaceae treatments for the floras of La Selva and Nicaragua. They also result from work towards a revision of the Central American members of the tribe Clusieae.

New Species

While studying the Clusiaceae at La Selva, two new species were encountered. Twenty-two species in ten genera of Clusiaceae are now known from this small field station in the lowlands of northeastern Costa Rica.

Clusia cylindrica Hammel, sp. nov.

FIGURES 1, 2, 4.

Frutices epiphytici grandes, dioecii; laminae anguste ellipticae; flores parvi, 4–5 mm diam., masculini 12–20 staminibus, feminei 4–8 staminibus; fructux anguste ovoidei, 1.5–2 cm longi, 0.5–0.7 cm lati, stigmatibus 4.

TYPE. Costa Rica, Heredia, La Selva Biological

Station, 10 May 1980, *Hammel 8635* (DUKE, holotype; CR, F, MO, isotypes).

Epiphytic shrubs often reaching tree-size proportions, the branches 4-8 m long; milky sap scant. Leaf blades mostly narrowly elliptic (rarely obovoid), 7.5–10(–12) cm long, 3–4.5 cm wide, the apex acute (very rarely obtuse or rounded), the base acuminate and often decurrent; midrib prominent above and below, the lateral veins very indistinct, 5-8 per cm, arising at an angle of (30-)40-45°(-50), submarginal vein about 1 mm from margin; petiole 0.4-1 cm long. Staminate inflorescence a small but open, globose panicle 3-5 cm wide; flowers small, inconspicuous, ca. 0.5 cm in diameter, the petals thick and rubbery, 4 mm long, pinkish to yellowish green, subtended by 3-5 pairs of decussate bracts, the upper 2 pairs being sepals with the inner sepals about twice as large as the others; stamens few, 12-20, distinct, often reddish, ca. 1.5 mm long with the filaments equal to or slightly longer than the anthers, elevated on a square receptacle; pollen grains globose-spherical, ca. 12 µm in diameter, tricolpate, exine gemmate-echinate and foveolate. Pistillate inflorescence fewer flowered than the staminate, ca. 1-2 cm wide; flowers same as the staminate but the ovary surrounded by 4-8 apparently normal stamens similar to those of the male flowers; stigmas 4, round, ca. 1 mm in diameter, slightly elevated and offset from the apex of the fruit. Fruits narrowly ovoid, 1.5-2 cm long, 5-7 mm in diameter; sepals and bracts accrescent in fruit.

SPECIMENS EXAMINED. Nicaragua. MATAGALPA: Neill 1718 (MO). ZELAYA: Moreno & Sandino 13297 (MO); Neill 4244 (MO); Stevens 7421, 8752 (MO). Costa Rica. ALAJUELA: Jimenez 4093 (MO); A. Smith 1763, 2597 (MO). HEREDIA: Finca La Selva, Folsom 9458, 9684, 10076; Grayum 2811; Hammel 8342, 8635, 8924, 8933, 9089, 9254, 9263, 9391, 9873, 10789; D. Smith 232; Wilbur & Jacobs 34467 (all DUKE). LIMON: Da-

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FIGURES 1, 2. Clusia cylindrica. 1. Photograph of plant with mature fruit (scale bar = 2 cm). 2. SEM of pistillate flower with corolla removed to show stamens (*Hammel 1896*, DUKE; scale bar = 1 mm).

vidson 7073 (US). SAN JOSE: Pittier 11956 (US); Skutch 2585 (US). **Panama.** BOCAS DEL TORO: Churchill 5329 (MO). COCLÉ: Hamilton & Davidse 2721; Hammel 1865 (MO). COLÓN: Duke 15276; McPherson & Merello 8236 (MO). PANAMÁ: Churchill 3821; Nee & Tyson 10960; Tyson & Nee 7320 (MO); Wilbur & Weaver 10860 (DUKE). SAN BLAS: Sugden 490 (MO).

HABITAT AND DISTRIBUTION. Nicaragua, Costa Rica, and Panama in low to middle elevations. A locally common, often quite large, epiphyte in primary forest at La Selva but also often found flowering and fruiting in pasture and fence-row trees in the area.

PHENOLOGY. Flowering mostly in the dry season, January–April (August), fruit maturing May– June (September).

RELATIONSHIPS. *Clusia cylindrica* is distinctive among Central American species for its relatively small, narrowly elliptic leaves with very indistinct lateral veins and its small, cylindrical 4-valvate fruits. The thick rubbery decussate petals and the stamens of the pistillate flowers clearly place this species in the *Clusia flava* group (see below). *Clusia cylindrica* resembles *Havetiopsis flexilis* Pl. & Tr., which is known in Central America from a few localities in Panama and from Belize. This latter species, however, has only 4 stamens in the staminate flowers, globose fruits, and twigs with reddish exfoliating bark.

Among Central American and West Indian species of *Clusia, C. cylindrica* may be most closely related to *C. gundlachii* Stahl of the West Indies. These two species are almost identical in details of the leaves and fruits, but the latter has only 6 stamens and is also unique in the genus for having fused petals. In the Flora of Panama C. cylindrica was included among specimens of C. dukei Maguire. This latter species is also a member of the C. flava group but has larger flowers and fruits and more distant, more divergent lateral veins. Although the relationship of Clusia cylindrica to South American plants has not been thoroughly investigated a strong resemblance to species now placed in Oedematopus cannot be denied. In fact, considering the distinguishing characters of the groups within Clusia discussed below, the C. flava group is only nominally distinct from such South American genera as Havetiopsis and Oedematopus.

Tovomitopsis silvicola Hammel, sp. nov. FIGURES 3, 5.

Frutices ad 6 m alti; laminae oblongae, (13–) 16–22 cm longae, 4–6.5(–8) cm latae, nervis secundariis obscuris plus minusve reticulatis; 2 sepali externi inaequalia; perianthium non striatum; fructus ovoidei, 1.5–2.5 cm diam.

TYPE. Costa Rica, Heredia, La Selva Biological Station, 1 Aug. 1980, *Hammel 9404* (DUKE, holotype; CR, F, MO, isotypes).

Dioecious shrubs or small trees to 6 m tall; sap of leaves and twigs distinctly milky. Leaf blades oblong, mostly (13–)16–22 cm long, 4–



FIGURE 3. Tovomitopsis silvicola. A, habit (scale bar = 2 cm). B, flower bud (scale bar = 2 mm). C, fruit (scale bar = 1 cm). (A, B, Hammel 9404; C, Gomez et al. 21129, MO.)

6.5(-8) cm wide, the apex broadly acute with a short acumen, to acuminate, the base narrowly acute, leaf surface dull or lustrous above and below, drying reddish brown; midrib prominent below, glabrous, major lateral veins ca. 10–16,

difficult to distinguish from the minor intermediate veins, arising at an angle of $(60-)70^{\circ}$, numerous, fine resin canals visible in dried material; petioles 1–2.5 cm long. Inflorescences more or less pendent, pyramidal, 6–10 cm long and as



FIGURES 4-7. Pollen types in *Clusia* and *Tovomitopsis*. 4. SEM of the pollen of *C. cylindrica* (Folsom 9458, DUKE). 5. SEM of pollen of *T. silvicola* (Wilbur 30243, DUKE). 6. SEM of pollen of the dioecious form of *C. minor* (Primack 301, DUKE). 7. SEM of pollen of *C. stenophylla* (Hammel 11371, DUKE). Scale bar = 10 μ m.

wide, many flowered, minutely puberulent to glabrous; buds 4–5 mm in diameter, the outer pair of sepals often unequal with the large sepal overtopping the bud and the smaller sepal ca. ¹/₂ the height of the bud or smaller, perianth not striate, red abaxially, white adaxially; staminate flowers with the stamens 1.5–3.5 mm long; pollen grains globose-spherical, ca. 18 μ m in diameter, tricolporate, exine foveolate; pistillate flowers with the stamens smaller, ca. 1 mm long. Fruits ovoid, 1.5–2.5 cm in diameter, red, infructescence branches pendent.

SPECIMENS EXAMINED. **Costa Rica.** HEREDIA: Finca La Selva, Chacon 452; Folsom 8775, 9030; Grayum 1498, 1902; Hammel 9404, 10965, 11031; Hammel & Trainer 12688, 13186; Schatz & Grayum 655; D. Smith 172; Sperry 1081; Wilbur 30243 (all DUKE). LIMÓN: Standley & Valerio 48487, 48772, 48790 (US). SAN JOSÉ: Gomez, Herrera & Chacon 21129 (MO).

HABITAT AND DISTRIBUTION. Known from the Caribbean lowlands of Costa Rica. At La Selva *Tovomitopsis silvicola* is restricted to ridges in primary forest.

PHENOLOGY. Flowering during the rainy season, June–September, fruits maturing mostly in the dry season, January–June.

RELATIONSHIPS. Although the present species is quite different in overall aspect and in habitat preference from the distinctive Panamanian species, *Tovomitopsis angustifolia* Maguire, it shares some apparently unusual features with that species and the two may be closely related. In both these species the primary lateral veins of mature leaves are obscure and nearly indistinct from the intermediate lateral veins. Both have bright red flower buds with one of the outer sepals longer than the other and over-topping the bud, and both have milky rather than clear sap.

The oblong, obscurely but many-veined leaves, which dry reddish brown, the red flower buds, and above all the milky rather than merely clear sap distinguish this species from *Tovomitopsis* glauca Pl. & Tr. and *T. nicaraguensis* Pl. & Tr. with which it is sympatric at La Selva.

TABLE 1. Three species groups of Central American Clusia.

| Clusia flava group | Clusia minor group | Clusia multiflora group |
|--------------------|--------------------|-------------------------|
| C. belizensis | C. croatii | C. coclensis |
| C. chanekiana | C. cupulata | C. conferta |
| C. cooperi | C. dicrophyllya | C. congestiflora |
| C. cvlindrica | C. divaricata | C. lusoria |
| C. dukei | C. erectistigma | C. massoniana |
| C. flava | C. fructiangusta | C. mayana |
| C. gracilis | C. liesneri | C. palmana |
| C. guatemalensis | C. lineata | C. perscariosa |
| C. lundellii | C. longipetiolata | C. pringlei |
| C. mexicana | C. minor | C. rotundata |
| C. oedmatopoidea | C. odorata | C. salvinii |
| C. orizabae | C. parvicapsula | C. shippii |
| C. osseocarpa | C. pratensis | C. stenophylla |
| C. ovigera | C. rosea | C. verapazensis |
| C. quadrangula | C. utilis | |
| C. suborbicularis | C. uvitana | |
| C. tetratrianthera | C. valerii | |
| C. torresii | | |
| C. uniflora | | |

CLUSIA IN CENTRAL AMERICA

Clusia is the largest genus in the Clusieae and most notorious for its need of general revision. Most species of *Clusia* are hemi-epiphytes; they germinate on the branches of other trees and later send roots to the ground. The genus contains about 150 species, approximately one-third of which occur in Central America. Much of the diversity in the genus has come to light relatively recently. Standley (1937), for example, reported just 11 species from Costa Rica; about 25 are now known. Likewise, D'Arcy (1980) reported 17 species from Panama but now about 27 species are known. Among the Central American species three morphological groups can be distinguished. These groups have been earlier recognized, e.g., Maguire (1979), but have not been described; they have only been roughly indicated by partial lists of the species included. It is still premature to equate these groups with formal sections established previously (Planchon & Triana, 1860). Here they are intended only as working hypotheses and as aids to identification.

Type specimens or descriptions of all names applied to Central American species of *Clusia* were examined. Each of the species can be placed in one of the three groups (TABLE 1). This list is not meant to imply that each name applies to an accepted species; numerous of them are here (see below) and elsewhere (e.g., D'Arcy, 1980) considered to be taxonomic synonyms. Pollen of some of the species in each group was removed from herbarium specimens, coated with goldpalladium, and examined using a scanning electron microscope (Hammel, 1984).

Clusia minor Group

Staminate flowers producing resin at anthesis; staminodia of the pistillate flowers forming a resinous ring about the base of the ovary, usually persistent in fruit; pollen grains tricolpate, exine scabrate and foveolate (FIGURE 6). The floral resin, which is produced only by members of the *Clusia minor* group, is gathered by bees for nest building (Skutch, 1971: 261–262; Armbruster, 1984).

Most species in the *Clusia minor* group, as here defined, are strictly dioecious; staminate plants bear only stamens and pistillate plants bear ovaries and sterile staminodia. *Clusia minor* itself, however, when broadly interpreted, contains apomictic, hermaphroditic, and dioecious forms (Maguire, 1976; pers. obs.). This complex may provide evidence for the evolution of hermaphroditism and apomixis from (or within) a dioecious species.

With only two species (*C. minor* and *C. rosea*) reaching north of Nicaragua the *C. minor* group is less diverse in northern Central America than the other two groups. This group is now well enough understood to provide a meaningful key to the Central American species.

Key to Species of the Clusia minor Group in Central America

1. Petioles usually less than 1 cm long, often lacking.

- 2. Inflorescences about as long as broad; fruits ovoid to broadly cylindrical; leaves obovate with very short and broad petioles, not clasping.
 - 3. Twigs reddish with exfoliating epidermis; marginal vein ca. 3-5 cm from margin; flowers 3-4 cm in diam.; fruits with the stigmas forming a conical cap. C. cupulata (Maguire) Maguire.
 - 3. Twigs green, without exfoliating epidermis; marginal vein 1–2 mm from margin; flowers 1–2.5 cm in diam.; stigmas forming a flat cap. *C. leisneri* Maguire.

Petioles usually 1 cm long or more, never lacking.
 Lateral veins nearly perpendicular (70-90°) to midrib; staminate flowers with a central resinous sterile

- 4. Lateral veins usually at an angle of 60° or less to the midrib; staminate flowers without a central sterile area, the stamens all apparently fused into a capitate, resinous cluster, or plants not dioecious.
 - 6. Leaf blades truncate to broadly rounded apically, acute and often truncate basally. . . C. rosea Jacq.
 6. Leaf blades usually acute to acuminate, rarely rounded apically, acute basally.

 - 7. Lateral veins at less than 50° to the midrib; resin canals of upper leaf surface arising along the midrib at an acute angle, running into the margin; sepals pink or green and pink; fruits lacking a bony endocarp.
 - 8. Outer sepals entirely fused in bud, the buds apiculate. (This species is not known in fruit. It is vegetatively very similar to and may only be a variant of the dioecious form of *C. minor.*) . . .

8. Outer sepals free to the base, the buds rounded.

- Tertiary venation obscure; leaf tips acute to obtuse.
 10. Epidermis of twigs exfoliating; plants always terrestrial.
 - 11. Fruits globose, ca. 1–1.5 cm in diam.; stigmas ca. 2 mm long; staminodial ring with pollen producing anthers; epidermis red.

Fruits ovoid, ca. 2-3 cm long, 1.5-2 cm in diam.; stigmas ca. 4 mm long; staminodial ring lacking anthers; epidermis tan.C. minor L. (apomictic form).
 Epidermis of twigs not exfoliating; plants usually epiphytic.

- Leaf blades 4–6 cm long, ca. 2 cm wide; fruits narrowly ovoid, 4–5 cm long, 1.5–2 cm in diam.; plants terrestrial; known only from the area of Volcan de Chiriqui in western Panama.
- - 13. Flower buds less than 1 cm in diam.; apex of leaf usually acute; fruits globose to ovoid, 1-2 cm long, 1-1.5 cm wide; stigmas 10-13, sessile or slightly elevated on styles less than 2 mm long. C. minor L. (dioecious form).

Clusia flava Group

Petals usually 4, decussate, thick and rubbery, greenish-pink to cream-colored; stamens short (usually less than 5 mm); staminodia of pistillate flowers anther bearing, often arranged symmetrically in 4 groups of 1–4 stamens around the base of the ovary, the filaments persistent in fruit; pollen grains tricolpate, exine gemmate-echinate and foveolate (FIGURE 4). Flowers of *Clusia flava* Jacq. at La Selva have a very strong sweet fragrance of imitation banana flavoring and appear to attract only small weevils.

Species of the *Clusia flava* group are apparently androdioecious; staminate flowers are totally without any kind of functional or residual gynoecium, but the pistillate flowers bear about 4–12 full-sized seemingly normal stamens (see FIGURE 2). This feature has been described numerous times for *C. flava* itself and related species (Planchon & Triana, 1860; Fawcett & Rendle, 1926; Maguire, 1979). In spite of the morphology of pistillate flowers, theoretical considerations predict that their pollen would not be fertile (Lloyd, 1975; Charlesworth & Charlesworth, 1978).

Clusia multiflora Group

Petals usually 5–6, imbricate, thin and membranaceous, waxy white or pale green; stamens long (often 1 cm); staminodia of pistillate flowers toothlike in a whorl around the base of the ovary, lacking anthers, deciduous in fruit; pollen grains tricolporate, exine foveolate (FIGURE 7). Some members of the *Clusia multiflora* group produce nectar and are probably visited by hawkmoths (Armbruster, 1984; Haber, pers. comm.). Others are visited by bees.

Pistillate plants of the *Clusia multiflora* group bear only tooth- or club-shaped staminodia, which are usually visible only in early flowering stages. This apparent lack of staminodia in fruiting material coupled with the usually short, broadly winged petioles helps identify members of this group. This is perhaps the most difficult group of the three; many forms of leaf size and shape are apparent but in many cases they appear to intergrade. More collections and further study are necessary before an adequate taxonomy of this group can be given.

SYNONYMY

Although some of the 50 names applied to *Clusia* in Central America (TABLE 1) are considered taxonomic synonyms, further study and collecting will probably account for at least that many species. A number of these taxonomic synonyms in *Clusia* and other Clusiaceae are discussed in detail below.

Clusia minor L., Sp. Pl. 510. 1753.

- ?Clusia odorata Seemann, Bot. Voy. Herald 89. 1853. TYPE: Panama, Chiriqui, Seemann 1638 (Mo!, photo).
- Clusia parvicapsula Vesque, Epharmosis 3: 10, plate 34. 1892. TYPE: Mexico, Bourgeau 1891 (US!).
- ?Clusia pratensis Seemann, Bot. Voy. Herald 89. 1853. Type: Panama, Panama, Seemann (MO!, photo).
- Clusia utilis Blake, Contr. U.S. Nat. Herb. 24: 14, plate 14. 1922. TYPE: Guatemala, Izabal, Blake 7859 (Us!, holotype; Mo!, isotype).

The two unquestioned species in synonymy here were erroneously treated as synonyms of *Clusia flava* in the Flora of Guatemala. Instead, they are identical to all the material of *C. minor* from the West Indies I have examined. These plants have a distinctive reddish exfoliating bark on their twigs, have small globose fruits, and pollen bearing anthers in the staminodial ring. It is not known whether this pollen is functional but since no strictly staminate plants have been found, the plants must be either apomictic or hermaphroditic.

Another entity in the *Clusia minor* complex also with exfoliating bark but of a light tan color, with larger fruits, and with reddish sepals occurs in Panama. Most significantly, this entity is quite common and likewise known only from pistillate

material, but the staminodial ring bears no pollen. Like C. rosea (Maguire, 1976) these plants are definitely apomictic. All of these non-dioecious plants are apparently restricted to seasonally, relatively dry habitats, e.g., the Pacific lowlands in Costa Rica and Panama. At least in Central America the apomictic entity in the C. minor complex is easily distinguishable from the hermaphroditic form and may warrant recognition as a distinct species, i.e., C. pratensis. The hermaphroditic form is primarily restricted to the West Indies and Central America north of Panama, whereas the apomictic form is restricted to Panama and northern South America. The latter has also been introduced and naturalized in Ceylon where it was misidentified as C. rosea (Kostermans, 1980).

The name Clusia odorata has been widely used for the common dioecious entity in the C. minor complex, which is wide-spread in wet mid- to low elevations of Costa Rica and Panama (primarily on the Caribbean slope). It has ovoid to somewhat cylindrical fruits and bark that does not exfoliate. However, on present evidence, it appears that C. odorata may actually be a narrowly endemic species, restricted to the slopes of Volcan Baru in western Panama, the type locality. Collections from this area have smaller, more narrow leaves, larger flowers, and longer fruits than other members of the complex. If recognized as a separate species, the common dioecious form of C. minor may have no name. Fieldwork, especially in western Panama is essential for unravelling the taxonomy and biology of this complex.

- Clusia quadrangula Bartlett, Proc. Amer. Acad. 43: 55. 1907. TYPE: Guatemala, Izabal, Deam 56 (US!).
 - Clusia cooperi Standley, Field Mus. Pub. Bot. 4: 234. 1929. TYPE: Panama, Bocas del Toro, Cooper 460 (F!).

Although *Clusia cooperi* was described from Panama, the type was not then available and this species was only briefly mentioned in the Flora of Panama (D'Arcy, 1980). The few other Panamanian collections of *C. quadrangula* were cited in the Flora under *C. lineata* (Wedel 884, 1906) or *C. minor* (Steyermark & Allen 17102, Wedel 814).

- Clusia uvitana Pittier, Contr. U.S. Nat. Herb. 13: 452. 1912. Type: Costa Rica, Limon, *Pittier* 12704 (US!).
 - Clusia erectistigma Maguire, Phytologia 39: 68. 1978. TYPE: Panama, Bocas del Toro, Maguire & Maguire 61473A (NY).

In the Flora of Panama this species was not recognized as an entity separate from *Clusia minor*. However, when variation within the *C. minor* complex is understood, the identity and integrity of *C. uvitana* becomes clear. It has larger, thicker obovate leaves with indistinct lateral veins, larger fruits with distinctly elevated stigmas, and is mostly restricted to the wet Caribbean lowlands from southern Nicaragua through Costa Rica and Panama. The fruits are similar to the apomictic form of *C. minor* (=*C. pratensis*), which is restricted to dry Pacific slopes in Panama. *Clusia uvitana* is common on Barro Colorado Island in Panama where it has gone under the name *C. odorata*.

- Havetiopsis flexilis Pl. & Tr., Ann. Sci. Nat. Bot. 14: 246. 1860. Type: Brasil, *Spruce 3294* (P, not seen).
 - Clusia gentlei Lundell, Contr. Univ. Michigan Herb. 6: 48. 1941. Type: Belize, Stan Creek, Gentle 3512 (MICH!, holotype).

Although *Clusia gentlei* is apparently known only from type material, which is pistillate, its reddish exfoliating branchlets, obovate leaves, 4 staminodia, and small globose fruits clearly identify it with staminate and pistillate collections of *Havetiopsis flexilis* from elsewhere, e.g., Barro Colorado Island in Panama. This species has not been reported from anywhere between Belize and Panama.

- Tovomita stylosa Hemsl., Biol. Cent.-Amer. 1: 88. 1879. TYPE: Panama, *Fendler 298* (MO!, lectotype).
 - Tovomita membranifolia Standley, Field Mus. Nat. Hist. Bot. Ser. 22: 160. 1940. TYPE: Panama, Darien, Terry & Terry 1478 (Mol, isotype).

In the Flora of Panama D'Arcy transferred *Tovomita membranifolia* to *Tovomitopsis*, however, the isotype of this species at MO is clearly a depauperate fruiting specimen of *Tovomita stylosa*. The other specimen of *T. membranifolia* cited in the Flora of Panama (*Kirkbride & Duke* 1312) is an undescribed species of *Clusia* in the *C. multiflora* group. It should also be noted that *Tovomitopsis*, for reason of priority, cannot include *Chrysochlamys* in synonymy as was indicated in the Flora of Panama.

- Tovomitopsis glauca Pl. & Tr., Ann. Sci. Nat. Bot., Ser. 4, 14: 264. 1860. Type: Costa Rica, Cartago, *Oersted 3589* (c!).
 - Tovomita gracilis Williams, Fieldiana Bot. 29: 357. 1961. TYPE: Costa Rica, Alajuela, Brenes 4217 (F!).

The holotype and only specimen of *Tovomita* gracilis is a mixed collection of a flowering branch with one attached leaf of *Tovomitopsis glauca* and a leafy, sterile shoot of an undetermined species of *Tetrapteris* (Malpighiaceae) (W. Anderson, pers. comm.). The hairs on this viny shoot are clearly dolabriform (i.e., malpighian) and the rather obvious interpetiolar stipules are even mentioned in Brenes' field notes on the herbarium label. The fertile element of this collection is here designated as the lectotype of *Tovomita* gracilis, a name that must then come into the synonymy of the earlier *Tovomitopsis glauca*.

- Tovomitopsis nicaraguensis Pl. & Tr., Ann. Sci. Nat. Bot., Ser. 4, 14: 266. 1860. Type: Nicaragua, Rio San Juan, *Oersted 3587* (c!).
 - Tovomitopsis standleyana (Williams) D'Arcy, Ann. Missouri Bot. Gard. 67: 1040. 1980. TYPE: Panama, Bocas del Toro, Wedel 1019 (Mo!, isotype).

Tovomitopsis nicaraguensis has been broadly interpreted as a widespread and common species ranging from Guatemala into South America. Although locally common at La Selva in northeastern Costa Rica, the real Tovomitopsis nicaraguensis is actually quite rare in collections, and restricted mostly to the wet Caribbean lowlands of southern Nicaragua, Costa Rica, and Panama. The type was collected along the Rio San Juan not far from La Selva and is identical to one of the three species at La Selva. It is distinguished by its large, somewhat succulent, glossy, and distantly veined leaves, which do not dry reddish brown and lack visible resin canals in dried material, by its large flower buds and its stout erect inflorescences and infructescences. Type material of Chrysochlamys pauciflora Standley (=Tovomitopsis standlevana) from Bocas del Toro Province of Panama, is also clearly identical to the original T. nicaraguensis.

The plants on Barro Colorado Island in Panama and many of the specimens cited as *Tovomitopsis nicaraguensis* in the Flora of Panama, belong to a species in a different genus, *Chrysochlamys eclipes* Williams, with leaves that do dry reddish brown, thick and succulent rather than membranaceous petals, monadelphous rather than separate stamens, and pollen with echinate rather than the psilate-foveolate exine of *Tovomitopsis* species examined.

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LITERATURE CITED

- ARMBRUSTER, W. S. 1984. The role of resin in angiosperm pollination: ecological and chemical considerations. Amer. J. Bot. 71: 1149–1160.
- CHARLESWORTH, B. AND D. CHARLESWORTH. 1978. A model for the evolution of dioecy and gynodioecy. Amer. Nat. 112: 975–997.
- D'ARCY, W. G. 1980. Flora of Panama. Guttiferae. Ann. Missouri Bot. Gard. 67: 969-1043.
- ENGLER, A. 1925. Guttiferae. *In* A. ENGLER AND K. PRANTL, eds., Die naturlichen Pflanzenfamilien 21: 154–237.
- FAWCETT, W. AND A. RENDLE. 1926. Flora of Jamaica 5: 190–202. British Mus. (Nat. Hist.), London.
- HAMMEL, B. E. 1984. Systematic treatments of the Cyclanthaceae, Marantaceae, Clusiaceae, Cecropiaceae, Lauraceae, and Moraceae for the flora of

a wet lowland tropical forest, Finca La Selva, Costa Rica. Ph.D. dissertation, Duke Univ., Durham, North Carolina.

- AND M. H. GRAYUM. 1982. A preliminary report on the flora of La Selva Field Station. Ann. Missouri Bot. Gard. 69: 420–425.
- KOSTERMANS, A. J. G. H. 1980. Clusiaceae. P. 110 in M. D. DASSANAYAKE AND F. R. FOSBERG, eds., A revised handbook to the flora of Ceylon, Vol. 1. Amerind, New Delhi.
- LLOYD, D. 1975. The maintenance of gynodioecy and androdioecy in angiosperms. Genetica 45: 325– 339.
- MAGUIRE, B. 1976. Apomixis in the genus *Clusia* (Clusiaceae).—A preliminary report. Taxon 25: 241–244.
- ——. 1979. On the genus *Clusia* (Clusiaceae) in Mexico. Taxon 28: 13–18.
- PLANCHON J. AND J. TRIANA. 1860. Memoire sur la famille des guttiferes. Ann. Sci. Nat. Bot. Ser. 4, 13: 306–376; 14: 226–367; 15: 240–319.
- SKUTCH, A. 1971. A naturalist in Costa Rica. Shorter Publ. Co., Inc., Gainesville.
- STANDLEY, P. C. 1937. Flora of Costa Rica. Guttiferae. Field Mus. Nat. Hist., Bot. Ser. 18: 703–712.