A re-examination of Sanango racemosum. 1. Morphology and distribution.

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A re-examination of Sanango racemosum. 1. Morphology and distribution

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Summary

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The history of the genus Sanango and its classification are reviewed. A detailed description is given of its gross morphology, trichome and seed surface micromorphology. Data on germination, phenology and distribution in Ecuador and Peru are presented. The author concludes that characteristics of the inflorescence, trichomes, fruit morphology and seed surface anatomy as well as seed development are consistent with the inclusion of Sanango in the Gesneriaceae.

Introduction

The genus Sanango G. S. Bunting & J. A. Duke (1961) and its single original species, S. durum G. S. Bunting & J. A. Duke, were based on two collections of Woytkowski from Amazonian Peru and placed in the Loganiaceae, subfamily Buddlejoideae, because of their presumed relationship to Buddleja L., Nuxia Lam. and Peltanthera Benth. The authors mention the following attributes which indicated to them affinity to the Buddlejoideae: small trees, opposite leaves with a line connecting the leaf bases, sympetalous corolla with hippocrepiform dehiscence of anthers (as in Nuxia and Peltanthera), a disc around the ovary, septicidal capsules, and multicellular hairs.

In Engler (1964) the Buddlejoideae including Sanango are treated as a family of the Tubiflorae next to the Scrophulariaceae. Cronquist (1981) followed this arrangement and noted Sanango's scrophulariaceous tendencies in the irregular 5-lobed corolla with four functional stamens and a staminode. Rauschert (1982) proposed Gomaranthus Rauschert when he recognized that Gomara Ruiz & Pav. was a later homonym of Gomara Adans. Barringer (1983), unaware of Rauschert's publication, found that Sanango had previously been discovered and described by Ruiz & Pavón (1794: 63; 1798: 162) under the names of Gomara Ruiz & Pav. and G. racemosa Ruiz & Pav. respectively. They had placed Gomara in "Didynamia Angiosperma" among scrophulariaceous genera. Barringer (1983), following Cronquist, transferred Gomara to the Buddlejaceae. He recognized that the genus was unusual in the Buddlejaceae because of its 5-merous corolla, the presence of a staminode and the somewhat swollen base of the corolla tube. However he argued that the following traits spoke against placing Gomara in the Scrophulariaceae: thickened pilose filaments, glandular petiole base, enlarged style, and fusiform, smooth-coated seeds. Barringer (1986), upon being informed by Mabberley of Rauschert's publication, made the new combination S. racemosum (Ruiz & Pav.) Barringer. Complete synonymy is given in his paper.

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Fig. 1. Distribution of Sanango racemosum (black dots).

Recently Sanango has been found growing in Ecuador and material has become available so that a more detailed evaluation of its alliance might be made. The aim of this paper is to review the general morphology of Sanango, its distribution and phenology, and to give detailed information on its trichomes, seed coat anatomy, and germination pattern. Other papers in the present series examine floral and vegetative anatomy, and phytochemistry. The concluding paper evaluates all the evidence for a reclassification of Sanango.

Materials and methods

The study collection comprises specimens from the five largest U.S. herbaria and from QCA, Ecuador. Collections of this genus under the name *Sanango* are almost absent from European herbaria. No search was made under the name *Gomara*.

Trichomes from a leaf base and from the inner surface of the corolla of the specimen *Woytkowski 5925* (MO) were coated with gold palladium, examined, and photographed with an AMR 1000. Seeds for SEM from *Woytkowski 5619* (MO) were coated with gold and examined with a Zeiss Novascan 30 and photographed.

For further study of trichomes and inflorescences FAA preserved material of *Neill 9458* was examined under a dissecting microscope and a calibrated light microscope. Mature fruits with viable seeds of this collection were studied, and seeds were planted either in pots filled with fine-grained soil and kept moist inside a plastic sleeve, or scattered on moistened filter paper in petri dishes and potted upon germination. Germinated seedlings were observed over a year's period.

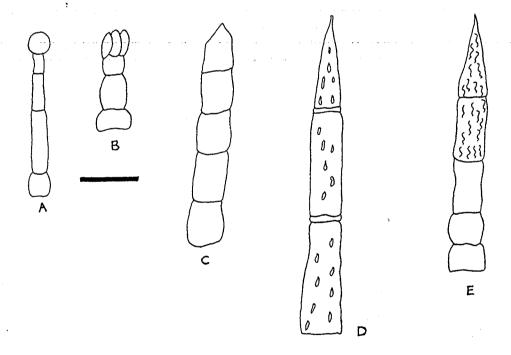


Fig. 2. Trichomes of Sanango. – A, from margin of cotyledon; B, from margin of corolla lobe; C, from base of calyx lobe; D, from tip of calyx lobe; E, from outside surface of corolla tube. – Scale bar = $50 \, \mu m$.

Results

General morphology. - Trees or shrubs 2-12 m high, with light brown to greyish bark with conspicuous linear lenticels. Young branches slightly puberulent. Leaves decussate, with an interpetiolar line; petiole 0.5-1 cm long. Blade elliptic or narrowly obovate, $10-28 \times 4.5-15$ cm, membranaceous when young, later subcoriaceous, glabrous above, strigulose below on the veins; lateral veins arcuate, conspicuous on the lower surface; apex shortly acuminate; base cuneate; margin denticulate in the distal part. Inflorescence terminal, thyrsoid, with 2-3 orders of branches, $5-20 \times 3-10$ cm; all branches and branchlets strigulose, opposite, subtended by bracts and prophylls respectively. Flowers in paired, bracteolate, secund cymes. Pedicels 1-2 mm long. Flowers 5-merous, slightly zygomorphic and gibbous. Calyx with conspicuous venation, puberulent; tube 0.8-1.4 mm long; lobes 1-1.8 mm long, ciliate at margin, becoming recurved around the mature fruit. Corolla white, subsalverform; tube curved, glandular outside, inside with glandular and warty hairs from the region of staminal insertion up to the mouth, 7-9 mm long; lobes imbricate in bud, subequal, $2-3.5 \times 2-2.5$ mm, rounded at the tip. Stamens inserted 3.5-4 mm above the corolla base; filaments pilose, curved inward, 2.5-3.5 mm long; anthers introse, $0.4\text{-}0.5 \times$ 0.5-0.8 mm, dehiscing by a curved confluent line. Staminode inserted 2.5 mm above the corolla base, 0.15 mm long. Pollen 3-colporate, sphaeroid to oblate-sphaeroid, $15-15.5 \times 12.5-16$ µm. Ovary semi-inferior, 2-celled, ellipsoid, 1-1.5 mm long, surrounded by a fleshy cup-shaped disc with 5 shallow lobes that is almost as high as the ovary. Style thick, 0.25-0.3 mm long; stigma peltate, bilobed, 0.6-0.75 mm long. Capsule bony, ovoid, glabrous, with conspicuous veins, $3-3.5 \times 1.7-2$ mm, dehiscing septicidally and loculicidally in mid regions but often remaining united at the apex. Seeds 0.6-0.8 × 0.12-0.2 mm, straight or sigmoid, wingless. (See Bunting & Duke, 1961: fig. 1.)

Ecology and distribution. — Rain forest, most often on limestone bluffs adjacent to a river. In the vicinity of Misahualli, Ecuador, and in similar habitats in northern and central Peru, at elevations of 300-750 m (Fig. 1). Flowering throughout the year but primarily from July to November.

Local names and usage. – Sanangu (Peru: Amazonas), Woytkowski; urcu chiri capsi = hill cold tree (Ecuador: Napo) Marles; Neill & Palacios. The latter collectors indicate that a leaf decoction is used as a bath before hunting.

Specimens examined. — Ecuador. Napo: Jatun Sacha, 4 Sep 1987, Ceron 2172 (MO); 8 km de Puerto Misahualli, margen derecha del Rio Napo, 8 Nov 1987, Ceron 2627 (MO, QCA); 24 Aug 1988, Ceron & Ceron 4530 (MO); Canton Tena, Ceron 7209 (MO); Rio Napo & Rio Huambuno junction, 8 Nov 1985, Marles EE106 (F, MO); Jatun Sacha, 21 Sep 1990, Neill 9458 (DLF, MO, US); 6 km rio abajo de Misahualli, 19 Nov 1985, Neill & Palacios 7017 (F); 3 km of entrance of Jatun Sacha, 30 Aug 1988, Palacios 2817 (MO); Via Payamino-Loreto, 4-6 km del rio, 12 Sep 1986, Zaruma 731 (MO). Peru. Amazonas: Quebrada Huampami, Rio Cenepa, Kayap 219 (MO); mouth of Rio Santiago on highland, Tessman 4045 (NY);

Fig. 3. Trichomes of Sanango. – A, B, on inner surface of corolla tube; C. on adaxial surface of leaf base.

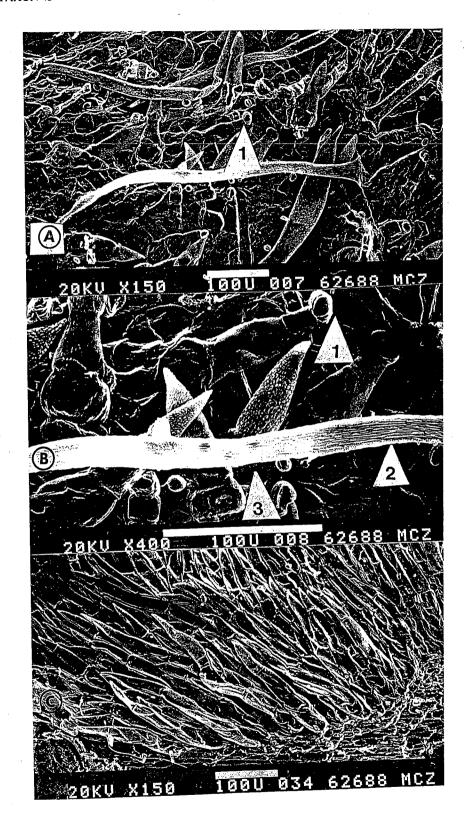
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Aramango, S of Názaret, 2 Apr 1960, Woytkowski 5619 (holotype of Sanango durum, MO; isotypes: US, K); left bank Rio Marañon, opposite Quebrada Mirana, above Cascadas de Mayasi, 16 Sep 1962, Wurdack 2018 (US). Huanuco: Tingo Maria, 3 Aug 1964, Dwyer 6228 (MO); Pozuzo, 17 Sep 1784, Ruiz & Pavón s.n. (holotype of Gomara racemosa, MA (n.v.), fragment F; photo F; isotype B†; photo F, GH); Rupa Rupa, Jacintillo left bank of Rio Monzón, 13 Jul 1978, Schunke 10354 (MO). Junín: Rio Paucartambo Valley near Perene Bridge, 19 June 1929, Killip & Smith 25254 (F, US); between Santa Rosa and Nieriatinami, Pichis trail, Jun 28 - Jul 28, 1929, Killip & Smith 26206 (NY, US); Satipo, Aug 1960, Woytkowski 5925 (MO). San Martín: km 28, Tarapoto-Yurimaguas road, trail to W of road, 17 Aug 1986, Knapp 8039 (F); mouth of Rio Chote, left bank of Rio Huallaga, 29 Jun 1970, Schunke 4076 (F).

Indumentum. – Two basic types of hairs develop, both are uniseriate, one is glandular and the other is not. The glandular trichomes are always multicellular while the non-glandular form may be either unicellular or multicellular. The indumentum on floral parts is much more varied than that on leaves and young stems.

Type 1, glandular hairs: Most commonly the stalk consists of three cells and the head has one to four cells. Trichome length ranges from 55 to 120 μm. Trichomes with a globose unicellular head are characteristic of margins of cotyledons, young leaves, and stems of seedlings (Fig. 2A); these heads are delicate, breaking off readily from the stalk. Glandular hairs are also distributed on both surfaces of the corolla. Those on the outer surface of the corolla tube have a bulbous base with two short stalk cells and an opaque head (Bunting & Duke, 1961: t. 4E). A similar type but with a three- to four-celled head may be found on margins of the corolla lobes (Fig. 2B). The inner surface of the corolla has trichomes with a longer stalk of three cells and a multicellular head (Fig. 3A1, 3B1).

Type 2, non-glandular hairs: There are six subtypes of non-glandular trichomes in Sanango. Two are unicellular and can be found inside the flower: smooth-walled unicellular trichomes 150-225 µm long are found on the filaments (Dickison, 1994, fig. 1E); unicellular hairs with striate walls, numerous and very long (0.2-0.6 mm), line the corolla tube from the insertion of the stamens to the mouth of the corolla (Fig. 3B2). The hairs on leaves, young stems, and branches of the inflorescence are three to six cells long (0.4-1.2 mm), with a pointed tip and an inflated base. As the leaves mature, these trichomes decrease in number but can still be abundant on the adaxial surface at the base of the petiole (Fig. 3C; Bunting & Duke, 1961: t. 4A). The most common hairs on the calyx are also three to six cells long but more rounded at the tip and shorter, 40-140 μm long, without an inflated base (Fig. 2C). Similar but 250 µm long hairs, with up to seven cells, are found on the inner surface of the corolla lobes. Near the tip of the calyx lobes more pointed hairs of three to four cells, 250-300 µm long, with verrucose walls are found (Fig. 2D). Finally are 2-5 celled, 50-150 µm long hairs that incorporate several features of other multicellular trichomes, having an inflated base and the apical one or two cells with warty protrusions on their walls, may be found on both the outer and inner surfaces of the corolla tube and on the calyx lobes. (Fig. 2E, 3B3).

Seeds. – Although there are 300-350 ovules per ovary (two counts) each mature fruit contains less than a hundred seeds (three counts). Seeds are minute and orange. The micropylar end can be recognized by its somewhat bulbous shape, while the

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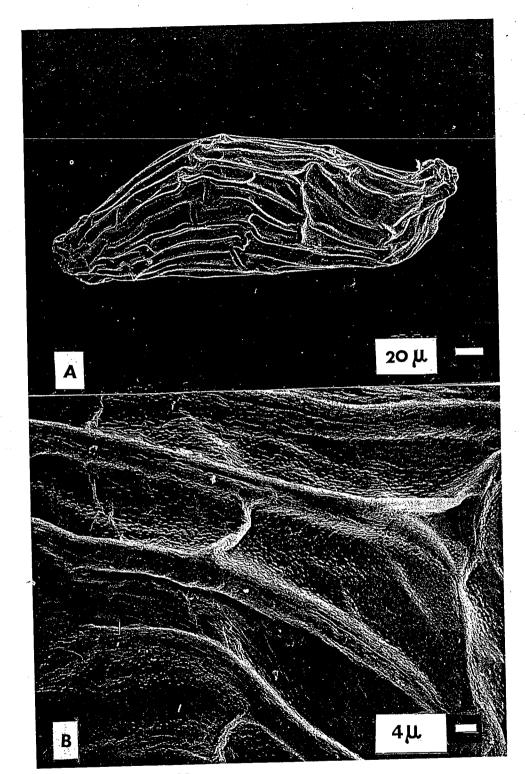


Fig. 4. A, B, seed surface of Sanango.

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chalazal end is rather pointed (Fig. 4A). Using the terminology of Beaufort-Murphy (1983), the seeds of Sanango are narrowly elliptic, constricted. Surface seed coat cells are lineate-polygonate with a slight spiral orientation. The individual cells have salient edges with discrete crests, and depressed papillate faces (Fig. 4B). When a hand section is made through seeds the abundant white endosperm is visible around the straight embryo. The embryo is 0.4-0.5 mm long, with the radicle slightly longer than the two equal cotyledons. It takes approximately three weeks for the seed to germinate when placed on moistened filter paper. When the seedling emerges from the testa, a dense halo of hairs, has already developed approximately 0.2-0.3 mm above the base. Within a week or two one or more roots form endogenously and project through the hypocotyl tissue, 0.4-0.5 mm from the base of the young plant. The cotyledons are 0.6×0.4 mm at this early stage. The plants grow very slowly. After one year they are only 6 cm high, with six pairs of leaves.

Discussion and conclusions

As monographer of New World *Buddlejaceae* the author has never thought *Sanango* was closely allied to *Buddleja* and its relatives (Norman, 1982). The main reasons for questioning its position in the *Buddlejaceae* were: (1) secund 2-flowered cymes; (2) 5-merous flowers with four functional stamens and a staminode; (3) a conspicuous fleshy cup-shaped disc surrounding the ovary; (4) bony septicidal capsules with additional dehiscence in the mid region of the locules; (5) absence of stellate trichomes; (6) ecological niche in rain forest. Some of these points will be discussed in more detail below.

The thyrsoid paniculate inflorescence with twin flowered bracteate cymes found in Sanango is widespread in the Gesneriaceae and is also present in several genera of Scrophulariaceae (Wiehler, 1983) but is absent from the Buddlejaceae. The inflorescence in this family is also thyrsoid but the flowers are in compound dichasial cymes, usually congested into heads of various sizes.

Bunting & Duke (1961) refer to the annular disc around the ovary of Sanango and some members of the Buddlejoideae such as Nuxia and Peltanthera. The alleged disc in Nuxia is the remnant of the corolla base which abscises regularly, leaving a 5-lobed ring around the ovary (Leeuwenberg, 1975). In Peltanthera, there is a low disc, approximately 0.5 mm high and much shallower than the ovary. The conspicuous five-lobed sinuate disc of the Gesnerieae (Skog, 1976) is similar to that found in Sanango.

The bony capsular fruit of *Sanango* is surrounded by reflexed sepal lobes. The dehiscence along the septum and the mid-vein of the locules results in two large oval windows. This type of dehiscence, in which the style often remains coherent during fruit maturation, is not uncommon in the *Gesneriaceae* (Ivanina, 1967; Wiehler, pers. comm.). In the *Buddlejaceae* the capsules also dehisce both septicidally and loculicidally, but by four apical valves when mature. The *Scrophulariaceae* typically have septicidal capsules.

The seeds of Sanango are extremely small, narrowly elliptic, with elongated seed coat cells and salient radial walls (Fig. 4A). The tangential walls have minute papillae (Fig. 4B). Dust seeds are the rule in the Scrophulariales but there is considerable variation in such micro characters as presence or absence of wings, or size, shape and thickenings of the outermost cells of the seed coat. Seeds approaching the shape and

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ated seed ute papilisiderable shape and hape and surface characters of Sanango are found in the African genus Nuxia and a very few species of Buddleja from southeastern Brazil (Norman, unpublished). However, the seeds in these two genera are twice as large as those in Sanango, lack an orange coloration, and their surface cells have smooth faces. The similarities in size and surface features of the seeds of Sanango and several species of Rhytidophyllum Mart. (Skog, 1976; Beaufort-Murphy, 1983) are unmistakable. A highly magnified SEM photograph of seed coat cells of R. auriculatum Hook. reveals the same sunken face of the tangential walls, with papillate projections.

The unusual presence of hairs so close to the seedling base has not been observed in *Buddleja*. Fritsch (1904) describes and illustrates this phenomenon in seedlings of *Streptocarpus* Lindl. Weber (1978) also notes the presence of a ring of hairs at the base of the hypocotyl in germinating seeds of *Rhynchoglossum gardneri* W. L. Theob. & Grupe. In that species adventitious roots form at the base of the hypocotyl

rather than at a short distance above it, as in Sanango.

The non-glandular and glandular hairs found in Sanango are commonly found in the Scrophulariales (Hummel & Staesche, 1962), whereas the non-glandular trichomes in the Buddlejaceae are typically stellate (Norman, 1967) and are unlike any found in Sanango. The non-glandular hairs in Peltanthera, another genus which Bunting & Duke (1961) compared to Sanango, has branched multicellular hairs (Hunziker & Di Fulvio, 1957), an unusual feature for the Buddlejaceae also absent in Sanango. The long unicellular hairs which line the corolla tube of Sanango have slight protuberances arranged in linear rows (Fig. 3B2). Similar hairs may be found on the inner corolla surface of Buddleja but here the wall thickenings are short and spirally arranged (Norman, unpublished). Members of the Scrophulariaceae commonly possess unicellular hairs with sculptured walls on the inside of the corolla (Raman, 1987). Long unicellular hairs are uncommon in the Gesneriaceae (Wiehler, pers. comm.). The glandular hairs, both short- and long-stalked, found in Sanango, are very similar to those in the Buddlejaceae. The range of indumentum type in Sanango corresponds well with the descriptions and illustrations for the family Gesneriaceae (Wiehler, 1983), tribe Gesnerieae (Skog, 1976). However, it must be said that there is no diagnostic trichome found in Sanango and otherwise unique to the Gesneriaceae.

The results of these morphological observations support the view that *Sanango* belongs to the *Gesneriaceae*. The characters which were thought to tie *Sanango* to the *Buddlejaceae* (woodiness, opposite leaves with interpetiolar line, septicidal capsule) are of a superficial nature and are found in the *Gesneriaceae* as well.

Acknowledgements

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