A REVISION OF COLICODENDRON (CAPPARACEAE)

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ABSTRACT

The South American genus *Colicodendron* (Capparaceae) is validated and amended. The taxonomic limits and the generic relationships are established and discussed. *Colicodendron* consists of four species, the previously established *Colicodendron* yco Mart. from northeastern Brazil, and *C. scabridum* (Kunth) Seem. from western Ecuador and Perú, plus two new species herewith described: 1) **Colicodendron bahianum** X. Cornejo & H.H. Iltis, restricted to the Atlantic coastal rainforests of the State of Bahia, eastern Brazil; and, 2) **Colicoden-dron valerabellum** H.H. Iltis, T. Ruiz & G.S. Bunting, a local endemic from the dry shrublands and forests in the environs of Valera, in the State of Trujillo, Venezuela. The new species are illustrated, a map and a key to the species of *Colicodendron* are herewith provided.

RESUMEN

Se valida y enmienda *Colicodendron* Mart., un género de Capparaceae restringido a América del Sur. Se establecen sus límites taxonómicos y se discuten sus relaciones con géneros afines. *Colicodendron* está representado por cuatro especies: Las previamente establecidas *Colicodendron yco* Mart., distribuida al noreste de Brasil, y *C. scabridum* (Kunth) Seem., localizada en los bosques secos y xerofíticos al oeste de Ecuador y norte de Perú; más dos nuevas especies aquí descritas: 1) **Colicodendron bahianum** X. Cornejo & H.H. Iltis, sólo conocida de los bosques húmedos del Estado de Bahía, al este de Brasil. Y, 2) **Colicodendron valerabellum** H.H. Iltis, T. Ruiz & G.S. Bunting, una endémica local restringida a los bosques secos del área de Valera, en el Estado Trujillo, Venezuela. Se ilustran las nuevas especies y se provee de una clave y mapa para las especies de *Colicodendron*.

KEY WORDS: Colicodendron, Capparaceae, Brazil, Ecuador, Perú, Venezuela, endemics

During our studies of the neotropical species of *Capparis* s.l. (Capparaceae), carried out to produce a generic realignment of this extremely polymorphic genus, it became clear that *Colicodendron* Mart. is a well defined South American genus of stellate shrubs and trees, characterized by having a 1-seriate valvate calyx with a dentate or lobed nectary-dish or nectary-cup, and thick-walled, indehiscent amphisarcous fruits.

Colicodendron was established by Martius (1839: 25), for two Brazilian species: *Colicodendron yco* Mart., the generic type, and *C. longifolium* Mart. (the latter recently placed in *Neocalyptrocalyx*, as *N. longifolium* [Mart.] X. Cornejo & H.H. Iltis [2008a]). Subsequently, Seeman (1852: 78) correctly transferred to *Colicodendron*: *Capparis scabrida* Kunth, but also the unrelated *Capparis avicennifolia* Kunth, and *Capparis pulcherrima* Jacq. (the latter as *Colicodendron pulchellum* Seem., nom. reject.), as well as the quite unrelated glabrous or simple-haired *Capparis subbiloba* Kunth (=*Cynophalla flexuosa* [L.] J. Presl). Two years later, Turczaninow (1854: 327–328) erratically described three species in *Colicodendron*, all of them synonyms of unrelated species of *Capparis* s.l., a contribution that obfuscated any clear concept of that genus.

Colicodendron was treated as a subgenus of Capparis L. s.l. (Eichler 1865: 272), and later as a section of Capparis (Pax & Hoffmann 1936: 181). In both mentioned infrageneric taxa, the members of Colicodendron were mixed up in a heterogeneous assemblage with the Mexican Capparis angustifolia Kunth (= Quadrella angustifolia [Kunth] H.H. Iltis & X. Cornejo), and the South American C. crotonoides Kunth and C. tweediana Eichler (both members of Capparicordis H.H. Iltis & X. Cornejo, a recently described stellate neotropical genus, Iltis & Cornejo 2007). Most recently Hutchinson (1967: 309), in his attempted generic realignment of Capparis s.l., made seven additional, but all inappropriate combinations to produce a poorly defined Colicodendron.

In this work, a revision of *Colicodendron* is presented. The genus is validated and amended, its morphological limits are defined, and the relationships with the morphologically closely related genera are discussed.

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Colicodendron Mart., Flora 22, Bleibl. 1:25. 1839, emend. X. Cornejo & H.H. Iltis. Type: Colicodendron yco Mart.

Destrugesia Gaudich., Bot. Voy. Bonite, t. 57. 1844–1846. Type: Destrugesia scabrida Gaudich.

Evergreen shrubs or trees, covered by stellate to echinate trichomes throughout. Leaves simple, short-petiolate to sessile, opposite to spirally or whorled. Inflorescences terminal, subterminal and/or axilar, a panicle, raceme or racemose spike, rarely a solitary axillary flower (in *Colicodendron yco*); floral bracts filiform or subulate, deciduous. Flowers with calyx 1-seriate, valvate, \pm cup-shaped, the 4 sepals free, \pm equal, distinct and entirely enclosing the corolla in bud, their margins and tips touching each other from early bud until near anthesis, at the base fused forming a hypantium, coated by a 4-dentate nectary dish or nectary cup or a 3-lobed nectary cup within. Petals 4, imbricate or torsivus in bud, sessile. Stamens 14 to 60, the filaments geniculate or spirally arranged in bud, at anthesis exserted, inserted on an expanded flat androgynophore, anthers basifixed. Fruits amphisarcous or pseudoamphisarcous (in *C. scabridum*), woody, thick-walled and multilocular, bearing white- or yellow-embryoned seeds, ca. 1–2 cm, cotyledons ca. 1–1.5 mm wide, convolute, testa crustaceous.

Due to the stellate pubescence, 1-seriate valvate calyx with the lobes covering the corolla from early bud until near anthesis, and the presence of a nectary cup or nectary dish, *Colicodendron* is related to the recently described neotropical genus *Capparicordis* H.H. Iltis & X. Cornejo. However, *Colicodendron* differs from the latter by having elliptic, lanceolate, oblong to oblanceolate, pinnately nerved leaf blades (vs. cordate to reniform or suborbicular and basally subpalmatly-nerved leaf blades); a 4-dentate nectary dish or 3-lobed nectary cup (vs. a nectary cup with four filiform to triangular-filiform appendages); higher number of stamens, 14 to 60 (vs. 4 to 8); and larger indehiscent thick-walled amphisarcous fruits, with an inflexible woody pericarp bearing larger seeds, ca. 1–2 cm (vs. smaller dehiscent fruits, with a soft and flexible, thinly coriaceous pericarp, which splits and falls off at maturity, bearing smaller seeds, ca. 5–7 mm, dispersed by birds, Cornejo pers. obs., 2002). *Colicodendron* is also related to the South American genus *Calanthea* (DC.) Miers, as was correctly stated by Martius in the original publication (p. 27, cf. with *Capparis pulcherrima* Jacq., the type of *Calanthea* [DC.] Miers). However, *Calanthea* mainly differs from *Colicodendron* by the very distinctive calyx with open aestivation, in which the not valvate linear-ligulate sepals are widely spaced from each other, exposing a valvate corolla from the very young bud; and by the seeds with barely folded, very thick cotyledons, 4–7 mm wide (Cornejo & Iltis 2008b).

Colicodendron could be also related to the stellate to peltate, Central American-West Indian genus *Quadrella* (DC) J. Presl. However, *Colicodendron* differs from the latter by having flowers with a hypanthium coated by a nectary dish or nectary cup (vs. flowers without hypanthium, but with a flat receptacle and four scales inserted on it in *Quadrella*); and indehiscent, ellipsoid to globose thick-walled woody amphisarcous fruits with larger seeds (vs. capsular, dehiscent, linear or oblong and few times to ovoid, with seeds distinctively smaller, usually arranged in a single row in *Quadrella*).

Colicodendron was previously known by two widely disjunct endemic species: *Colicodendron yco* from eastern Brazil, and *C. scabridum* (Kunth) Seem., restricted to the dry forests of western Ecuador and adjacent Peru. In this work, two additional South American endemic species, both with whorled subsessile leaves and beautiful inflorescences are added to this genus.

 Colicodendron bahianum X. Cornejo & H.H. Iltis, sp. nov. (Figs. 1, 2, 7). Type: BRAZIL. BAHLA: Antiga rodovia que liga a Estacion Ecologia do Pau – Brasil a Sta. Cruz, 7 km ao NE da estacao, ca. 12 km ao NW de Porto Seguro, 16°23'S 39°8'W, Regiao de Mata Higrofila Sul Baiano, ca. 80–100 m, 14 Aug 1979 (fl), S.A. Mori, L.A. Mattos Silva & S.A. Euponino 12710 (HOLOTYPE: CEPEC; ISOTYPES: NY, US, WIS).

Colicodendrum species novum cum pubescentia stellata, calyx valvatis 1-seriatis cum nectarius cupularibus et fructus amphysarcum, affinis *Colicodendrum yco* Mart., a qua differt frutex pauciramosis cum foliis subverticillatis et subsessilis (nec ramosissimis cum foliis oppositis et petiolatis), inflorescentiis racemosiis (nec paniculatiis), staminis 30 ad 42 (nec 14 ad 20), gynophoriis 1.6–2 cm longiis, glabriis (nec gynophoriis 3.5–5 cm longiis et stellatis pubescentiis).

Sparsely branching shrubs or slender treelets, $1-6 \text{ m} \times 4 \text{ cm}$ dbh; terminal branches densely stellate-echinate; stipules absent. Leaves subverticillate, grouped in whorls at the end of the terminal branches, sessile or

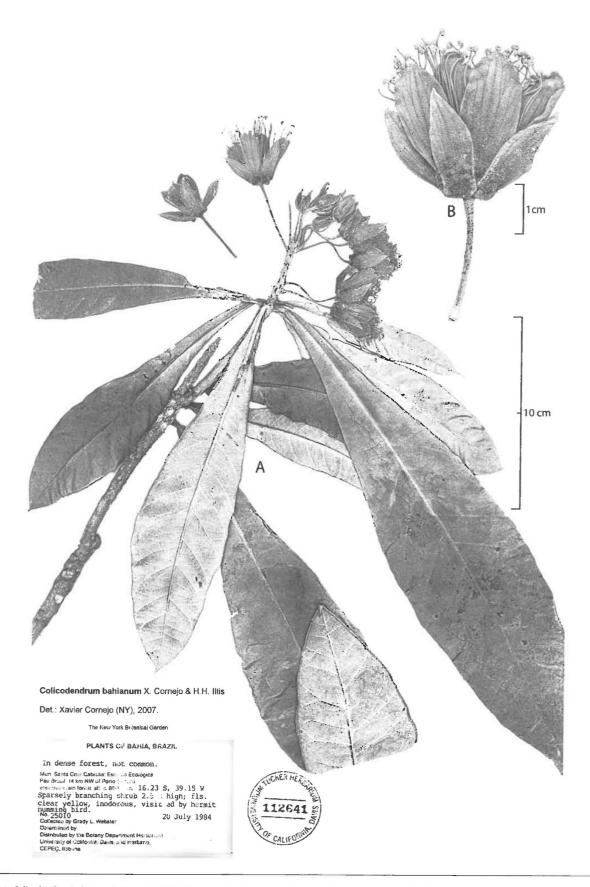


Fig. 1. Colicodendron bahianum X. Cornejo & H.H. Iltis. A. Terminal branch with whorled leaves and terminal inflorescence. B. A flower nearly to anthesis. (A, B. G. Webster 25010, DAV).

subsessile, with blades narrowly oblanceolate to narrowly elliptic, $13-40 \times 3-7(-10)$ cm, stiff, coriaceous (alive), chartaceous (dry), attenuate and revolute at the base, acute and apiculate to sometimes shortly rostrate at the apex, shiny green (alive) with an impressed to often sulcate midvein, nerved and glabrous above, paler green (alive) and with a strongly prominent glabrous or echinate-stellate midvein beneath, margin inconspicuosly thickened, with 15 to 25 major upward-arching lateral nerves on each side of the midvein. Inflorescences terminal and subterminal racemes, sometimes cauliflorous in older wood, densely stellate-echinate; axis short, 1–5 cm, stout, bearing to 25 flowers at the same time. Floral bracts linear, 3–7 mm, deciduous, densely echinate-stellate. Pedicels 1.8-4 cm, articulate to the axis. Sepals oblong-elliptic or ellipsoid to lanceolate, $12-22 \times 6-8$ mm, abaxially keeled, mainly toward the base, \pm acute at apex, yellow (alive), rusty brown (when dry), stellate-echinate abaxially; hypanthium 4–6 mm deep, coated by a subtetragonal 4-dentate nectary dish within, nectary appendages broadly deltoid to semiorbicular, 1.5 × 2.5-4 mm, glandular, stellate. Petals torsivae in bud, apparently inserted at the edge of the nectary cup, oblong to obovate-oblong, 20–28 × 7–12 mm, widely obtuse to rounded at apex, longitudinally nerved, sulfur yellow and erect at anthesis (Mori, pers. com.), dull rusty-brown (when dry), stellate on both sides. Stamens 30 to 42, filaments 2-3 cm, geniculate in bud, glabrous, inserted on a white-stellate-tomentose expanded toruslike androgynophore, anthers ca. 2 mm, white (alive). Gynophore 1.6–2 cm, glabrous; ovary oblong, 5–6 \times 2–3 mm, longitudinally sulcate, glabrous; stigma sessile, capitate. Infructescences with gynophores ca. 2–2.5 × 0.3–0.5 cm, pedicels ca. 3–3.5 cm. Amphisarcous oblong-ellipsoid, 7–12 × 2–4 cm, subpendulous; fruit wall 3–7 mm thick, mature seeds 1.3–1.7 mm in diam.

Colicodendrum bahianum is somewhat related to the equally yellow-flowered *C. yco*, is allopatric in the dry Caatinga to the north (Fig. 7). However, the more mesophytic *C. bahianum* can be easily distinguished by dense whorls of subsessile leaves, arranged toward the end of the terminal branches (Fig. 1A, vs. sub-opposite and pedicellate leaves, more spaced out along the branches). The inflorescences of *Colicodendrum bahianum* are short dense racemes (vs. larger and longer, paniculate inflorescences, or rarely solitary axillary flowers in *C. yco*), bearing flowers with erect (vs. reflexed) sepals at anthesis, higher number of stamens (30 to 42 vs. 14 to 20 in *C. yco*), smaller anthers (ca. 2 mm vs. 4 mm), shorter glabrous gynophores (1.6–2 cm vs. 3.5–5 cm, pubescent) and glabrous (vs. pubescent) ovaries.

Due to the whorled subsessile leaves, *Colicodendron bahianum* seems morphologically more closely related to the herein also described *Colicodendron valerabellum* H.H. Iltis, T. Ruiz & G.S. Bunting (for differences see comment under the latter species).

Phenology.—Collected in flower in February, July, August, November and January, and fruit in August. The sulfur yellow flowers are visited by hermit hummingbirds (*Webster 25010*).

Cytology.—Unknown.

Distribution.—Eastern Brazil, restricted to the southern extension of the moist or wet evergreen Atlantic rain forests (ca. 2000 mm) into southeastern Bahia State (Fig. 7).

Conservation concern.—Habitat is under intense human pressure from both agriculture and wood harvesting, especially for so decorative species *Colicodendrum bahianum* (Scott Mori, per. comm., Sep 1979; "It was one of the most beautiful species that I've ever seen"). Images of this potential ornamental species are available at the New York Botanical Garden Web site (NYBG, 2003).

PARATYPES. **BRAZIL. Bahia:** Mun. Santa Cruz Cabrália, mata costeira, 15 Jul 1966, *R.P. Belem & R.S. Pinheiro 2580* (F, UB, WIS). Est. Ecológica Pau Brazil, 14 km NW of Porto Seguro, evergreen rainforest, 39°15'W 16°23'S, ca. 80–100 m, 20 Jul 1984, *G.L. Webster 25010* (CEPEC, DAV, WIS). Porto Seguro, Parq. Naca. Monte Pascoal, 15 Jan 1973 (fl.), *T.S. Santos 2692* (CEPEC, NY, WIS); ibidem, trail to peak, upper slopes and top of Monte Pascoal, 40°34'29"W 15°15'53"S, 250–536 m, 14 Nov 1996, *W. Thomas et al. 11256* (NY). Estrada a Santa Cruz, Itaju do Colônia, 15 Jan 1971 (fl), *T.S. Santos 1329* (CEPEC, WIS). Guaratinga, plantacao de Cacau, 10 Aug 1966, *R.P. Belem & R.S. Pinheiro 2749* (UB, WIS). Potiraguá, Fazenda Independencia, Rod. Itaimbe, Potiraguá, ca. 15 km a partir da BR 101, 15°42'12"S 39°34'31"W, 6 Feb 2004, *P. Fiaschi et al. 2283* (CEPEC, NY [NY photo in WIS]). Pastaria, Itaimbe – Potiraguá, 10 Nov 1967, *R.S. Pinheiro 214 & T.S. Santos 77* (CEPEC, UB, WIS). Potiraguá a Itaimbe km. 10, 29 Jan 1972, *R.S. Pinheiro 1801* [1802] (CEPEC, WIS); km 10 da rod. Potiraguá para Itaimbé; 24 Jul 1973, *R.S. Pinheiro 2202* (CEPEC, WIS). Entre Eunápolis et Tabela, ± km 15, 28 Nov 1970, *E. de Mello Filho 2988 & M. Emmerich 3526* (CEPEC [CEPEC photo and fragm. at WIS]). "Mun. Itabello, Bahia" [there is no such place, perhaps a mistake

for Itabuno, a prominent town in the Cacao region, where the CEPEC herbarium is located], Cascalheira, mata pluvial, 13 Aug 1995 (fl, fr), *C. Hatschbach, M. Hatschbach & J.T. Motta 63068* (US [US photo at WIS]).

- 2. Colicodendron scabridum (Kunth) Seem., Bot. Voy. Herald 78. 1852. (Fig. 7). BASIONYM: Capparis scabrida Kunth, Nov Gen. Sp. 5:95. 1821. Octanema scabrida Rafin., Sylva Tellur. 112. 1838. Destrugesia scabrida (Kunth) Gaudichaud, nomen, Voyage de La Bonite [text unpubl.], Atlas pl. 57. 1842. Colicodendron scabridum (Kunth) Hutch., Gen. Fl. Pl. 2:309. 1967, hom. illeg. Type: ECUADOR or PERU: Habitat in America meridionali, without data, Humboldt & Bonpland s.n. (LECTOTYPE, designated here: P [microfiche at NY!]; ISOLECTOTYPE: B-W 10055-01 0! [B-W photo 9478 at WIS!]).
 - Capparis angulata Ruiz & Pav. ex DC., Prodr. 1:253. 1824. Colicodendron angulatum (Ruiz & Pav.) Hutch., Gen. Fl. Pl. 2:309. 1967. Capparis canina Tafalla, nomen. Tipe: ECUADOR: Guayas, Guayaquil, 1799 (fl), "Zapote de perro," Ruiz s.n. (=Tafalla) (LECTOTYPE, designated here: MA [MA photo 29269 at WIS!]; ISOLECTOTYPES: B 10 0242738! [B photo 342 at WIS!], G! [G fragm. at WIS!]).
 - Capparis gaudichaudiana Eichl. in Mart, Fl. Bras. 13:273. 1865. Colicodendron gaudichaudianum (Eichl.) Hutch., Gen. Fl. Pl. 2: 309. 1967.
 TYPE: PERU: Piura, Paita, Voyage de la Bonite, Jul 1836 (fl, fr), M. Gaudichaud s.n. (LECTOTYPE, designated here: B 10 0242739!; ISOLECTOTYPES: B 10 0242737! ["misit 1841"]; F 876547!, F 894168!, F [fragm.] 609130!, G [G photo 8472 at WIS!], P!).

Nomenclatural note.—The herein selected lectotype of *Capparis scabrida* housed at P, has a label with a correct origin of the specimen, "in America equatoriale," and the number "19" added. The B isolectotype of *Capparis scabrida* consist of a branch with a terminal inflorescence, with the two leaves, one inflorescence, and floral pieces detached and remounted. That isolectotype, originally only identified as *Capparis*, was named *Capparis speciosa* (a Willdenow's nomen nudum, non *Capparis speciosa* Griseb. [1879], = *Anisocapparis speciosa* [Griseb.] X. Cornejo & H.H. Iltis), as reads the label which is at the upper left corner of the photo 9478, now in a separate sheet (B-W 10055 -00 0). That label has the following handwritten information: "Polyandria Monoginia *Capparis speciosa* racemi(?) terminali, foliis ovato-lanceolatis obtusis mucronatis supra nitidis glabris subtus tomentosis foliola elliptica. Habitat in America meridionali." The discussed isolectotype later was correctly identified by Eichler himself, in a handwritten label of determination, which reads: "*Capparis (Colicodedron) scabrida* H.B.K."

Multi-branched shrubs to trees, to 10 m and 25 cm dbh, erect to low and widely spreading; the stem when injured produces a gum (Little 6725); terminal branches complanate or ± tetragonal, densely stellate throughout. Leaves spirally-alternate, few times opposite-decussate, petioles 8-30 mm, lacking pulvini; blade coriaceous (rigidly coriaceous when dry), lanceolate to oblong, $(6-)8-23 \times 2-7$ cm, acute to rounded, sometimes emarginate, apiculate at apex, cuneate to rounded, sometimes retuse at base, olive green (alive), but drying to a bright sulfur-yellow in herbarium material, thinly stellate-tomentose when young, soon glabrescent and smooth or scabrous above, pale grayish or "ashen" greenish-yellow and densely pale stellate-tomentose with a prominent midvein beneath; (7–)12–23 lateral nerves on each side of the midvein. Inflorescences simple, densely corymbose racemes, solitary and terminal or lateral in the axils of leaves, or branched, terminal racemes compounded into complex, stout, (sub)erect, corymbose panicles, to 30 cm, densely stellate, each raceme with only 1–4 open flowers at its end at one time. Floral bracts filiform, 5–12 mm, soon deciduous. Pedicels 2.5–4 cm, densely brown stellate and sparsely dendroid. Flowers dark brown to greenish-brown, densely stellate. Flowers asymmetrical, in perfect flowers the androgynophore-gynophore off-centered within the calyx cup, arching out and upward. Sepal lobes broadly ovate to lanceolate, $10-15 \times 10^{-15}$ 5–8 mm, at anthesis cucullate-ascending, acute at the apex, densely brown stellate on both sides, eventually caducous, broadly inserted on the rim of a wide bowl-shaped calyx cup, $9-13 \times 6-8$ mm, with a 3-lobed nectary cup coating the hypanthium within. Petals narrowly to broadly ovate, oblong or elliptic, $15-23 \times$ 10-15 mm, reflexed and outrolled at the tip at anthesis, widely cuneate to truncate at the sessile base, obtuse to rounded at the apex, white to cream or yellowish, sometimes greenish, stellate on both sides. Stamens 24 to 35, borne in a ring on top of the short 2–3 mm androgynophore, filaments (3.5–)5–7(–8) cm, stellate and dendroid, adnate to each other for 0.5–2 mm at the base; anthers 3–4 mm, white (alive). Gynophore 5–8 cm, creamish-white, maturing to purple (alive), sparsely stellate; ovary ovoid to ellipsoid, $4-6 \times 3-5$ mm, densely stellate; stigma truncate, sessile. Infructescences with gynophores 7–10 × 0.4–0.6 cm, pedicels 2.5–3.5(–4) cm. Pseudoamphisarcum oblongoid, ovoid, or ellipsoid, slightly asymmetrical, $8-15 \times 5-9$

cm, pendulous, \pm umbonate at the apex, densely stellate, when mature exhibiting 8 longitudinal \pm sulcate (dried) lines (usually 4 major, indicating the valves); fruit wall fibrous, 6–10 mm thick, pulp bright orange at maturity, insipid; seeds 15 to 60, subspherical-reniform, often strongly beveled, ca. $1-2 \times 1-1.5$ cm, surrounded by a densely orange sarcotesta infiltrated by many hairs from the crustaceous reddish-brown testa; embryo yellow.

The amphisarcum is a simple, indehiscent fruit, provided with a thick, woody to subwoody fruit-wall, which retains the shape upon removal of sarcocarp, and never splits in valves after maturity (Spjut 1994: 23, 37). In *Colicodendron scabridum*, the fruits at maturity fall on the ground to eventually decompose and release the seeds, leaving usually four thickly-subwoody, elliptical, abaxially convex, unattached, persistent valves. That fruit type of *Colicodendron scabridum*, which doesn't fit in any of the fruit types known (Spjut 1994), is herein proposed as Pseudoamphisarcum (pseudo + amphisarcum) X. Cornejo (mod. nov.), which means a false amphisarcum.

Local names.—ECUADOR: Sapote (Spanish, Little 6725), sapote de campo (Spanish, Van den Eynden et al. 1999: 42), sapote de perro (Spanish, *Cornejo & Bonifaz* 7583), sapote gomoso (Spanish, *Steyermark* 54842); Zapotillo (Spanish, *Brandbyge* 42789); Zapote de perro (Spanish, *Acosta-Solis* 8521, Mille 1940, Madsen 64103). PERU: Sapote (Spanish, *Díaz & Baldeón* 2374), sapote de perro (Spanish, *Woytkowski* 5672). Zapote (Spanish, Vargas 42), Zapotillo (Spanish, *Simpson & Schunke* 567).

The bright orange color of the mature fruit pulp of *Colicodendron scabridum* strongly resembles the color of the pulp of a locally (in Ecuador) well known edible fruit called "Sapote" (*Quararibea cordata* [Bonpl.] Vischer, Bombacaceae). This is the origin for the several similar and derived local names of *Colicodendron scabridum*.

"Sapote de perro," one of the local names, refers to *Pseudalopex sechurae* Thomas. This is an endemic canid locally known as "Perro de monte" (Spanish) or "Sechura fox" (English), that has a distributional pattern similar to that of *Colicodendron scabridum* in the dry coastal areas of Ecuador and Peru. When the food is really scarce, the *Pseudalopex sechurae* facultatively eats the fruits of *Colicodendron scabridum* (Bruning 1985; Cornejo 2005).

Zapotillo (Spanish), a town located in a dry forest at the Province of Loja in Southwestern Ecuador, owes its name to the local name of the locally well known *Colicodendron scabridum*.

Phenology.—Flowering mostly between February to October, fruiting mostly September to December. A single tree 4–6 m high, produces 20 to 60 flowers at anthesis per night. Within the nectary cup, three droplets of nectar start to be produced at 19:00 h., each droplet from below of each nectary lobe. By 19:30 h, the nectary cup is full of nectar. But by the next morning at 6:00 h, the flowers don't have nectar anymore, perhaps due to the intense bat activity during the night. The nectar is secreted during one night per flower only. The flowers live one night only and don't produce any scent (Cornejo field obs. in Bahía de Caráquez, Ecuador, July 2004).

Cytology.—n = 8 [!Pazy, ECUADOR. Manabí: Iltis and Iltis 243 WIS, Iltis unpublished ms).

Distribution.—Colicodendron scabridum is a characteristic floristic element of dry to very dry or xerophytic areas of western Ecuador and Perú, where is a dune former. This species ranges from sea level in Ecuador from the Province of Manabí, to ca. 2500 m in the mountains of the Province Loja, and in Perú south to Dept. Ancash (Fig. 7).

Ecological interactions and field observations.—The flowers of *Colicodendron scabridum* are visited by the common domestic honey bee, *Apis mellifera* L. Dozens of buzzing bees can be heard from under a tree when the nocturnal flowers are just about to open. The honey bee's activity peaks in and around the flowers of *Colicodendron scabridum* is between 18:30 to 19:30 h. The domestic bees re-start re-visiting the flowers the next morning, as well between 6:00 to 8:00 h. Nocturnal, presumably pollen predator bees such as Halictidae (*Megalopta?*), also visit the flowers at 19:00 h. While both species of bees touch the anthers and the ovaries, it seems however that the true pollinators are bats. From 20:00 to 5:50 h, many small bats frequent the flowers of *Colicodendron scabridum*, which are exposed on long peduncles high above the foliage. The bats beat their wings hovering in the air while licking the nectar from each flower during less than one second,

as hummingbirds are apt to do. The bats do not hold themselves from the flowers as happens to the African Bignoniaceae, *Kigelia africana* [Lam.] Benth. (seen in Bahía de Caráquez, Ecuador, the same locality where *Colicodendron scabridum* was studied by the senior author). When leaving the flower, the bat shakes the inflorescence, presumably helping pollination. It is interesting to note that only the individuals of *Colicodendron scabridum* growing in total darkness are visited by bats. These conspicuously have a higher fruit productivity per tree than the remaining individuals located around the nocturnal lights along the roadsides in the same locality. Additionally, the flowers of *Colicodendron scabridum* are also visited by *Amazilia amazilia*, a hummingbird who visits the old (previous night's) flowers between 7:00 to 8:00 h, and the new flowers just about to open at ca. 18:00 h. Finally, the flowers of *Colicodendron scabridum* are commonly visited by wasps, coleoptera and several species of ants (Cornejo field obs. in Bahía de Caráquez, Ecuador, July 2004).

Uses.—The fruits have been reported as edible for humans and as medicinal against colds and coughs. They are commonly eaten by cattle and donkeys (*C. Cerón et al.* 22424, Van den Eynden et al. 1999: 42, Cornejo field obs.), while the wood is used for fuel and to make handicrafts (*Cornejo & Bonifaz* 7583, Van den Eynden et al. 1999: 42). Finally, a "glue" for paper can be obtained from the cut, gum-oozing ends of the stems (*Cerón 11876*).

Conservation biology.—A characteristic common species in the dry landscape, it does not appear to be in danger of extinction.

Specimens studied. ECUADOR. Manabí: Bahía de Caráquez, 6 Jun 1955, E. Asplund 16569 (S); 10 m, Apr 1944, M. Acosta-Solís 8521 (F); km 8 carr. Bahía-Tosagua, Universidad Católica, bosque muy seco-seco tropical, intervenido, 80°32'W 00°45'S, 30 m, 31 Oct 1997, X. Cornejo & C. Bonifaz 5852 (AAU, GB, GUAY, WIS [voucher for DNA]); 20 km carr. a Chone, monte espinoso tropical, 80°25'W 00°38'S, 100 m, 4 Jun 1989, C. Cerón et al. 6174 (MO, QAP, QCNE, WIS); frente a la Isla Corazón, 80°22'W 00°40'S, ca. 190 m, 18 Feb 1994, X. Cornejo & C. Bonifaz 1739 (GUAY). 1 km NW of San Vicente, ca. 10 m, 9-12 Jul 1977, H.H. Iltis & M. Iltis E-228 (WIS); Cantón Sucre, 21-22 km S of Leonidas Plaza, 80°25'W 0°46'S, ca. 100 m, 16 Sep 1993, G. Webster et al. 30666 (DAV, QCNE); Moteles la Playa, deciduous thorn scrub vegetation, ca. 10 m, 9 Jul 1977, H.H. Iltis & M. Iltis E-182 (WIS). 10 km SE of Bahía de Caráquez, at km 11-14 along road to Chone near the highest point, ca. 150 m, 8 Jul 1977, H.H. Iltis & M. Iltis E-243 (B, QCA, WIS [2]); Ad El Recreo, ca. 100 m, 1897, Eggers 15528 (F, PR). Entre La Salina y Chone, 26 Jul 1945, M. Acosta-Solfs 10638 (F); 1 km N of Portoviejo on main road; hill overlooking town, common on dry coastal hills, 7 Aug 1980, B. Hansen et al. 7980 (AAU, RSA, SEL, USF, WIS); Portoviejo-Jipijapa road, ca. 1 km S of La Pila, grazed deciduous forest, ca. 200 m, 4 May 1985, G. Harling & L. Andersson 24821 (GB, QCA, WIS); Jipijapa, 80°35'W 1°21'S, 30 m, 25 Mar 1981, B. Sparre 20020 (GH, S); 10 km N of Montecristi, 180 m, 29 Dec 1961, C. Dodson & Thien 1786 (MO, WIS); 11 km W of Puebloviejo, 22 km E of Manta, extremely dry scrub with large bombacaceous trees, ca. 100 m, 28 Oct 1974, A. Gentry et al. 12203 (MO, WIS); 14 km SW of Manta on new road to San Lorenzo, 80°47'W 1°01'S, 300 m, 2 Jun 1997, D. Neill & M. Asanza 10706 (MO, QCNE, WIS); between Puerto López and Machalilla, 80°48'W 1°32'S, 70 m, 29 Sep 1984, J. Brandbyge 42789 (AAU, MO, NY, QCA); Parque Nacional Machalilla, Norte de Puerto López, monte espinoso Tropical, 80°48'W 1°31'S, 70 m, 3 Apr 1994, X. Cornejo & C. Bonifaz 2326 (GUAY, WIS); comuna Agua Blanca, 80°42'W 1°35'S, 30 m, 7 Jan 1994, X. Cornejo & C. Bonifaz 1147 (GUAY, QCNE); ibidem, 350 m, 21 May 1995, X. Cornejo & C. Bonifaz 3900 (GUAY); 80°44'W 1°31'S, 125 m, 2 Aug 1990, C. Cerón et al. 11671 (MO, QCNE, WIS); 25 Jun 1993, Salaite, Cerro Viejo y punta de Las Sillas, C. Cerón et al. 22424 (QAP); Joa hacia Mero Seco, desvío a la derecha del cerro La Jacinta y de ahí hasta el cerro Las Colembras, 80°41'W 1°25'S, ca. 420 m, 6 Sep 1991, C. Josse 638 (AAU, QCA); camino a la Playa de Los Frailes, ca. 25 m, 29 Jul 1992, M. Gavilánez et al. 966 (NY, QCA, QCNE [2]); Playa Los Frailes, ca. 2 m, 23 Jan 1991, A. Gentry & C. Josse 72703 (MO, QCNE); Río Blanco-Vuelta Larga, 80°47'W 01°29'S, 150 m, Sep 1986, C. Bonifaz 1076 (GUAY); Bosque seco aledaño al Parque Nacional Machalilla, 100 m, 25 Nov 1990, P. Mena & M. García 87 (NY, QCA, WIS); Estero Seco, bosque muy seco tropical, 80°37'W 01°39'S, 150 m, 29 Nov 1993, X. Cornejo & C. Bonifaz 924 (GUAY); without locality, 80°32'W 0°04'S, ca. 200 m, 9 Jul 1978, G. Webster 2262 (MO). Guayas: Between Daule and Lomas, 9 Oct 1952, F. Fagerlind & G. Wibom 501 (LD, MO, S); "Prope Guayaquil," Mar 1865, R. Spruce 4403 (K); Ad Bahía et prope Guayaquil, Apr 1942, L. Mille 1940 (US); Guayaquil-Playas, Feb 1965, G. Sánchez 1 (GUAY, WIS); Casas viejas, 22 km W of Guayaquil on road to Salinas, ca. 60 m, 25 Sep 1981, C. Dodson & P. Dodson 11508 (SEL); El Azúcar, bosque muy seco tropical, 10 m, 19 Jul 2002, X. Cornejo & C. Bonifaz 7583 (AAU, GUAY, WIS); between Progreso and Playas, ca. 30 m, 27 Oct 1958, G. Harling 3096 (S); 10 km W of Progreso, ca. 20 m, 29 Oct 1958, G. Harling 3100 (S); along road between Progreso and Baños San Vicente, 16 Apr 1941, H. K. Svenson 11501 (BKL); above Palmar on coast north to Santa Elena, 50 m, 13 Mar 1982, C. Dodson & P. Dodson 12943 (QCNE, SEL, WIS); Cerca a Playa Rosada, ca. 1 m, Jul 1993, X. Cornejo & C. Bonifaz 275 (GUAY, WIS); Chanduy, "in litore Maris Pacifi," R. Spruce 6403 (BM, CGE, K); E of Ancón, 20 Sep 1952, F. Fagerlind & G. Wibom 220 (S); Muey, May 1978, F. Valverde 23 (GUAY, MO, SEL); Island of Puná, 24 Aug–8 Sep 1836 [voyage of H.M.S. Sulphur], G. W. Barclay 422 (BM, NY, WIS); Aug 1847, B. C. Seeman 915 (K); "Insula Puná," Oct 1892, H. Eggers 14735 (GH, K, LE, M, US); ibidem, 1852, Andersson s.n. (S); Isla Puná, path from Puná Vieja to Campo alegre, 80°08'W 02°49'S, ca. 50 m, 4 Nov 1987, J. Madsen 64103 (AAU); path Río Hondo to Cerro Yanzún, 80°03'W 02°44'S, 50 m, 2 Oct 1987, J. Madsen 63987 (AAU[2], QCA, QCNE). El Oro: Parroquia San Antonio, Hcda. Montecarlo, 22 Mar 1967, C. Pineda 89 (GUAY, MO, S); entre Arenillas y Puerto Pitahaya, Dec 1978, L. Albert de Escobar 913 (QCA, WIS); camino entre Puerto Pitahaya y Arenillas, 15 Apr-15 May 1979, L. Albert de Escobar 1248 (NY, QCA, WIS); at Arenillas, 6 km S, 25 Jun 1943, E. Little 6725

(NY, US); 2 km S de Chacras cerca de la entrada a Balsalito en la carretera de la Reserva Militar de Arenillas, suelo Paleustalf, rojo con profundidad variable, 80°14'W, 3°33'S, 200 m, 16 Feb 1997, H. Vargas et al. 1158 (WIS); ca. 1 km N of Huaquillas, 1 May 1980, G. Harling & L. Andersson 18813 (GB, WIS); Huaquillas, dry thorn scrub forest, 80°13'W 3°27'S, 5 m, 7 Apr 1980, L. Holm-Nielsen 22842 (AAU). Loja: Cantón Saraguro, caserío Chayasapa, 79°12'W 4°17'S, 2500 m, 5 Sep 1990, C. Cerón 11876 (MO, QAP, QCNE, WIS); 10 km N El Empalme on Macará-Celica road, 800 m, 12 Feb 1991, Kessler 2463 (AAU); Rd. Macará-Loja, 16 km S of Catamayo, 79°23'W 4°05'5, 1400 m, 13 Feb 1987, J. Bohlin et al. 1331 (GB, QCA); between Loja and Portovelo, 3-6 Oct 1918, J. Rose et al. 23327 (NY, US); El Saucillo, Las Casas Viejas, 80°11'20"W 4°15'40"S, 360 m, 15 Feb 1996, Van den Eynden et al. 615 (LOJA, QCNE); above Catamayo towards Loja, very dry slope, ca. 1650 m, 9 Oct 1955, E. Asplund 18077 (B, K, LD, NY, S); between El Tambo and La Toma, 1000-2200 m, 3 Sep 1923, A. Hitchcock 21330 (GH, NY, US); carr. La Toma-El Tambo, monte espinoso premontano, 79°25'W 4°02'S, 1500 m, 26 Dec 1991 (fr), D. Rubio et al. 2287 (MO, QCNE, WIS); between Gonzanamá y La Toma, 1400 m, 21–23 Jul 1959, G. Harling 6065 (S); Catamayo, 1 km SE de La Toma, 79°22'W 4°00'S, 1500 m, 6 Sep 1994, E. Little et al. 252 (NY, QCNE, WIS); Cerca a Catamayo, 79°21'W 4°00'S, 1238 m, 22 Mar 1994, X. Cornejo & C. Bonifaz 2148 (AAU, GUAY, QCNE, WIS); Rd. Catamayo–La Toma, ca. 1500 m, 24 Apr 1980, G. Harling & L. Andersson 18600 (AAU, GB); dry rocky desert hills above La Toma, ca. 1675 m, 24 Oct 1943, J. Steyermark 54842 (GH, NY); Catamayo valley, Lehmann 4939 (F, K, LE); along the Río Guayaba, 4800 ft, 8 Oct 1944, W. H. Camp E-651 (NY, WIS[2]); Río Guayabas, 5 km NW of Catamayo (La Toma), 1300 m, 10 Feb 1945, F. Fosberg & M. Giler 22933, 22934 (WIS); E side of Catamayo valley, 3 km E of Catamayo, 1690 m, 10 Feb 1945, F. Fosberg & M. Giler 22927 (WIS); near la Toma, 79°04'30"W 4°00'00"S, 1300 m, 20 Oct 1965, D. Knight 439 (LE, WIS); ibidem 14 Feb 1965, D. Knight 609 (WIS); La Toma, 1400 m, R. Espinoza 537 (F, NY); SW Catamayo, valley along Río Catamayo, 79°21'W 3°59'S, 1355 m, 10 Jul 1989, L. Dorr & I. Valdespino 6584 (NY, QCA, QCNE, WIS); La Toma-El Tambo, km 5–11 (along gravel roads), vic. Río Catamayo, dry rocks with cacti, 79°21'W 04°03'S, 1300–1500 m, 15 Oct 2000, J. Madsen & J. Gálvez 7441 (AAU, NY); Rd. San Pedro de La Bendita-Catamayo, km 6.5 (4 km from Catamayo), 79°23'W 3°57'S, ca. 1325 m, 16 Jul 1996, G. P. Lewis et al. 2451 (K, LOJA, QCNE); Cerro Villonaco, 1800 m, 13 Feb 1985, G. Harling & L. Andersson 22023 (GB, NY, QCA, WIS). PERU. Tumbes: Prov. Tumbes, Dtto. Pampas del Hospital, Huapalas, 100m, 26 Jun 1964, J. Vargas 42 (NY); Dtto. San Juan de la Virgen, along Quebrada Las Peñas, betw. San Juan de la Virgen and Matapalo, 6 Jan 1968, D. Simpson & J. Schunke 567 (F, NY). Piura: Prov. Piura, Piura, 1928, O. Haught F-69 (F); Prov. Paita, Paita, D'Urville (Lesson?) s.n., 1825 (B [2]); 25 Jun 1914, Mr. & Mrs. J.N. Rose 18513 (NY); ibidem, 25 Jul 1901, R. Williams 2927, 2928 (NY); Prov. Sullana, Sullana, 260 m, 16 Apr 1987, C. Díaz & S. Baldeón 2374 (MO). Lambayeque: Lambayeque, 1150 m, 8 Jan 1964, P. Hutchinson & J. Wright 3518 (MO); Lambayeque, km 698 betw. Lima and Sullana, chief dune former in desert, sea level, 5 Oct 1959, B. Maguire & C. Maguire 44389 (F, MO, NY). Cajamarca: Prov. Celendín, Balsas-Celendín rd., 1–5 km from Balzas, 78°04W 6°50'S, 910–1160 m, desert slopes, Río Marañon Valley, 23 Feb 1984, D. Smith 6145 (MO, NY); Río Marañón Valley, Celendín-Balsas rd. 25 km and onward from Celendín, 78°05'W 06°51'S, 1000-2500 m, 16 Jul 1983, D. Smith & I. Sánchez 4330 (MO, NY); Prov. San Ignacio, San Ignacio, 600–700 m, 78°46'W 5°12'S, 16 Apr 1996, J. Campos y P. Díaz 2615 (MO). La Libertad: Prov. Trujillo, Trujillo, 15 Apr 1988, C. Díaz & S. Baldeón 2784 (MO); Cerro Campana, 800 m, 25 Oct 1983, A. Sagástegui 10965 (MO); ibidem, 100 m, 14 Jul 1973, A. López & E. Araujo 7978 (MO, NY); banda occidental, 215 m, 10 Sep 1949, N. Angulo 1250 (NY); base del Cerro Campana, 60 m, 23 Oct 1983, A. Sagástegui s.n. (NY); in quebrada bottom on SE side of Cerro Campana, 150-200 m, 24 Sep 1957, P. Hutchinson 1358 (NY); Prov. Pacasmayo, Pacasmayo, 79°24'W 7°33'S, 120 m, 13 Jul 1983, D. Smith 4221 (MO); just S of San Pedro de Lloc, 100 m, 31 Dec 1963, P. Hutchinson & J. Wright 3352 (F, G, GH, HEID, K, LE, MO, MICH, M, NY, P, S, US, USM); ca. 96 km N of Trujillo on Panamerican hwy, coastal desert dunes, 60 m, 16 Oct 1984, M. Dillon & M. Whalen 4014 (F, MO); 84 km N of Trujillo, 3 Mar 1973, A. Richardson 2029 (NY). Ancash: 78°06'W 10°11'S, 11 Oct 1958, K. Rahn 318 (MO, ex Tropicos).

3. Colicodendron valerabellum H.H. Iltis, T. Ruiz & G.S. Bunting, sp. nov. (Figs. 2–7). TYPE: VENEZUELA: Edo. Trujillo, Distr. Valera, "Arbusto de 3 m de alto; hojas brillantes por el haz, envés con pubescencia estrellada de color amarillo y caediza al tacto. Pedúnculo de la inflorescencia secundaria castaño claro e inclinado con respecto al eje caulinar. Botones con néctar. Sépalos castaño oscuro, ásperos al tacto; pétalos color crema. Estambres en número de 64, sobre un corto androginóforo, gineceo gris oscuro y atrofiado en las flores masculinas examinadas. La inflorescencia con hormigas y 'pegones' [Himenopteros]." Se observaron 17 individuos en un área de 3 m² [3 km²?]," Carretera vieja Valera-Motatán, saliendo de Valera por el barrio La Floresta. Selva decidua muy intervenida, 550 m, 70°36'W 9°20'N, 16 Mar 1991 (fl, y fr), *T. Ruiz-Zapata & C. Benítez de Rojas 4671* (HOLOTYPE: MY; ISOTYPES: K, MO, US, VEN, WIS; photocopies together with individual leaves F, IRBR, MER, NY, PORT, S, UC.).

Colicodendrum species novum cum pubescentia stellata, calyx valvatis 1-seriatis cum nectarius cupularibus et fructus pachycarpus, affinis *Colicodendrum yco* Mart., a qua differt frutex vel arbusculis pauciramosis cum foliis subverticillatis (nec ramosissimis cum foliis oppositiis), inflorescentiis racemosiis (nec paniculatiis), staminis (35–)50–64(–70) (nec 14 ad 20), gynophoriis ca. 8–9 cm longiis, (nec gynophoriis 3.5–5 cm longiis), et fructis subglobosis (nec ellipsoidiis).

Evergreen palmoid treelets [or in damaged plants with one or two additional unbranched stems from near the base, some of these decumbent and sending forth 1 to 3, erect, leaf- and sometimes flower-bearing lateral-horizontal shoots], to 5 m long and 3–5 cm dbh often crowded (colonal?); young branch(es) dark-brown echinate or echinate-stellate; stipules absent. Leaves subsessile to short-petiolate, to 1.5 cm, grouped in crowded whorls at the end of the terminal branches exposing mostly leafless internodes, nodes of leaf insertions ca. 3–6 cm, swollen, blades oblanceolate to narrowly elliptic, (16–)20–50 × 4–9 cm, stiffly coriaceous

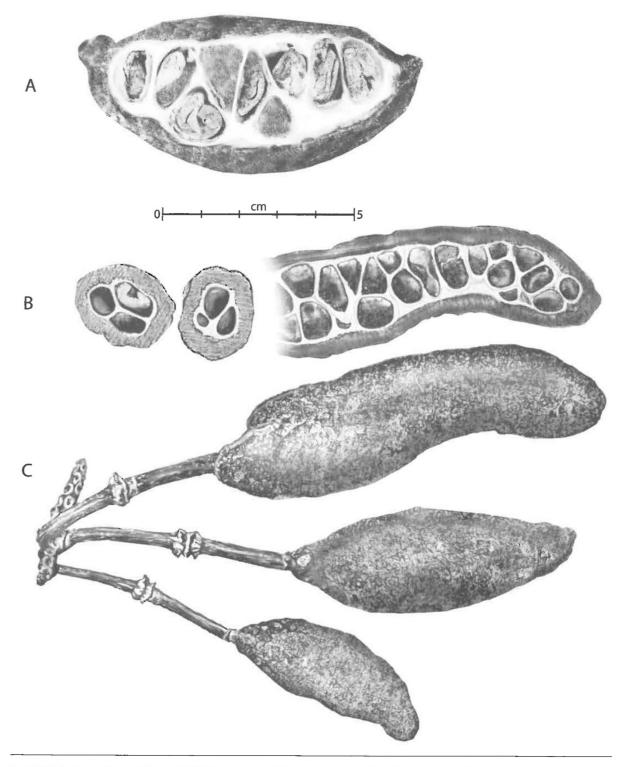


Fig. 2. Colicodendron bahianum X. Cornejo & H.H. Iltis. A. Longitudinal section of a mature fruit. B. Transversal and longitudinal sections of immature fruits. C. Infructescence. (A. Hatschbach & Motta 63068, US. B–C. de Mello Filho 2988, CEPEC).

and hard but somewhat flexible (alive), chartaceous (dry), attenuate but rounded-retuse to subcordate at the base, acuminate or acute to widely obtuse at the apex, margin inconspicuosly thickened and revolute, lustrous green (alive) with a impressed to sulcate midvein, prominently and coarsely rugose (i.e., bullate), with the blade surface between the deeply impressed midrib and main nerves prominently convex and smooth, ap-

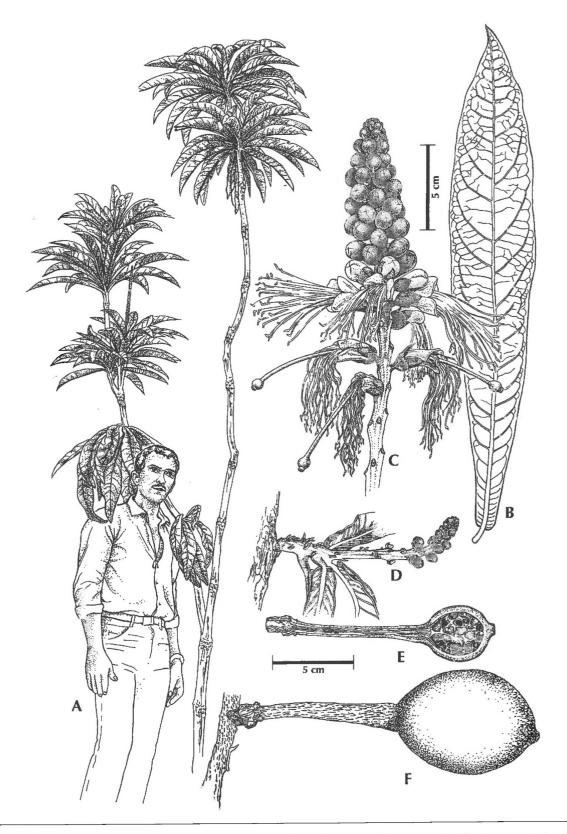


FIG. 3. Colicodendron valerabellum H.H. Iltis, T. Ruiz & G.S. Bunting. A. Habit. B. A leaf blade. C. An inflorescence with three hermaphrodite flowers in postanthesis at base; four male flowers above them in full bloom and three beginning to wilt; and, above these, some 50 male flower buds. D. An inflorescence bearing (sub)sessil flowerbuds. E–F. Immature fruit. (A. After photo of *Bunting & Trujillo 13120*. B–D. *Iltis et al. 30547*, WIS. E–F. *Ruiz & Villafañe 4764*, MY). A–E, drawings by Marian Firmani; F, by T. Ruiz Z.

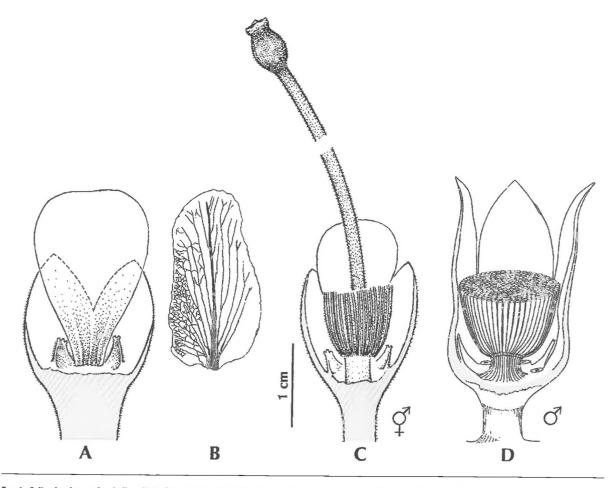


Fig. 4. Colicodendron valerabellum H.H. Iltis, T. Ruiz & G.S. Bunting. A. Schematic section of flower, showing calyx in relation to one petal and the alternating scaly nectary appendages. B. Petal, with its detailed nervature shown only in lower left area. C. Hermaphrodite flower, showing columnar androgynophore arising from the nectary dish, cut-off bases of staminal filaments, and abbreviated gynophore tipped by a young ovary. D. Male flower, showing scaly nectary appendages, three petal bases and phalanx of stamens touching petals and sepals to create an inner nectar chamber. (A–D. *Iltis et al. 30547*). A, C by Manara; B, D by Iltis.

parently glabrous (glabrescent) above; paler green (alive) and with a strongly prominent midvein and densely stellate beneath; 14 to 26 pairs of lateral nerves. Inflorescences terminal, racemose spike, stiffly erect and densely coarsely echinate-stellate throughout, rough to the touch, arising from the center of a leaf whorl, axis eventually elongating to 40 cm (or more?) × 6–10 mm tick, stout, bearing 20 to 100 or more subsessile, rustybrown (alive) flower buds, but only 2 to 5 flowers opening each night in successive acropetal circles. Floral bracts subulate, ca. 5–7 mm, deciduous, densely brown-echinate. Pedicels 2–3 × 3–4.5 mm. Sepals ovate to lanceolate, 15–25 × 8–12 mm, ± acute at apex, densely yellow-brown (alive) echinate abaxially; hypanthium ca. 2–3 mm depth, coated by a 4-dentate nectary dish within, nectary appendages deltoid, ca. $3-4 \times 3-4$ mm, emarginated to bifid at the apex. Petals apparently inserted at the edge of the nectary cup, at anthesis obovate to obovate-oblong, $25-32 \times 10-15$ mm, widely obtuse to truncate at apex, longitudinally nerved, bright yellowish or cream (alive), densely pale-brown echinate-stellate abaxially. Stamens (35–)50–64 (–70), filaments (4-)6-7 cm, stellate at the base, inserted on a expanded torus-like androgynophore, at anthesis projecting forward in a narrow phalanx, anthers 3.8-5 mm. Gynophore 8-9 cm, densely stellate; ovary 6-7 × 4-5 mm, subglobose, 8-ribbed, densely stellate; stigma sessile, truncate, discoid. Infructescences a stout gynophore, ca. 10 mm wide. Amphisarcous subglobose, ca. 9 × 7 cm (immature), subpendulous, apex umbonate with an apically stigmatic depression at the umbo, densely rusty-brown echinate, yellow when

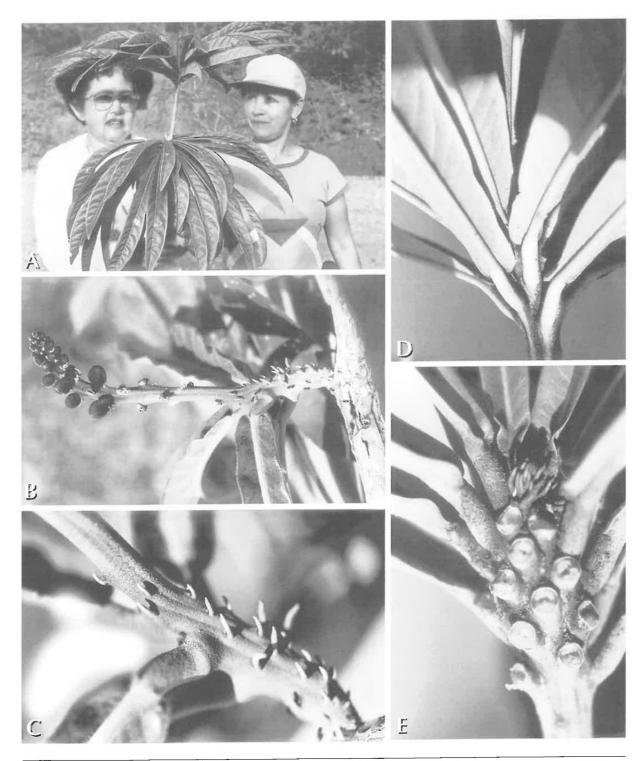


Fig. 5. *Colicodendron valerabellum* H.H. Iltis, T. Ruiz & G.S. Bunting. A. Terminal two leaf whorls of unbranched, 4 m tall treelet, showing conduplicate arched leaves and leafless inter-whorl stem segment (Thirza Ruiz Zapata on right, Carmen E. Benítez de Rojas on left). **B.** Lateral secondary shoot, terminating in a small spike. **C.** Enlarged base of spike shown in B, with bract-like processes and base of a petiole. **D.** Pseudoverticil of leaves showing leaf bases. **E.** Pseudoverticil of D, with leaves removed to show crowding of petioles and a densely bracted terminal bud of future replacement stem or inflorescence. (A–D, photos by Iltis of *Iltis et al. 30547*, from near type locality).



Fig. 6. Colicodendron valerabellum H.H. Iltis, T. Ruiz & G.S. Bunting. F. Rigid, massive peduncle of primary inflorescence, covered with symmetricallyspaced pedicel scars. G. Terminal pseudoverticil of primary stem, showing base of old, now decomposed peduncle and six branch buds covered with bract-like processes. H. Two immature fruits near base of rigid, stout, erect peduncle. (F–G, photos by Iltis of *Iltis et al. 30547*, from near type locality. H, photo by G. Bunting).

ripe (fide a local informant, *Iltis et al. 30547*); fruit wall thick, pulp whitish or cream, seeds numerous (ca. 30?), reniform, $20-25 \times 13-14$ mm (immature), seed coat red-purple (fide Bunting).

Colicodendron valerabellum differs widely from *C. yco* by the characters written in the Latin diagnosis. Due to the leaves arrangement in crowded whorls at the end of the terminal branches (Fig. 3A, 5A) and unbranched inflorescences (Fig. 3C), *Colicodendron valerabellum* seems more closely related to the Brazilian *C. bahianum* (Fig. 1A). However, *Colicodendron valerabellum* differs from the latter by having spicate inflorescences with a larger central axis, 10–30 cm (Fig. 3C, vs. racemose, with shorter central axis, 1–5 cm, Fig. 1A), bearing subsessil (vs. 1.8–4 cm, pedicellate) flowers, longer gynophore, 8–9 cm (vs. 1.6–2 cm), subglobose (vs. oblong) ovaries; subglobose fruits (Fig. 6H, vs. oblong-ellipsoid, Fig. 2) and by its localized distribution, in northwestern Venezuela (vs. eastern Brazil, Fig. 7).

Phenology.—Colicodendron valerabellum apparently begins to flower in November, not long after the end of the rainy season, and continues to bloom into April or May (or "does it flower twice a year, once in May and again in November?"), with older hermaphrodite flowers beginning fruit enlargement with the commencement of the rainy season at the beginning of May, forming young fruits by July, "when new growth was just starting," and completing their growth by the following January or February.

The terminal inflorescence of Colicodendron valerabellum is apparently an extension of the apical mer-

istem that continues to grow from the center of the upper-most leaf whorl. It is, however, a structure most unusual in many respects, not the least of which is the fact that its flowers are essentially sessile or subsessile on the peduncle axis, with the pedicels very short and thick, so that this structure, rather than a *raceme*, could better be called a *racemose spike*. The remaining species of *Colicodendron* and even of the neotropical *Capparaceae* s.s. have flowers borne on well developed pedicels. In this comparatively specialized species, this loss of pedicel is linked to a basically primitive, racemose inflorescence, while its three relatives, *C. bahianum*, *C. yco* and *C. scabridum*, have pedicellate flowers in racemes or panicles, presumably the derived condition. Correlated with this loss of pedicel in *C. valerabellum* may be the great length, thickness and stiffness of the peduncle, truly spike-like in the non-botanical meaning of the word, ultimately becoming a full centimeter thick and to 40 cm long, which eventually decompose. Around the stubby remains of the old inflorescence in the center of the leaf whorl, several axillary buds, densely covered with subulate bracts, may be initiated. These in turn may produce 1 to 3 replacement axes, essentially by continuing the unbranched growth upward and the production of another flowering spike, or else lead to the branching of the stem into 2 or 3 axillary branches.

Although variable in particulars among individuals, the primary terminal spikes bear flowers in the following sequence: the lowest floral buds soon abort, leaving only pedicel scars on the peduncle (these buds are usually naked, but in some inflorescences subtended by up to 20 or so small leaves rapidly decreasing in size upward and spaced over a distance of some 10 cm). Moving upward, the next 3 to 6 flower buds, well spaced and the first to burst into bloom, develop into fully functioning hermaphrodites, in which the many stamens are exceeded for about 1 cm by a gynophore bearing its well-developed ovary. Finally, towering above the circle of hermaphrodite flowers, and densely aggregated at first into a narrowly conical inflorescence, are some 20 to 100 staminate flower buds, with only 2–3(–5) of these blooming at one time, beginning at base and continuing upward. The whole inflorescence thus has a long-extended flowering period lasting perhaps a month, and in the process gradually elongating the peduncle to its maximum length. Once the staminate flowers finish blooming, they soon wilt and fall off, leaving only the symmetrically placed, oval pedicel scars on the peduncle.

If the hermaphrodite flowers at the base of the spike become fertilized and commence fruit development, the peduncle above them eventually dries up and eventually decomposes. But if these hermaphrodite flowers are not fertilized, not only do they fall off, but also the peduncle then often retains its stiff, thick structure to eventually produce a new set of hermaphrodite flowers near its tip some 30 cm or more up from its base. This double insurance that seeds will eventually be produced may be the key to understanding the function of so massive a structure.

Clues to the enigmatic reproductive morphology of *Colicodendron valerabellum* must lie in its pollination agents. Of the eight main attributes of the bat pollination syndrome (Chiropterophily) cited by various authors (Pijl 1961: 51; Faegri & Pijl 1966: 114; Vogel 1958: 492), the following six would seem to apply to *Colicodendron valerabellum*: 1) Nocturnal anthesis, the flowers lasting only one night. 2) Flowers and inflorescences strong enough to carry the weight of a bat (subsessile, often many flowers on the strong pedicels, thick calyx, powerful peduncle, i.e., racemose spike axis). 3) Honey abundant, mucilaginous, accessible (to sphingid moths as well). 4) Flower (corolla) yellowish or creamy. 5) Pollen abundant. 6) Inflorescence exposed high above the foliage.

Biological interactions.—According to a local informant, the fruits of *Colicodendron valerabellum* are eaten by deer (Iltis et al. 30547, WIS).

Why the big fruits of *Colicodendron valerabellum* should be borne high above the leaves is a curiosity, when in its close relatives, as in most *Capparaceae*, heavy fruits hang down. Or were the fruits/seeds of *Colicodendron valerabellum* dispersed internally by the now extinct megafauna as the giant Gomphotheres (Janzen & Martin 1982), as suggested for *Neocalyptrocalyx muco* (H.H. Iltis, Cumaná, Delgado & Aymard) X. Cornejo & H.H. Iltis, another giant-fruited Capparaceae of northern Venezuela and Colombia? (Iltis et al. 1996: 379, see *Capparis muco*).

Cytology.—Unknown.

Distribution.—Colicodendron valerabellum is known only from one limited metapopulation of several, scattered minute populations, with perhaps a total of 20 to 40 plants, growing in extremely disturbed, open tropical deciduous forest remnants and thickets on top of 10–20 m high, steep and badly eroding road cuts and local trash dumps scattered for 3 to 7 km north of Valera (654 m) along and immediately above the *old* highway to Motatán (ca. 500 m), in northwest Venezuela (Fig. 7). Growing in seasonally dry, semi-deciduous to deciduous open forest or woodlands of medium-sized trees, the "bosques higrófilos y mesófilos de las sierras en la región Andina" (Hueck 1960), or in degraded secondary thorn thickets (matorral).

Conservation biology.—Colicodendron valerabellum appears to be close to extinction, but with all known populations restricted to the edge of the old yet easily accessible Valera-Motatán highway, and the rest of the landscape barely explored, the possibility exists that the extensive woodlands covering the hills above the road may well hold more extensive stands. In fact, this is also suggested by the presence of a common name, "fruto de venado" (fruit of the deer), since rare species are generally not honored with common names.

The few plants known to exist are certainly in trouble reproductively: except for the inflorescence with two young fruits photographed by Bunting in 1983, the two somewhat older fruits collected by Ruiz-Zapata in 1997, and the five hermaphrodite flowers with developing ovaries at the tip of an inflorescence collected by Ruiz-Zapata in 1998, no other fruits, young or old, have ever been located despite assiduous searching. Perhaps, like many a taxon at the end of its evolutionary career, *C. valerabellum* is not reproducing well. Negative human influences such as firewood gathering, land clearing, and grazing by cattle as well as the unknown but negative impact of pesticide spraying can also not be discounted.

What is clear, in any case, is that the limited fruit production in all the examined populations (by H.H. Iltis) may be due to one or more of the following: 1) The often densely crowded stems may be clones, and, if self-incompatible, cannot form fruit unless cross-pollinated; 2) land clearing may have reduced genetic diversity to the point of no return; 3) the population is inbred, reducing seed production; 4) populations of the pollinating agents (sphingid moths, bats, or hummingbirds) have been much reduced by pesticide application to the local maize fields; 5) the species is adapted to an undisturbed summergreen open wood-land periodically cleared by fire, and now these relictual stands have to compete with weeds in a liana-rich, secondary community induced by human disturbance; 6) A remarkable number of Capparoids in the region, have extra-large, more or less woody, indehiscent fruits that, as one of us suggested (Iltis et al. 1996) may have had Gomphotheres, now extinct, as their dispersal agent (Janzen & Martin 1982).

PARATYPES. **VENEZUELA: Edo. Trujillo:** Dtto. Valera, carr. vieja Valera-Motatán, E-facing slopes of Río Motatán Valley, foothills of the Cordillera de Mérida of the Andes, on top of heavily eroding road cuts, 20 m above the old highway from Valera to Motatán, ca. 4 km N of Valera (1.4 km N of entrance to old hwy. from new hwy.), [ca. 70°36'W 9°21'N], 600 m, 10 Jan 1991 (y fl), *H.H. Iltis, T. Ruiz & C. Bentitez 30547* (WIS); 7 km N. of Valera (2 km. S of Motatán), *H.H. Iltis et al. 30548* (MO, MY, US, WIS); carr. vieja, en ladera, matorral deciduo, 600 m, 31 Mar 1996 (fl), *T. Ruiz & Villafañe 4740* (MY); alrededores de Valera, en bosque deciduo intervenido por deforestación para conucos [maize fields] y también el uso como basurero, 435 m [?], 10 Jan 1997 (fl., fr), *T. Ruiz & Villafañe 4764* (MY); carr. vieja, en matorral deciduo, 590 m, 31 Jan 1998 (old fl.), *T. Ruiz, Villafañe & Hernández 4801* (MY, WIS), 1 May 1998 (fl), *T. Ruiz, Hernández & Noguera 4802* (MY), carr. vieja, ca. 3 km N de Valera (from the last gas station), en ladera a la izquierda de la vía, en zona de bosque semideciduo ahora alterado, ca. 450 m, 6 Jun 1983 (y fr), *G. Bunting & Trujillo 13120* (W1S); carr. vieja, Zona perturbada, 9 May 1980 (fl), *J. Szwarcbort & A. Stoddard 14* (US, VEN).

- 4. Colicodendron yco Mart., Flora 22, Bleibl. 1:25. 1839. (Fig. 7). Capparis yco (Mart.) Eichler in Martius, Fl. Bras. 13:272. 1865. Type: BRAZIL. BAHIA: Habitat in silvis Catingas ad Caitete, Rio de Contas etc. Provinciae Bah. et ad Malhada ad Salgado usque in P. Min. Ger., Sep–Oct, C. Martius s.n. (LECTOYPE, designated here: M [M photo at WIS!]; ISOLECTOTYPES: BM, K, M).
 - Capparis speciosa Moric. nomen nudum (non Capparis speciosa Griseb., 1879), cited in Eichler in Mart., Fl. Bras. 272. 1865. Brazil, Bahia, Serra da Jacobina, 1839 (fl), J. Blanchet 2564 NY 387633! (from C. Meisner herb.). NOTE: J. Blanchet 2564 B 10 0242727!, it has been determined by error (by H.H. Iltis 1983) as the isotype of Capparis yco Mart..

Many branched shrubs to trees, 2 to 6 m tall; terminal branches complanate, angulate, often ± subtetragonal, densely stellate. Leaves opposite, petioles 0.5–2 cm, lacking pulvini; blades coriaceous, lanceolate to

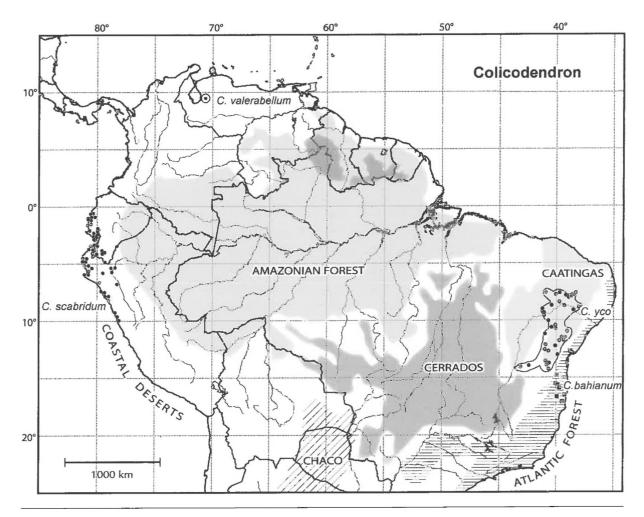


FiG. 7. Distribution of *Colicodendron* Mart. The pronounced morphological differentiation of these four species, disjunct in widely separated regions on the far edges of the Amazon Basin speak for an ancient evolutionary history: 1) *Colicodendron scabridum*: locally common, ranging from the dry-season deciduous, xeric, coastal woodlands near Canoa, Prov. Manabí, Ecuador, south through the dry thorn scrub of coastal Ecuador to the extremely arid deserts of Peru as far as Casma, Prov. Ancash; and inland to the dry, inter-Andine valleys near Loja, Ecuador and the upper Río Marañón, Prov. Amazonas, Perú. 2) *Colicodendron valerabellum* H.H. Iltis, T. Ruiz & G.S. Bunting: A highly local endemic, restricted to a stretch of road ca. 3–6 km north of Valera along the old highway to Motatán, Est. Tujillo, Venezuela, in open to dense but sunny, deciduous to semi-evergreen, tropical, mesophyllous dry forests or ceroid woodlands and thickets, at elevation of ca. 600 m. 3) *Colicodendron yco* Mart.: Widespread in the northeastern Brazilian states of Bahia and Pernambuco (and, barely, Ceara), in the Caatinga, and drought-frequented land, where the vegetation is xerophytic, summer-deciduous, and droughtadapted. 4) *Colicodendron bahianum* X. Cornejo & H.H. Iltis, restricted to moist and wet forests at SE of Bahia State, at Eastern Brazil. (Distribution of *C. yco* in Pernambuco adapted from Costa e Silva 1995).

oblong or oblong-elliptic, $9-25 \times 3-8.5$ cm, usually retuse to cordate at the base, acute to widely obtuse and apiculate, few times rounded to truncate or notched at the apex, margin entire to sinuate, dark green, glossy (alive) and glabrescent above, whitish, whitish-grey, pale green or pale tan (alive), with prominent nerves and densely stellate beneath; (8–)10–16 pairs of lateral nerves. Inflorescences axillary and terminal, paniculate, rarely solitary axillary flower (*Pinheiro 1453*), densely stellate. Floral bracts linear-subulate, 5–10 mm. Pedicels 1–2 cm, articulated. Sepals 1–1.8 × 4–7 mm, the lobes acute to obtuse at apex, reflexed at anthesis, cream or dull-yellow, densely stellate, deciduous; nectary a 4-dentate cup, the teeth 3–5 × 2–4 mm, triangular, acute. Petals oblanceolate to oblong, 15–30 × 5–7 mm, at anthesis all together erect resembling a tubular corolla, reflexed at the upper third, yellow to orange-yellow, stellate adaxially, densely stellate abaxially. Stamens 14 to 20, filaments 3.5–4 cm, stellate at the base, inserted on a stellate androgynophore, anthers ca. 3–4 mm, yellow (alive). Gynophore 3–5 cm; ovary ovate, 3–5 mm, both densely stellate; stigma

capitate-disciform. Infructescences with gynophores 3-5 cm, pedicels 1-4 cm; amphisarcous ellipsoid, $6-10 \times 4-6$ cm, subpendulous, apex umbonate with an apically stigmatic depression at the umbo, densely stellate, bearing 10 to 20 seeds, testa light brown, crustaceous, glabrous.

Icones.—Colicodendron yco is illustrated in detail in Flora Brasiliensis (Eichler in Mart. 1865, tab. 60, see *Capparis yco*).

Local names.—Icó (Portuguese, R. Santos & A. Castellanos 24350), icó branco (Portuguese, Laurênio et al. 262), icó de cavalo, icó preto (Portuguese, Costa e Silva 1995: 75).

Biological interactions.—The base of the flower is visited by small ants (Harley 27133).

Cytology.—*n* = 8 [!Pazy, BRAZIL. BAHIA: *Mori et al.* 11218, WIS, Iltis unpublished ms).

Distribution and ecology.—Widespread in the northeastern Brazilian states of Bahia and Pernambuco (and, barely, Ceara), in the Caatinga, a semi-arid (300–800 mm/year rainfall), hot (23°–28° C yearly average) and drought-frequented land, where the vegetation is xerophytic, summer-deciduous, and drought-adapted (Costa e Silva 1995: 74).

Specimens studied. BRAZIL. Pernambuco: Mun. Belém de São Francisco, ilha do Meio, 18 Jul 1967, E. Tenório 314 (IPA); Mun. Cabrobó, entre Cabrobó e Terra Nova, 15 Apr 1971, D. Andrade-Lima et al. 767 (IPA); Mun. Inajá, Reserva Biologica de Serra Negra, chapadão arenítico, solo arenoso recoberto por matéria orgânica em decomposição, 15 Sep 1995, M. Tschá et al. 236 (NY, PEUFR); 16 Sep 1995, M. Tschá et al. 247 (NY, PEUFR); ibidem, 9 Dec 1995, A. Laurênio et al. 262 (NY, PEUFR); Mun. Petrolina, Fazenda Santa Maria, proximo a divisa com Santa Maria da Boa Vista, 3 Sep 1968, G. Carvalho 54 (HST). Bahia: Mun. Vitoria da Conquista e Jequié, 26 Sep 1963, R. Santos & A. Castellanos 24350 (NY); Mun. Jequié, Estrada que liga Jequié a Lafayete Coutinho, ca. 11–17 km a W de Jequié, caatinga herbáceo-arbustiva, 19 Nov 1978, S. Mori et al. 11207, 11218 (NY); Jequié, 28 Sep 1979, K. Kubitzi & H. Poppendieck 79-262 (NY); De Jequié para Milagres, 20 Sep 1965, A. Duarte 9545 (NY, RB); Serra do Castanhão, 14.5 km S of Jequié on BR 116 to paved road (at Churrascaria Corujão), then 7.3 km W of BR 116, 40°11.35'W 13°57'S, arborescent caatinga, 575 m, 19 May 2001, W. Thomas & S. Sant' Ana 12527 (NY); 40°11.46'W 13°56.52'S, 600 m, high elevation semi-deciduous forest with some caatinga species, 23 Oct 2001, W. Thomas et al. 12567 (MO, NY); Mun. Juazeiro, N end of Serra da Jacobina at Flamengo, 11 km S of Barrinha (ca. 52 km N of Senhor do Bonfim) at Fazenda Pasto Bom, 42°12'W 10°00'S, Quartz formation and surrounding caatinga, 24 Jan 1993, W. Thomas et al. 9632 (NY); Serra da Jacobina, 1839, J. Blanchet 2564 (B, NY); Mun. Rui Barbosa, 8.5 km from Rui Barbosa along right side of old road going via Povoado Alagoas to Itaberaba, dense tall, partly deciduous seasonal forest, 40°23'W 12°15'S, 29 Jan 1993, J. Kallunki & J. Pirani 392 (NY); Mun. Rio de Contas, 7 km da cidade na Estrada para Livramento do Brumado, 41°50'W 13°38'S, 650 m, Caatinga, 12 Dec 1988, R. Harley et al. 27133 (MO, NY); Serra do Rio de Contas, by the waterfall of Rio Brumado just N of Livramento Brumado, ca. 41°50'W 13°38'S, ca. 460 m, 20 Jan 1974, R. Harley et al. 15339 (MO, NY); Mun. Riachao do Jacuipe, ca. 30 km na Estrada de Riachao do Jacuipe para Capim Grosso, caatinga, 14 Mar 1990, A. de Carvalho & J. Saunders 2765 (CEPEC, NY); Lagoa da Eugenia S end near Camaleão, ca. 10°40'S 39°43'W, 300 m, 21 Feb 1974, R. Harley 16284 (NY); Quemaidas, 9–11 Jun 1915, J. Rose & P. Russel 19843, 19871 (NY); 5 km al S de Ichu, camino a Tanquinho, ca. 39°09'W 11°48'S, ca. 300 m, 15 Jan 1997, Arbo M.M. et al. 7261 (CTES, NY); 30 km N of Serrinha, ca. 39°00'W 11°30'S, 2 Nov 1972, T. Ratter & Da Fonsēca 2704 (NY[2]); Ba. Maracás x Pouso Alegre km. 27, caatinga, 8 Jul 1971, R. Pinheiro 1453 (CEPEC, NY); Salgada, 15 May 1918, H. Curram 277 (GH, NY).

KEY TO THE SPECIES OF COLICODENDRON

1.	Many branched trees or shrubs; the leaves arranged along the branches, distinctively petiolate.	
	2. Leaves opposite; flowers yellow, sepals reflexed at anthesis, nectary a 4-dentate cup, adrogynophores	
	centered, gynophores 3–5 cm, densely stellate; petals 5–7 mm wide; E Brazil	С. усо
	2. Leaves spirally, rarely subopposite on the same branch; flowers brown to greenish-brown, sepals erect	
	at anthesis, nectary a 3-lobed cup, androgynophores off-centered, gynophores 5–8 cm, sparsely stellate;	
	petals 10–15 mm wide; W Ecuador and adjacent northern Peru	. scabridum
	Unbrached to sparsely branched shrubs or treelets; the leaves whorled at the end of the terminal branches, sessile to 2 cm petiolate.	
	3. Inflorescence a raceme with the flowers distinctively pedicellate, pedicels 1.8-4 cm, relatively laxly ar-	
	ranged on a short axis, 1–5 cm; gynophore 1.6–2 cm, ovary oblong; fruit oblong-ellipsoid; eastern Brazil	
		. bahianum
	3. Inflorescence a racemose spike with the flowers subsessile, pedicels to 3 mm, densely arranged along	
	the axis, 10–40 cm; gynophore 8–9 cm, ovary subglobose; fruits subglobose; NW Venezuela, near Valera	
	C. va	alerabellum

Rejected names

Colicodendron anceps Shuttl., nomen in Chapman, Fl. South. U.S. 32. 1860. = Quadrella jamaicensis (Jacq.) J. Presl.

- Colicodendron angustifolium (Kunth) Hutch., Gen. Fl. Pl. 2:309. 1967. = Quadrella angustifolia (Kunth) H.H. Iltis & X. Cornejo.
- Colicodendron avicenniafolium (Kunth) Seem., Bot. Voy. Herald 78. 1852. = Beautempsia avicennifolia (Kunth) Gaudich.
- Colicodendron crotonoides (Kunth) Hutch., Gen. Fl. Pl. 2:309. 1967. = Capparicordis crotonoides (Kunth) H.H. Iltis & X. Cornejo.

Colicodendron lepidotum Turcz., Bull. Soc. Nat. Mosc. 27:327. 1854. = Quadrella odoratissima (Jacq.) Hutch.

Colicodendron longifolium Mart., Flora 22:26. 1839. = Neocalyptrocalyx longifolium (Mart.) X. Cornejo & H.H. Iltis.

Colicodendron obovatum Turcz., Bull. Soc. Nat. Mosc. 27:327. 1854. = Monilicarpa tenuisiliqua (Jacq.) X. Cornejo & H.H. Iltis. Colicodendron pulchellum Seem., Bot. Voy. Herald 78. 1852, nomen = Calanthea pulcherrima (Jacq.) Miers.

Colicodendron salicifolium (Griseb.) Hutch., Gen. Fl. Pl. 2:309. 1967. = Sarcotoxicum salicifolium (Griseb), X. Cornejo & H.H. Iltis.

Colicodendron subbilobum (Kunth) Seem., Bot. Voy. Herald 78. 1852. = Cynophalla flexuosa (L) J. Presl.

Colicodendron tweedianum (Eichl.) Hutch., Gen. Fl. Pl. 2:309. 1967. = Capparicordis tweediana (Eichl.) H.H. Iltis & X. Cornejo.

Uncertain name

Colicodendron obliquifolium Turcz., Bull. Soc. Nat. Mosc. 27:328. 1854.

We have not seen *Linden 1370*, the cited type specimen of *Colicodendron obliquifolium*, collected from "Nova Grenada, prov. Pamplona at ripas Rio Zulia" (Colombia). However, *Colicodendron obliquifolium*, originally described as "glabrum...," evidently does not belong to *Colicodendron*.

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