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# A new and endangered species of *Iochroma* (Solanaceae) from the cloud forests of central Peru and its phylogenetic position in Iochrominae

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## Abstract

*Iochroma amicorum* M. Cueva, S. D. Sm. & S. Leiva (Solanaceae), a new species from cloud forests of Central Peru, is described and illustrated. Phylogenetic analyses of DNA sequence data suggest that *Iochroma amicorum* is closely related to *I. nitidum*, *I. umbellatum*, *I. grandiflorum* and *I. tingoanum*, which collectively form the "U" clade of Iochrominae. Certain morphological characteristics of calyx and corolla as well as the type of habitat appear to be common in species of this clade. *Iochroma amicorum* is easily distinguished from other members of the "U" clade by its campanulate or funnel-shaped corolla with short and slightly reflexed lobes, the presence of an expanded stapet at the point of filament insertion with short lateral extensions united to the corolla, and its globose usually white fruits with tinges of purple at the base. Distribution, phenology and are discussed together with the position of the new species in Iochrominae. *Iochroma amicorum* is assessed as Endangered according to IUCN criteria B1ab (i, iii).

**Key words**: Andes, South America, taxonomy, Cloud forest

## Resumen

Se describe e ilustra a *Iochroma amicorum* M. Cueva, S. D. Sm. & S. Leiva (Solanaceae) una especie nueva procedente de los bosques nublados del centro del Perú. Según el análisis filogenético molecular, *I. amicorum* está relacionada a *I. nitidum*, *I. umbellatum*, *I. grandiflorum* y *I. tingoanum*, las cuales forman el clado "U" de Iochrominae. Ciertas características morfológicas del cáliz y corola además del tipo de hábitat parecen ser comunes en las especies de este clado. *Iochroma amicorum* se distingue fácilmente de los otros miembros del clado "U" por su corola campanulada infundibuliforme con lóbulos cortos y ligeramente reflexos, filamentos estaminales insertados en el borde basal del tubo corolino formando un petalostemo extendido con pequeñas prolongaciones laterales unidas a la corola, y por sus frutos globosos blancos con la parte basal púrpura. Se adicionan datos sobre la distribución y fenología de esta nueva especie y se discute sobre su posición filogenética en Iochrominae. *Iochroma amicorum* es considerada En Peligro según los criterios B1ab (i, iii) de la IUCN.

**Palabras clave**: Andes, Sudamérica, taxonomía, bosque nublado

## Introduction

*Iochroma* Bentham (1845: 20) is a Neotropical genus whose center of diversity is in the Andes, between Colombia and northern Peru (Smith & Baum 2006). This group of unarmed shrubs and treelets comprises an estimated 25 species (Leiva 1995, 2006, 2007, 2009, Leiva & Quipuscoa 1998, Leiva & Lezama 2005, Leiva *et al.* 1998, 2003, Lezama *et al.* 2007, Smith *et al.* 2008, Smith & Leiva 2011). The species generally present showy colorful flowers (Smith & Baum 2006) that are pollinated by hummingbirds and various types of insects (Smith *et al.* 2008). Accordingly, several *Iochroma* species have become popular as ornamentals (Shaw 1998, Meerow *et al.* 2004). The fruits of *Iochroma* are globular or elongated berries with sclerosomes, and they are usually accompanied by an accrescent calyx (Hunziker 2001, Smith & Baum 2006, Lezama *et al.* 2007). *Iochroma* species typically inhabit cloud forest gaps, clearings, and disturbed areas between 1800 and 2800 m.

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Within the Solanaceae, *Iochroma* falls in the tribe Physaleae (sensu Olmstead *et al.* 1999, 2008), in the large berry-fruited subfamily Solanoideae. Members of *Iochroma*, together with species of *Acnistus* Schott (1829: 1180), *Dunalia* Kunth (1818: 55), *Saracha* Ruiz & Pavón (1794: 34), *Eriolarynx* Hunziker (2000: 66) and *Vassobia* Rusby (1907: 422), form a well-supported Andean clade in Physaleae, designated the subtribe Iochrominae by Olmstead *et al.* (1999, 2008). However, the genus itself, as traditionally delimited is not monophyletic (Smith & Baum 2006). For example, *I. australe* Grisebach (1874: 218) belongs to a clade together with species of *Eriolarynx, I. parvifolium* (Roemer &Schultes 1819: 698) D' Arcy (1993: 1259) is more closely related to *Dunalia* than to other *Iochroma* species, and *I. cardenasianum* Hunziker (1977: 21) appears to belong to the Datureae, a tribe comprising *Brugmansia* Persoon (1805: 216) and *Datura* Linnaeus (1753: 179) (Olmstead *et al.* 2008). Excluding these three species (Smith & Leiva 2011), *Iochroma* sensu Smith & Baum (2006) is confined to the Andes of Colombia, Ecuador, and Peru. Smith & Baum (2006) identified two major clades of *Iochroma*, one with four subclades designated with the letters A, C, L, and F, and another smaller clade, the U clade, which appears to be sister to the remainder of Iochrominae. The ACLF clade species are generally distinguished by their funnel-shaped or tubular corollas where stamens are inserted near the base, and most of them are distributed between 5°N in Colombia and 8°S in the North of Peru. By contrast, the U clade species develop salverform flowers with inserted stamens in the middle of the corolla tube or higher, coming to possess, in some cases, more or less sessile anthers. These taxa are distributed from 4°S in the south of Ecuador to 10°S in the center of Peru (Smith & Baum 2006). Among the U clade species, only *I. umbellatum* (Ruiz & Pavón 1799: 45) Hunziker (1982: 101) possesses a wide distribution, reaching 10°S in the departments of Ancash, Húanuco, and Lima (Brako & Zarucchi 1993). The remaining species are more restricted and are apparently endemic from certain localities in southern Ecuador and northern Peru (Leiva & Quipuscoa 1998, Leiva 2009).

In the present study, we describe a new member of the U clade from the province of Oxapampa in central Peru. This area, on the easternside of the cordillera in the department of Pasco, comprises a vast region of montane cloud forest with immense biodiversity (Young & León 2000). The Solanaceae is one of the richest families in this flora (Vásquez *et al.* 2005), and currently is estimated to be represented by 27 genera and 150 species, 10 of which are thought to be endemic (M. Cueva, unpublished). During collecting expeditions carried out in 2009, 2013 and 2014 in Yanachaga-Chemillen National Park, the authors identified a new species with affinities to *Iochroma.* Nonetheless, it presented peculiar physical characteristics that have not been described to date in the genus. The morphological and phylogenetic analyses presented here confirm its placement in *Iochroma* and its distinctiveness relative to other species in the genus.We provide a description of this new species, *I. amicorum*, and provide analyses of DNA sequence data to support its phylogenetic position within *Iochroma*.

## Material and Methods

**Taxonomy**—Our description is based on material of *I. amicorum* collected in the province of Oxapampa, in the department of Pasco, in Yanachaga-Chemillén National Park and adjacent zones. The collections were deposited in seven herbaria: MO, USM, HOXA, HUT, HUSA, HSP and HAO. The morphological description is based on the external characters observed in living plants and material from the herbaria. The vegetative parts were examined in detail as well as the interior of the flowers and fruits. The fine scale morphological details were observed with an Olympus SZX7 stereoscope (8x–56x) and a Leica optic microscope (40x–100x). The distribution of *I. amicorum* is based on the information taken from all the examined specimens and presented in a map using the geographic coordinates of each individual. To assess the conservation status of this new species, the guidelines, criteria and categories of the IUCN (2012) were used.

**Phylogenetic analysis**—We used phylogenetic analysis of two nuclear and one nuclear ribosomal gene to confirm the placement of *Iochroma amicorum*. Sequences for this species were added to the 41-taxon dataset of Muchhala *et al.* (2014) and Smith & Baum (2006).We amplified *LEAFY* (*LFY*) intron II, exons 2 through 9 of the granule bound starch synthase (*waxy*), and the internal transcribed spacer (ITS) from *I. amicorum* genomic DNA using protocols described in Smith & Baum (2006). All products were directly sequenced commercially, and sequences were edited and aligned in MacClade 4.0 (Maddison & Maddison 2000). The genbank numbers for these sequences are KM514684 (*LFY*), KM521199 (*waxy*), and KM514683 (ITS). Support for the phylogenetic placement of *I. amicorum* was assessed with bootstrap analyses of the combined dataset in PAUP 4.0b10 (Swofford 2002). Heuristic searches were completed for 500 bootstrap replicates with 10 random addition replicates (holding one tree at each step), TBR branch swapping, and maxtrees set to 100.

## Results

### Taxonomy

***Iochroma amicorum*** M. Cueva, S. D. Sm. & S. Leiva *spec. nov.* (Fig. 1, 2)

Type:—PERÚ. Oxapampa: Distrito de Huancabamba, sector Oso Playa, Parque Nacional Yanachaga-Chemillén, camino hacia el campamento, 2362 m, 10° 19′ 27″S 75° 35′ 20″W, 15 Octubre 2009, *M. Cueva, A. Monteagudo, L. Valenzuela, A. Peña, J. Mateo & R. Rivera 646* (holotype: HOXA!; isotypes: MO!, USM!, HUT!, HUSA!, HSP!).

*Iochroma amicorum* can be distinguished from the most similar *Iochroma* species (*I. umbellatum* and *I. tingoanum*) by its funnel-shaped to campanulate corolla, its staminal filaments inserted in the basal part of the corolla tube to form a visible stapet with small lateral extensions joined to the corolla tissue, and its mature globular fruits, usually white with a purple base.

Shrub or small tree, 2–5 m high.Stem cylindrical, older parts of creamy colour, glabrous and with lenticels white-yellowish or brownish, the main trunk with a diameter of 3–5.5 cm, old branches with a diameter of 0.9–1.5 cm; young stems dark green or creamy green with a diameter of 3.5–7 mm, puberulent, internodes 0.5–2 cm, the indumenta appressed along the surface of the stem, with simple and branched whitish hairs. Leaves simple, entire, 17–32 × 5.5–10.1 cm, elliptic or narrow elliptic, membranaceous, apex generally acuminate or sometimes acute, base attenuate, with primary venation pinnate, prominent on the abaxial surface, 19–27 secondary veins uniformly spaced born approximately at right angles from the midrib; adaxial surface glabrescent dark green, with simple and branched hairs generally appressed to the lamina's surface; abaxial surface light green, densely pubescent, with whitish hairs simple and branched, more or less erect or curled, iridescent, 0.5–1.5 mm long; petioles 2–4 cm long, puberulent, with similar hairs to the ones present in the lamina. Flowers 2–10 arranged in fascicles on short shoots of 0.5–5 cm long, simulating umbels; pedicels green and puberulent at anthesis, 16–45 mm long, with a diameter of 1.5 mm expanding up to 3.5 mm beneath the calyx; flower buds ovoid or oblong protruding from the calyx tube. Calyx 4–6 mm x 6.5–9.5 mm, cupulate to urceolate, thick, green turning white towards its apical border, truncate with short rounded uneven lobes or obtuse, external surface puberulent with protruding venation, internal surface smooth with minute papillae scattered. Corolla 11–19 mm × 6–8 mm, campanulate to funnel-shaped, slightly thick or membranaceous, limb 12–21 mm in diameter at the anthesis, generally lilac or purple fading to white at the base, with 5 green to purple maculae in its interior, rarely completely white with green maculae, puberulent in its exterior, with simple hairs whitish, glabrous internally, lobes of 4–4.5 mm × 5 mm, deltoid short, apex acute, extended or slightly reflexed, puberulent in both surfaces. Stamens equal, inserted 2 mm from the basal edge of corolla tube, free portion of filaments 5.5 mm long and with a diameter of 0.5–1 mm, glabrous, white, filament base abruptly widening at the insertion zone with the corolla, forming a visible stapet that develops two small lateral extensions which are not free, anthers 3–3.5 × 1.5–2 mm, oblong, creamy white. Gynoecium 3–3.5 × 3 mm with globose, glabrous ovary; style 6 × 0.8 mm towards the base, with a diameter of 1.5–1.8 mm towards the apex, claviform, white, glabrous; stigma 0.6 × 2 mm, expanded, bilobed, green, papillose. Fruit 12–14 × 14–15 mm, a globose berry, slightly compressed apically, smooth, usually white with purple base, occasionally entirely white or entirely purple, coriaceous pericarp with sclerosomes, and well-developed placenta tissue. Fruiting calyx 7–8 × 13.5–14 mm, persistent, accrescent, truncate, with an irregular border. Fruiting pedicels 30–50 mm × 2 mm near the base, expanding up to 4 mm in diameter underneath the calyx. Seeds 150–178 per fruit, 1.5 × 1 mm, brownish flattened reniform, testa foveolate.

*Etymology*:—the specific epithet comes from the Latin *amicus*. The species is dedicated to the generosity of friends and botanical colleagues who assisted with the discovery and description of this new species by donating their time and energy to help the authors conduct this research. These parties are listed in acknowledgements.

*Distribution and habitat*:—*I. amicorum* is one of only two *Iochroma* species of the genus that extends south to 10°S latitude in central Peru. At present it is known from the province of Oxapampa, in the districts of Oxapampa and Huancabamba, Oso Playa, Milpo and San Alberto sectors inside Yanachaga-Chemillén National Park and in other adjacent zones (Figure 3). It grows in cloud forests between 2300–2600 m. The majority of individuals of this riparian species grow in lightly disturbed or open areas along riverbanks or small streams. Occasionally, they are found in the shade of primary forest but still always adjacent to moving water.

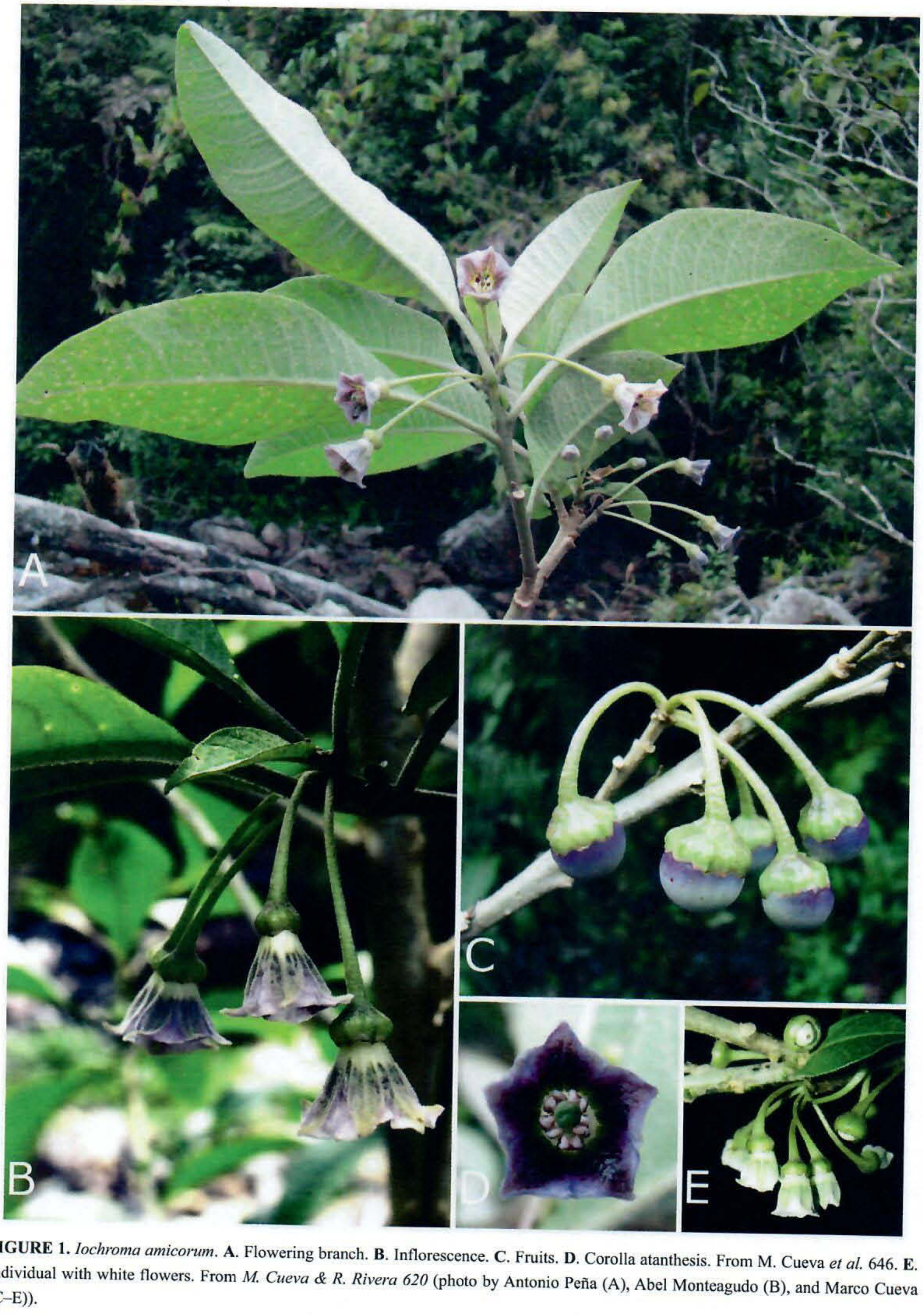


**FIGURE 1.** *Iochroma amicorum*. **A**. Flowering branch. **B**. Inflorescence. **C**. Fruits. **D**. Corolla atanthesis. From M. Cueva *et al.* 646. **E**. Individual with white flowers. From *M. Cueva & R. Rivera 620* (photo by Antonio Peña (A), Abel Monteagudo (B), and Marco Cueva (C–E)).

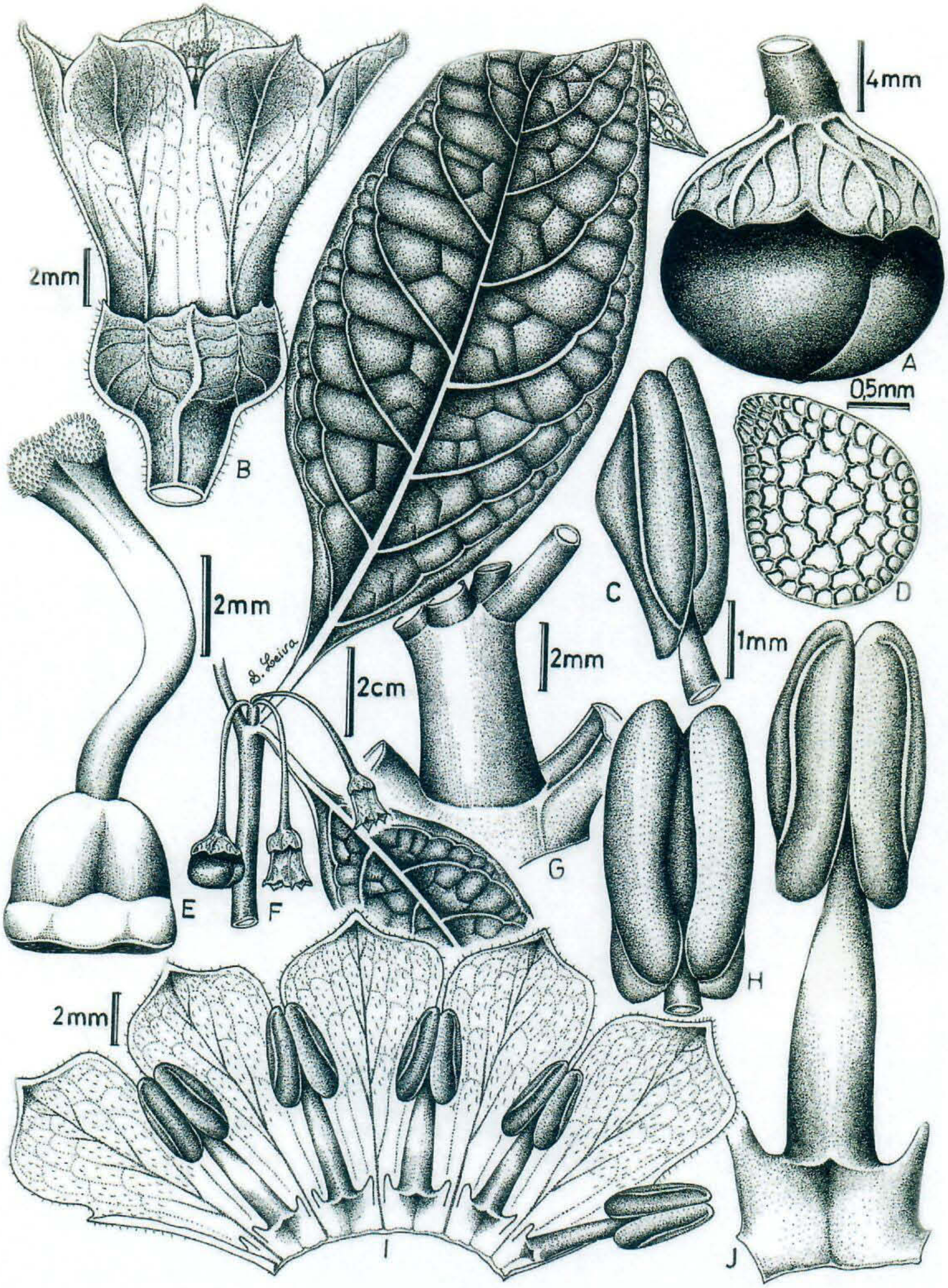


**FIGURE 2.** *Iochrom aamicorum*. **A**. Fruit. **B**. Flower. **C**. Anther lateral view. **D**. Seed. **E**. Gynoecium. **F**. Flowering branch. **G**. Inflorescence. **H**. Anther dorsal view. **I**. Open corolla. **J**. Stamen isolated, showing anther in ventral view, and stapet with lateral projections which was separated from the tissue of the corolla. From *M. Cueva et al. 646*. Drawing by Segundo Leiva.

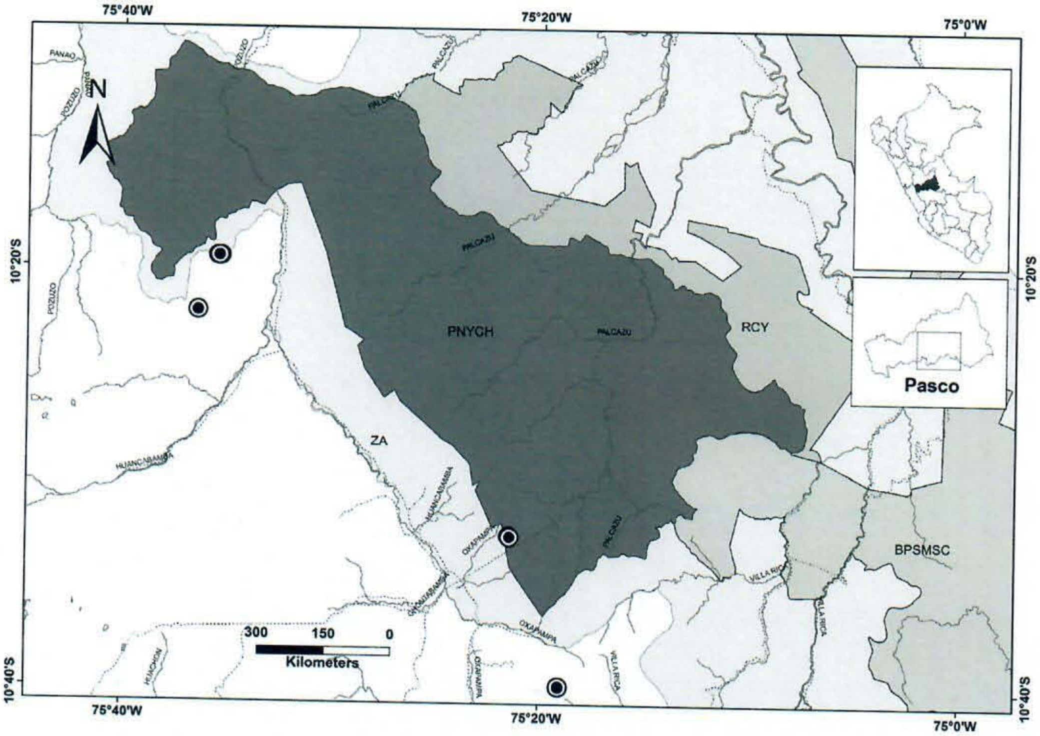
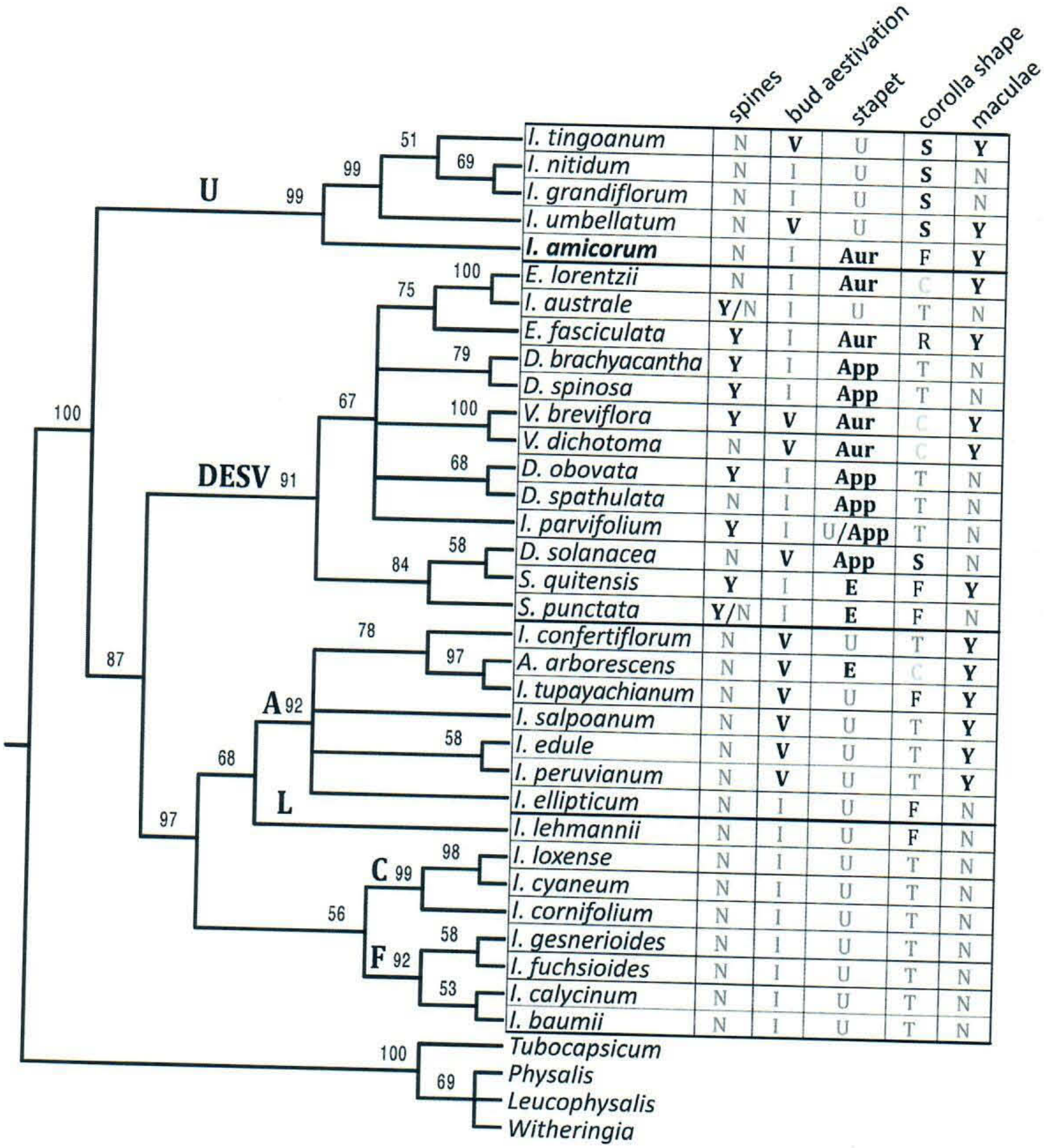


**FIGURE 3.** Distribution of *I. amicorum*. (PNYCH= Yanachaga-Chemillén National Park. ZA= Buffer Zone. RCY= Communal Reserve Yanesha. BPSMSC= Protected Forest of San Matias-San Carlos).

*Phenology*:—This species' phenology appears variable. In October 2009, the individuals in Sector Oso Playa were either flowering or in a fruiting state. In the same month in 2013 the majority of individuals at this site were vegetative and only a few possessed flowers or fruits. Other individuals collected at the Sector San Alberto in April 2009 had flowers and fruits whereas in October 2013 only vegetative plants were found. A return trip in March 2014 revealed only plants in a vegetative state at Sector San Alberto but fruiting individuals at Sector Oso Playa and Sector Milpo. Thus, it appears that *I. amicorum* flowers sporadically February through April and perhaps again September through October.

*Conservation status*:—According to the IUCN (2012) categories, *I. amicorum* is considered endangered (EN) following the B1ab (i, iii) criteria. This species is only known in four localities and its present range is approximately 220.9 km$^2$. The known populations are mostly in the buffer zone of Yanachaga-Chemillen National Park or outside the strictly protected area. In these areas, settlers are actively clearing land for agriculture and livestock breeding. In the future, these human activities could reduce the available riparian habitat for *I. amicorum* and/or eliminate some of its few known populations.

*Additional specimens examined*:—PERÚ. Oxapampa: Distrito de Oxapampa, Parque Nacional Yanachaga-Chemillén, Sector San Alberto, alrededores del Refugio el Cedro, 2483 m, 10º 32′ 43,3″S 75º 21′ 29,5″W, 26–27 Abril 2009, *M. Cueva* & *R. Rivera 620* (HOXA, USM, MO, HUT, HUSA); Camino Refugio el Cedro-Abra Esperanza, 2528 m, 10º 32' 45.5"S 75º 21' 26.2"W, 21 Octubre 2013, *S. Smith et al. 551* (HOXA, MO); carretera nueva Oxapampa-Bosque Shollet-Villa Rica, 2324 m, 10º 39' 51.2"S 75º 19' 2.4"W, 25 Octubre 2013, *S. Smith et al. 571* (HOXA, MO, USM); Distrito de Huancabamba, Parque Nacional Yanachaga-Chemillen, Sector Oso Playa, path to the camping area, 2362 m, 10º 19' 26.7"S 75º 35' 27.9"W, 20 Octubre 2013, *S. Smith et al. 542* (HOXA, MO, USM, HAO); path to the camping area, 2362 m, 10º 19' 26.9"S 75º 35' 24"W, 20 Octubre 2013, *S. Smith et al. 543* (HOXA, MO); path to the camping area, 2362 m, 10º 19' 26.9"S 75º 35' 24"W, 20 Octubre 2013, *S. Smith et al. 544* (HOXA, MO); camino Lanturachi-Cueva Blanca-Milpo, 2546 m, 10º 22' 3.7"S 75º 36' 25.4"W, 24 Octubre 2013, *S. Smith et al.563*, (HOXA, MO, USM).



| | spines | bud aestivation | stapet | corolla shape | maculae |
|---|---|---|---|---|---|
| *I. tingoanum* | N | **V** | U | **S** | **Y** |
| *I. nitidum* | N | I | U | **S** | N |
| *I. grandiflorum* | N | I | U | **S** | N |
| *I. umbellatum* | N | **V** | U | **S** | **Y** |
| ***I. amicorum*** | N | I | **Aur** | F | **Y** |
| *E. lorentzii* | N | I | **Aur** | C | **Y** |
| *I. australe* | **Y**/N | I | U | T | N |
| *E. fasciculata* | **Y** | I | **Aur** | R | **Y** |
| *D. brachyacantha* | **Y** | I | **App** | T | N |
| *D. spinosa* | **Y** | I | **App** | T | N |
| *V. breviflora* | **Y** | **V** | **Aur** | C | **Y** |
| *V. dichotoma* | N | **V** | **Aur** | C | **Y** |
| *D. obovata* | **Y** | I | **App** | T | N |
| *D. spathulata* | N | I | **App** | T | N |
| *I. parvifolium* | **Y** | I | U/**App** | T | N |
| *D. solanacea* | N | **V** | **App** | **S** | N |
| *S. quitensis* | **Y** | I | **E** | F | **Y** |
| *S. punctata* | **Y**/N | I | **E** | F | N |
| *I. confertiflorum* | N | **V** | U | T | **Y** |
| *A. arborescens* | N | **V** | **E** | C | **Y** |
| *I. tupayachianum* | N | **V** | U | F | **Y** |
| *I. salpoanum* | N | **V** | U | T | **Y** |
| *I. edule* | N | **V** | U | T | **Y** |
| *I. peruvianum* | N | **V** | U | T | **Y** |
| *I. ellipticum* | N | I | U | F | N |
| *I. lehmannii* | N | I | U | F | N |
| *I. loxense* | N | I | U | T | N |
| *I. cyaneum* | N | I | U | T | N |
| *I. cornifolium* | N | I | U | T | N |
| *I. gesnerioides* | N | I | U | T | N |
| *I. fuchsioides* | N | I | U | T | N |
| *I. calycinum* | N | I | U | T | N |
| *I. baumii* | N | I | U | T | N |

**FIGURE 4.** Phylogeny of Iochrominae showing placement of *I. amicorum*. Majority-rule consensus of 500 bootstrap replicates. Bootstrap support is indicated above branches. Abbreviations for genera of Iochrominae are *I.* = *Iochroma*, *A.* = *Acnistus*, *V.* = *Vassobia*, *S.* = *Saracha*, *E.* = *Eriolarynx*, *D.* = *Dunalia*. Physalinae outgroups are *Tubocapsicum anomalum*, *Physalis peruviana*, *Witheringia solanacea*, and *Leucophysalis grandiflora*. Two more distantly related outgroups (*Cuatresiahar lingiana* and *Larnax sachapapa*) were pruned from the tree. The table shows variation for five characters: spines (Y=yes, N=no), bud aestivation (V=valvate, I=induplicate), stapet (U=unexpanded, E=expanded, Aur=expanded with auricles, App=expanded with appendages), corolla shape (S=salverform, F=funnel-shaped, C=campanulate, T=tubular, R=rotate), and maculae on inside of corolla (Y=yes, N=no). Scoring for corolla shape and stapet morphology from Smith & Baum (2007).

## Phylogenetic position

The phylogenetic analysis carried out with the nuclear genes *waxy*, ITS, and *LFY* shows that *I. amicorum* is part of a clade (the "U" clade) that is sister to the rest of Iochrominae (Figure 4). This clade, comprising *I. umbellatum*, *I. tingoanum* Leiva (2009: 18), *I. grandiflorum* Bentham (1845: 20), *I. nitidum* Leiva & Quipuscoa (1998: 172) and *I. amicorum*, has a bootstrap value of 99%. Within this U clade, *I. amicorum* appears to be sister to the remaining four species in the clade (BS 99% also). This analysis also upholds the monophyly of Iochrominae (BS 100%) and provides moderate support (BS 87%) for the sister relationship between the U clade and the large clade containing the other *Iochroma* species as well as the smaller genera *Acnistus, Eriolarynx*, *Vassobia*, *Dunalia* and *Saracha* (Figure 4). Relationships among those species are similar to previous studies (Smith & Baum, 2006; Muchhala *et al.* 2014).

## Discussion

According to the phylogenetic analysis, *I. amicorum* is most closely related to *I. umbellatum*, *I. tingoanum*, *I. grandiflorum* and *I. nitidum,* members of the U clade of Iochrominae (Smith & Baum 2006). The recently described *I. lilacinum* Leiva (2009: 14) may also belong in this clade as it has a strong morphological affinity with *I. umbellatum*. The phylogenetic placement of *I. amicorum* within the U clade is supported by several morphological synapomorphies. The cupulate urceolate calyx of *I. amicorum*, with its protruding ribbing, is very similar to that of *I. nitidum* and *I. grandiflorum* (Leiva & Quipuscoa 1998). The close proximity of the anthers to the style observed in the flowers of *I. amicorum* (Figure 1 D) is shared with the majority of the U clade species, especially with *I. umbellatum* and its relatives *I. tingoanum* and *I. lilacinum* (Leiva 2009). Another feature of species in this clade is the preference for riparian habitats. *I. grandiflorum*, *I. nitidum*, *I. tingoanum* and *I. lilacinum* are also often found near streams (S. Smith, pers. obs.) and *I. umbellatum* commonly occurs with roots partially in the water. Following this pattern, *I. amicorum* grows exclusively along streams and rivers, and may have its roots partially submerged. The flower colour of *I. amicorum*, with lilac or purple towards the limb with 5 green maculae is quite similar to *I. tingoanum* and *I. umbellatum* (Leiva & Quipuscoa 1998, Smith & Baum 2007, Leiva 2009) although *Iochroma nitidum* and *I. grandiflorum* develop completely purple corollas. *Iochroma amicorum* can also develop flowers completely white with green maculae in its interior (Figure 1 E), but this form is less frequent. White flowers with green maculae are also known in *I. confertiflorum* Miers (1849: 31) Hunziker (1982: 100), *I. smithianum* Lezama, Limo & Leiva (2007: 24) and *I. tupayachianum* Leiva (2006: 277), all members of the ACLF clade that are closely to related with *Acnistus arborescens* Schlechtendal (1832: 67) and share valvate bud aestivation (Smith & Baum 2006). Unlike these taxa, bud aestivation in *I. amicorum* is induplicate with visible interlobular folds typical in *Iochroma* (Hunziker 2001). The globose fruit form of the *I. amicorum* is also present in the majority of the species from the U clade. *I. nitidum*, *I. grandiflorum* and *I. tingoanum* develop globose berries accompanied by an accrescent calyx (Leiva 1998, 2009), while in *I. umbellatum* and *I. lilacinum*, the berries are ovoid or conical. However, the white apex with the purple base of the *I. amicorum* fruits seems to be a peculiar feature not found in the other species of this group.

*Iochroma amicorum* possesses several other morphological characters that distinguish it from the other species in the U clade and the ACLF clade. Whereas *I. nitidum*, *I. grandiflorum*, *I. umbellatum* and *I. tingoanum* possess salverform corollas and corolla limbs with distinct triangular and well-reflexed, even revolute lobes (Leiva & Quipuscoa 1998, Smith & Baum 2007, Leiva 2009), *I. amicorum* has campanulate to funnel-shaped corollas with short, indistinct, and only slightly reflexed lobes. Another character that easily distinguishes *I. amicorum* is the insertion of the stamens in the base of the corolla tube. In this species, the staminal filaments expand abruptly at the insertion zone forming a visible stapet that develops two small lateral extensions joined to the corolla tissue (Figure 2). The other species from the U clade possess stamens inserted near the middle zone of the corolla tube and the stapet does not expand nor develop lateral extensions. *Iochroma* species in ACLF clade similarly lack a stapet, but their filament insertion point is at the base of the corolla (Smith & Baum 2006, 2007). The expanded stapet with small to prominent lateral projections is also present in other genera of Iochrominae, namely *Vassobia*, *Eriolarynx* and *Dunalia* (Hunziker 2001; Figure 4). *Vassobia*, distributed in Bolivia, Argentina, Uruguay, Paraguay and Brazil is distinguished from other Iochrominae by its small flowers with rotate or rotate-campanulate purple or maroon corollas (Hunziker 1984, 2001). *Eriolarynx* possesses rotate or campanulate corollas with a dense ring of trichomes in its interior, and its species are distributed in Bolivia and Argentina (Hunziker 2000). Finally *Dunalia*, a widely distributed genus across the Andes, has tubular flowers like many *Iochroma* species, but it is typically spiny and its well-developed stapets often form visible free lateral projections or auricles (Hunziker 2001, Smith & Baum 2006).

Considering the pattern of character variation across the molecular phylogeny it is clear that many characters previously thought to be of taxonomic significance do not correspond to natural groups. Although previous studies suggested that bud aestivation matches well with generic divisions (Baehni 1946, Hunziker 1982), a closer examination as part of this study suggests that valvate aestivation has evolved several times in Iochrominae (Figure 4). The elaborate stapet, which was the basis for the generic delimitation of *Dunalia*, is clearly homoplasious (Figure 4, see also Smith & Baum 2007) and indeed appears in other distantly related Solanaceae, e.g. *Jaltomata* (Hunziker 2001). More detailed anatomical studies could reveal differences in the way this structure and its lateral appendages develop in the distinct lineages, but its presence alone does not appear to be taxonomically informative. Similarly, the expression of patches of chloroplasts in the corolla forming green to yellow maculae seems relatively common in Iochrominae (Figure 4). Species in the A clade have these maculae on the corolla lobes (Smith and Baum 2006). They are found deeper in the corolla in *I. amicorum* and other taxa. The ability to express colored plastids in the corolla may thus be pleisiomorphic and the absence of these spots in the C and F clades of *Iochroma* (e.g. *I. cyaneum* and *I. fuchsioides*) may represent the derived state. Despite their homoplasy across the phylogeny, combinations of these characters (e.g., spines plus stapet appendage) are still useful for diagnosing species and genera within Iochrominae.

Given the morphological distinctiveness of the U clade of *Iochroma* and its present placement as sister to the rest of Iochrominae, one possibility for future taxonomic revision is the recognition of these five species as a separate genus. This would reduce the paraphyly of *Iochroma*, although not render it monophyletic as *Acnistus* is also nested within *Iochroma* (Figure 4). We have chosen not to segregate the U clade species at this point because its phylogenetic position remains inconclusive. Although concatenated analyses support its sister group position (BS 87%), one of the loci (*waxy*) places the U clade as sister to ACLF when analyzed separately (Smith and Baum, 2006). Ongoing studies (Gates and Smith, unpublished) are examining additional nuclear and plastid loci to determine the consensus position for the U clade and to better resolve relationships within Iochrominae as a whole. With a more resolved phylogeny and detailed analyses of morphological variation we will be able to produce a stable and useful revision for the entire clade that best reflects evolutionary history.

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