

GENERIC LIMITS AND TAXONOMY OF BRAYOPSIS
AND EUDEMA (BRASSICACEAE)IHSAN A. AL-SHEHBAZ¹

Brayopsis colombiana subsp. *colombiana*, *B. colombiana* subsp. *ecuadoriana*, and *Eudema incurva* are described as new. They represent first generic records from Colombia, Ecuador, and Peru, respectively. A new combination, *Eudema nubigena* subsp. *remyana*, is proposed. The limits of *Brayopsis* and *Eudema* are critically evaluated, and keys to the species of both genera are given. The sectional classification of *Eudema* is discussed, and its value is questioned.

In his treatment of the Brassicaceae (Cruciferae) for the *Flora of Peru*, Macbride (1938) followed Baehni and Macbride (1937) in uniting *Brayopsis* Gilg & Muschler with the earlier-published *Englerocharis* Muschler. Evidence supporting the maintenance of both genera was given in Al-Shehbaz (1989a); there I pointed out that *Brayopsis* and *Englerocharis* are unrelated to each other, and that their nearest relatives are *Eudema* Humb. & Bonpl. and *Catadysia* O. E. Schulz, respectively.

During the study of some Colombian species of *Draba* L. (Al-Shehbaz, 1989b), I discovered an undescribed species of *Brayopsis* among undetermined material. The new species, hereafter *Brayopsis colombiana* Al-Shehbaz, raised some taxonomic and phylogeographic questions. First, the genus had not previously been reported from Colombia; second, *B. colombiana* is disjunct from the nearest range of *Brayopsis* in Peru by at least 1600 air kilometers; and third, one of the close relatives of this plant is a Bolivian species that Schulz (1924) treated as *Eudema diapensioides* (Wedd.) O. E. Schulz (= *B. diapensioides* (Wedd.) Gilg & Muschler). The phylogeographic disjunctions of *Brayopsis* are not surprising, and several other South American genera of the Brassicaceae show even more dramatic distributional gaps; these will be dealt with in a forthcoming paper. Adequate material of this complex was not available to me 18 months ago when I submitted a revision of *Brayopsis* for publication (Al-Shehbaz, 1989a). The subsequent discovery of *B. colombiana* and *E. incurva* and the study of almost all the types of *Eudema* have prompted a critical reevaluation of the boundaries between these two genera.

Brayopsis resembles *Eudema* in habit and in having few to several solitary flowers borne on peduncles that arise from the center of a well-developed rosette. The maturation of these flowers follows a racemose, centripetal pattern; the direction of anthesis is from the periphery to the center. No other South

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American genera have such a synapomorphy, and therefore *Brayopsis* and *Eudema* are sister groups. The somewhat remotely related *Dactylocardamum* Al-Shehbaz and *Xerodraba* Skotts. have only one pedunculate or sessile flower from the center of the leaf cluster terminating a given branch (Al-Shehbaz, 1989c).

Schulz (1924, 1936) separated *Brayopsis* from *Eudema* solely on the basis of its having siliquose instead of siliculose fruits. Additional morphological differences between the two genera, particularly in funicle length and seed-coat sculpture, are also found (see TABLE, FIGURE 1). These differences strongly support the maintenance of both genera.

Brayopsis colombiana is a perfectly good representative of the genus, and characters of the fruits, as well as the filiform funicles and the seed sculpture (see FIGURES 1, 2; TABLE), strongly define its generic identity. Schulz's (1924) initial assignment of *B. diapiensoides* to *Eudema* was based solely on his study of a fragmentary isotype at Berlin. Although I have seen only three additional specimens of the type collection, the fruit shape and dimensions, funicle type, and seed-coat sculpture are characteristic of *Brayopsis* and not *Eudema* (see TABLE). Therefore, I believe that Gilg & Muschler's (1909) placement of *B. diapiensoides* in *Brayopsis* is more acceptable than its assignment by Schulz (1924) to *Eudema*.

BRAYOPSIS

The taxonomy of *Brayopsis alpaminae* Gilg & Muschler, *B. calycina* (Desv.) Gilg & Muschler, and *B. monimocalyx* O. E. Schulz has been studied in some detail (Al-Shehbaz, 1989a), and therefore an account need not be repeated here. The addition of *B. diapiensoides* has expanded the morphological diversity within the genus only a little. A key to the five species of *Brayopsis* and a taxonomic account of *B. colombiana* and *B. diapiensoides* are given below.

- A. Styles in fruit 1–3 mm long; sepals erect, somewhat coherent; fruit valves densely covered with long, straight trichomes. *B. alpaminae*.
- A. Styles in fruit obsolete or 0.2–0.8(–1) mm long; sepals ascending, free; fruit valves glabrous or rarely with short, crisped trichomes.
 - B. Leaves 0.4–0.8(–1) mm wide, ciliate with trichomes 0.2–0.3 mm long; fruits stipitate; gynophores 1.2–2.5 mm long, thinner than fruiting peduncle. *B. diapiensoides*.
 - B. Leaves 1.5–4 mm wide, glabrous or ciliate with trichomes (0.8–)1–1.5 mm long; fruits sessile, or if stipitate, then gynophores up to 0.5 mm long and thicker than fruiting peduncle.
 - C. Sepals persistent even after fruit dehiscence; leaves ovate, densely pubescent on upper surface. *B. monimocalyx*.
 - C. Sepals usually caducous shortly after anthesis; leaves oblong, lanceolate, or linear, glabrous or pubescent on upper surface.
 - D. Fruits short-stipitate; fruiting peduncles 3–15 mm long; leaves spatulate to oblanceolate or rarely lanceolate; styles conspicuous, to 1.5 mm long; Colombia and Ecuador. *B. colombiana*.
 - D. Fruits sessile; fruiting peduncles (9–)12–42(–55) mm long; leaves linear to lanceolate; styles obsolete or very rarely to 0.8 mm long; Argentina, Bolivia, Peru. *B. calycina*.

Comparison between *Brayopsis* and *Eudema*.

CHARACTER	TAXON			
	<i>Brayopsis</i>	<i>B. colombiana</i>	<i>B. diapensioides</i>	<i>Eudema</i>
Fruits				
Shape	Linear, lanceolate, or oblong-linear	Lanceolate	Lanceolate	Oblong, ovoid, suborbicular, obovoid, or pyriform
Length/width quotient	(3.5-)5-8(-10)	5-6.5	3.5-5	1-1.5(-2.5)
Funicle	Long, filiform	Long, filiform	Long, filiform	Short, thick
Septum	Complete	Complete	Complete?	Complete or reduced to rim
Seed-coat sculpture	Colliculate-reticulate	Colliculate-reticulate	Colliculate-reticulate	Coarsely reticulate*

*Mature seeds of only *E. incurva*, *E. nubigena*, and *E. rupestris* were available.

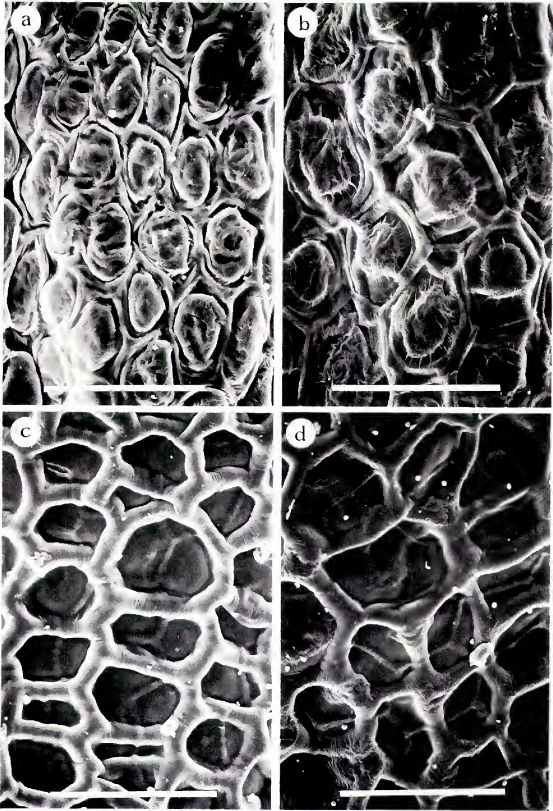


FIGURE 1. Scanning electron micrographs of seeds of *Brayopsis* and *Eudema*: a, *B. alpaminae* (Macbride & Featherstone 887, GH); b, *B. colombiana* subsp. *colombiana* (holotype, GH); c, *E. nubigena* subsp. *nubigena* (Mexico 7652, F); d, *E. rupestris* (Jameson s.n., us). Scale bars = 100 μ m.

Brayopsis colombiana Al-Shehbaz, sp. nov.

FIGURE 2.

Herba perenna dense caespitosa, caudicibus ramosis, foliis emortuis persistentibus vestitis. Folia rosulata, spathulata vel oblanceolata, ciliata, 4–12 mm longa, 1.5–4 mm lata, pilis simplicibus (0.8–)1–1.5 mm longis. Pedunculi fructiferi tenui, 3–15 mm longi. Petala alba, spathulata 2.2–2.5 mm longa, 0.7–0.9 mm lata. Siliqua lanceolata, subtereta, breve stipitata, 6–8 mm longa, 1.2–1.5 mm lata; septum hyalinum completum; locula 4–6 sperma; stylus 0.4–1 mm longus. Semina oblonga notorrhiza, brunnea, 1.4–1.6 mm longa, 0.7–0.9 mm lata; funiculi filiformi, 1.2–2 mm longi.

Cespitose, cushion-forming perennials; caudices woody, branched, covered with whole leaves of previous years. Leaves forming dense rosettes, spatulate to oblanceolate, 4–12 mm long, 1.5–4 mm wide, obtuse to subacute at apex, ciliate with trichomes (0.8–)1–1.5 mm long, cuneate at base. Sepals erect, ovate, ca. 2 mm long. Petals white, spatulate, 2.2–2.5 mm long, 0.7–0.9 mm wide. Filaments 1.2–1.8 mm long; anthers ovate, ca. 0.6 mm long. Fruiting peduncles erect, slender, 3–15 mm long, sparsely pubescent. Fruits lanceolate, 6–8 mm long, 1.2–1.5 mm wide, dehiscent, subterete, exserted well above leaf rosette; gynophores stout, to 0.5 mm long; valves glabrous, acute at both ends, inconspicuously veined; septa hyaline, complete; styles 0.4–1 mm long. Seeds 4 to 6 per locule, oblong, 1.4–1.6 mm long, 0.7–0.9 mm wide, brown, pendulous; cotyledons incumbent; funicles filiform, 1.2–2 mm long.

TYPE. Colombia, Depto. Boyacá, Cordillera Oriental, Sierra Nevada del Cocuy, Alto Ritacuva, 11 April 1959, 4600 m alt., *H. G. Barclay & P. Juajibioy 7355* (holotype, GH; isotype, MO).

KEY TO THE SUBSPECIES

- Leaves ciliate; sepals ca. 2 mm long; petals 2.2–2.5 mm long; styles in fruit 0.4–1 mm long; Colombia. 2a. subsp. *colombiana*.
 Leaves not ciliate; sepals 3–4.5 mm long; petals 4–5.5 mm long; styles in fruit 1–1.5 mm long; Ecuador. 2b. subsp. *ecuadoriana*.

2a. **Brayopsis colombiana** subsp. *colombiana*

ADDITIONAL SPECIMENS EXAMINED. Colombia. DEPTO. BOYACÁ: Cordillera Oriental, Sierra Nevada del Cocuy, Alto Ritacuva, 4400 m alt., *Barclay & Juajibioy 7410* (GH); same locality, 4600 m alt., *Grubb, Curry, & Fernández-Pérez 304* (K, US).

Brayopsis colombiana subsp. *colombiana* is the sole representative of the genus in Colombia. It grows on unstabilized, fine, sandy soil in crevices of bedrock above moraines of the Ritacuva glacier at an altitude of ca. 4400–4600 m.

2b. **Brayopsis colombiana** subsp. *ecuadoriana* Al-Shehbaz, subsp. nov.

Folia glabra, nonciliata; sepala 3–4.5 mm longa; petala 4–5.5 mm longa, ca. 1.5 mm lata; stylus 1–1.5 mm longus.

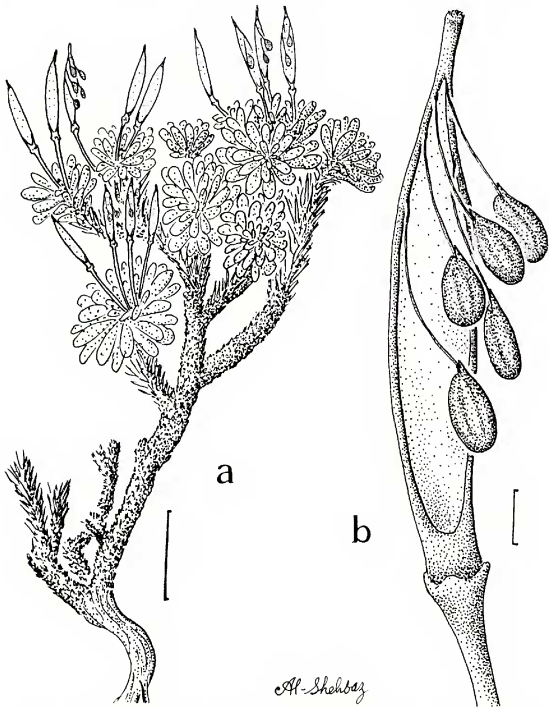


FIGURE 2. *Brayopsis colombiana* subsp. *colombiana* (holotype): a, plant; b, fruit with valves removed. Scale bars = 1 cm (a), 1 mm (b).

Leaves glabrous, lanceolate to oblanceolate, not ciliate. Sepals oblong, 3–4.5 mm long. Petals white, spatulate, 4–5.5 mm long, ca. 1.5 mm wide. Fruits 5–6 mm long; styles 1–1.5 mm long.

TYPE. Ecuador, Prov. Azuay, páramo de las Cajas, Lagunas Suerochocha, 35 km on Cuenca-Molleturo road; mountain 1 km NW of pass, 79°14'W, 2°48'S, 4200–4400 m alt., 30 Jan. 1988, *U. Molau & B. Eriksen* 2787 (holotype, GB).

The type collection of *Brayopsis colombiana* subsp. *ecuadoriana* represents

the first record of *Brayopsis* from Ecuador, and the type locality somewhat bridges the gap between the main range of the genus and that of subsp. *colombiana*. The differences in flower size between the two subspecies is significant. In the absence of additional material, and because of the evident similarity in all other morphological characters, I have refrained from recognizing these taxa as separate species. The presence vs. absence of leaf trichomes, which is a good distinguishing character, should not be overemphasized: the same pattern occurs within *B. calycina*.

Brayopsis colombiana resembles *B. diapensioides* in several features, particularly in having lanceolate, stipitate fruits, short styles, and filiform funicles. It is easily distinguished, however, by its spatulate to oblanceolate or lanceolate leaves 1.5–4 mm wide, its stout gynophores to 0.5 mm long, and its either glabrous or ciliate leaves with fine trichomes (0.8–)1–1.5 mm long. In contrast, *B. diapensioides* has narrowly lanceolate to linear leaves 0.4–0.8(–1) mm wide, slender gynophores 1.2–2.5 mm long, and stouter trichomes 0.2–0.3 mm long. Perhaps the nearest relative of *B. colombiana* is *B. calycina*, from which it is easily distinguished by several characters given in the key above.

Brayopsis diapensioides (Wedd.) Gilg & Muschler, Bot. Jahrb. Syst. 42: 484. 1909.

Draba diapensioides Wedd. Ann. Sci. Nat. Bot. 5(1): 285. 1864. *Eudema diapensioides* (Wedd.) O. E. Schulz, Pflanzenr. IV, 105(Heft 86): 245. 1924. TYPE: Bolivia, Prov. Larecaja, vicinity of Sorata, between Ancouma and Turelague in Cerro de Aosas, 4500 m alt., November 1860, Mandon 894 (holotype, ♀; isotypes, ♂ (photos, ♀, ♂!), BM!, G!).

Densely caespitose perennials, with thick, much-branched caudices covered with persistent petiolar remains of previous years. Leaves narrowly lanceolate to linear, forming well-developed rosettes, 4–8 mm long, 0.4–0.8(–1) mm wide, subacute, ciliate with unbranched trichomes 0.2–0.3 mm long; blades thin, shorter than persistent, conspicuously thickened petioles. Sepals erect, ovate, 2–2.5 mm long, 1.2–1.3 mm wide, membranaceous at margin, glabrous. Petals obovate, 2.5–3.5 mm long, 1.2–1.5 mm wide, cuneate at base. Filaments 2–2.5 mm long; anthers ovate, 0.5–0.6 mm long. Fruiting peduncles 5–8 mm long, thick, up to 1 mm wide, sparsely pubescent with trichomes to 0.3 mm long. Fruits lanceolate, subterete, 3.5–5 mm long (excluding style and gynophore), stipitate, glabrous; styles 0.4–0.7 mm long; gynophores 1.2–2.5 mm long, slender, about half as wide as fruiting peduncle. Seeds oblong, 1.2–1.4 mm long, 0.7–0.8 mm wide, borne on filiform funicles ca. 1.2 mm long.

Hardly anything can be said about the variation and biology of this species, which is apparently known only from the type collection. *Brayopsis diapensioides* can easily be distinguished from the remainder of the genus in having slender gynophores much narrower than the thickened fruiting pedicels.

EUDEMA

As interpreted here, *Eudema* consists of six species, including only five of the eight recognized by Schulz (1924, 1936). One species, *E. remyana* (Wedd.)

O. E. Schulz, is reduced here to a subspecies of *E. nubigena* Humb. & Bonpl. Another, *E. diapensioides*, is treated above as a species of *Brayopsis*. The third species, *E. colobanthoides* (Skotts.) O. E. Schulz, is reassigned to *Xerodraba*. The sixth species, *E. incurva*, is described below as new.

Schulz (1924, 1936) recognized the heterogeneity of *Eudema* and divided the genus into four sections. The monotypic sect. *Gynophoridium* O. E. Schulz was defined solely on the basis of having stipitate instead of sessile fruit. Its single species is recognized here as *Brayopsis diapensioides*.

Section *Lepteudema* O. E. Schulz is separated from the rest of the genus mainly on the basis of having slender, scaly, loosely branched rhizomes instead of a thick caudex. Two species of this section, *Eudema friesii* O. E. Schulz and *E. werdermannii* O. E. Schulz, have dendritic leaf trichomes that are lacking in the rest of the genus. This section might justifiably be raised to a separate genus, but in the absence of adequate material at my disposal, I refrain from taking such an action.

The monotypic sect. *Xereudema* O. E. Schulz is based on a species that was originally described as *Xerodraba colobanthoides* Skotts. Schulz (1924) transferred the species to *Eudema* because it allegedly lacks the expanded leaf bases, subsaccate sepals, and somewhat fleshy petals characteristic of *Xerodraba*. However, these features are unreliable in this complex, and *Xerodraba* is easily separated from *Eudema* by its solitary terminal flowers, usually complete septum, and densely imbricate, minute, fleshy, wholly persistent leaves. *Eudema* has several flowers at the branch apex, a usually rudimentary septum, and nonimbricate, large, unfleshy leaves with persistent petioles.

Boelcke (1982) transferred *Xerodraba colobanthoides* to the later homonym *Skottsbergiella* Boelcke and then (in Boelcke & Romanczuk, 1984) to *Skottsbergianthus* Boelcke. However, the single character on which the latter genus is based, the presence of a minute, scalelike appendage at the base of each petal, might not justify its recognition as distinct from *Xerodraba*. I have not seen adequate material of *X. colobanthoides*, but the species does not belong to *Eudema*. I have concluded that Schulz's (1924, 1936) sectional classification of *Eudema* is artificial and does not improve the taxonomy of the genus.

Eudema Humb. & Bonpl. Pl. Aequinoct. 2: 133. 1813. LECTOTYPE (here designated): *E. rupestris* Humb. & Bonpl.

Cespitose, scapose perennials with thick, branched caudices or slender rhizomes, the branches covered with petiolar remains of previous years and terminated by rosettes; trichomes simple or dendritic, sometimes absent. Leaves rosulate, petiolate, somewhat fleshy, entire or rarely pinnately lobed; petioles persistent, thick or flattened at base. Flowers solitary, borne on peduncles originating from center of rosette, maturing centripetally. Sepals erect, ovate, nonsaccate at base, caducous. Petals white to creamy white, obovate, spatulate, oblanceolate, or sublinear, usually not differentiated into blade and claw. Stamens 6; anthers oblong to ovate. Nectar glands 4, 1 on each side of a lateral stamen. Fruits dehiscent, suborbicular, ovoid, obovoid, pyriform, or rarely oblong, subterete to conspicuously flattened parallel or rarely perpendicular to

replum, glabrous; septa reduced to narrow rim or rarely complete; stigmas subentire. Seeds few to many, coarsely reticulate; cotyledons incumbent; funicles short, thick.

KEY TO THE SPECIES OF EUDEMA

- A. Leaves with dendritic trichomes; plants with slender rhizomes.
 - B. Leaves pinnately lobed, rarely coarsely toothed, upper surface sparsely pubescent. 6. *E. friesii*.
 - B. Leaves entire, upper surface densely pubescent. 5. *E. werdermannii*.
- A. Leaves glabrous or with simple trichomes; plants with thick caudices (if with rhizomes, then leaves glabrous and fruits flattened).
 - C. Fruits obovate to pyriform, conspicuously flattened parallel to replum; plants rhizomatous. 4. *E. hauthalii*.
 - C. Fruits oblong or ovoid, subterete or slightly flattened; plants with thick caudex.
 - D. Fruits oblong; seeds 10 to 30 on each placenta; petioles flattened at base; leaves linear to narrowly oblanceolate, glabrous.
 - E. Leaf blades ciliate; septa complete; fruits strongly incurved; seeds plump, 15 to 30 on each placenta, 0.7–0.8 mm long. 1. *E. incurva*.
 - E. Leaf blades not ciliate; septa reduced to rim; fruits straight; seeds flattened, 10 to 13 on each placenta, 1.2–1.7 mm long. 2. *E. rupestris*.
 - D. Fruits ovoid; seeds 1 to 5 on each placenta; petioles thick at base; leaves spatulate to ovate or oblanceolate, ciliate or glabrous. 3. *E. nubigena*.

1. *Eudema incurva* Al-Shehbaz, sp. nov.

FIGURE 3.

Herba perenna caespitosa scaposa, caudicibus tenuibus. Folia rosulata lineari vel lineari-lanceolata, ciliata, 5–15 mm longa, 0.6–1.4 mm lata, petiolis persistentibus, ad basin complanatis. Pedunculi fructiferi glabri, 4–10 mm longi. Siliqua oblonga, incurva, angustiseptata, 4–8 mm longa, 2.5–3.5 mm lata; septum hyalinum completum; locula 15–30-sperma; stylus 0.4–0.7 mm longus. Semina late ovoidea, notorrhiza, biseriata, reticulata, 0.7–0.8 mm longa, 0.5–0.6 mm lata.

Cespitose, perennial herbs with slender, simple, or few-branched caudices covered with petiolar remains of previous years. Leaves rosulate, petiolate, linear to linear-lanceolate, 5–15 mm long, 0.6–1.4 mm wide, ciliate with unbranched, straight trichomes to 2 mm long; petioles persistent, not ciliate, flattened at base, 2–7 mm long. Flowers not seen. Fruiting peduncles glabrous, 4–10 mm long. Fruits oblong, strongly incurved, glabrous, 4–8 mm long, 2.5–3.5 mm wide, flattened contrary to septum, rounded at apex and base; septa complete, hyaline; styles 0.4–0.7 mm long. Seeds 15 to 30 per locule, broadly ovoid, plump, 0.7–0.8 mm long, 0.5–0.6 mm wide, dark brown, conspicuously reticulate, biserially arranged in each locule; funicles 0.2–0.5 mm long; cotyledons incumbent.

TYPE. Peru, Depto. Ancash, Prov. Huaraz, Punta Callán and above, summit area of the Huaraz-Casma road, 30 km from Huaraz, 1–3 km N of road, heavily grazed puna with rock outcrops, 77°37'W, 9°32'S, 4200–4400 m alt., 7 April 1988, *U. Molau & B. Eriksen 3512* (holotype, GB (photocopy, GH)).

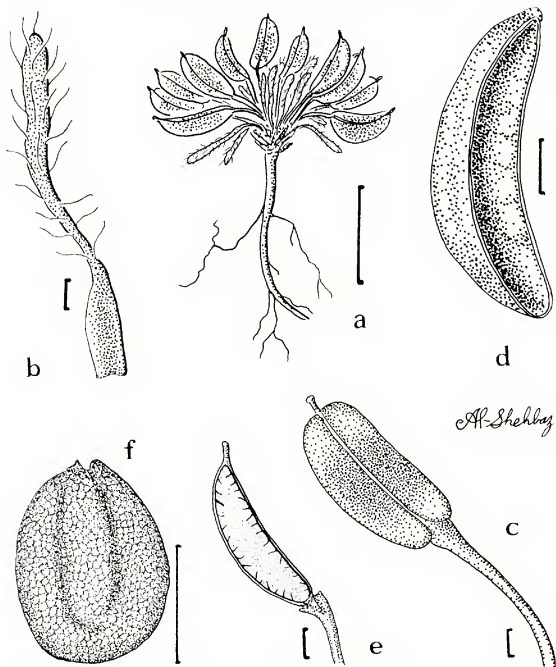


FIGURE 3. *Eudema incurva* (holotype): a, plant; b, leaf; c, fruit; d, valve; e, replum and septum; f, seed. Scale bars = 1 cm (a), 1 mm (b-f).

Eudema incurva is closely related to the Ecuadorian endemic *E. rupestris*. It is easily distinguished from the remainder of the genus in having angustiseptate, strongly incurved fruits, a complete septum, many (15 to 30 per locule) biserially arranged, small seeds to 0.8 mm long, and conspicuously ciliate leaf blades with trichomes to 2 mm long. No flowers are found on any of the six plants of the holotype. However, floral remains on a young fruit reveal that the sepals are oblong, pubescent, and ca. 2.5 mm long, and that the filaments and the oblong anthers are ca. 2 and 0.8 mm long, respectively.

Eudema incurva is somewhat anomalous in the genus because it has a com-

plete instead of a rimlike septum and numerous seeds per locule. In these characters it resembles *Brayopsis*, but the overall morphology strongly supports its placement in *Eudema*.

2. *Eudema rupestris* Humb. & Bonpl. Pl. Aequinoct. 2: 133. 1813.

Sisymbrium rupestre (Humb. & Bonpl.) Wedd. Ann. Sci. Nat. Bot. 5(1): 290. 1864; *Hesperis rupestris* (Humb. & Bonpl.) Kuntze, Revis. Gen. Pl. 2: 935. 1891; *Draba humboldtii* Desv. J. Bot. (Desvaux) 3: 171. 1815; *Eutrema humboldtii* (Desv.) Sprengel, Syst. Veg. 2: 880. 1825. TYPE: Ecuador, between Quito and Cuenca, Montaña del Assuay, *Humboldt & Bonpland s.n.* (holotype, P (IDC 6209. 119: 1. 6!); isotype, B!).

Eudema grandiflora Planchon in W. J. Hooker, London J. Bot. 3: 620. 1844; *Sisymbrium grandiflorum* (Planchon) Wedd. Ann. Sci. Nat. Bot. 5(1): 290. 1864; *Hesperis planchoniana* Kuntze, Revis. Gen. Pl. 2: 936. 1891; *Brayopsis grandiflora* (Planchon) Gilg & Muschler, Bot. Jahrb. Syst. 42: 482. 1909. TYPE: Ecuador, Andes, monte Assuay, 15,000 ft [ca. 4570 m] alt., *Jameson s.n.* (holotype, MPU or NA; isotype, NY!).

Cespitose, glabrous perennials with much-branched caudices covered with petiolar remains of previous years. Leaves numerous, rosulate, petiolate; blades linear to narrowly oblanceolate, rounded at apex, entire, attenuate at base, 7–17 mm long, 1–3 mm wide; petioles conspicuously flattened at base, 7–10 mm long. Sepals erect, narrowly oblong to suboblanceolate, 6–7 mm long, ca. 2 mm wide, scarious at margin, with few subapical trichomes. Petals oblong to sublinear, 11–12 mm long, ca. 2 mm wide. Filaments erect, slender, 5.5–6.5 mm long; anthers narrowly oblong, 1.2–1.5 mm long. Fruiting peduncles glabrous, 10–14 mm long. Fruits oblong, subterete to slightly compressed contrary to replum; valves thin, glabrous, with conspicuous midvein; septa reduced to rim; styles slender, 3–3.5 mm long. Seeds about 10 to 13 on each placenta, ovoid, slightly compressed, 1.2–1.7 mm long, 0.8–1.1 mm wide, dark brown to blackish, conspicuously reticulate; funicles thick, ca. 0.2–0.5 mm long.

REPRESENTATIVE SPECIMENS. **Ecuador:** Andes above Quito, 14,000 ft [ca. 4267 m] alt., *Jameson s.n.* (US, 2 sheets).

Eudema rupestris is apparently a very rare species. I have examined only a few specimens, which were collected around the middle of the last century. It is easily distinguished from its nearest relative, *E. nubigena*, in having oblong fruits with 10 to 13 seeds on each placenta, larger flowers with longer sepals, petals, and anthers, and linear to narrowly oblanceolate leaves with flattened petioles. In *E. nubigena* the ovoid fruits have 1 to 5 seeds on each placenta, the flowers are smaller, and the leaves are usually spatulate to ovate with thick petioles.

3. *Eudema nubigena* Humb. & Bonpl. Pl. Aequinoct. 2: 136. 1813.

Densely cespitose perennials forming well-developed cushions. Caudices woody, much branched, densely covered with persistent petioles of previous years. Leaves numerous, forming dense rosettes, somewhat fleshy; blades spatulate to oblanceolate or ovate, (3–)4–8(–9) mm long, 1.5–4(–5) mm wide, entire,

obtuse to somewhat subacute, nonciliate or ciliate throughout, with unbranched trichomes to 1.2 mm long; petioles persistent, thick, (2-)3-10 mm long. Sepals ovate to oblong, (2-)2.5-3.5(-6) mm long, (1.2-)1.5-2 mm wide, scarios at margin. Petals broadly obovate, 3-5 mm long, 1.5-2.5(-2.8) mm wide, rounded at apex, not clawed, white to creamy white. Filaments 2-3(-3.5) mm long; anthers oblong, 0.7-1 mm long, usually violet. Fruiting peduncles 2-5(-10) mm long. Fruits broadly to narrowly ovoid, subterete, (2-)3-5(-6) mm long, 2-3 mm wide; septa usually reduced to narrow rim; styles 0.4-2.5(-3) mm long. Seeds (1 or) 2 to 4 (or 5) on each placenta, oblong-ovate, (1.4-)1.6-2 mm long, (0.8-)1-1.3(-1.4) mm wide; dark brown, conspicuously reticulate; funicles thick, to 0.6 mm long.

KEY TO THE SUBSPECIES

- Leaf blades conspicuously ciliate; fruits usually broadly ovoid, styles 0.4-1.5(-3) long. 3a. subsp. *nubigena*.
 Leaf blades usually not ciliate; fruits narrowly to broadly ovoid, styles (1.2-)1.5-2.5(-3) mm long. 3b. subsp. *remyana*.

3a. *Eudema nubigena* subsp. *nubigena*

Draba nubigena (Humb. & Bonpl.) Desv. J. Bot. (Desvaux) 3: 171. 1815; *Sisymbrium nubigenum* (Humb. & Bonpl.) Wedd. Ann. Sci. Nat. Bot. 5(1): 290. 1864; *Hesperis nubigena* (Humb. & Bonpl.) Kuntze, Revis. Gen. Pl. 2: 935. 1891; *Eutrema bonplandii* Sprengel, Syst. Veg. 2: 880. 1825. TYPE: Ecuador, between Quito and Cuenca, Montaña del Assuay, *Humboldt & Bonpland s.n.* (holotype, P (IDC 6209. 119: I. 7!)).

Leaf blades ciliate throughout, with trichomes to 1.2 mm long. Fruits broadly or rarely narrowly ovoid, usually plump; styles stout to rarely slender, 0.4-1.5(-3) mm long.

REPRESENTATIVE SPECIMENS. **Ecuador**, PROV. IMBABURA: volcano Cotacachi, *Boysen Larsen, Eriksen, Kvist, Nissen, & Korning 45635* (AAU); Imbabura, *Hirsch 155* (GH); Cayambe Mt., *Cazalet & Pennington 5735* (UC). PROV. PICHINCHA: Cerro Antisana, *Grubb, Lloyd, Pennington, & Whitmore 632* (NY); Pichincha and Antisana, *Sodirol 52* (B); Loma Pilongo, NE slope of Nevado Iliniza, *Molau & Eriksen 2269* (GB); Cerro Iliniza, near border to Cotopaxi, *Harling 11175* (GB); W Rucu Pichincha, Padre Encantado, *Molau, Eriksen, & Klitgaard 2407, 2408* (GB); Mt. Corazón, *Asplund 17499* (G, NY, S); Volcán Iliniza, *Sparre 17457* (S); summit of Cerro Pichincha, *Holmgren & Heilborn 175* (S, 2 sheets); Mt. Pichincha, near Quito, *Hitchcock 21064* (GH, NY, US); Rucu Pichincha, *Asplund 17310* (NY, S); Volcán de Pichincha, *Bell 362* (BM, 2 sheets), *Mexia 7652* (F, UC, US); Andes above Quito, *Jameson 11* (LE), *33* (G, GH, P), *752* (BM, G, LE); on Chimborazo and Pichincha, *Jameson s.n.*, Sept. 1824 (E).

Subspecies *nubigena* grows on consolidated moraine and sandy soil between rocks or in crevices, as well as in grass paramo at altitudes of 4000-4820 m.

Plants of this subspecies vary in flower color from white (*Boysen Larsen et al. 45635*) to greenish yellow (*Grubb et al. 632*). Style length is also variable: styles of most plants that I have examined are usually less than 1.5 mm long, while those of plants comprising *Sparre 17457* are up to 3 mm. Although the

septum in almost all collections of subsp. *nubigena* is reduced to a narrow rim, it is unusually complete in *Boysen Larsen et al.* 45635.

3b. *Eudema nubigena* subsp. *remyana* (Wedd.) Al-Shehbaz, comb. nov.

Based on *Sisymbrium remyanum* Wedd. Ann. Sci. Nat. Bot. 5(1): 290. 1864; *Hesperis remyana* (Wedd.) Kuntze, Revis. Gen. Pl. 2: 935. 1891; *Brayopsis remyana* (Wedd.) Gilg & Muschler, Bot. Jahrb. Syst. 42: 482. 1909; *Eudema remyana* (Wedd.) O. E. Schulz, Pflanzenr. IV. 105(Heft 86): 244. 1924. TYPE: Ecuador, Chimborazo, *Remy s.n.*, 3 Nov. 1856 (holotype, ♀! (photo and fragment, ♀!)).

Aschersoniodoxa chimborazensis Gilg & Muschler, Bot. Jahrb. Syst. 42: 470. 1909. TYPE: Ecuador, Chimborazo, *Hall s.n.*, 1853 (holotype, ♀!).

Leaf blades glabrous throughout, rarely sparsely ciliate. Fruits narrowly ovoid, rarely broadly so; styles slender to rarely stout, (1.2-)1.5-2.5(-3) mm long.

REPRESENTATIVE SPECIMENS. Ecuador. PROV. BOLIVAR: W base of Volcán Chimborazo, *Maguire & Maguire* 61738 (NY), 61746 (NY, US); ca. 33 km N of Guaranda, W of Volcán Chimborazo, *Luteyn & Cotton* 11076 (GH). PROV. CHIMBORAZO: E slope of Mt. Chimborazo, *Asplund* 7934 (s); S slope of Mt. Chimborazo, *Asplund* 8384 (CAS, GH, NY, s, US), 8392 (s); WSW slope of Mt. Chimborazo, below Whympfer refuge, *Molau & Eriksen* 2991 (GH); Chimborazo, *Hirsch* E330 (GH), *Whympfer s.n.*, Jan. 1880 (BM); slope of Chimborazo, above Tortorillas, *Penland & Summers* 702 (GH); between Urbina and Mt. Chimborazo, *Hitchcock* 21976 (GH, NY, US); Riobamba, *Primbach* 219 (US). PROV. TUNGURAHUA: Las Minas, SE of Volcán Carihuayrazo, *Brandbyge* 42383 (AAU); Tungurahua volcano, *Korning & Thomsen* 47335 (AAU); paramo of Minza, *Penland & Summers* 387 (GH, US).

Subspecies *nubigena* and *remyana* are remarkably similar in almost all aspects of habit, leaf morphology, floral dimensions, and size and sculpture of seeds, as well as the reduction of the septum to a narrow rim. They are somewhat different in leaf pubescence, style length, fruit shape, and geographic distribution.

Schulz (1924) separated the two subspecies (as species) solely on the basis of the leaves being ciliate in subsp. *nubigena* and nonciliate in subsp. *remyana*. This difference holds for the majority of collections that belong to the latter taxon. However, in *Luteyn & Cotton* 11076 leaf blades and/or petioles vary continuously from completely glabrous to sparsely pubescent. Ciliate and nonciliate petioles have also been observed in *Asplund* 8384 (NY).

The fruits of subsp. *nubigena* are usually broadly ovoid, while those of subsp. *remyana* tend to be narrower. However, some collections of the latter (e.g., *Asplund* 8384; s) have broadly ovate fruits. Styles of subsp. *remyana* are usually longer than those of subsp. *nubigena*. In *Sparre* 17457 and *Asplund* 17499 (NY), both of subsp. *nubigena*, style length is 2-3 and 1.2-1.8 mm, respectively. Similarly, in a few plants of subsp. *remyana* (e.g., *Asplund* 8392) the styles are 1.2-1.6 mm long.

A critical evaluation of these slight differences in style length, fruit shape, and leaf pubescence reveals that there is no justification for recognizing *Eudema remyana* as a species distinct from the earlier-published *E. nubigena*. The taxonomy of the group is best served by reducing the former to a subordinate taxon of the latter.

Plants of subsp. *remyana* apparently occupy similar habitats at about the same altitude as those of subsp. *nubigena*.

4. ***Eudema hauthalii*** Gilg & Muschler, Bot. Jahrb. Syst. 42: 471. 1909.

Brayopsis hauthalii (Gilg & Muschler) Skottsberg, Kongl. Svenska Vetenskapsakad. Handl. 56(5): 236. 1916. TYPE: Argentina, [Prov.] Santa Cruz, Río Gallegos, Cerro Buitres, R. Hauthal 10618 (holotype, v! (photo, f!)).

Brayopsis skottsbergeri Gilg in Skottsberg, Kongl. Svenska Vetenskapsakad. Handl. 56(5): 236. 1916. TYPE: Patagonia, Sierra de los Baguales, Paso Centinela-Baguales, Skottsberg s.n., 1909 (not seen).

Prostrate, glabrous perennials with slender, branched rhizomes, the branches terminated by rosettes and covered with petiolar remains of previous years. Leaves rosulate, petiolate, oblanceolate-spatulate to narrowly oblanceolate or linear, (6-)9-15(-22) mm long, (0.7-)1-1.5(-2) mm wide, entire, rounded at apex, attenuate at base; petioles glabrous, as long as or longer than blades, conspicuously flattened at base. Sepals erect, ovate, 2.5-3.5 mm long, glabrous, rounded at apex. Petals oblanceolate, (4.5-)5.5-6.5 mm long, (1.2-)1.5-1.8 mm wide, rounded at apex, attenuate at base, creamy white. Filaments slender, 2.5-3.5 mm long; anthers 0.5-0.6 mm long. Fruiting peduncles (3-)5-10 mm long, few to several from center of rosette. Fruits sessile, obovate to pyriform, rarely ovate, flattened parallel to replum, (4-)5-11(-12) mm long, 4-7 mm wide, dehiscent from apex downward; valves thin, glabrous, inconspicuously nerved; septa hyaline, reduced to narrow rim; styles 0.5-1 mm long. Seeds 2 to 5 on each placenta, oblong, 2-2.5(-3) mm long, 1.1-1.3(-1.8) mm wide, light brown, obscurely flattened at distal end; funicles thick.

REPRESENTATIVE SPECIMENS. **Argentina.** PROV. SANTA CRUZ: Depto. Lago Argentino, Ea. Pérez, Río de las Vueltas, Meseta Quemada, *Sleumer 1386* (G, US); Cerro Corona, La Victorina, Lago Paine, *Pisano & Pisano 5603* (GH, HIP); Güer Aike, Ea. Las Viscachas, Ensenada de Riques, *TBPA 2679* (HIP); Co. Sin Nombre, *TBPA 2674* (HIP); Co. Pto. la Piedra, *TBPA 2542* (HIP). **Chile.** MAGALLANES: Depto. Ultima Esperanza, Sierra de los Baguales, Ea. La Cumbre, Co. Sin Nombre, *TBPA 757* (HIP).

Eudema hauthalii is most closely related to *E. werdermannii*, from which it is easily distinguished in having glabrous leaves, obovate to pyriform fruits (4-)5-11(-12) mm long, and seeds 2-2.5(-3) mm long. In contrast, *E. werdermannii* has densely pubescent leaves with dendritic trichomes, suborbicular fruits 2.5-3 mm long, and seeds 0.9-1.2 mm long. The two species resemble each other in habit, leaf morphology, flower size and color, flattening of the fruit, reduction of the septum to a rim, and number of seeds on each placenta.

Eudema hauthalii and *E. werdermannii* form dense cushions in moist seepage areas of rocky steppes. They often produce a tangled growth among fine gravel, particularly at altitudes of 700-1500 m.

5. ***Eudema werdermannii*** O. E. Schulz, Notizbl. Bot. Gart. Berlin-Dahlem 10: 462. 1928. TYPE: Chile, Prov. Atacama, Depto. Copiapó, Cord. Río Figueroa, Co. Paredones, ca. 4300 m alt., Jan. 1926, *E. Werdermann 974* (holotype, v! (photos, f!, GH!, NY!); isotypes, f!, GH!, M!, MO!, NY!, s!, uc!, us!, z!).

Cespitose, rhizomatous perennials forming dense cushions; rhizomes branched, 1–2.5 mm wide, with sessile, ovate to lanceolate scales at nodes. Leaves rosulate, somewhat fleshy, narrowly oblanceolate to spatulate, (3–)8–20(–30) mm long, (0.7–)1–2(–3.5) mm wide, obtuse to rounded at apex, entire, attenuate at base, glabrous on lower surface, usually densely pubescent on upper surface with dendritic trichomes; petioles ciliate with simple or furcate trichomes, somewhat expanded at base. Sepals erect, oblong, 3–4 mm long, 1.4–1.8 mm wide, obtuse at apex, scarious at margin, sparsely pubescent on back with dendritic trichomes. Petals oblanceolate, (4.5–)5–7 mm long, 1.5–2.2 mm wide, rounded at apex, cuneate at base, white to creamy white. Filaments 2.5–3.5 mm long; anthers oblong, 0.8–1 mm long. Fruiting peduncles glabrous, 3.5–20 cm long. Fruits sessile, suborbicular, strongly compressed parallel to replum, 2.5–3 mm in diameter; septa reduced to narrow rim; styles 0.2–0.8 mm long; stigmas capitate, slightly 2-lobed. Seeds 3 to 5 on each placenta, ovoid, 0.9–1.2 mm long, 0.6–0.8 mm wide.

REPRESENTATIVE SPECIMENS. **Argentina:** PROV. SAN JUAN: Quebrada Ortiga, E part of Cordillera de la Ortiga, *Johnston 6174* (BA, GH, S), 6290 (GH); Quebrada de Coucoute, between Las Vicuñitas and el Portezuelo de Coucoute, *Moreau 30/87* (BA); Iglesia, Río Blanco cerca del Baño del Bollete, *Castellanos 15523* (US).

Eudema werdermannii forms prostrate mats in wet gravel at altitudes of 3800 to 4300 m. Field notes on *Johnston 6174* (GH) indicate that the plant produces much-branched rhizomes that form a tangled growth in the gravel, and that the plants are smaller and less branched in drier sites than in wetter areas.

Eudema werdermannii is highly variable in habit and leaf size and shape. Plants of the type collection have much-shortened rhizomes that terminate in a compact, few-branched caudex. In contrast, those of *Johnston 6174* are rather lax and have long, slender rhizomes with a conspicuous, sessile scale at each node. The variation in leaf size and shape is evident within each population, and apparently plants of the drier sites have smaller leaves with shorter petioles than those of the wetter ones.

6. *Eudema friesii* O. E. Schulz, Pflanzenr. IV. 105(Heft 86): 245. 1924. TYPE: Argentina, Prov. Salta, Incachuli bei San Antonio de las Cobras, ca. 5000 m alt., 30 Oct. 1901, *Fries 703* (holotype, B! (photos, F!, GH!, NY!); isotype, UPS!).

Prostrate rhizomatous perennials; rhizomes slender, branched, with conspicuous, sessile scale at each node; branches terminated by rosettes and covered below leaves with petiolar remains of previous years. Leaves rosulate, petiolate, lanceolate to linear, (5–)9–16 mm long, (1.5–)2–3 mm wide, obtuse at apex, pinnately lobed to rarely dentate at margin, glabrous on lower surface, sparsely pubescent on upper surface and margin with dendritic trichomes. Flowering peduncles originating from center of rosette, 2–4 mm long. Sepals erect, ovate, 2.5–3.5 mm long, ca. 1.5 mm wide, glabrous or sparsely pubescent below apex, scarious at margin. Petals spatulate, 5–6.5 mm long, 1.2–1.5 mm wide, creamy white, rounded at apex, attenuate to clawlike base. Filaments 3–3.5 mm long; anthers oblong, 0.9–1 mm long. Young fruits ovate, apparently

compressed parallel to replum, glabrous; septa reduced to narrow rim; styles ca. 0.5 mm long. Seeds not seen.

ADDITIONAL SPECIMEN EXAMINED. **Bolivia**. DEPTO. ORURO: Prov. Carangas, Sajama, 4200 m alt., *Asplund* 3988 (s).

Eudema friesii is a very rare species that apparently grows on fine gravel. Its nearest relative is *E. werdermannii*, which it resembles in having branched trichomes, slender rhizomes, and creamy white flowers. It is easily distinguished from the remaining species of *Eudema* by its pinnately lobed instead of entire leaves.

EXCLUDED NAMES

- Eudema colobanthoides* (Skotts.) O. E. Schulz, Pflanzenz. IV. **105**(Heft 86): 246. 1924. = *Xerodraba colobanthoides* Skotts. Kongl. Svenska Vetenskapsakad. Handl. **56**(5): 234. 1916.
- Eudema diapensioides* (Wedd.) O. E. Schulz, Pflanzenz. IV. **105**(Heft 86): 245. 1924. = *Brayopsis diapensioides* (Wedd.) Gilg & Muschler, Bot. Jahrb. Syst. **42**: 484. 1909.
- Eudema glebaria* (Speg.) Gilg & Muschler, Bot. Jahrb. Syst. **42**: 472. 1909. = *Xerodraba glebaria* (Speg.) Skotts. Kongl. Svenska Vetenskapsakad. Handl. **56**(5): 362. 1916.
- Eudema lycopodioides* (Speg.) Gilg & Muschler, Bot. Jahrb. Syst. **42**: 471. 1909. = *Xerodraba lycopodioides* (Speg.) Skotts. Kongl. Svenska Vetenskapsakad. Handl. **56**(5): 362. 1916.
- Eudema microphylla* (Gilg) Gilg & Muschler, Bot. Jahrb. Syst. **42**: 472. 1909. = *Xerodraba pycnophylloides* (Speg.) Skotts. var. *microphylla* (Gilg) O. E. Schulz, Pflanzenz. IV. **105**(Heft 86): 250. 1924.
- Eudema monantha* (Gilg) Gilg & Muschler, Bot. Jahrb. Syst. **42**: 472. 1909. = *Xerodraba monantha* (Gilg) Skotts. Kongl. Svenska Vetenskapsakad. Handl. **56**(5): 362. 1916.
- Eudema patagonica* (Speg.) Gilg & Muschler, Bot. Jahrb. Syst. **42**: 471. 1909. = *Xerodraba patagonica* (Speg.) Skotts. Kongl. Svenska Vetenskapsakad. Handl. **56**(5): 362. 1916.
- Eudema pectinata* (Speg.) Gilg & Muschler, Bot. Jahrb. Syst. **42**: 471. 1909. = *Xerodraba pectinata* (Speg.) Skotts. Kongl. Svenska Vetenskapsakad. Handl. **56**(5): 235. 1916.
- Eudema pycnophylloides* (Speg.) Gilg & Muschler, Bot. Jahrb. Syst. **42**: 471. 1909. = *Xerodraba pycnophylloides* (Speg.) Skotts. Kongl. Svenska Vetenskapsakad. Handl. **56**(5): 362. 1916.
- Eudema thlaspiforme* Philippi, Anales Univ. Chile **41**: 675. 1872. = *Draba philippii* O. E. Schulz, Notizbl. Bot. Gart. Berlin-Dahlem **10**: 559. 1929.
- Eudema trichocarpa* Muschler, Bot. Jahrb. Syst. **40**: 276. 1908. = *Weberbaueria trichocarpa* (Muschler) J. F. Macbr. Candollea **5**: 356. 1934.

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