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The genus *Plethadenia* (*Rutaceae*)

Abstract

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The genus *Plethadenia* is revised. It consists of two species, which are distributed in the Greater Antilles and are likely endangered, viz. *P. cubensis* from E Cuba and *P. granulata* from N Haiti and the SW Dominican Republic. The species differ in the indument, the morphology of the sepals and disc, and in the size of the flowers and follicles. The genus and its species are described, and distributional data, a distribution map, illustrations and a key to the species are provided. The systematic position of *Plethadenia* within the *Rutoideae* sensu Engler is briefly discussed.

Introduction

The small genus *Plethadenia* is distributed in Cuba and Hispaniola only. The plants are densely covered with oil glands which produce a wonderful lemon-like odour. For their oil the leaves are used in the Dominican Republic for tea and also as medicine against influenza. The composition of the oil of *P. granulata* was investigated by Adams & al. (1990). Flowers and infructescence resemble the fresh green colour of the leaves.

The first collection of *Plethadenia* was made in Hispaniola by Bertero in 1819 or 1820 (Stafleu & Mennega 1993: 118), a second collection in Cuba in 1909 (Britton 1993, NY). The specimens from Hispaniola were described as *Fagara granulata* (Urban 1896: 594). While preparing a treatment of the *Rutaceae* for the North American Flora, P. Wilson mailed a fragment of Britton's specimen to Urban at Berlin-Dahlem asking "whether or not this is the same as *Fagara granulata*" (August 30, 1910). Urban answered: "This is exactly *Fagara granulata*. Leaflets only a little broader, as far as I can judge by sterile material" (September 8, 1910; copies of the letters are mounted on Britton's specimen at NY). Wilson (1911: 199) noted for *Fagara granulata* "Known only from sterile material collected in Santo Domingo and Cuba" and "Probably not of this genus"(!). Somewhat later, when Urban was able to inspect fertile plants from Hispaniola, he described the new genus *Plethadenia* and wrote about the Cuban material: "Plantam valde affinem, sed foliis omnibus oppositis" (Urban 1912: 238). Again twelve years later, when fertile specimens of Ekman's collection from Cuba arrived at Berlin-Dahlem, Urban (1924: 177) described the new Cuban species *P. cubensis* (to which Britton's specimens belong). Probably

due to these circumstances, the occurrence of two *Plethadenia* species was erroneously reported for Cuba by Léon & Alain (1951: 388). This was corrected by Liogier (1969: 84).

Material and methods

This paper is a result of studies undertaken for the Flora of the Greater Antilles Project and for the Flora de la República de Cuba, mainly based on herbarium specimens from these herbaria: BM, HAJB, HPPR, JBSD, K, NY, P, S, US (abbreviations according to Holmgren & al. 1990). The dried flowers were boiled in aqua dest. together with a drop of detergent. For SEM studies the dried flowers were soaked with a mixture (6:1) of aqueous Aerosol OT (dioctyl sodium sulfosuccinate, Peterson & al. 1978) and 95% acetone, dehydrated with FDA, critical point dried and cool-sputtered with 20 nm gold-palladium. Dried seeds and leaflets were sputtered with gold-palladium without prior preparation. The Cuban provinces are given according to the administrative division of 1975; the phytogeographical division follows Samek (1973). The distribution map is based exclusively on examined material.

Taxonomy

Plethadenia Urb., Symb. Antill. 7: 237. 1912. – Type: *Plethadenia granulata* (Krug & Urb.) Urb. (≡ *Fagara granulata* Krug & Urb.)

Unarmed, small, evergreen shrubs; all parts glandular-verrucose and very fragrant. *Leaves* alternate, subopposite or opposite; petiole and rachis slightly winged (Fig. 1B, 3B-C), paripinnate; leaflets (2)4-10(11), sessile, opposite or subopposite, shiny adaxially, coriaceous. *Inflorescences* small, cymose, axillary (Fig. 1G, 3D, 4A); peduncles 0.5-1.6 cm long. *Flowers* 2-3 mm long, subsessile, perfect. *Sepals* 4, free, persistent. *Petals* 4, free, ovate, slightly navicular, cucullate at apex, obliquely truncate at base (Fig. 3E), conspicuously glandular (Fig. 3D, 4A), valvate in aestivation (Fig. 3E, H). *Stamens* 8 (4+4?), free, the episepalous ones longer and with larger anthers; filaments broadened towards base and minutely pubescent, anthers nearly basifixed (Fig. 3F-G, H). *Gynoecium* tetracarpellate, carpels sessile, subconnate centrally toward base, styles free, short, stigmata connate at anthesis, ovary conspicuously glandular (Fig. 3E, 4B), ovule 1, anatropous?; disc undulate, entire, nearly flat or short-cupulate with an unequal sinuate margin (for an empirical flower diagram see Fig. 3H). *Fruit* short-stipitate, aggregated of 1-4 modified follicles (fruitlets), abortive follicles persistent (Fig. 1C); peduncles at fruiting nearly of the same length as at anthesis. *Follicles* 2.8-4.2 mm long, (sub)connate centrally and laterally toward the base, subsessile, ovoid and laterally somewhat compressed, short-apiculate, one-seeded; endocarp yellowish, main part elastic, horny, smaller part membranaceous. *Seeds* small, reniform (known only from *P. granulata*), ejected by a catapult mechanism.

Two geographically vicarious species endemic to Cuba and Hispaniola (Haiti, Dominican Republic), respectively (Fig. 2).

The genus name comes from the Greek *πληθος* (multitudo) and *αδην* (glandula) for “numerous glands”.

Key to the species of *Plethadenia*

- 1 Leaves, branchlets and inflorescences densely minutely pubescent; sepals elliptic to oblong, differing in size, longer than the petals (at least in bud); fruitlets about 3 mm long 1. *P. granulata*
- Leaves sparsely hairy to glabrous; branchlets and inflorescences densely minutely pubescent, powdered or glabrous; sepals triangular-lanceolate, all of same size; petals longer than the sepals; fruitlets about 4 mm long 2. *P. cubensis*

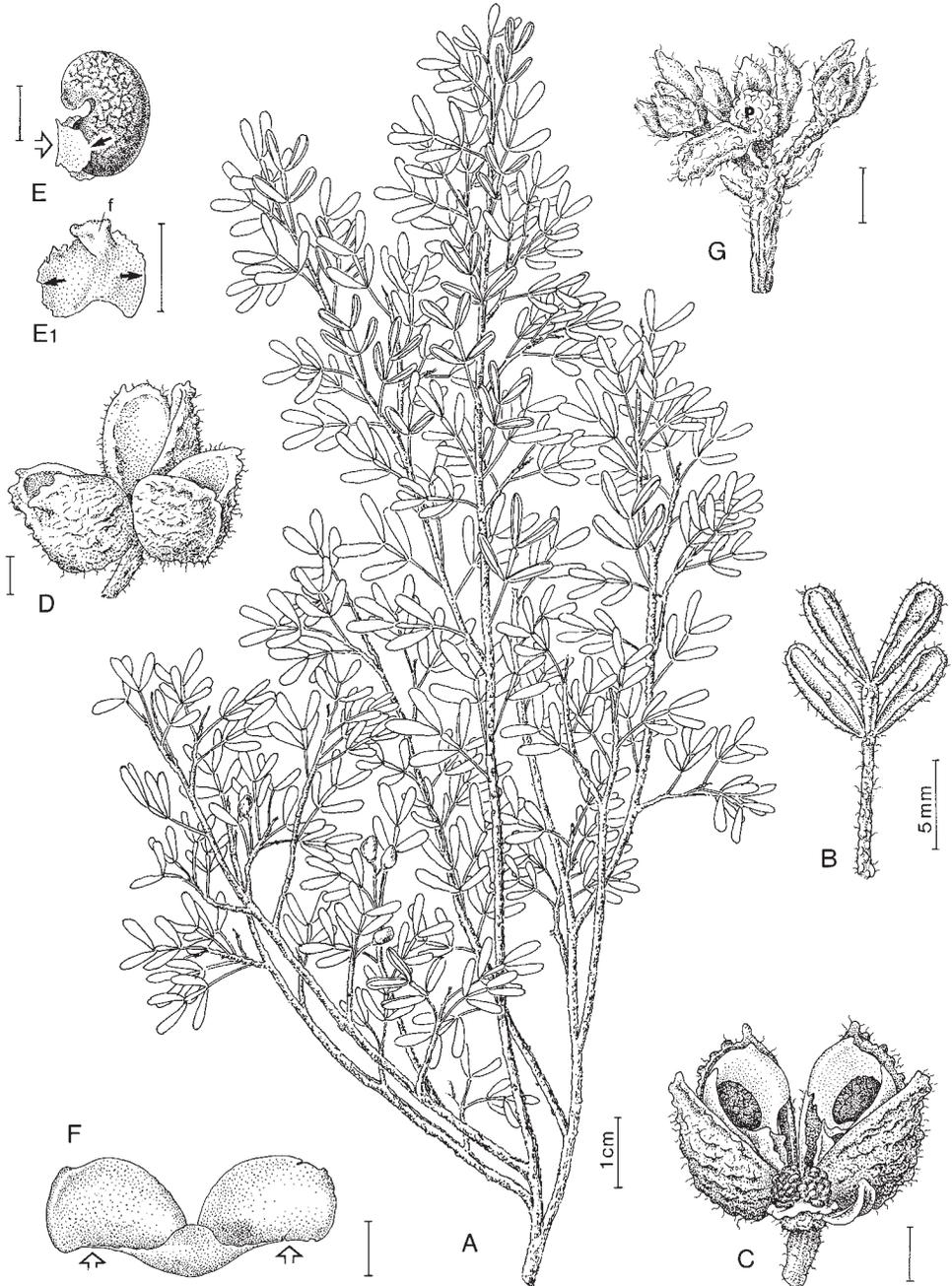


Fig. 1. *Plethadenia granulata* – A: habit; B: leaf (abaxial view); C: fruit with two ripe and two abortive follicles, sepals partly removed; D: remaining exocarpic cases of a fruit of three ripe fruitlets; E: seed (lateral view) with remaining placental endocarp; E1: placental endocarp and placenta or placental bundle (or funicle?), abaxial view; F: endocarp after outshooting (adaxial view); G: inflorescence with flower buds, each with sepals of different size, apical flower bud opened. – A-F: *Beurton & Mory* 975 (B), G: *Zanoni & Pimentel* 40402 (NY); f = funicle?, p = petals in bud, further explanations see text; bars without given size = 1 mm

1. *Plethadenia granulata* (Krug & Urb.) Urb., Symb. Antill. 7: 238. 1912 \equiv *Fagara granulata* Krug & Urb. in Bot. Jahrb. Syst. 21: 594. 1896 \equiv *Zanthoxylum granulatum* (Krug & Urb.) P. Wilson in Bull. Torrey Bot. Club 37: 86. 1910. – Lectotype (designated here): Santo Domingo, [1819 or 1820], Bertero (NY! [leaf fragments and a pencil drawing probably from the destroyed Berlin(B)-type]; isolectotype: P! [leaf fragments]). – Fig. 1, 4A-E.

Note: According to the protologue *Plethadenia granulata* was collected “in Sto. Domingo, in montibus aridis prope Biazomar”. This location is not traceable.

Much-branched shrub, 1-2 m high; branchlets, inflorescences and leaves mostly densely minutely pubescent of simple trichomes, probably with a tendency to stellate biangulate trichomes (Fig. 4E). *Leaves* alternate, subopposite to opposite, petiole 0.3-1 cm long, rachis 0.2-0.6(0.8) cm long, leaflets opposite or sometimes subopposite, 2-6(9), obovate or oblong, 0.5-1.0 \times 0.1-0.4 cm, margins often strikingly revolute, apex rounded or subtruncate, base oblique; leaflets hypostomatic (Fig. 4E), light green. *Peduncle* 0.6-1.4 cm long. *Sepals* elliptic to oblong, 1-2 mm long, differing in size (Fig. 1G, 4A, C), glandular-verrucose and somewhat fleshy. *Petals* in bud shorter than the sepals (and enclosed by them), strikingly glandular-verrucose (Fig. 1G, 4A). *Disc* undulate, flat (Fig. 4B). *Follicles* ribbed, 2.7-2.9 \times 2.0 \times 1.8 mm, light green when ripe (Fig. 1C-D). *Seeds* 2.0-2.3 \times 1.0-1.7 \times 0.8-1.4 mm, reniform, adaxial face concave, opaque black with irregularly reticulate shiny ribs (Fig. 1C, E).

Follicle dehiscence and seed release: The direction of dehiscence is from apex toward base. The exocarpic splitting is ventricidal and partly dorsicidal (toward the middle; Fig. 1D). The endocarpic dehiscence is ventricidal toward the middle, dorsicidal toward the base (Fig. 1C; the adaxially non-separated lower part is marked with a white arrow in Fig. 1E) and laterally along

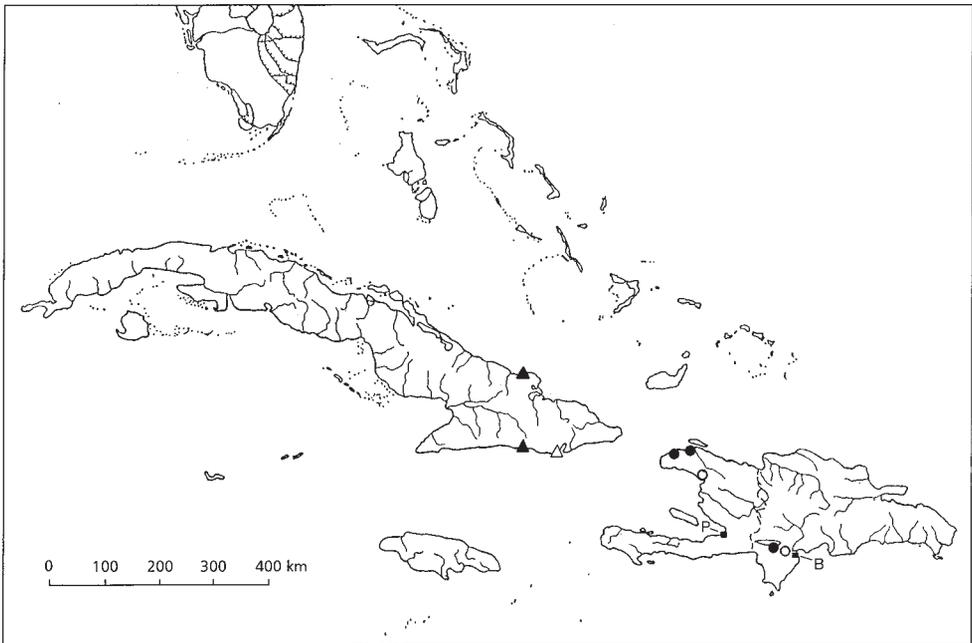


Fig. 2. Distribution of *Plethadenia cubensis* (▲, △) and *P. granulata* (●, ○). – Empty symbols: location not exactly known, B: Barahona, P: Port-au-Prince.

the border between an elastic horny part (the main part) and a smaller membranaceous part (dividing lines are marked with black arrows in Fig. 1E-E1 and white arrows in 1F). The elastic horny part of the endocarp remains undivided basally (Fig. 1F). The seed is ejected when the elastic horny part of the endocarp jumps out of the fruitlet and opens its free “valves” like wings (Fig. 1F). The exocarp cases still remain attached to the plant (Fig. 1D), and the small membranaceous organ remains for some time attached to the dispersed seed (Fig. 1E-E1, 4D). The nature of this organ, whether “placental endocarp” (term according to Wilson 1970, 1998) as I believe because it appears to be true endocarp or aril (Corner 1976, cf. Engler 1931: fig. 111H in case of *Zieria*) is still unclear. Seed ejection distance is unknown; the seeds are light-weight.

Plethadenia granulata occurs on coastal terraces in the northern mountain ranges of Haiti (from Mole St Nicolas to the vicinity of Cabaret and near Gonaives) and in the “foothills” of the Sierra de Bahoruco along the Valle de Neiba in the southwestern part of the Dominican Republic. According to Weyl (1966: 101), the whole area of the Hoyo de Enriqueillo (from Port-au-Prince to Barahona, Plaine de Cul-de-Sac in Haiti and Valle de Neiba in the Dominican Republic) was covered by the sea in the Pleistocene. Thus, the foothills of the Sierra de Bahoruco are coast terraces too (see Fig. 2).

Flowers were collected in February, March and August; ripe fruits and seeds were collected in March only.

Plethadenia granulata is a rather rare species and the statement by Liogier (1985: 349) “in Hispaniola alga frecuente” is questionable. Today the species is probably endangered through destruction of the vegetation by cutting wood for cooking (Haiti) and by rubbish discarding near the villages (e.g. near Puerto Escondido, Dominican Republic). Unfortunately the foothills of the Sierra de Bahoruco are not part of the Parque Nacional Sierra de Bahoruco (cf. Hoppe 1989).

Specimina alia visa: HAITI: DEPARTMENT NORD-QUEST: Vicinity of Cabaret, 1929, *Leonard & Leonard 11881* (NY); Mole St. Nicolas, 1985, *Zanoni, Mejía & Pimentel 33531* (NY). — DEPARTMENT ARTIBONITE: Near Gonaives, Coupe á Pintade [not located = La Coupe?], 1927, *Ekman H.9448* (K).

DOMINICAN REPUBLIC: PROVINCE INDEPENDENCIA: Foothills of the Sierra de Bahoruco, between Puerto Escondido and Duverge, *Humbert 27602* (P); *ibid.*, 1978, *Alain & Liogier 27469* (NY); *ibid.*, *Zanoni & Pimentel 26458* (JBSD); *ibid.*, 1987, *Zanoni & Pimentel 40402* (JBSD, NY); *ibid.*, 1992, *Zanoni & Garcia 47188* (JBSD); *ibid.*, 1998, *Beurton & Mory 975* (B). — PROVINCES INDEPENDENCIA/BARAHONA?: Ad Las Salinas, *Fuertes 819* (BM, K, NY).

2. *Plethadenia cubensis* Urb., Symb. Antill. 9: 177. 1924. — Type: Cuba, Santiago de Cuba, “near Aguadores”, 4.11.1917, *Ekman 8697* (S [n.v.], NY!).

Much-branched shrub, 1-2 m high; branchlets and inflorescences sparsely to densely minutely pubescent, leaf stalk, rachis and leaflets abaxially sparsely hairy, powdered or glabrous. *Leaves* opposite, subopposite to alternate, petiole 0.3-1.2(-2) cm long, rachis 0.3-1.8 cm long, leaflets opposite or subopposite at base and subopposite toward the apex, (2)6-10(11), oblong-cuneate, 0.5-1.2 × 0.1-0.4 cm, margins slightly to strikingly revolute, apex rounded or subtruncate, base oblique; leaflets hypostomatic (Fig. 3A-C, 4F). *Peduncle* 0.5-1.5 cm long. *Sepals* triangular-lanceolate, about 0.8 mm long, glabrous and with some glands. *Petals* c. 2.5 mm long, conspicuously glandular-verrucose (Fig. 3D). *Disc* short-cupulate, with an unequal sinuate margin (Fig. 3E). *Follicles* slightly ribbed, 4-4.2 × 2.5 × c. 2 mm (only the exocarp cases are known). *Seeds* unknown.

This rare species occurs in the E Cuban provinces Santiago de Cuba, Guantanamo and Holguin on terraces of the SE coast around the Bahía de Santiago de Cuba in the vicinity of Guantanamo, and also on the N coast E of Bahía de Naranjo (Fig. 2). The precise location in the “vicinity of

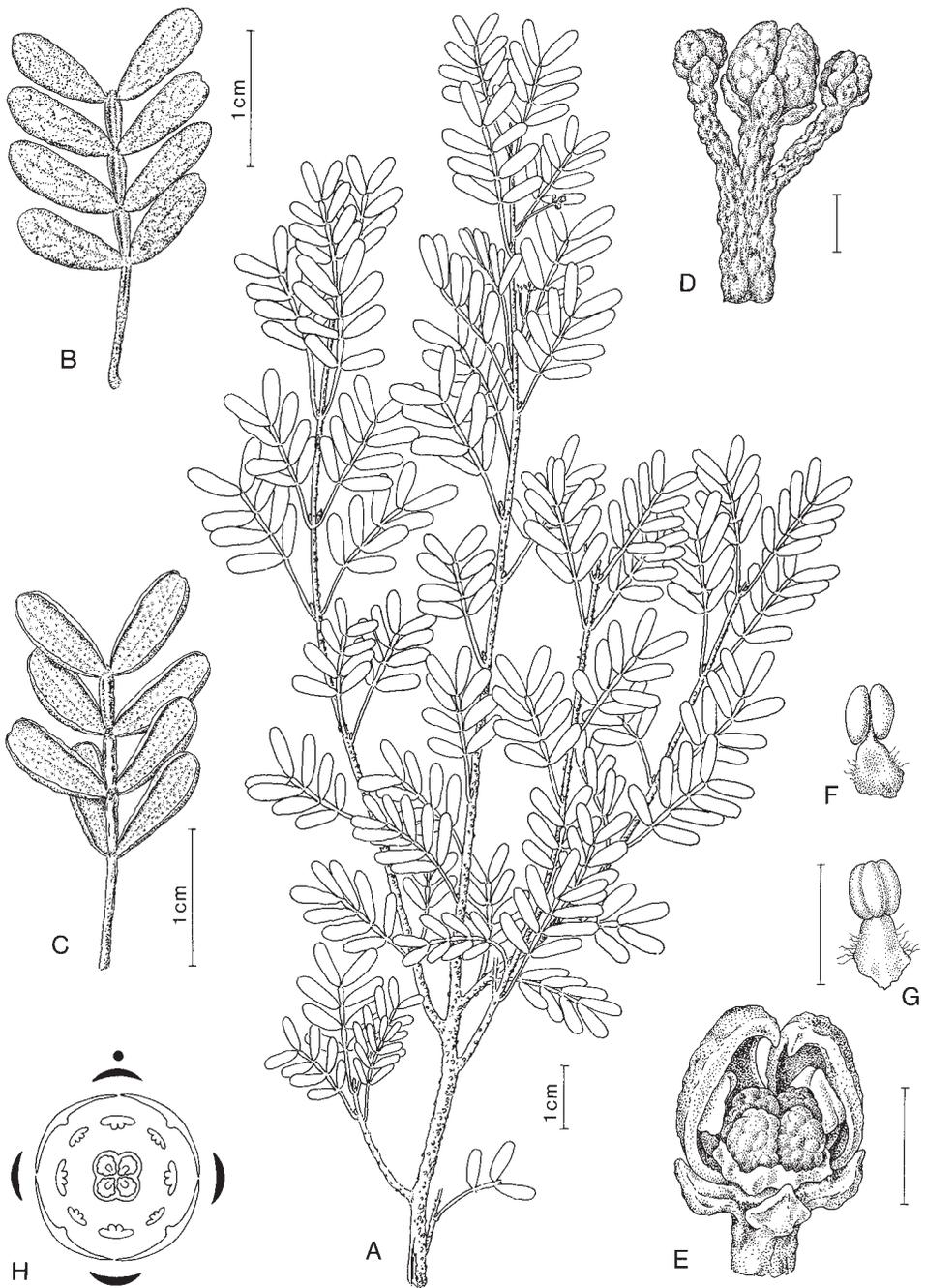


Fig. 3. *Plethadenia cubensis* – A: habit; B-C: leaf (B: adaxial view, C: abaxial view); D: inflorescence with three flower buds; E: opened flower bud with carpels, disc and two stamens (two petals and six stamens removed [base of filaments not visible], stigma complex breaks off); F-G: stamen (F: dorsal view, G: ventral view); H: empirical flower diagram. – All from *Lopez Figuerira 896* (HAJB); bars without given size = 1 mm.

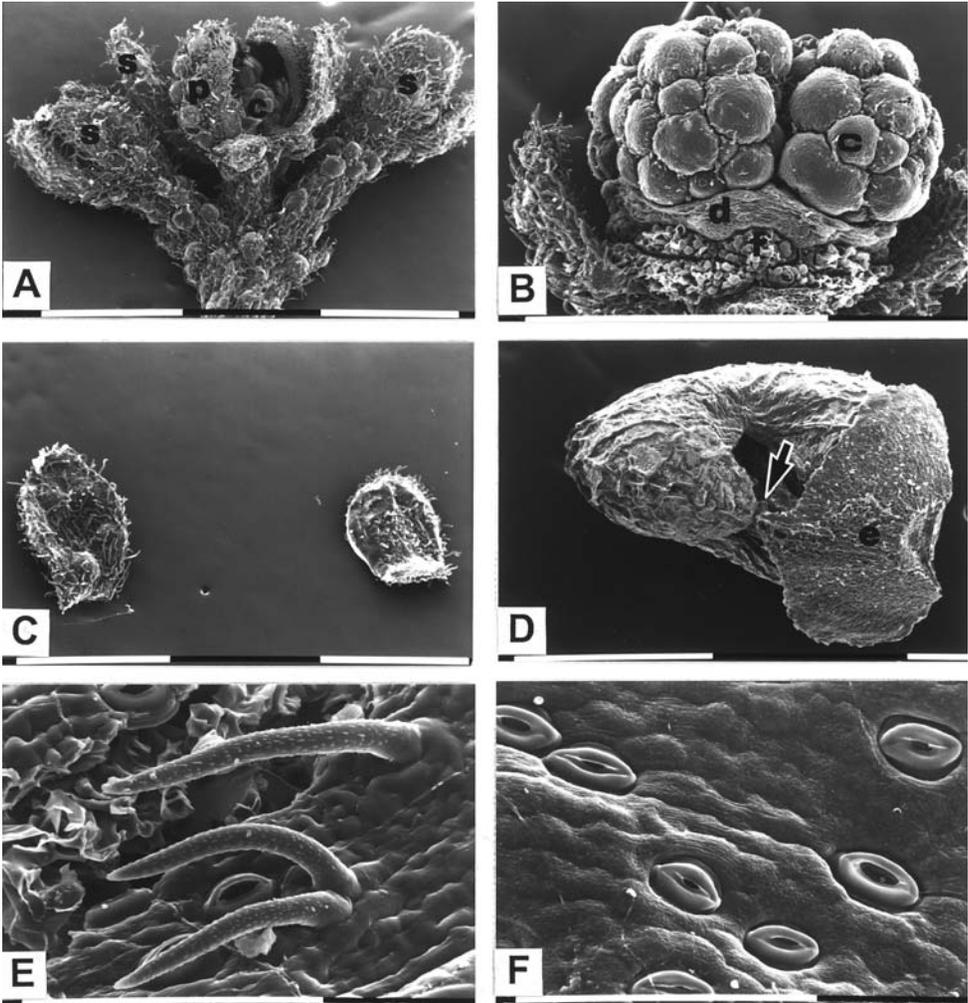


Fig. 4. *Plethadenia granulata* (A-E) and *P. cubensis* (F), SEM photographs – A: inflorescence with three flower buds, apical flower bud opened, sepals and petals partly removed; B: opened apical flower bud of A with carpels, disc, filament base of three of the eight stamens, petals base of two petals (sepals and petals mainly removed); C: two sepals of the flower bud of B; D: seed with remaining placental endocarp (e), and placenta or placental bundle (or funicle?), adaxial/lateral view; E-F: leaflet, abaxial view. – Bars: A-D = 1 mm, E-F = 0.1 mm; c = carpels, d = disc, f = base of filament, p = petal, s = sepal, e = placental endocarp, arrowed = funicle(?).

Guantanamo” is unknown. This year I traced in the herbarium of Pinar del Rio (HPPR) specimens collected for the first time in the Province Holguin in 1990.

Flowers were collected in February, March and November. Dehisced follicles (without endocarp and seeds) were collected in March. *P. cubensis* is endangered, especially in the vicinity of Santiago de Cuba.

Specimina alia visa: CUBA: S. loc., *Ramon de la Sagra* (P). — PROVINCE HOLGUIN: Estero Ciego, east of Bahía de Naranjo, 28.3.1990, *Verdecia Gongora & al.* (HPPR 6081). — PROVINCE SANTIAGO DE CUBA: Bahía de Santiago de Cuba, Club Punta Gorda, 1912, *Britton, Britton & Cowell*

12630 (NY, US); *ibid.*, 1953, *Lopez Figueira* 896 (HAJB); between Aguadores and El Morro, 1922, *Ekman* 15622 (BM); Playa de Aguadores, 1956, *Alain & Lopez Figueira* 4886 (HAJB). — PROVINCE GUANTÁNAMO: Vicinity of Guantánamo, 19.-31.3.1909, *Britton* 1993 (NY).

Conclusions and discussion

Plethadenia consists of two geographically vicarious species in E Cuba and Hispaniola (Haiti, Dominican Republic). The small shrubs grow on limestone in dry thorn scrub vegetation, in coastal thickets and dry forests. Flowers and fruits are extremely small. Ripe fruits and seeds were unknown until 1998, when a fruiting plant was found by the author in the Dominican Republic. The dehiscence of the follicles and the seed presentation are described. The seed is ejected by a catapult mechanism.

The genus fits into Engler's subfamily *Rutoideae* but not into any of his tribes (Engler 1896: 111ff, 1931: 213ff). It combines features of the pantropical *Rutoideae-Xanthoxyleae-Evodinae*, into which the genus was placed by Engler together with the genera of the Australian *Rutoideae-Boroniaceae*. These features are, e.g., the morphology of the disc, the number of ovules per ovary, the follicle dehiscence and the seed ejection. Relations between paleotropical, especially Australasian, and neotropical *Rutaceae* seem to be very close, indicating an old age of this family. Interestingly, the secondary metabolites and their biosynthesis (Da Silva & al. 1988: 125) support the suggestions made by Diels (1936) that the Australian *Boroniaceae* originated from "*Proto-Zanthoxyleae*". The present findings form an additional argument for a systematic revision of the *Rutaceae*, as demanded by Da Silva & al. (1988) and recently also by Chase & al. (1999).

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