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A study of Bellonia L. (Gesneriaceae).

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KEYWORDS:

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A STUDY OF BELLONIA L. (GESNERIACEAE)

Xu Zhaoran L. E. Skog*

ABSTRACT

This paper discussed the taxonomy of *Bellonia* of Gesneriaceae. According to the development and the morphological characters of the inflorescences, it is evidently that the single flowered *Bellonia spinosa* Swartz is differed from *B. aspera* Linn., and suggested to retain *B. spinosa* Swartz as an independent species, and supposed that the single flowered species is an offspring of the cymed ones.

Keywords: *Bellonia*, *B. aspera*, *B. spinosa*

INTRODUCTION

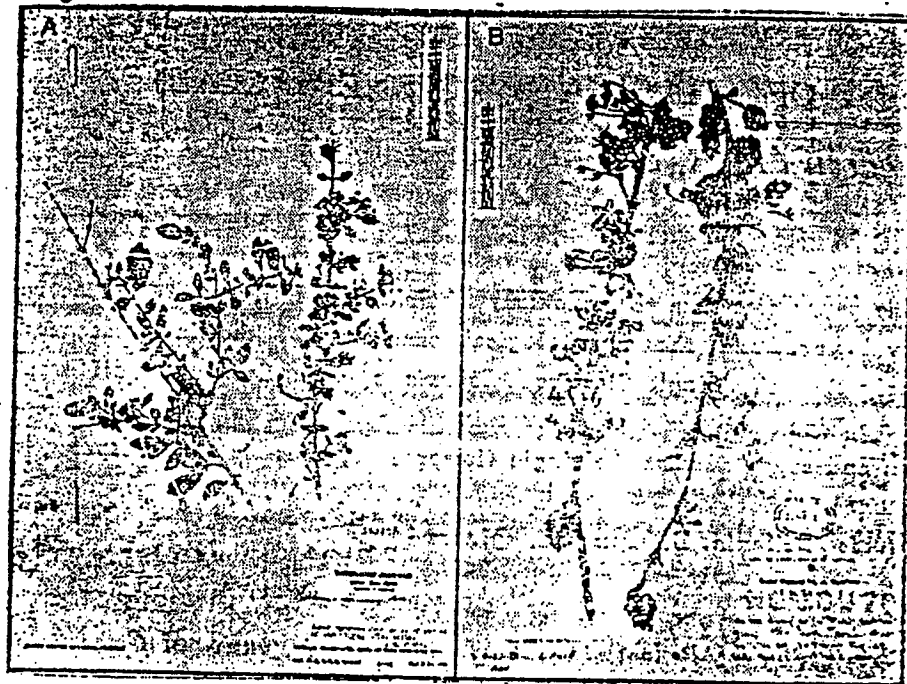
This study of *Bellonia* L., a West Indian genus of Gesneriaceae, is based mainly on the herbarium material available. In addition, SEM (scanning electron microscope) techniques were used to study the morphology of the seeds and pollen grains.

Bellonia was first described and illustrated by Plumier (1703)⁽¹⁾, a French missionary, explorer and botanist, as "*Bellonia frutescens, folio melissae aspero*". The genus name commemorates the French naturalist and traveler Pierre Belon (1517-1564) (Everett, 1981)⁽²⁾. The binomial name "*Bellonia aspera*" was adopted by Linnaeus (1753)⁽³⁾ in "Species Plantarum" based on plumier's epithet. Swartz (1788)⁽⁴⁾ published a second species in this genus, *B. spinosa*. Since Swartz, however, the genus has remained with 2 species (pl. 1).

Bellonia L. is unique in the Gesneriaceae, remote from other genera in morphology, by lacking a conspicuous corolla tube (or rather, the tube is extremely short), and by being the only member of the family with spines. This genus is also distinctive in its anatomy. The ovary is half inferior, with no apparent disk, and the vascular plan of the flower is quite different from any other taxon with an inferior or partly inferior ovary in this family. According to Wilson (1974)⁽⁵⁾, five of the

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pl. 1 Specimen photo

A: *Bellonia spinosa* Sw. (Howard & Howard 8904 (US));

B: *Bellonia aspera* L. (Ekman 2374 (US)).

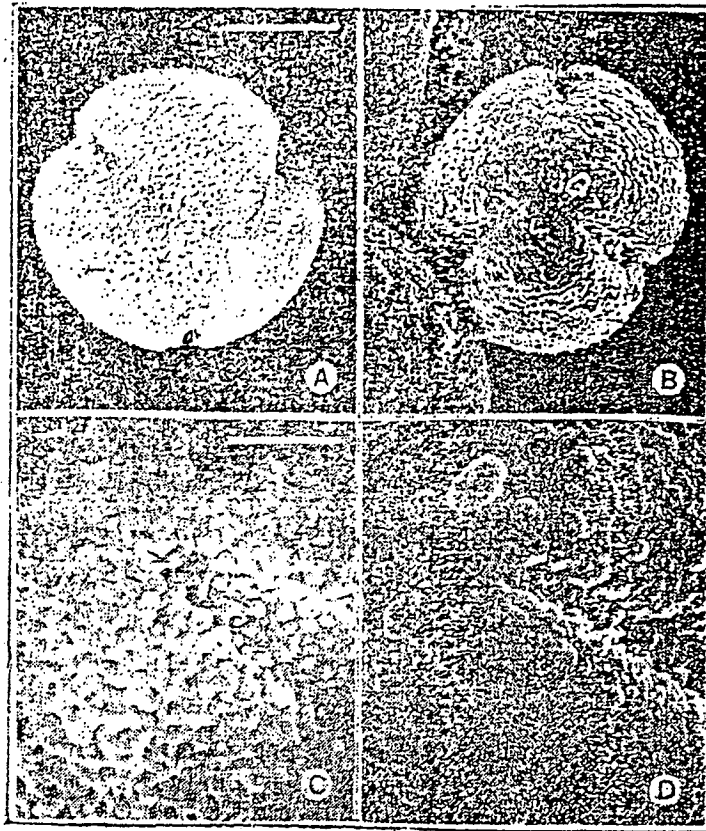
10 bundles of floral vascular tissue that emerge from the central cylinder are sepal medians and five are petal-sepal lateral traces. The stamen traces emerge at a higher level, in the same radius as the sepal medians. Characteristically, the stamen traces arise independently, and are not adnate to the sepal medians. Wall bundles are conspicuous.

The number of fertile stamens is also unusual in *Bellonia*. *B. spinosa* normally has 5 fertile stamens, but some flowers do exist with 6 fertile stamens. In *B. aspera*, 6 fertile-stamened flowers are normally seen, and in the literature an 8 fertile-stamened flower has been recorded (Candolle 1873)⁽⁶⁾. This high stamen number is very unusual in *Gesneriaceae* for plants in this family usually have either 2 or 4 fertile stamens. However, the fruits show a characteristic of the *Gesneriaceae* subfamily *Gesnerioideae*, that of a unilocular bicarpellate ovary.

There is no doubt that *Bellonia* is closely related to both *Phinaea* Bentham and *Niphaea* Lindley which also have very short corolla tubes and rotate limbs. Fritsch (1894)⁽⁷⁾ placed the three genera together in the Tribe *Bellonieae* which included two others, *Monopyle* Moritz ex

Bentham and *Anodiscus* Bentham. Recently Wiehler (1983)⁽⁸⁾ combined these five with others in a much larger tribe, *Gloxinieae* Fritsch. However, according to Beaufort-Murphy (1983)⁽⁹⁾, the seed morphology supports Fritsch's tribal concept.

Since Swartz (1788)⁽⁴⁾, the status of the two species of *Bellonia* L. has been unquestioned until Lourteig (1983)⁽¹⁰⁾ who combined the two species into one. At first glance, however, the two species would appear to be only variations of a single species for the spiny habit appears to have intermediate forms (see Discussion after *B. aspera*). But when compared carefully with the earliest published illustration of the habit (Plumier in J. Burman ed. 1756), two species are clearly recognizable. The true "*B. aspera*" of Plumier has both terminal and axillary cymose inflorescences, without spines, while *B. spinosa* has single



pl. 2 Pollen grain SEM micrograph

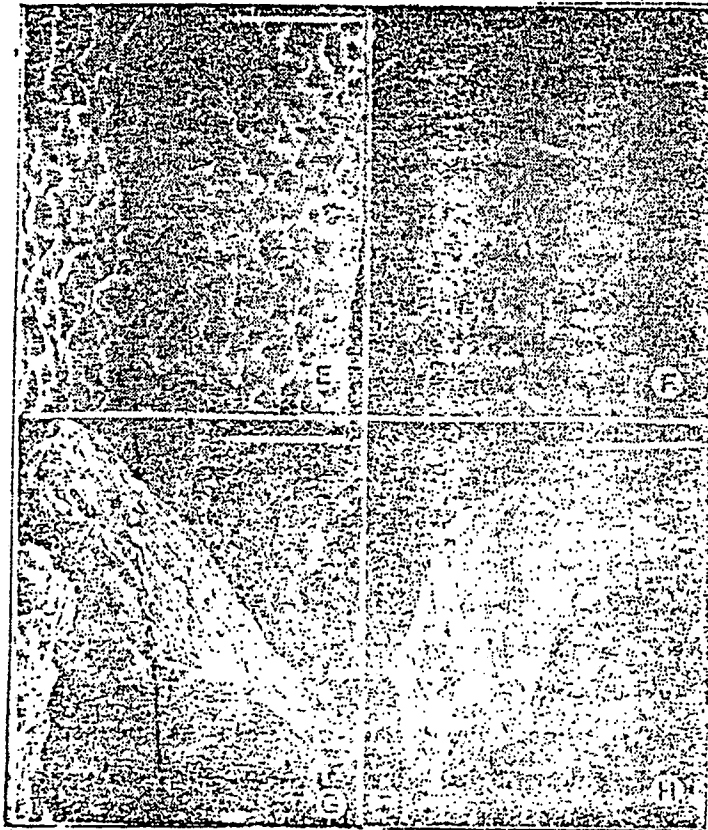
A, C: *B. aspera* L., (Skog & Hodapp 5454 (US)). B, D: *B. spinosa* Sw. (Valeur 852 (US)); A, B: polar view ($\times 8.0$ k, scale=3.8 μ m); C, D: colpate view ($\times 20.0$ k, scale=1.5 μ m).

axillary flowers, and is obviously spiny. Lourteig (1983)⁽¹⁰⁾ considered the drawing of Plumier (in J. Burman ed. 1756) to represent plants influenced by the humid environment from which they were collected. This may or may not be true. Although Plumier left no type specimen for us to examine, we do find out that the specimens of *Ekman* 2374 typically agree with the habit of the Plumier drawing (in J. Burman ed. 1756). They were collected from a limestone habitat, but which does not indicate a humid environment. The leaves of the specimen are coriaceous, which often results from water stress. Also, it is unreasonable to explain the non-spiny habit as the result of a humid environment (see discussion below).

As in other *Gesneriaceae*, the pollen morphology of this genus has little obvious value in correlation with the plant's habit. The exine of the grain is rugulose in both species, but the tectum of *B. spinosa* is somewhat smoother on the surface than that of *B. aspera* (pl. 2, 3). As we do not have mature seeds of *B. aspera*, we cannot compare the seed morphology of these two species (pl. 3).

The presumed evolution of the morphology in these two species is remarkable. It is likely that the cymose inflorescence is the more primitive, and the single-flowered inflorescence is the derived form, reduced and simplified from the cyme by the shortening of the peduncle and the reducing of the flower number in the cyme. In addition, some single-flowered inflorescences degenerate to a spine. Evidence of the reduction can still be seen in the morphology of the two species. In *B. aspera*, cymes on the same plant have flowers from 4 to only 2, or even rarely, single flowers. In the single-flowered "cyme", 2 small bracts persist on the peduncle, demonstrating that the single-flowered "cyme" resulted from the reduction of a true cyme of two or more flowers. In *B. spinosa*, the single-flowered inflorescence has no bracts on the peduncle, evidence that the peduncle has been reduced to only the base, or rather, the peduncle has disappeared, and the so-called "inflorescence" is composed of only the flower and its pedicel. Thus, the single-flowered inflorescence in *B. aspera* is obviously different from that in *B. spinosa*.

It appears that the spines are the result of degeneration of the inflorescence. The axillary single-flowered inflorescence and the axillary spines (of the same length) are normally found on the same plant. On one branch, the fertile structures (inflorescences) are on the upper part, and the sterile (spines) on the lower. Sometimes, an inflo-



pl. 3 SEM micrographs

E, F: tectum surface of pollen grain. E: *B. aspera* L. (Chao & Hodapp 5454 (US)); F: *B. spinosa* SW. (Vickrey 852 (US)).

G, H: seed morphology. G: *B. aspera* L. (Ehman 2374 (US), immature seed, $\times 1.5k$, scale=30 μ m); H: *B. spinosa* SW. (Jimenez & Liogier 5730 (US), mature seed, $\times 220$, scale=100 μ m).

rescence is opposite to a spine at the same node and both are axillary. The reason for an inflorescence degenerating to a spine is unknown at present, but it seems possible that the reduction of the flower number may be a way to reduce the nutritional expense, and so allowing the plant to better survive environmental stress. Many plants of *Bellonia* grow on exposed coastal or roadside cliffs. Water and nutritional stress may therefore be limiting to these plants' production of flowers.

The usual provenance of *B. aspera* is exposed limestone rock. This means the more primitive species *B. aspera* (and probably the ancestral genus) may have originated in a limestone flora. Its descendant, *B. spinosa*, seems to have escaped from the strict limestone habitat and

become distributed in a much broader area that includes both limestone and non-limestone substrates. The latter species appears to be more adaptive than its apparent ancestor. The adaptive advantage may be partly due to the reduction of the flower number (from a cyme to a single-flowered inflorescence and further, to a spine).

One might expect that the limestone environment, because of its normally dry conditions, often results in more spiny plants. Contrary to this supposition, the spiny species of this genus, *B. spinosa*, is not common on limestone, but rather it is the spineless *B. aspera* that is exclusive to the limestone substrate. At least in this genus, it is evident that the spiny morphology has little relationship with the limestone substrate, and the limestone substrate may not necessarily mean a dry environment. It is possible that here the phylogeny of species is more important in the development of its morphology.

Bellonia aspera is possibly endangered. Until now, nearly 300 years since the first published report of this species (Plumier 1703), only a few specimens are known. Although, on a specimen collected by Ekman (2374), the only typical specimen available at present, was written: "Common along River Bras Gauche, on limestone", it has not been found or recorded from other places. This might suggest that the primitive species is generally less adaptive and so has a narrower distribution than the more advanced species, *B. spinosa*.

TAXONOMY

Bellonia L., Gen. Pl. 50. 1737, ed. 5 1754, Sp. Pl. 1: 172. 1753; Alain in Leon & Alain, Fl. Cuba 4: 451. 1957; A. DC in DC, Prodr. 17: 290. 1873; Fritsch in Engl. & Plantl, Nat. Pflanzenfam. 4 (3b): 172. 1894; J. Hanst., Linnaea 34: 255, 429-430. 1865; Lam., Encycl. 1: 397. 1783; Plum. in J. Burman (ed.), Pl. Amer. 35, pl. 47. 1756; Sw., Prodr. 42. 1788; Sw., Fl. Ind. Occid. 1: 382. 1798; Urb., Symb. Antill. 2: 367. 1901, 8: 645. 1921.

Type species: *B. aspera* L.

Shrubs, sturdy, spiny or not (in *B. aspera*). Leaves opposite, sessile to shortly petiolate; petioles sessile to 0.2 cm long; blades small, coriaceous and hirsute. Inflorescences axillary, cymose with 1 or 2 to 4 flowers. Flowers subactinomorphic, with an inconspicuous floral tube; calyx campanulate, with 5(-8) calyx lobes, calyx lobes as long as floral tube, triangular, lanceolate or linear; corolla broadly campanulate.

with a very short tube, limb rotate, of 5(-8) spreading lobes, obtuse, entire, membranaceous; stamens 5(-8) adnate to the base of the corolla tube, all fertile, erect and tightly pressed against each other but not coherent, filaments short, anthers ellipsoid, apically apertured; pollen grains rugulose on the exine; disk absent; ovary semi-inferior, with one locule and 2 parietal placentae, ovules many, style linear, longer than the stamens, stigma not conspicuously enlarged. Fruit a 2-valved dry capsule, surrounded by the persistent calyx, subellipsoid, with a curved beak at the apex; seeds numerous. Chromosome number $n=13$.

2 species distributed in the Caribbean Islands fo Cuba and Hispaniola, usually growing on limestone substrate (fig. 1).

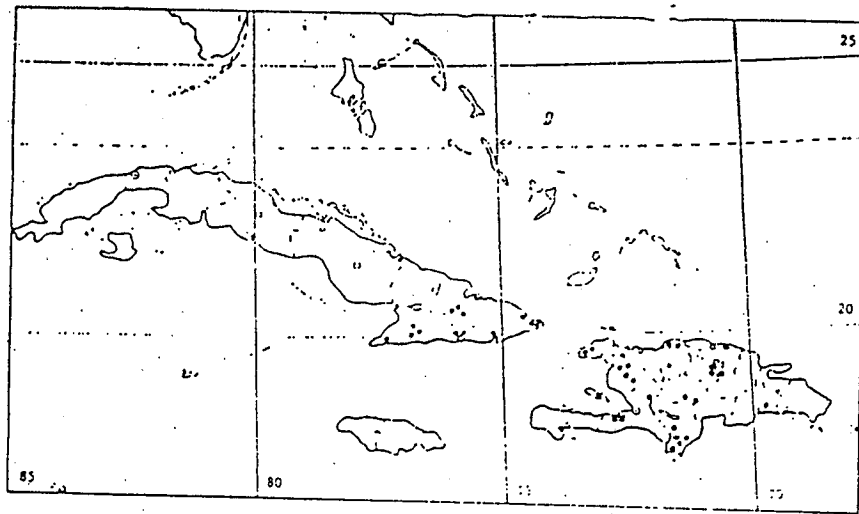


fig. 1 Distribution of *Bellonia* L. *B. aspera* L. *B. spinosa* Sw.

KEY TO THE SPECIES

- a. Plants non-spiny (for exceptions see Discussion after *B. aspera*); inflorescences cymose of 2-4 flowers, terminal or axillary; corolla tube ca. 4 mm long, limb ca. 3 cm across; pollen grains with rough tectum. Haiti 1. *B. aspera* L.
- a. Plants spiny; inflorescences single-flowered, axillary; corolla tube ca. 2 mm long; limb 1-2 cm across; pollen grains with smoother tectum. Cuba, Dominican Republic, and Haiti 2. *B. spinosa* Sw.
1. *B. aspera* L., Sp. Pl., ed. 1: 172. 1753; A: DC in DC, Prodr. 17: 290. 1873; J. Hanst., Linnaea 34: 255, 429. 1865; Lam., Encycl. 1: 397, pl.

149, 1783; Plum. in J. Burman (ed.), Pl. Amer. 35, pl. 47. 1756; Sw., Prodr. 42. 1788; Urb., Symb. Antill. 2: 367. 1901, 8: 646. 1921.

Type: Plumier, Nov. Pl. Amer. 19, pl. 31. 1703.

Erect shrubs, sturdy. Stem and mature branches grayish, young branches brown in dried specimens, minutely pubescent. Leaf blades ovate or elliptic, unequal in each pair, 1.2-2.8 x 0.6-2.0 cm, cuneate or subrounded at the base, obtuse at the apex, dentate, especially toward apex, pubescent below and scabrous above; secondary veins 4-6 pairs, with the midvein prominent below, and deeply immersed above. Inflorescences cymose and normally 2-4-flowered, sometimes reduced to a single flower, terminal or axillary, pubescent, peduncles 0.2-1.5 cm long with 2 linear bracts; pedicels 0.5-1.5 cm long. Flowers about 3 cm in diameter when fully open. Calyx of 6(-8) sepals, lobes sublinear, 6-7 x 1 mm, with multicellular pubescence. Corolla tube about 4 mm long, limb lobes 6(-8), suborbicular, broadly elliptic or ovate, ca. 1.0 x 0.8-1.0 cm, glabrous inside, minutely pubescent outside. Stamens 6(-8), anthers 3.2-4.0 x 1.2 mm, filaments 1.0 x 0.6 mm, glabrous. Ovary ca. 3-4 x 2.0-3.5 mm, with multicellular pubescence, style 1-5 x 0.3 mm, sparsely pubescent, stigma not enlarged, and indistinct from the style, with dense short pubescence. Capsule 4-valved, opening from the apex, valves ca. 0.4 mm thick, with a line of pubescence inside along the parietal margin. Seeds multifaced, mature seeds not seen. Chromosome number $n = 13$ (Oliver & Skog 1984).

ECOLOGY: Plants growing on limestone along river banks.

DISTRIBUTION: In southern Haiti, the specimen that agrees most closely with the Plumier drawings only recorded from Trouin, on the banks of a tributary of Riviere Gauche (fig. 1).

SPECIMENS EXAMINED: HAITI: Dept. du Sud: Trouin, 5 Nov 1924 (fl), Ekman 2374 (K, NY, US); Nov 1966 (fl), Taipey s. n. (E).

CULTIVATED: Originally collected by Taipey from Haiti, 23 Nov 1966 and grown at Cornell University, Ithaca, NY, S. I. Acc. no. 77-251. 14 May 1980 (fl), Skog & Hodapp 5451 (US), 29 Apr 1983 (fl), Skog & Linett 5563 (US).

DISCUSSION: When Linnaeus (1737) first described *Bellonia* and *B. aspera* (1753), he cited the publication of Plumier (1703). As the types of Plumier's American plants are his drawings (Stafleu & Cowan 1983), the description and illustration of Plumier (1703) may serve as the type for *Bellonia aspera* L. and so for *Bellonia* L. Because "Plumier 1703" has

only drawings of flower and fruit, and while "Plumier in J. Burman ed. 1756" has a drawing of the habit, we also take the latter publication into consideration for the specific concept of *B. aspera* L. (the plate in the Burman edition is cited in the second edition of Linnaeus' *Species Plantarum* 1762). The Plumier's drawings are related to the Surian collection for Surian accompanied Plumier to the West Indies in 1689-1690 and made the collections (Stafleu & Cowan 1986). Further work is needed to examine the Surian collection in (P) to determine if there is any Surian material that matches the Plumier type of *Bellonia*.

Several specimens that bore the name of *B. aspera* do not belong to this species but rather to *B. spinosa* when compared with the original publication of Plumier (1703), and with the Burman edition (1756). Only Ekman 2374 typically matches the original illustration. Skog & Linett 5563 and Skog & Hodapp 5451 are likely from the same source as Talpey s. n. (E). These latter three specimens have smaller leaves, inconspicuous spines, but have some untypical cymes with 2 flowers or so. They are now placed in this species according to the cyme morphology. The Talpey collection notes report that the location was in the area of Gauche, Grande and Gossline Rivers, on limestone rock which is near the locality of Ekman 2374, but the relationship between the Talpey collection and the Ekman collection needs further investigation in the field. Miller s. n. (US) collected in Haiti may be this species, but is too fragmentary to be positively identified.

2. *B. spinosa* Sw., Prodr. 42. 1788; Sw., Fl. Ind. Occid. 382. 1798; Alain in Leon & Alain (ed.), Fl. Cuba 4: 452. 1957; A. DC in DC, Prodr. 17: 290. 1873; Griseb., Fl. Wright. 2: 526. 1862; Griseb., Cat. Pl. Cub. 198. 1866; J. Hanst., Linnaea 34: 429. 1865; Poiret in Lam., Encycl. Suppl. 1: 610; Sauvalle, Fl. Cub. 92. 1873; Tussac, Fl. Antill. 197, pl. 30. 1808-13; Urb., Symb. Antill. 2: 367. 1901, 8: 645. 1921.

TYPE: Swartz s. n. (SBT, holotype; B-WILLD, BM, M, isotypes; photos from M and B-WILLD in US).

Shrubs, 0.5-2.0 m tall, spiny; branches brown or grayish, more or less pubescent; internodes 0.5-1.5 cm long; spines single and axillary, needlelike, pungent, 0.5-1.5 cm long. Leaf blades ovate or oblong, 0.5-2.5 x 0.5-1.5 cm, cuneate or suborbicular at the base, obtuse at the apex, sparsely and shallowly dentate on the margin, hirsute above, pubescent below, secondary veins 3-4 pairs, together with the midvein

immersed above, prominent below. Flowers usually single and axillary, rarely 2 or more congested in the same axil without a conspicuous peduncle; pedicels 1-1.5 cm long (or more), pubescent, without bracts. Calyx of 5(-6) sepals, lobes triangular or lanceolate, 2-4 x 1.0-1.5 mm, nearly patent, outside pubescent, inside glabrous; corolla 1-2 cm in diameter in open flower, tube about 2 mm long, lobes 5(-6), ovate, elliptic, or suborbicular, 5.5-8.0 x 4-5 mm, outside pubescent, inside glabrous. Stamens 5(-6), erect, glabrous, 2.5-5.5 x 0.7-1.5 cm, filaments adnate to the corolla tube for ca. 0.2 mm, 1.0-1.5 x 0.3-0.6 mm. Ovary 4 x 2 mm, the exposed part with glandular hairs; style 3.5-5.0 x 0.2-0.3 mm, very sparsely glandular-pilose; stigma slightly rugose. Capsule subellipsoid, 0.5-0.7 x 0.2-0.4 cm, curved at the apex and seemingly with a short beak. Seeds irregularly multifaced, elliptic (ca. 1:2.4), about 0.5 x 0.3 mm, spiral in shape, apices obtuse, cells polygonate or lineate-polygonate, edges of cells elevated, faces of cells depressed and smooth. Chromosome number $n = 13$ (Lee, 1966).

ECOLOGY: On river banks, cliffs, or in thickets on hillsides, growing on both limestone and non-limestone substrates, alt. 100-900 m.

DISTRIBUTION: Cuba and Hispaniola (Haiti and Dominican Republic) (fig. 1).

DISCUSSION: On the label for the isotype photo in US is indicated erroneously "Locality: Jamaica". According to Swartz (1788), the type locality is "Hispaniola". The species has never been found in Jamaica.

SPECIMENS EXAMINED:

CUBA:

CAMAGUEY: Pta. Ganado, 10 Aug 1927 (fl), *Ekman* 8874 (K, NY, US). LAS VILLAS (SANTA CLARA): Trinidad Mts, hillside near San Jose, Jun-Aug 1941 (fl), *Howard* 5176 (NY, US). ORIENTE: Central Almeida, Sept 1944 (fl), *Acuna s. n.* (US); Sierra Maestra, Rio Yara, May 1948 (fr), *Acuna s. n.* (US); Guantanamo, Valle del Caujeri, 14-15 Sept 1952 (ster), *Acuna* 17891 (HAC, US), Baracoa, Paredones del Rio Yumuri, 5 Feb 1952 (ster), *Acuna & Diaz-Barreto* 14759 (HAC, US); vicinity of Daiquiri, hillside, 300 m, 14-16 Mar 1912 (fr), *Britton & Cowell* 12655 (NY); Ens. de Mora, on cliffs, 26-29 Mar 1912 (fr), *Britton et al.* 12934 (NY, US); Jimbainbay, Cayo Rey, 3 Sept 1942 (fr), *Clemente* 2481 (US); Sardiñero, Santiago, Jan 1948 (fr), *Clemente* 5830 (US); El Salado, Santiago, Oct. 1945 (fl), *Clemente* 6265 (US); Sierra Maestra, ad

Rio Yara, 100-200 m, 28 Jul 1922 (ster), *Ekman* 5627 (US), 14665 (k); Sierra de Nipe, Carrascales at Rio Piloto, 350 m, 9 Sept 1922, *Ekman* 15062 (K); Pico Turquino, banks of Rio Yara, Jul 1922 (fl, fr), *Leon* 10951 (NY, US); S. Baracoa Region, Caleta, E of Jauco, 17 Jul-4 Aug 1924 (fl), *Leon* 11868 (NY); Mesa del Chivo, Maisi, Jan 1940 (fl), *Leon* 17549 (US) Salto del Sojo, Sierra de Nipe, Jul 1940 (fl, fr), *Leon* 17969 (US); Terraza de Maisi, 19 Aug 1939 (ster), *Leon & Victorin* 17117 (NY); Rio Yao, dry pastures, Mar 1943 (fr), *Marie-Victorin* 60019 (US); Farallones de Sardinero, 5 Jan 1956, *Morton* 8728 (ster) (US), 8742a (fl, fr) (US); cliffs near the mouth of Rio Yumuri, E Baracoa, near sea level, 13 Jan 1956 (ster), *Morton & Alain* 9034 (US); vicinity of Baracoa, 1-17 Feb 1902 (fl), *Pollard et al.*, 210 (NY, US); Rio Yumuri, 6, 12 Dec 1910 (fl, fr), *Shafer* 7757 (NY, NY, US); Rio Yao, S of Breycito, Mar 1943 (fr), *Victorin & Clemente* 22388 (US), Mayari, Sa. del Cristal, 18 Feb 1948 (fr), *Zayas & Ferras s. n.* (US). NO EXACT LOCALITY: a. 1860 (fl), *Wright* 370 (K); a. 1955 (fl), *Alain* 333 (US).

DOMINICAN REPUBLIC:

BARAHONA: on cliff, 100m, Mar 1910 (fl, fr), *Fuertes* 157 (BM, E, K, NY, US); on wet dripping cliff face, Palo Mino, 21 Jul 1950 (fl), *Howard* 12090 (BM, US). MONTECRISTI: Moncion, near Arroya Seco, 275 m, 3 Jul 1929 (fl), *Ekman* 13086 (US); Moncion, 300-400 m, 18 Apr 1933 (fl), *Valeur* 852 (K, NY, US). PEDERNALES: near Banano, Pedernales R. 400 m, 24-27 Jun 1975 (fr), *Liogier & Liogier* 23327 (NY), 26961 (NY). PUERTO PLATA: Cofrese, 100 m, 24-25 Feb 1973 (fl, fr), *Liogier* 18819 (NY). SAN JUAN: vicinity of Rio Arriba del Norte (N, San Juan), 9-14 Sept 1946 (fl), *Howard & Howard* 8904 (BM, NY, US); 3 km N Presa de Sabaneta, Rio San Juan, 24 Jun 1982 (fl), *Mejia & Pimentel* 20995 (NY, US). SANTIAGO: La Bosua near Janico, ca. 800 m, 29 Apr 1970 (fl), *Burch & Jimenez* 2516 (BM, NY); 12 miles from Santiago, La Bosua, limestone, 22 Jun 1969 (fl), *Jimenez & Liogier* 5730 (NY); La Bosua, 250 m, 6 May 1968 (fl, fr), *Liogier* 11133 (NY, US), 9 May 1969 (fl), *Liogier* 15170 (NY); La Bosua, 22 Jun 1969 (fr), *Jimenez et al.* 5730 (US); 15 km SW of Santiago, on limestone cliff, 9 Jul 1970 (fl, fr), *Skog* 1590 (US); Bao R. at Sabana Iglesia, 18 Feb 1965 (fr), *Talpey* 31 (US); San Jose de las Matas, 250 m, 25 Mar 1930 (fl), *Valeur* 424 (US). SANTO DOMINGO: 8 May 1887 (fl, fr), *Eggers* 1823 (K).

HAITI:

ARTIBONITE: La Victoire, 400 m, 16 Jun 1942 (fl), *Holdridge* 1270

(BM, NY, US); vicinity of Ennery, 900 m, 21 Jan 1926 (fl), *Leonard* 9060 (NY, US); S. Ennery, 325-900 m, 4 Feb 1926 (ster), *Leonard* 9506 (US); San Michel to Marmelade, ca. 700 m, 6 Aug 1905 (fl), *Nash & Taylor* 1474 (NY, US). CENTRE: Montagnes Noire, Lacde Petigre, 13.5 km NE Mirebalais, 11 Nov 1982 (fl), *Zanoni et al.* 23999 (NY). NORD: vicinity of St. Michel de l'Ataleye, 350 m, 7 Dec 1925 (fr), *Leonard* 7792 (US). NORD-OUEST: vicinity of Jean Rabel, 29 Jan 1929 (fl), *Leonard & Leonard* 12642 (US), 1-13 Mar 1939 (fl), 13685 (E, US); vicinity of Bambardopolis, 610 m, 22 Feb 1929 (fr), *Leonard & Leonard* 13449 (US). OUEST: Fondverrettes, 13 Sept 1955 (fl), *Proctor* 10695 (US); Montagnes Noires, near Poste de Flande, 22 Sept 1955 (fl), *Proctor* 10911 (US, US). ILE DE LA GONAVE: Pte-a-Raquettes, 8 Oct 1927 (fl, fr) *Ekman* H8874 (NY, US); near village of La Mahantiere, 26 Jul 1927 (fl), *Eyerdam* 85 (NY, US). ILE DE LA TORTUE: vicinity of La Vallee, 28 Dec 1928-9 Jan 1929 (fl), *Leonard & Leonard* 11245 (NY, US), 11484 (K, US).

CULTIVATED: originally collected by Talpey (31), from Dominican Republic, S. I. Acc. 80-156, *Skog & Linett* 5557 (US); Jardin Botanico Nacional, Santo Domingo (originally from Prov. Pedernales, Dominican Republic), 21 Nov 1980 (fr), *Zanoni* 9306 (NY).

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拜伦苣苔属 (*Bellonia* L.) 的研究

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摘 要

对拜伦苣苔属 (*Bellonia* L.) 作了订正, 讨论了它的种间关系和与其他属的联系, 对本属的进化方向作了论述。研究工作主要依据世界各地的馆藏植物标本, 并采用扫描电子显微镜技术分析了孢粉和种子的形态。

拜伦苣苔属隶于苦苣苔科 (*Gesneriaceae*) 苦苣苔亚科 (*Gesnerioideae*), 含 2 种, 分布于加勒比海地区的古巴和海地岛。法国 Plumier 于 1703 年发表了这个属, 取名为 "*Bellonia*", 后来林奈 (Linnaeus, 1737) 确认了这个属, 并为本属的模式种采用了双名 (*Bellonia aspera* L.)

拜伦苣苔属在形态上十分独特。它是苦苣苔科中唯一具刺的属。它的花被管中的雄蕊维管束单独发生而有别于同一科中的其他属。它的可育雄蕊数目 5~8 个, 和苦苣苔科一般的 2 或 4 个可育雄蕊截然不同。它的花冠结构也独具一格, 没有明显的花冠管, 辐射对称; 苦苣苔科一般花冠两侧对称。花冠管明显。不过, 这个属的子房和果实结构符合苦苣苔亚科的特征, 一室两个侧膜胎座。

本属含两个种: 糙叶拜伦苣苔 (*B. aspera* L.) 和刺拜伦苣苔 (*B. spinosa* Sw.), 它们从形态学上是独立的明显可分的种。前者具有明显的聚伞花序, 植株无刺, 孢粉的表面纹饰较为粗糙; 后者的花序明显单花, 植株多刺, 孢粉表面纹饰较为平滑。分析它们的形态学, 糙叶拜伦苣苔是原始的, 刺拜伦苣苔是次生的。形态演化的方向比较明显: 从聚伞花序通过花的数目的减少和花序轴的短缩而简化为单花; 花序的来源是一个叶腋内生的短缩的枝条; 植株上的刺和花序同源, 是花序不育化而形成的。推测在进化过程中, 为了减少营养的消耗而减少了花的数目, 从而以尽可能好的营养保证可育花的质量。

这个属可能起源于石灰岩植物区系。比较原始的糙叶拜伦苣苔仅发现于海地岛南部的石灰岩上。较为进化的刺拜伦苣苔则在石灰岩和非石灰岩基质上都有分布, 分布区遍布于海地岛并延伸至古巴岛上。这符合一般的规律, 进化的后代常常适应能力较强, 分布区也较广。

一般认为石灰岩植物区系具较多的有刺植物, 但在本属中无刺的糙叶拜伦苣苔反倒是一个石灰岩特有植物, 而多刺的刺拜伦苣苔则广布到非石灰岩生境上。这表明, 石灰岩生境和植物的刺形态学没有直接的联系, 可能种系发生学对植物的形态具有比环境更大的影响。

关键词 苦苣苔科, 拜伦苣苔属, 糙叶拜伦苣苔, 刺拜伦苣苔



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