
New Species and Combinations in *Larnax* (Solanaceae)

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ABSTRACT. Based on phylogenies generated using morphological and molecular data, *Deprea glabra* and *D. sylvarum* are transferred to *Larnax*, and a new subspecies, *L. sylvarum* subsp. *novogranatensis*, is described. Four new species are described and illustrated: *Larnax cuyacensis* from Peru, similar to *L. glabra* and *L. sylvarum*, but with a rotate, fleshier corolla much lighter in color, and a fruiting calyx tightly appressed to the berry; *L. grandiflora* from Peru, intermediate between *L. andersonii* and *L. sachapapa*; *L. parviflora* from Peru, similar to *L. psilophyta* of Ecuador, but differing in vegetative and reproductive characters and having the smallest flowers in the genus; and *L. darcyana* from Colombia, similar to *L. subtriflora* of Peru, but differing vegetatively and with much shorter, non-branching hairs, a smaller corolla, shorter filaments, and apiculate anthers. Keys are provided for selected genera and for *Larnax*. In addition, some synonymies are noted.

Key words: *Deprea*, *Larnax*, Solanaceae, South America.

The genus *Larnax* (Miers) Hunziker, native to montane regions of northwest South America, is among a group of approximately 12 so-called "physaloid" genera in the large tribe Solaneae (Avrett, 1979; D'Arcy, 1991). Although closely aligned with *Deprea* Rafinesque, *Larnax* is certainly distinct in its floral and pollen morphology (Sawyer, 1999). The known diversity in *Larnax* has expanded in recent years to include 18 species (Hunziker, 1977; Hunziker & Barboza, 1995; Leiva, 1996; Leiva et al., 1998a, 1998b; Sawyer, 1998).

Species of *Larnax* are tropical Andean shrubs or small trees 0.3–5 m tall, occurring from northern Peru to Colombia. The taxonomic revisions herein extend their distribution as far north as Costa Rica. With few exceptions species are of limited distribution. Although infrequent in most habitats, they are recognized easily, like many shrubby taxa in this family, by their plagiotropic upper stem and leaf growth and by the axillary fascicles of from 1 to several flowers per node. Corolla color ranges from cream to yellow to purple, and can be variable within species (Sawyer & Benítez, 1998). Fruits are

fleshy orange berries usually containing from 60 to over 100 small seeds. *Larnax* has been taxonomically associated with the genus *Deprea* Rafinesque (Barboza & Hunziker, 1994; Hunziker, 1977). Heteranthery is one character that delimits *Larnax* from *Deprea*. In *Deprea*, anthers in the same flower are of equal size, whereas in *Larnax*, the 5 anthers are grouped in arrays of either 2 or 3 different size classes. Other characters that separate these genera include the presence of thickened filament bases forming a stamen petalum (see Barboza & Hunziker, 1991) in *Larnax* (filament bases are never thickened in *Deprea*), the degree of corolla fusion (in *Deprea* corollas are infundibular, with the limb shorter than or equal to the tube; in *Larnax* corollas are always rotate-campanulate, the limb always longer than the tube), and the echinate pollen morphology in *Larnax* vs. rugulate in *Deprea* (Barboza & Hunziker, 1994; Sawyer, 1999). A list of *Larnax* species and their synonymies is presented in Appendix 1. Not included are nomina nuda I have encountered in the literature and among museum specimens. These include "*Athenaea costaricensis*" applied by Bitter to *L. sylvarum*, "*A. weberbaueri*" applied by Bitter to *L. subtriflora*, and "*L. nieva*" (see Leiva et al., 1998b). Character-based cladistic analysis of *Deprea* and *Larnax* will be presented elsewhere.

Based on analyses from both morphological and molecular data (Sawyer, 1999) to be expanded upon elsewhere, the following new combinations are necessary.

Larnax glabra (Standley) N. W. Sawyer, comb. nov. Basionym: *Athenaea glabra* Standley, Trop. Woods 42: 32. 1935. *Deprea glabra* (Standley) Hunziker, Kurtziana 10: 25. 1977. TYPE: Ecuador. [Bolívar] Western cordillera above Balsapampa, 2600 m, 14 Dec. 1934, A. Rimbach 239 (holotype, F lost, F photo; isotypes, B destroyed, G, GH, NY, WIS photo, Y not seen).

Results of canonical variates analysis have demonstrated that *Larnax glabra* is distinct from its sister species *L. sylvarum* (Fig. 1). *Larnax glabra* is

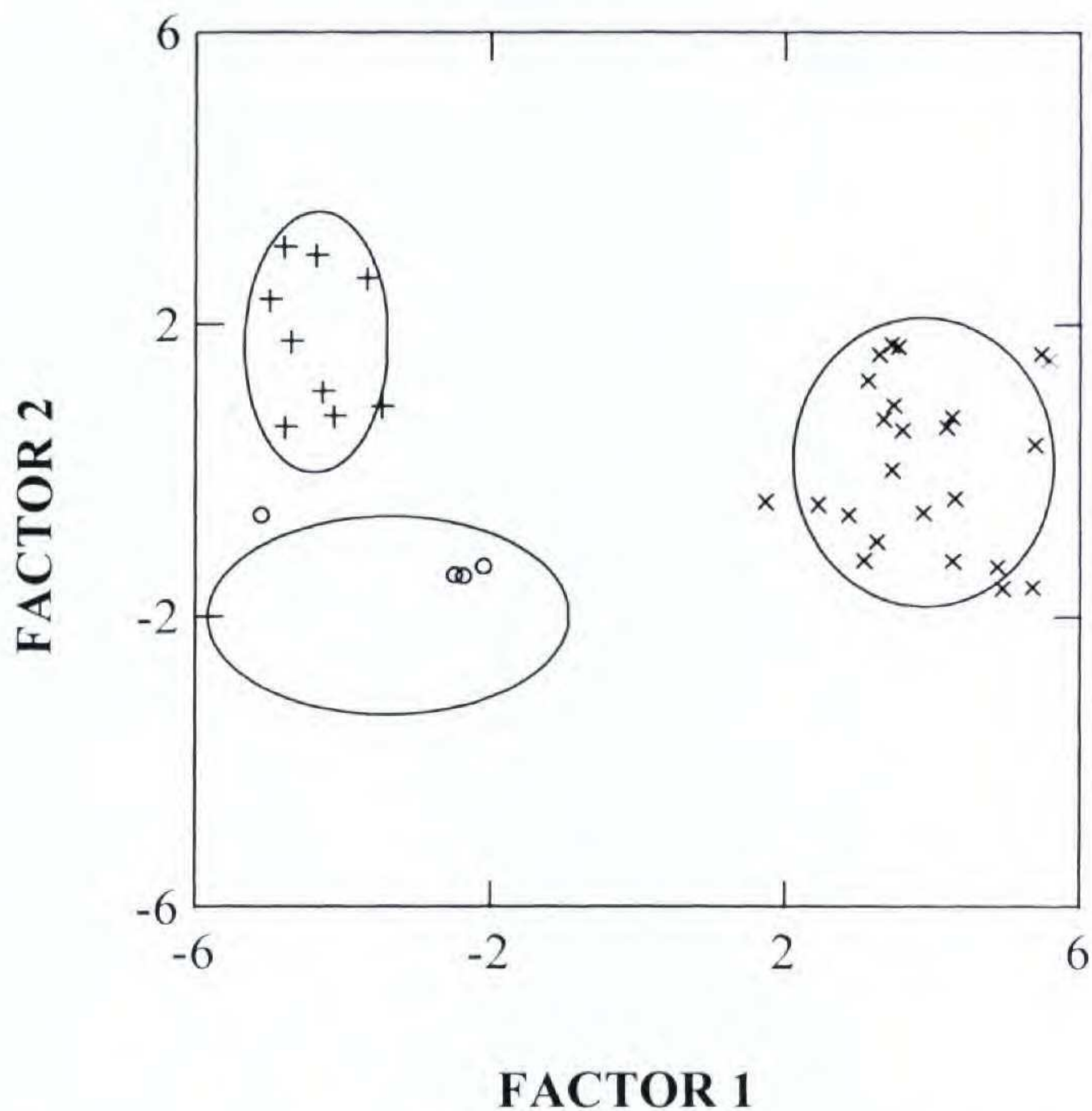


Figure 1. Canonical variates analysis using 10 continuous variables for Central American and Colombian populations of *Larnax sylvarum* and *L. glabra* from Colombia and Ecuador. Factor 1 accounts for 89.6% of the total variance; factor 2 accounts for the remaining 10.4%. Central American *L. sylvarum* = (0); *L. glabra* = (x); Colombian *L. sylvarum* = (+).

distinguished by its glabrous, somewhat fleshy and falcate leaves; the relatively large purple, campanulate corollas with lobes about equal to the corolla tube; and the presence of a stamen petalum with projections at the shoulders.

Habitat and distribution. *Larnax glabra* inhabits cloud forest and wet middle montane habitats from 1800 to 3700 m. This species has a relatively broad distribution in relation to many *Larnax* species, occurring from southern Ecuador to central Colombia.

Larnax sylvarum (Standley & C. V. Morton) N. W. Sawyer, comb. nov. Basionym: *Athenaea sylvarum* Standley & C. V. Morton, Field Mus. Nat. Hist. Bot. Ser. 18: 1036. 1938. *Deprea sylvarum* (Standley & C. V. Morton) Hunziker, Kurtziana 10: 25. 1977. TYPE: Costa Rica. San José: Finca La Cima, N of El Copey, 2100–2400 m, 21–22 Dec. 1925, Standley 42812 (holotype, US; GH, WIS photos).

Characters that delimit *Larnax sylvarum* from *L. glabra* include its geminate leaves, the corolla usually with some green coloration present, the small size of the corolla and perianth, the occurrence of calcium oxalate crystals in the pollen sac, the occurrence of a stamen petalum without projections at the shoulders, the lustrous pale to whitish green

fruiting calyx with purple veins, and the small berry.

Habitat and distribution. This species inhabits cloud forest and wet middle montane habitats from 1500 to 2900 m. This subspecies has been collected only in Central America in western Panama and Costa Rica. This is the only species in the group that occurs in Central America. It is entirely possible that this species has evolved by allopatric speciation of *L. glabra* following dispersal into Central America.

Larnax sylvarum (Standley & C. V. Morton) N. W. Sawyer subsp. **novogranatensis** N. W. Sawyer, subsp. nov. TYPE: Colombia. Antioquia: Mpio. Jardín, km 20 of road Jardín–Riosucio (Dpto. Caldas), ca. 15 km SSE of Jardín, Alto de Ventanas, 5°31'N, 75°48'W, 2700–2790 m, Oct. 1988, J. Zarucchi, McPherson & Roldán 6926 (holotype, TEX; isotypes, COL, HUA).

A *L. sylvarum* subsp. *sylvarum* distinguitur foliis et staminum filamentis brevioribus; distantis brevioribus inter folii nervos secundarios; pedicellis, corollis, calycis lobisque longioribus; corollae tubo, et calyce fructifero longiore; et fructu grandiore.

Morphometric analyses using the methods of Sawyer and Benítez de Rojas (1998) have shown individuals (10 from 3 populations) of *Larnax sylvarum* from northern Colombia group together, distinct from the Central American individuals (10 from 6 populations from northern Panama and Costa Rica) of *L. sylvarum* and *L. glabra* (10 from 10 populations from Colombia and Ecuador; Fig. 1). Of the 10 variables used (leaf apex width, leaf length, petiole length, hair length, corolla length, anther length, anther length/filament length, fruiting calyx length, fruiting calyx lobe length, and seed diameter), loadings for anther length, leaf apex width, and leaf length were highest for factor 1, and loadings for corolla length, anther length, and fruiting calyx length were highest for factor 2. Mahalanobis distances from a canonical variates analysis (SYSTAT 7, 1997, SPSS, Inc., Chicago) between group centroids showed all pairs to be significantly different ($P < 0.0001$). Wilks's lambda values (SYSTAT 7, 1997, SPSS, Inc., Chicago) also were highly significant ($P < 0.0001$). For these reasons, the subspecies *novogranatensis* is here described.

Habitat and distribution. This subspecies occurs only in north-central Colombia, disjunct and distinct from the distribution of subspecies *sylvarum*, which appears restricted to Central America. It occurs in wet montane and cloud forests from 2300 to nearly 3000 m. Its occurrence in northern

Colombia may be explained by recent dispersal events from Costa Rica to Colombia.

KEY TO SUBSPECIES OF *LARNAX SYLVARUM*

- 1a. Leaves to 7 cm long, secondary leaf veins to 7 mm apart; flowering pedicels to 10 mm long, corolla 7.5–10 mm long, corolla tube 3.3–5 mm long; filaments to 4.5 mm long; fruiting calyx 8–14 × 8–14 mm, fruiting calyx lobes 0.7–1.5 mm long, maximum fruit length 10 mm
 *Larnax sylvarum* subsp. *novogranatensis*
- 1b. Leaves to 11 cm long, secondary leaf veins to 15 mm apart; flowering pedicels to 9 mm long, corolla 6.5–9.5 mm long, corolla tube 3–4.5 mm long; filaments to 6.2 mm long; fruiting calyx 7–8.5 × 6–7.8 mm, fruiting calyx lobes 0.3–1.4 mm long, maximum fruit length 7.5 mm
 *Larnax sylvarum* subsp. *sylvarum*

Paratypes. COLOMBIA. **Antioquia:** Jardín, vía Jardín–Riosucio, bosque húmedo premontano, 7 km de Jardín, a orilla de riachuelo, 05°30'N, 75°50'W, 2020 m, June 1987 (fr), *Callejas et al.* 3748 (COL); Vereda Ventanas, Jardín–Ventanas–Riosucio road, ca. 19.3 km SSE of Jardín, at border with Caldas, forest at highpoint of road (Ventanas), ca. 5°40'N, 75°47'W, 2830 m, May 1989 (bd, fl, fr), *Luteyn & Escobar* 12750 (COL, HUA); carretera Jardín (Antioquia) Riosucio (Caldas), Sitio Ventanas, cerca a la torre repetidora de T.V., 2900 m, Apr. 1987 (bd, fl, fr), *Marulanda & Jaramillo* 264 (HUA); carr. Jardín–Riosucio Sitio Ventanas, 2900 m, June 1987 (bd, fl, fr), *Marulanda et al.* 481 (HUA). **Huila:** Comisaría del Caquetá, Cordillera Oriental sobre el filo divisorio, en Gabinete, 2300–2450 m, Mar. 1940 (bd, fl, fr), *Cuatrecasas* 8458 (COL). **Nariño:** road to Laguna La Cocha, ca. 10 km E of Pasto, 1°12'N, 77°10'W, 3000 m, Jan. 1981 (fl, fr), *Gentry et al.* 30404 (COL).

Larnax cuyacensis N. W. Sawyer & S. Leiva, sp. nov. TYPE: Peru. Piura: Ayabaca, Mpio. of Yacupampa, 8 km NE of Ayabaca above Las Cuyas, in quebrada, 4°37'S, 79°42'W, 2600 m, 6 June 1997, *N. W. Sawyer* 797 (holotype, MO; isotypes, CONN, HAO, NY).

Species nova *L. glabrae* affinis, a qua corolla rotata carnosiora subviolacea, calyce fructifero adpresso arcte baccae, seminibus paucioribus differt.

Shrub or small tree, 0.8–5 m tall. Stems purple with branchlets strongly or weakly flexuous; nodes often swollen, glabrate; young stems sparsely puberulent. Leaves membranous, occasionally paired, elliptic, somewhat falcate, the apex acuminate, the base oblique, cuneate-attenuate, 4.5–10.5 × 1.5–4 cm, glabrous below and on the veins, sparsely puberulent above and along margins with multicellular, simple or occasionally branched, non-glandular hairs 0.3–0.8 mm long, leaves glabrate. Petiole 0.2–1.8 cm long, glabrous. Inflorescence axillary; flowers 3 to 6 per node in fascicles from a much reduced peduncle to 1.5 mm long and ad-

nate to the stem. Flowers somewhat pendent or perpendicular to the stem on glabrate pedicels 3–12 mm long. Flowering calyx green with purple veins, glabrate, ca. 5 mm long, ca. 4 mm diam., with subulate lobes 1–1.2 mm long. Corolla campanulate-rotate, pale violet, somewhat fleshy, 2–3 mm wide at the base, 11–12.5 mm long, sparsely to moderately puberulent externally with non-glandular and branched hairs and sessile glands, the interior puberulent with 11–33 non-glandular hairs/mm², the tube 6–7 mm long, the lobes narrowly triangular, flared at anthesis, 5–6.5 mm long. Stamens exerted from the corolla tube, slightly exerted from the corolla limb. Filaments sparsely puberulent at their base with non-glandular hairs, the free portion 4.5–5.5 mm long, adnate to the basal quarter of the corolla tube and there broadened and thickened forming a stamen petalum, the bases separated by the corolla vasculature, the adnate portion 1–1.5 mm long. Anthers dorsifixed, white, ovate-elliptic, occurring in two or three size arrays, 2–2.3 × 1.2–1.5 mm, the bases of thecae connivent, calcium oxalate crystals occurring as druses in pollen sacs. Pollen echinate. Ovary glabrous, conical, ca. 1.5 mm long, ca. 1.5 mm diam., ringed basally by a nectary. Style glabrous, to ca. 9 mm long at anthesis, exerted prior to anthesis; stigma clavate. Fruiting pedicels glabrate, ca. 14 mm long. Fruiting calyx accrescent, tightly investing the fruit, open at the apex, greenish white with purple veins, globose, ca. 10 mm long, ca. 11 mm diam., sparsely puberulent externally, the interior with scattered sessile glands and 2-celled stalked glands with unicellular heads; lobes shallowly triangular-subulate, 0.6–1.2 mm long, of unequal lengths. Fruit a berry, immature berry cream, globose, 9–10 mm diam.; seeds ca. 12, 2.7–3.1 mm diam.

Larnax cuyacensis is similar to *L. glabra* and *L. sylvarum* but possesses a corolla that is rotate and fleshier, with much lighter coloration; calcium oxalate crystals in the pollen sac; a fruiting calyx that is tightly appressed to the berry; and fewer seeds.

Habitat and distribution. This species is only known from the region around Ayabaca, north of the Huancabamba deflection in northern Peru, from 2400 to 2600 m in montane forest. The distribution of this species and *L. glabra* and *L. sylvarum*, with which it is affiliated, forms a continuum extending from northern Peru to Costa Rica.

Paratypes. PERU. **Piura:** Montaña de Cuyas, 8 km NE of Ayabaca, 4°32'S, 79°44'W, 2400–2410 m, Sep. 1991 (fr), *Gentry et al.* 75121 (MO); Ayabaca, Yacupampa, May 1971 (bd, fl, fr), *López et al.* 7722 (NY); Ayabaca, Las Cuyas, 2580 m, 6 June 1997 (bd, fl, fr), *Sawyer* 799 (CONN).

Larnax darcyana N. W. Sawyer, sp. nov. TYPE: Colombia. Huila: forest around Mehrenberg, road from Popayán, 2350 m, 6 July 1984, W. G. D'Arcy, Gentry, Monsalve & Silverstone 15626 (holotype, MO; isotype, CONN). Figure 2.

A *L. subtriflora* ramulis non flexuosis, foliis glabris parvioribus pilis haud ramosis multo brevioribus, corolla brevior, filamentis brevioribus, antheris apiculatis, calyce fructifero glabro costis adpressis differt.

Shrub to 2 m tall. Stems with branchlets seldom or weakly flexuous, glabrous; young stems sparsely to moderately puberulent. Leaves membranous, occasionally paired, elliptic, the apex acuminate, the base oblique, cuneate-attenuate, 3–9 × 1.4–5.2 cm, sparsely puberulent beneath, along veins and margin with multicellular, simple hairs 0.2–0.5 mm long; leaves glabrate. Petiole 0.4–1.5 cm long, sparsely to moderately puberulent, glabrate. Inflorescence axillary; flowers 1 to 4 per node in fascicles from a much reduced peduncle to 2.2 mm long either free or partially adnate to the stem. Flowers pendent on sparsely to moderately pubescent pedicels 3–7 mm long. Flowering calyx green, sparsely hirsute, ca. 2 mm long, ca. 3 mm diam., with lobes absent or with very shallow triangular or subulate lobes < 0.6 mm long. Corolla campanulate, pale greenish yellow, membranous, 7.8–10 mm long, ca. 2.5 mm wide at the base, sparsely hirsute and with sessile glands externally, the interior glabrous or with a few non-glandular hairs, the tube 2–3 mm long, the lobes triangular-acute, 5.5–7.2 mm long. Stamens exerted from the corolla tube, included in the corolla limb. Filaments glabrous, unequal in length, the free portion 1.8–3.1 mm long, adnate to the basal half of the corolla tube and there broadened and thickened forming a stamen petalum, the bases separated by the corolla vasculature, the adnate portion 1–1.5 mm long. Anthers dorsifixed, connivent, ovate-elliptic, apiculate, occurring in 3 size arrays, 1.8–2.5 × 1.2–1.5 mm, the bases of thecae sagittate; calcium oxalate crystals occurring as druses in pollen sacs. Pollen surface type unknown. Ovary glabrous, conical, 1–1.1 × 0.8–1 mm, ringed basally by a nectary. Style glabrous, 4.5–5.5 mm long; stigma clavate. Fruiting pedicels sparsely to moderately puberulent, 7–14 mm long. Fruiting calyx accrescent, the basal half tightly investing the fruit, open at the apex, lustrous green and purple with dark green or purple veins, somewhat pyriform-urceolate, 11–16.5 × 9.5–11 mm, glabrous within and without; lobes subulate, < 0.8 mm long, of unequal lengths. Fruit an orange berry, globose, 8–11 mm diam.; seeds 40–65; 2.9–3.8 mm diam.

This species is similar to *L. subtriflora* of Peru, but *L. darcyana* lacks the flexuous stems of *L. subtriflora*. *Larnax darcyana* has smaller, sparsely puberulent leaves with much shorter, non-branching hairs, a smaller corolla, shorter filaments, apiculate anthers, calcium oxalate crystals in the pollen sac, and glabrous fruiting calyces with appressed costae.

Habitat and distribution. Known only from the wet montane forests of the Mehrenberg region in Huila Province and to the north in the Parque Regional Ucumarí in Risaralda, Colombia, from 2200 to 2400 m where it occurs with *L. hawkesii*.

Paratypes. COLOMBIA. **Huila:** forest around Mehrenberg, road from Popayán, 2300 m, July 1984 (bd, fl), D'Arcy et al. 15595, 15627 (MO); finca Mehrenberg E of Volcán Puracé, near Cauca border, 02°16'N, 76°12'W, 2300 m, Apr. 1986 (bd, fl, fr), Gentry 53988 (NY, MO). **Risaralda:** Mpio. Pereira, Parque Regional Ucumarí, Cordillera Central, 4°45'N, 75°35'W, 1600 m, Aug. 1995 (bd, fr), Murcia 390 (MO).

Larnax grandiflora N. W. Sawyer & S. Leiva, sp. nov. TYPE: Peru. Cajamarca: Mpio. San Ignacio, in forest along road from San Martín to El Chaupe, 5°11'S, 79°03'W, 1700 m, 26 June 1997, N. W. Sawyer 827 (holotype, NY; isotypes, CONN, HAO, MO). Figure 3.

Planta inter *L. andersonii* et *L. sachapapa* quasi intermedia; a *L. andersonii* lobis calycis multo grandioribus, corolla multo grandiore differt; a *L. sachapapa* lobis calycis haud subulatis, intervenio corollae maculato atrovioleaceo differt.

Shrub, 0.5–1.5 m tall. Stems with branchlets seldom or weakly flexuous, sericeous. Leaves membranous, always geminate, heterophyllous, the larger (major) leaves elliptic, the apex acuminate, the base oblique, cuneate-attenuate, 3–10.5 × 2–5 cm, the smaller (minor) leaves ovate or elliptic-ovate, the apex cuspidate, the base truncate, 1.5–2.5 × 1.2–2 cm, strigose to sericeous above, hirsute to sericeous below, especially along the veins with long, multicellular, simple hairs 0.6–1.8 mm long. Petiole 0.6–1.5 cm long on major leaves, 1–2 mm long on minor leaves, sericeous. Inflorescence axillary, distal on a branch; flowers solitary; peduncle lacking. Flowers pendent or perpendicular to the stem, on sericeous pedicels 5–15 mm long. Flowering calyx green, sericeous, to 9.4 mm long, ca. 4 mm diam., with lanceolate lobes 2–7 mm long, of unequal lengths. Corolla campanulate to rotate, pale greenish cream with lustrous violet maculations internally between the veins, membranous, 19–20 mm long, sericeous externally, the interior glabrate with 0 or 1 non-glandular hairs/mm², the

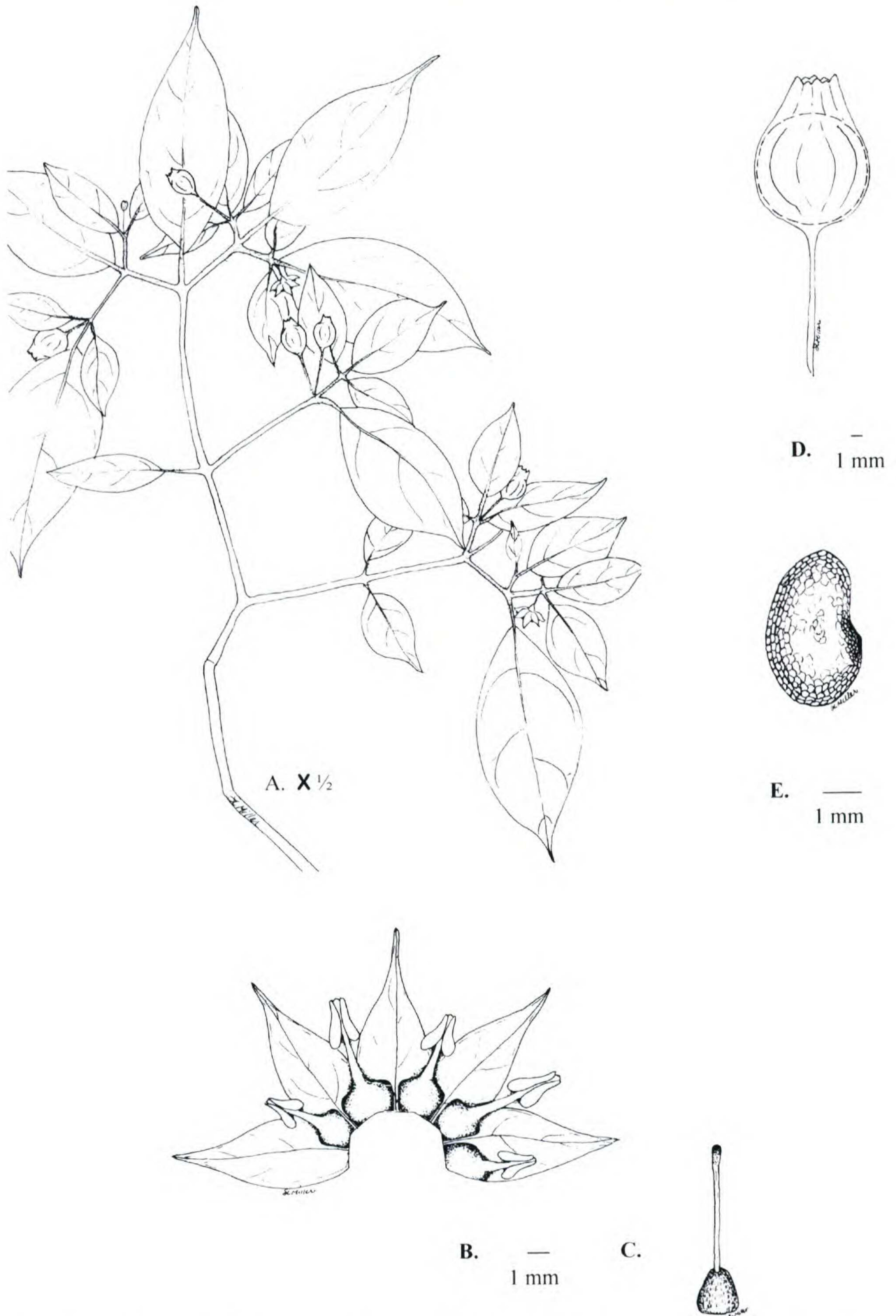


Figure 2. *Larnax darcyana* N. W. Sawyer (*D'Arcy et al. 15626*). —A. Branch apex. —B. Interior of mature corolla and androecium. —C. Mature gynoecium. —D. Mature fruiting calyx. —E. Mature seed.

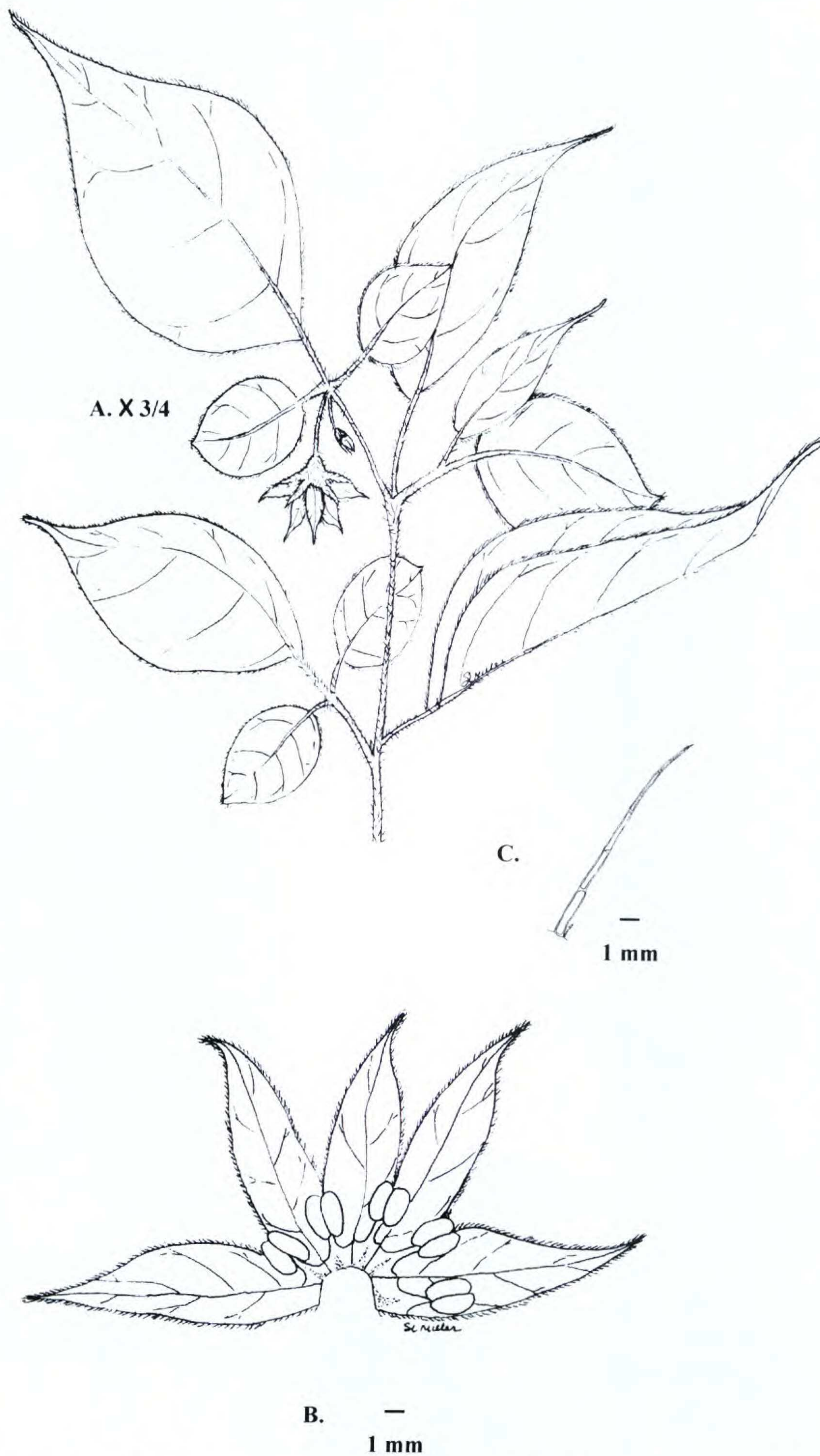


Figure 3. *Larnax grandiflora* N. W. Sawyer & S. Leiva (Sawyer 827). —A. Branch apex. —B. Interior of mature corolla and androecium. —C. Non-glandular leaf trichome.

tube 2–4 mm long, lobes narrowly triangular, reflexed at the apex, ca. 17 mm long, 4–4.5 mm wide at the base. Stamens exerted from the corolla tube, included within the corolla limb. Filaments glabrous, unequal in length, the free portion 2.5–3.5 mm long, adnate to the basal half of the corolla and there broadened and thickened forming a stamen petalum, the bases separated by the corolla vasculature, the adnate portion 1–1.6 mm long. Anthers dorsifixed, connivent, white to violet tinted, ovate to elliptic, occurring in 2 or 3 size classes, 1.8–2.3 × 1.5–1.9 mm, the bases of thecae sagittate; calcium oxalate crystals occurring as druses in pollen sacs. Pollen surface type unknown. Ovary glabrous, obovate to conical, 1.7–1.8 × 1.5–1.8 mm, ringed by a basal nectary. Style glabrous, ca. 5 mm long; stigma clavate. Fruit not known.

Similar to *L. andersonii*, this is the only other species in the genus displaying heterophyllous, geminate leaves and solitary flowers. Although the indumentum is abundant and composed of long hairs as in *L. andersonii*, bifurcating hairs are lacking. *Larnax sachapapa* and *L. grandiflora* have the largest flowers in the genus, both to 2 cm long. Unlike the well-collected *L. sachapapa*, the single known population of three individuals of *L. grandiflora* severely limits our knowledge of corolla size variation in this species. Unlike *L. sachapapa*, which has a yellowish green or white corolla, the corolla of *L. grandiflora* contains lustrous purple maculations between the primary and secondary veins internally, similar to that of *L. sagasteguii*. The flowering calyx of *L. grandiflora* possesses very long and narrow triangular lobes to 7 mm, a character unique to this species. The vegetative morphology of *L. grandiflora* appears intermediate between *L. andersonii* and *L. sachapapa*, both of which occur in northern Peru.

Habitat and distribution. This species has been collected only in Mpio. San Ignacio, Peru, in wet, relict montane forest at an elevation of ca. 1700 m.

Larnax parviflora N. W. Sawyer & S. Leiva, sp. nov. TYPE: Peru. Cajamarca: Mpio. Cutervo, Bosque Cutervo, Parque Nacional de Cutervo, NW corner of Cordillera Tarros, Chorro Blanco sector, ca. 10 km WNW of San Andreas, 6°12'S, 78°46'W, 2650 m, 4 Nov. 1990, M. Dillon, Sánchez & Guevara 6141 (holotype, F; isotype, HAO). Figure 4.

Ab aliis speciebus generis distinguitur caulibus et foliis glabris, 1–3 floribus axillaribus, corolla sulphurea et minus quam 5 mm longa petalis reflexis, limbo interioris corollae pilis brevibus annularibus, fructu assurgenti, et sem-

inibus paucis. Ab affinibus *L. psilophytæ* aequatorialis praeclare differt amplitudine et colore corollae et habitu arboris.

Shrub or small tree from 0.3 to 5 m tall. Stems dull greenish brown with branchlets seldom or slightly flexuous, glabrous. Leaves somewhat fleshy, occasionally paired, elliptic, the apex acute, the base oblique, cuneate, 2.5–11.5 × 1–4.5 cm, glabrous. Petioles on mature, more terminal leaves 0.2–0.7 cm long to 2.8 cm long on lower (shaded) leaves, sparsely puberulent with short pluricellular, non-glandular hairs. Inflorescence axillary, flowers 1 to 3 per node from a peduncle ca. 0.6 mm long, this adnate to the stem. Flowers somewhat pendent or perpendicular to the stem on sparsely puberulent pedicels 3–6 mm long. Flowering calyx green, 1–1.8 × 2.5–3 mm, sparsely pubescent externally with 1- or 2-celled non-glandular hairs and sessile, unicellular glands, the lobes absent or shallowly triangular, < 0.2 mm long. Corolla campanulate to rotate, pallid yellow, somewhat fleshy, 3.5–4.8 mm long, with sessile glands, otherwise glabrous externally, the interior sparsely to moderately puberulent with 6–25 non-glandular hairs/mm², tube 1.3–1.6 mm long, the lobes triangular, rotate-reflexed, 2–2.5 mm long, ca. 1.5 mm wide at the base. Stamens completely exerted in anthesis. Filament base sparsely hirsute with short uni- or bi-cellular hairs, otherwise glabrous; filaments unequal in length, the free portion 1.3–1.9 mm long, adnate to ca. the basal half of the corolla and there broadened and thickened forming a stamen petalum, the bases separated by the corolla vasculature, the adnate portion 0.5–1 mm long. Anthers dorsifixed, connivent, white, ovate to elliptic, occurring in 2 or 3 size classes, the shortest anther commonly aborting when 3 size classes present, 0.8–1.6 × 0.7–1.3 mm, the bases of thecae sagittate; calcium oxalate crystals occurring as druses and blocks in pollen sacs. Pollen echinate. Ovary glabrous, ovate to conical, 1–1.2 × 1 mm, ringed at the base by a nectary. Style often involute, 3.5–4.2 mm long, exerted prior to anthesis; stigma clavate. Fruiting pedicels assurgent, 11–20 mm long, sparsely pubescent. Fruiting calyx accrescent, tightly investing the fruit, open at the apex, green with inconspicuous ribs, urceolate with apex narrowing and slightly lengthened above the berry, 5–6 × 5–5.2 mm, exterior and interior glabrous, sessile glands present externally; lobes lacking or with minute teeth of unequal lengths no longer than 0.5 mm. Berry turning from green to orange to purple, glo-



Figure 4. *Larnax parviflora* N. W. Sawyer & S. Leiva (*Dillon et al.* 6141). —A. Branch apex. —B. Mature flower. —C. Interior of mature corolla and androecium. —D. Mature gynoecium. —E. Mature fruiting calyx.

bose, ca. 5 mm diam., seeds 15 to 20, 1.6–2.6 mm long.

This species is very similar to the Ecuadorian endemic *L. psilophyta*, its counterpart north of the Huancabamba deflection of northern Peru. Several shared attributes separate these from other *Larnax* species, which include the small, glabrous, fleshy leaves; more or less pendent inflorescences that become assurgent in fruit; small corollas with rotate limbs that lack anthocyanins; corollas that are essentially glabrous externally with an annular ring of hairs on the interior surface; and relatively few seeds.

Habitat and distribution. *Larnax parviflora*, collected from only two sites, appears to be endemic and limited in its distribution to the region around Cutervo, Cajamarca, in northern Peru. It has been found in relict montane and cloud forests and in somewhat disturbed primary forests from 2350 to 2650 m.

KEY TO *LARNAX PARVIFLORA* AND *L. PSILOPHYTA*

- 1a. Shrub or tree to 5 m tall; leaves pliant; corolla 3.5–4.8 mm long and yellow; anthers 0.8–1.6 mm long; fruiting pedicels 11–20 mm long
 *Larnax parviflora*
- 1b. Shrub to 2 m tall; leaves indurate; corolla 4–7 mm long and green; anthers 1.2–1.9 mm long; fruiting pedicels 6–9 mm long *Larnax psilophyta*

Paratypes. PERU. **Cajamarca:** Mpio. Cutervo, San Andreas, in La Pucarilla, 2350 m, 12 Aug. 1996 (bd, fl), *Sawyer 776* (CONN); Cutervo, above El Verde on road to Sto. Domingo de La Capilla, 6°19'S, 78°50'W, 2540 m, 15 June 1997 (bd, fl, fr), *Sawyer 819* (CONN); Mpio. Cutervo, San Andreas, en la Pucarilla, 2500 m, June 1988 (bd, fl, fr), *Vega 451* (F).

Larnax longipedunculata S. Leiva, Rodríguez & Campos, *Arnaldoa* 5: 194. 1998. TYPE: Peru. Cajamarca: Prov. San Ignacio, Caserío La Bermeja, bosques de neblina La Bermeja, Dist. Tabaconas, 1830 m, 4 Jan. 1998, *S. Leiva et al. 2098* (holotype, HAO not seen; isotypes, CONN, CORD not seen, F not seen, HAO not seen, HUT not seen, M not seen, MO not seen).

Larnax macrocalyx S. Leiva, Rodríguez & Campos, *Arnaldoa* 5: 197. 1998. Syn. nov. TYPE: Peru. Cajamarca: Prov. San Ignacio, Dist. Tabaconas, Caserío La Bermeja, bosques de neblina La Bermeja, La Bermeja-Huaquillo, 1700–1940 m, 20 Nov. 1997, *Rodríguez & Cruz 2052* (holotype, HUT not seen; isotypes, AMAZ not seen, CONN, CORD not seen, F not seen, HAO not seen, HUT not seen, M not seen, MO not seen, MOL not seen, NY not seen, USM not seen).

Thorough study by Sawyer of the isotype of *S.*

Leiva et al. 2098 (*L. longipedunculata*) and *Rodríguez & Cruz 2052* (*L. macrocalyx*) at CONN has provided evidence for synonymizing *L. macrocalyx* with *L. longipedunculata*. All the collections, only five in total, of *L. longipedunculata* and *L. macrocalyx* are from the same locality. The major differences listed by Leiva et al. (1998b) between these species are in the size of the leaves, the fruiting calyx, and the length of the accompanying fruiting pedicel. These discrepancies may be due solely to differences in age or local ecology. Considering the amount of variation that has been demonstrated in the genus (Sawyer, 1999), these minor differences do not, in my opinion, form enough of a basis for delineation, and *L. macrocalyx* is here treated as a synonym of *L. longipedunculata*.

Larnax sachapapa Hunziker, *Kurtziana* 10: 13. 1977. TYPE: Ecuador. Azuay: forested slopes between Cruz Pamba and Loma de Canela, in region of Río Sadracay (tributary of Río Mehuír), N of Molleturo, 2300–2500 m, 12 July 1943, *Steyermark 52965* (holotype, VEN).

Larnax pilosa S. Leiva, Rodríguez & Campos, *Arnaldoa* 5: 200. 1998. Syn. nov. TYPE: Peru. Cajamarca. Prov. San Ignacio, Dist. San José de Lourdes: Estrella del Oriente, 1600 m, 4°50'S, 78°55'W, 8 Jan. 1998, *S. Leiva, Campos & Rodríguez 2108* (holotype, HAO not seen; isotypes, CONN, CORD not seen, F not seen, HAO not seen, HUT not seen, M not seen, MO not seen, USM not seen).

Thorough study by Sawyer of an isotype of *S. Leiva et al. 2108* (CONN) described by Leiva et al. (1998b) as the new species *L. pilosa* has provided evidence for synonymizing *L. pilosa* with *L. sachapapa*. *S. Leiva et al. 2108* is undoubtedly a specimen of *L. sachapapa* as evidenced by its vegetative, floral, and fruiting characteristics, particularly the distinctive strongly subulate calyx lobes > 0.7 mm long. This collection extends the distribution of this species into Peru, making it the most widely distributed of any *Larnax* species (Colombia to Peru).

Evidence from morphology and ITS nrDNA sequence data indicates that *Deprea* and *Larnax* are distinct (Sawyer, 1999). Phylogenies generated from these data provide the basis for the transfer here of *D. glabra* and *D. sylvarum* to *Larnax*. Morphometric analyses have revealed notable differences between the Colombian and Central American representatives of *L. sylvarum* (Fig. 1), providing evidence for the circumscription of a Colombian subspecies, designated here *L. sylva-*

rum subsp. *novogranatensis*. In this article, four new species of *Larnax* are described and synonymies are noted. Hence, to date, 22 *Larnax* species are known from northwestern South America.

Within the last several years, many new species of *Larnax* have been described. When annotating museum specimens, it rapidly becomes evident that an enormous amount of confusion exists

among taxonomists as to the identity of *Larnax* species. In order to provide researchers with relevant taxonomic information and to aid researchers and herbaria in identifying museum material, the following keys are provided for selected genera within tribe Solaneae that share valvate corolla aestivation with *Larnax* (and *Deprea*) and for species of *Larnax*.

SYNOPTIC KEY TO SELECTED GENERA OF TRIBE SOLANEAE WITH VALVATE COROLLA AESTIVATION

- 1a. Calyx not accrescent.
 - 2a. Corolla lobes shorter than tube; filaments longer than anthers; fruiting calyx margin torn by expanding berry; Mexico to Brazil *Acnistus* Schott
 - 2b. Corolla lobes longer than tube; filaments shorter than anthers; fruiting calyx margin intact; Bolivia, Brazil, Uruguay *Aureliana* Sendtner
- 1b. Calyx accrescent.
 - 3a. Seeds fabiform and spherical; more than 9 flowers per inflorescence; Central America . . . *Brachistus* Miers
 - 3b. Seeds reniform and compressed; 1–7 flowers per inflorescence.
 - 4a. Corolla infundibular; filament gradually expanding basipetally where adnate to corolla; anthers equal in size.
 - 5a. Filaments adnate to corolla for ≥ 2.5 mm, calyx lobes unequal, distribution exclusively New World; Venezuela to Peru and Bolivia *Deprea* Raffinesque
 - 5b. Filaments adnate to corolla for < 1.8 mm, calyx lobes equal, distribution exclusively Old World; Europe and northern Africa to Nepal *Withania* Pauquy
 - 4b. Corolla campanulate-rotate; filament base abruptly expanded where adnate to corolla; anthers heterodynamous; Costa Rica to Peru *Larnax* (Miers) Hunziker

SYNOPTIC KEY TO THE SPECIES OF *LARNAX* (*L. GRANDIFLORA* EXCLUDED)

- 1a. Fruiting calyx tightly investing berry.
 - 2a. Fruiting calyx appressed to berry, urceolate.
 - 3a. Corolla ≥ 9 mm long, the lobes flared.
 - 4a. Mature fruiting calyx incompletely investing berry, the lobes ≥ 1.3 mm long.
 - 5a. Corolla yellow and lacking anthocyanins, the annulus of only non-glandular hairs; mature fruiting calyx intact; anthers ≤ 2.2 mm long; seeds < 50 per fruit; Peru *L. lutea* S. Leiva
 - 5b. Corolla greenish white with anthocyanins, the annulus of non-glandular and glandular hairs; mature fruiting calyx splitting; anthers ≥ 2.2 mm long; seeds > 50 per fruit; Peru *L. sagasteguii* S. Leiva, V. Quipuscoa & N. W. Sawyer
 - 4b. Mature fruiting calyx completely investing berry, the lobes ≤ 1.2 mm long.
 - 6a. Corolla unicolored, pale violet; Peru . . . *L. cuyacensis* N. W. Sawyer & S. Leiva, sp. nov.
 - 6b. Corolla bicolored, yellow with purple or brown maculations.
 - 7a. Mature leaves to 6 cm wide; 1–4 flowers per node; filaments 3.5–6 mm long; corolla with branched hairs; fruiting calyx > 50 mm²; fruit orange; Ecuador and Peru *L. suffruticosa* (Dammer) Hunziker
 - 7b. Mature leaves < 1.5 cm wide; 1–2 flowers per node; filaments 2.5–3 mm long; corolla lacking branched hairs; fruiting calyx < 50 mm²; fruit purple; Ecuador *L. steyermarkii* Hunziker
 - 3b. Corollas ≤ 9 mm long, the limb rotate.
 - 8a. Corolla > 7 mm long with anthocyanins present; berry at least 10 mm diam.; Peru *L. sawyeriana* S. Leiva, Rodríguez & Campos
 - 8b. Corolla < 7 mm long with anthocyanins lacking; berry < 8 mm diam.
 - 9a. Corolla green, 4–7 mm long; fruiting pedicel 6–9 mm long; leaves fleshy-indurate; anthers 1.2–1.9 mm long, shrub; Ecuador *L. psilophyta* N. W. Sawyer
 - 9b. Corolla yellow, < 5 mm long; fruiting pedicel 11–20 mm long; leaves somewhat fleshy; anthers < 1.6 mm long, shrub or tree; Peru *L. parviflora* N. W. Sawyer & S. Leiva, sp. nov.
- 2b. Fruiting calyx other than entirely appressed to berry, at least a portion of calyx apex free from berry, pyriform, or elongate-elliptic.
 - 10a. Fruiting calyx pyriform; berry globose or pyriform.
 - 11a. Corolla ≥ 8 mm long and yellow or white, the limb flared or without flexion; nodes green.

- 12a. Corolla yellow or yellow with purple or brown; berry globose; fruiting calyx lobes absent or dentate, < 0.5 mm long.
- 13a. Corolla glabrous within, yellow.
- 14a. Corolla > 10 mm long; plant pubescent with hairs > 1.2 mm long, branched hairs present; fruiting calyx pubescent, apex free of fruit; Peru *L. subtriflora* (Ruiz & Pavón) Miers
- 14b. Corolla < 10 mm long; plant sparsely puberulent with hairs < 0.9 mm long, branched hairs absent; fruiting calyx glabrescent, upper ½ free of fruit; Colombia *L. darcyana* N. W. Sawyer, sp. nov.
- 13b. Corolla pubescent within, yellow with purple or brown; Ecuador and Peru *L. suffruticosa* (Dammer) Hunziker
- 12b. Corolla greenish white; berry pyriform; fruiting calyx lobes strongly subulate, > 0.7 mm long; Colombia, Ecuador, and Peru *L. sachapapa* Hunziker
- 11b. Corolla ≤ 6 mm long and green, limb rotate; nodes with purple striations *L. vasquezii* S. Leiva, Rodríguez & Campos
- 10b. Fruiting calyx elongate-fusiform; berry elongate-elliptic.
- 15a. Petiole > 2 cm long; fruiting calyx lobes to 4 mm long; corolla < 8 mm long, green with anthocyanins; anthers < 2 mm long; Colombia and Ecuador *L. hawkesii* Hunziker
- 15b. Petiole < 1 cm long; fruiting calyx lobes < 0.5 mm long; corolla > 10 mm long, green without anthocyanins; anthers > 2 mm long; Ecuador . . . *L. harlingiana* Hunziker & Barboza
- 1b. Fruiting calyx loosely enveloping berry.
- 16a. Fruiting calyx urceolate; calyx ribs appressed or elevated.
- 17a. Flowers solitary, calyx ribs appressed, corolla interior glabrous or nearly so; Ecuador and Peru *L. andersonii* N. W. Sawyer
- 17b. Flowers > 3 per inflorescence; calyx ribs elevated; corolla interior densely pubescent.
- 18a. Leaves glabrescent on veins and margins; anthers < 1.6 mm long; filaments < 5 mm long; corolla < 9 mm long; fruiting pedicels ≤ 8 mm long; berry < 6 mm diam.; Colombia, Panama, and Costa Rica . . . *L. sylvarum* (Standley & C. V. Morton) N. W. Sawyer, comb. nov.
- 18b. Leaves glabrous on veins and margins; anthers > 1.7 mm long; filament > 7 mm long; corolla > 9 mm long; fruiting pedicels 10–14 mm long; berry > 6 mm diam.; Colombia and Ecuador *L. glabra* (Standley) N. W. Sawyer, comb. nov.
- 16b. Fruiting calyx pyriform–pyriform-invaginate; calyx ribs plicate.
- 19a. Corolla lobes uni-colored.
- 20a. Corolla white, the tube sometimes purple-spotted within; leaves membranous, geminate, to 24 cm long; berry 9–10 mm diam.; fruiting calyx lobes usually absent or triangular and somewhat subulate; seeds < 55; Ecuador and Peru . . . *L. peruviana* (Zahlbruckner) Hunziker
- 20b. Corolla purple; leaves lustrous, fleshy, attached singly, to 18 cm long; berry to 14.5 mm diam.; fruiting calyx lobes prominent, triangular; seeds > 55; Ecuador and Peru *L. purpurea* S. Leiva
- 19b. Corolla lobes bicolored.
- 21a. Peduncle adnate to stem; leaves to 13 cm long; corolla green with interior solid violet-purple, ≥ 5 mm long, the limb longer than the tube; berry 7–9 mm diam.; Ecuador and Peru *L. dilloniana* S. Leiva, V. Quipuscoa & N. W. Sawyer
- 21b. Peduncle free from stem, ≥ 5 mm long; leaves to 35 cm long; corolla green with interior violet maculations, ≤ 5 mm long, the limb equaling the tube; berry 8–12 mm diam.; Peru *L. longipedunculata* S. Leiva, Rodríguez & Campos

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- Appendix 1. Revised nomenclature for species of *Larnax*.
Accepted names are in boldface.
1. **L. andersonii** N. W. Sawyer
 2. **L. cuyacensis** N. W. Sawyer & S. Leiva
 3. **L. darcyana** N. W. Sawyer
 4. **L. dilloniana** S. Leiva, V. Quipuscoa & N. W. Sawyer
 5. **L. glabra** (Standley) N. W. Sawyer
Athenaea glabra Standley
Deprea glabra (Standley) Hunziker
 6. **L. grandiflora** N. W. Sawyer & S. Leiva
 7. **L. harlingiana** Hunziker & Barboza
 8. **L. hawkesii** Hunziker
 9. **L. longipedunculata** S. Leiva, Rodríguez & Campos
L. macrocalyx S. Leiva, Rodríguez & Campos
 10. **L. lutea** S. Leiva
 11. **L. parviflora** N. W. Sawyer & S. Leiva
 12. **L. peruviana** (Zahlbruckner) Hunziker
Athenaea peruviana Zahlbruckner
Withania peruviana (Zahlbruckner) Macbride
 13. **L. psilophyta** N. W. Sawyer
 14. **L. purpurea** S. Leiva
 15. **L. sachapapa** Hunziker
L. pilosa S. Leiva, Rodríguez & Campos
 16. **L. sagasteguii** S. Leiva, V. Quipuscoa & N. W. Sawyer
 17. **L. sawyeriana** S. Leiva, Rodríguez & Campos
 18. **L. steyermarkii** Hunziker
 19. **L. subtriflora** (Ruiz & Pavón)
Physalis subtriflora Ruiz & Pavón
Withania subtriflora (Ruiz & Pavón) Dunal
 20. **L. suffruticosa** (Dammer) Hunziker
Lochroma suffruticosa Dammer
 21. **L. sylvarum** (Standley & C. V. Morton) N. W. Sawyer
Athenaea sylvarum Standley & C. V. Morton
Deprea sylvarum (Standley & C. V. Morton) Hunziker
 22. **L. vasquezii** S. Leiva, Rodríguez & Campos