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Morphological and anatomical characterization of a new natural hybrid between *Cohniella ascendens* and *C. brachyphylla* (Oncidiinae: Orchidaceae)

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Abstract

A putative natural hybrid between *Cohniella ascendens* and *C. brachyphylla* (Orchidaceae, Oncidiinae) from western Costa Rica, *C. ×francoi*, is herein newly described, illustrated and characterized based upon both morphological and anatomical characters. This taxon hybrid is most similar to *C. ascendens* but the flowers show intermediate characters between the putative parents. *Cohniella ×francoi* is similar to *C. ascendens* in its semipendulous inflorescences, callus shape, cylindrical column base with linear oblong wings, and obovate stigmatic cavity plus several anatomical characters. On the other hand, it is similar to *C. brachyphylla* in the oblong to subquadrate lateral lobes of the labellum that are in the same plane as the central lobe, and the rectangular disc of the labellum with a lateral extension of the callus in the margins. A table of diagnostic characters for the new hybrid and its putative parents, a comparative figure, and a map showing their geographical distributions are also provided.

Resumen

Cohniella ×francoi, un híbrido natural entre *Cohniella ascendens* y *C. brachyphylla* (Orchidaceae, Oncidiinae) del oeste de Costa Rica es aquí descrito, ilustrado y caracterizado por caracteres morfológicos y anatómicos. El nuevo híbrido es más similar a *C. ascendens* pero las flores presentan caracteres intermedios entre sus padres putativos. *Cohniella ×francoi* se parece a *C. ascendens* en la inflorescencia semipéndula, la forma del callo, la columna cilíndrica con las alas linear oblongas y la cavidad estigmática obovada, además de varios caracteres anatómicos. Por otro lado, es similar a *C. brachyphylla* por los lóbulos laterales del labelo oblongos a subcuadrados y extendidos en el mismo plano que el lóbulo central y el disco rectangular con extensiones laterales del callo en los márgenes. Adicionalmente, proporcionamos una tabla de caracteres diagnósticos para el nuevo híbrido y sus padres putativos, una figura comparativa y un mapa detallando las distribuciones geográficas de los tres taxones.

Key words: Anatomy, Costa Rica, morphology, natural hybridization, *Cohniella ×francoi*

Introduction

The genus *Cohniella* Pfitzer (1889: 194) is distinguished from others members of the Oncidiinae by the relatively small and subspherical, 1-leaved pseudobulbs, succulent, terete leaves, and *Oncidium*-like flowers

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(Carnevali *et al*. 2010). At the present, the genus includes 22 species and one natural hybrid (Cetzal-Ix *et al*. 2013). Most species in the genus show disjunct distributional patterns (e.g. *C. leptotifolia* Cetzal & Carnevali (2010: 198), *C. pendula* Carnevali & Cetzal (in Carnevali *et al.* 2010: 171), *C. lacera* (Lindley 1844: 30) Cetzal (2012a: 139), etc.). However, a few species share distributional ranges with one or more congeneric taxa; these include *C. ascendens* (Lindley 1842: 4) Christenson (1999: 177), *C. cepula* (Hoffmannsegg 1843: 833) Carnevali & Romero (in Carnevali *et al.* 2010: 167), and *C. nuda* (Lindley 1837: 1994) Christenson (1999: 177). In all cases of sympatry of parapatry, the species involved are not sister taxa. For example, *C. cebolleta* (Jacquin 1760: 30) Christenson (1999: 177), a member of the *C. cebolleta* complex (Cetzal-Ix *et al.* 2013) is para- or sympatric with *C. nuda*, a member of the *C. ascendens* complex, whereas *C. cepula* (a member of the *C. cepula* complex) occurs in the same habitats as *C. jonesiana* (Reichenbach 1883: 781) Christenson (1999: 177), a member of the *C. jonesiana* complex (Cetzal-Ix *et al.* 2012b). No instances of natural hybrids between these pairs of species are known to occur.

Cohniella ascendens is unique in the genus in that it overlaps its distributional range with three other congeneric taxa, all members of the *C. brachyphylla* (Lindley 1842: 4) Cetzal & Carnevali (in Carnevali *et al.* 2010: 163) complex. *Cohniella ascendens* usually grows in evergreen to semi-evergreen forest but, more rarely, it also occurs in semi-deciduous forest and several types of secondary vegetation at elevations of 0–500 (–900) m. Thus, in Mexico, along the Gulf drainage north of the Tehuantepec isthmus, this species is sympatric with *C. biorbicularis* Balam & Cetzal (in Carnevali *et al.* 2010: 162). Also in Mexico, it is sympatric or parapatric with *C. yucatanensis* Cetzal & Carnevali (2010: 206) in the northern Yucatan Peninsula (Carnevali *et al*. 2010, Cetzal-Ix & Carnevali 2010) whereas it shares these habitats with *C. brachyphylla* in western Chiapas through extreme NW Costa Rica, along the Pacific drainage of Central America. The flowering period of these four species broadly overlap (Table 1), but so far no natural hybrids have been recorded or described.

TABLE 1. Flowering period comparison throughout the geographic range of each taxon of four species of *Cohniella* (based on Carnevali *et al*. 2010 and Cetzal-Ix & Carnevali 2010) and the putative natural hybrid *C. francoi*.

Taxa	Months of the year											
	J	F	M	A	M	J	J	A	S	O	N	D
Cohniella ascendens	*	*	*	*	*			+	+		+	+
Cohniella biorbicularis	+	+	*	*	+			+			+	
Cohniella brachyphylla	*	*	*	*	+		+	+	+	+	+	*
Cohniella yucatanensis	*	*	*		+			+	+	+		+
Cohniella ×francoi		+										

(+) Flowering. (*) Peak bloom.

As found in other genera in subtribe Oncidiinae (e.g. *Oncidium* Swartz (1800: 239), *Lophiaris* Rafinesque (1838: 40), and many others) *Cohniella* species feature a generalized floral architecture resembling blooms of the family Malpighiaceae, which are mainly pollinated by oil-gathering *Centris* bees (Dodson 1972, Carmona-Díaz & García-Franco 2009). Therefore, it is possible that these insects are able to visit and pollinate flowers of orchid species of the same or different genera, opening the possibility for intrageneric and intergeneric hybridization to occur, of which several examples are known in the group of genera related to *Cohniella* (e.g. *Lophiaris ×haematochila* (Lindley & Paxton (in Lindley 1850: 21)) Braem (1993: 19), *L. ×oerstelurida* Cetzal & Balam (2012: 139), and *×Cohnlophiaris quintanarooensis* Cetzal & Carnevali (in Cetzal-Ix *et al.* 2012a: 41)).

Despite all this, there is just a single natural intrageneric hybrid in *Cohniella* formally described. This is *Cohniella ×marvraganii* (Lückel 1998: 90) Christenson (1999: 177), the natural cross of *C. jonesiana* and *C. stacyi* (Garay 1973: 301) Christenson (1999: 177). This nothospecies was described from Santa Cruz, Bolivia,

and it is only known from two collections, each one morphologically more similar to one parent than to the other. These two, otherwise closely related species, are very different, rendering the natural hybrid readily identifiable by a combination of characters, some found in neither of the parents, others intermediate between the two.

However, other sympatric species of *Cohniella* are not as obviously distinct and the possibility that other events of natural hybridization may have been overlooked cannot be ruled out. To recognize other nothospecies within the genus would require knowledge of the morphology (and its variation) and biogeography of the putative parents.

Recently, in an area of tropical evergreen forest in the southern portion of the Guanacaste province (Santa Rosa National Park), Costa Rica, a plant was collected with intermediate floral characteristics between those of *C. ascendens* and *C. brachyphylla.* We here interpret this combination of morphological and anatomical characters as evidence of a hybrid status for this plant, which is herein proposed as the new nothospecies, *Cohniella ×francoi* Cetzal & Carnevali.

Material and methods

Plant material

All the specimens studied were prepared from plants collected in the field. Representative samples of each taxon were deposited in the Herbarium CICY: *Cohniella ascendens* (Chiapas, Mexico, *Cetzal 36*), *C. brachyphylla* (Chiapas, Mexico, *Carnevali 7310*), and the new hybrid (*Carnevali 7257*). Morphological characters of the new natural hybrid and putative parents were revised under the dissecting microscope. Additionally, we assessed morphological characters of additional putative parents from the taxonomic revisions of Carnevali *et al.* (2010) and Cetzal-Ix & Carnevali (2010). Images of live flowers were obtained with an Epson Expression 1640 XL scanner. Digital images of flowers were captured at several resolutions, ranging from 600 to 1200 dpi. Digital line drawings were produced with Canvas, Version X Build 925, using the digital images previously captured to provide outlines. A distributional map was produced by plotting the locality data cited here and previous studies of Carnevali *et al*. (2010) and Cetzal-Ix & Carnevali (2010) on an image data "shaded and colored SRTM elevation model" (NASA/JPL/NIMA 2002) using ArcView 3.2 (ESRI 1999).

Foliar anatomy

Samples of mature leaves for anatomical study from the same plants mentioned under "Plant Material" above. Sections were taken from the middle portion of the leaf and fixed in FAA (5% formaldehyde, 5% acetic acid, 40% water, and 50% ethanol) (Sass 1958). The sections were cut transversely freehand, stained with 0.5% aqueous Toluidine blue, mounted in 50% glycerin, and sealed with clear nail polish. The slides are included in the holotype specimen. For the study of leaf epidermis, 0.5 cm wide leaf sections were placed in an approximately 3.75% sodium hypochlorite solution for three hours, washed with distilled water, cleaned of mesophyll remnants with a brush, and stained and mounted in the same manner as the transverse sections. Observations were made using a Leica-DME microscope, and pictures were taken with a Nikon Eclipse E 200 microscope equipped with a camera.

Taxonomy

Cohniella ×francoi Cetzal & Carnevali, *nothosp. nov.* (Figs. 1–5)

Cohniella ×francoi is a nothospecies intermediate between *C. ascendens* and *C. brachyphylla*. It resembles the former in the semi-pendulous habit, the general morphology of the callus, the linear-oblong column wings, and the obovate

stigmatic cavity. It is similar to *C. brachyphylla* in the oblong to subquadrate, spreading lateral lobes of the labellum and in the rectangular disc of the labellum with a conical lateral extension on the margins. It is distinguished from both parental taxa by the brown callus with white teeth as well as the combination of the *Cohniella ascendens* type callus with a rectangular disc bearing conical lateral extensions on the margins.

Type:— COSTA RICA. Guanacaste: near Santa Rosa National Park, 19 February 2009, *Pupulin s.n. sub Carnevali 7257* (holotype, CICY!; isotypes, AMES!, JBL!).

Epiphytic, semipendulous herbs. Pseudobulbs 9–12 × 9–12 mm, subspherical to broadly ovoid, apically 1-leaved, red-purple tinged, totally enclosed by 3 imbricate sheaths. Leaves (13.6–)17.8–52.0 × 0.5–0.7 cm, terete, thickly fleshy-coriaceous, dark green, usually purple spotted. Inflorescences solitary from the base of the pseudobulbs, 9.7–21.0 cm long, a 5–10-flowered raceme; peduncle 5 cm long, and rachis 1.5 cm long, both dark green, purple tinged. Flowers 18–19 mm diameter, resupinate, with widely spreading perianth parts and the petals and sepals somewhat reflexed; ovary with pedicel 10–11 mm long, of which 2.5–3.0 mm correspond to the ovary, this 1 mm thick. Sepals basally clawed, spreading or somewhat reflexed, dorsal sepal 6.0–7.0 × 4.0–4.3 mm, oblanceolate, apically obtuse and minutely apiculate, concave in the upper half, the claw 1.0–1.2 × 1.1–1.2 mm. Lateral sepals fused at the very base, then free, similar to dorsal, 7.0–7.5 × 3.5–3.8 mm. Petals 6.5–7.0 × 3.5–4.0 mm, oblong to oblanceolate, somewhat oblique, the apex rounded, somewhat reflexed in natural position. Labellum deeply 3-lobed, 10–11 mm long from the base to the apex of the central lobe, 11–12 mm wide across the apices of the lateral lobes, the lateral lobes in the same plane as the central lobe and +/- perpendicular to it; central lobe 7.0–8.0 × 12.0–12.5 mm, spathulate to transversely oblate or circular in outline, apically rounded to subquadrate, basally produced into a short isthmus, 2.0–3.0 × 1.0–1.5 mm; lateral lobes 4.0–4.5 × 3.0–3.5 mm, patent, somewhat reflexed in natural position, oblong to subquadrate, apically truncate-rounded, the upper and lower margins of the lateral lobes flat to rounded; disc (the basalmost section of the labellum that carries the callus) 4.0–4.5 × 3.0–3.5 mm, rectangular, bearing a well-developed callus, 4.0–4.2 × 2.5–2.6 mm, brown, consisting of a large, elevated, +/- flat, hemicircular platform, 2 × 2 mm, proximally with two small, lateral, white, divergent teeth, that are obconical and point upward, 1.0–1.5 × 0.3–0.5 mm; distally with two lateral teeth, broadly rectangular to conical, these 1.8–2.0 × 0.8–1.0 mm; the central tooth or keel laterally compressed, ca. 2 mm long; the basal portion of the callus with conical lateral extensions. Column 3.0–3.2 × 1.2–1.5 mm, the ventral face in the same plane as the labellum lobes, oblong, tabula infrastigmatica longitudinally channeled, stigmatic cavity rounded, 1 × 1 mm; column wings small, 2 × 1 mm, linear-oblong. Anther cap 1.8 × 1.5 mm, apical, operculate, ellipsoid. Pollinarium 1 mm long, tegula spathulate, 0.5 × 0.3 mm, viscidium disciform, pollinia 0.5–0.8 mm long, yellow. Capsule 38.5 × 7.0 mm, elliptical, pale green with reddish spots.

Anatomical description (Fig. 4):—**Dermic tissue system**. Cuticle: Smooth (Fig. 4E) Epidermis: monostratified, cells with external periclinal walls thick and convex. In frontal view, the cells are arranged in rows, are isodiametric to slightly elongated, hexagonal, with thick, straight anticlinal walls, with angulose tapering end walls. Bulliform cells: absent. Stomata: tetracytic, guard cells without papillae, striations absent. **Fundamental tissue system**. Mesophyll: leaf unifacial, parenchyma homogeneous, cells of variable sizes, arrangement and morphology, with some cells bearing reticulate thickenings in the walls (Fig. 4F); numerous bundles of extravascular fibers arranged in two series (Fig. 4D–E), the outermost one layer of cells from the epidermis, the other 3–7 layers of cells deeper. Hypodermis: absent. Cellular inclusions: druses in some mesophyll cells toward 2–6 cell apart from the epidermis. **Vascular tissue system**: comprised by closed, collateral vascular bundles (Fig. 4B–C), arranged in two central, concentric series (Fig. 4A), made up of bundles of a larger size and many of smaller dimensions which are scattered in the mesophyll.

Distribution and ecology:—*Cohniella ×francoi* is only known from the vicinity of the Santa Rosa National Park in Guanacaste province, Costa Rica. This hybrid grows in tropical dry forest (Holdridge 1967) where the distribution ranges of its putative parents, *C. ascendens* and *C. brachyphylla*, overlap (Fig. 2). The Santa Rosa National Park and surrounding areas are located in the Santa Rosa Plateau at 300 m of elevation, between the Pacific Coast and the Guanacaste Cordillera (Heinrich & Hurka 2004); in this area both putative

parents have been recorded; the *C. brachyphylla* parent was misidentified by these authors as *Oncidium cebolleta* (Jacquin 1760: 30) Swartz (1800: 240) and the *C. ascendens* parent as *O. ascendens* Lindley (1842: 4). Vouchers for these two species from the general Guanacaste area are cited in Cetzal-Ix & Carnevali (2010).

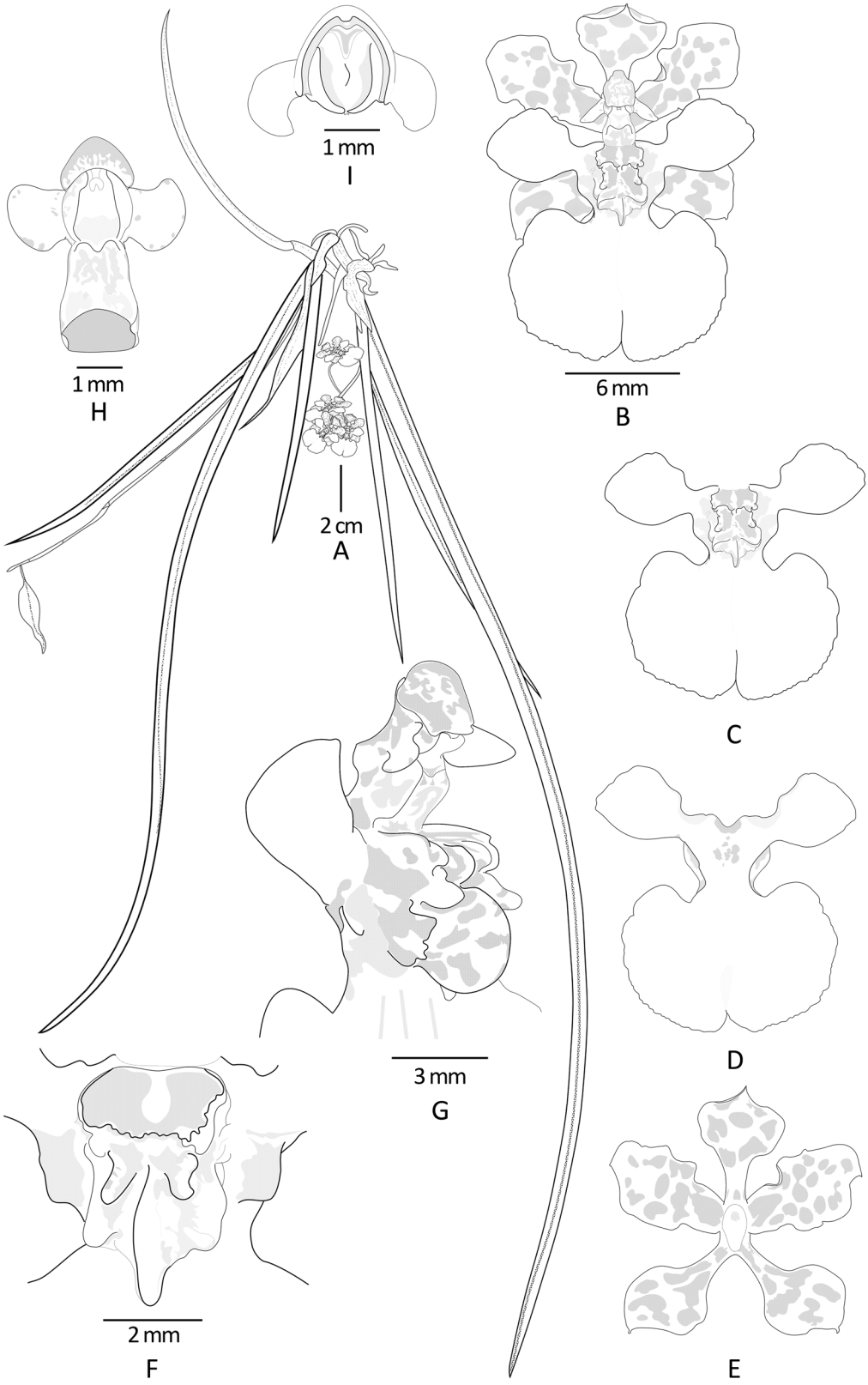

FIGURE 1. *Cohniella ×francoi*. **A.** Habit with inflorescence. **B.** Flower. **C.** Labellum front view. **D.** Labellum back view. **E.** Sepals and petals. **F.** Disc and callus. **G.** Column and base of labellum, lateral view. **H.** Column, ventral view. **I.** Column, front view. Scale: B-E. 6 mm. Drawing by W. Cetzal-Ix.

In most localities along their distributional range, both parental taxa are allopatric (Fig. 2, map scale is too large in some areas to clearly show this). However, in a few known localities both species appear to be parapatric, i.e. occurring in the same general area but growing in different vegetation types; *Cohniella ascendens* always found growing in the more humid, shadier places. Thus, the two taxa can grow within flying distance of a potential common pollinator. The occurrence of this natural hybrid between *C. ascendens* and *C. brachyphylla* suggests that, where the existence of vegetation mosaics allow for the habitats of both parental taxa to coexist within pollinator flying distance, gene exchange between these clearly different taxa may occur. We know little about the pollinators of these two taxa. We have observed oil-gathering *Centris* bees visiting *C. brachyphylla* both in the field as in cultivation (where the visits result in the successful production of capsules), whereas have never seen any pollinator on *C. ascendens*. There is a report of *Trigona nigra* Cresson as a pollinator of *C. ascendens* (Parra-Tabla *et al*. 2000) but the reported locality (Dzilam de Bravo in northern Yucatan State, México) makes it highly unlikely that they were actually studying this species (most likely it was *C. yucatanensis*). Since there are no plant vouchers reported in the Parra-Tabla *et al*. (2000) study, we have to disregard the report at this time.

FIGURE 2. Distributional records of *Cohniella ×francoi* and putative parents (based upon Cetzal-Ix & Carnevali, 2010). BE= Belize. CR= Costa Rica. GT= Guatemala. NI= Nicaragua. SV= El Salvador.

Eponymy:—Named after Franco Pupulin, Professor at the University of Costa Rica and researcher at the Lankester Botanical Garden, who collected the type specimen.

Morphological analysis:—The morphology of this specimen from Costa Rica is intermediate between *C. ascendens* and *C. brachyphylla*. The semipendulous habit, the callus type, the linear-oblong column wings, and the obovate stigmatic cavity are similar to those of *C. ascendens*. On the other hand, the erect, oblong to subquadrate lateral lobes of the labellum as well as the rectangular disc of the labellum with conical lateral

extension on the margins are similar to those of *C. brachyphylla*. Comparisons between the putative hybrid and its putative parental species are featured in Table 2 and Figure 3.

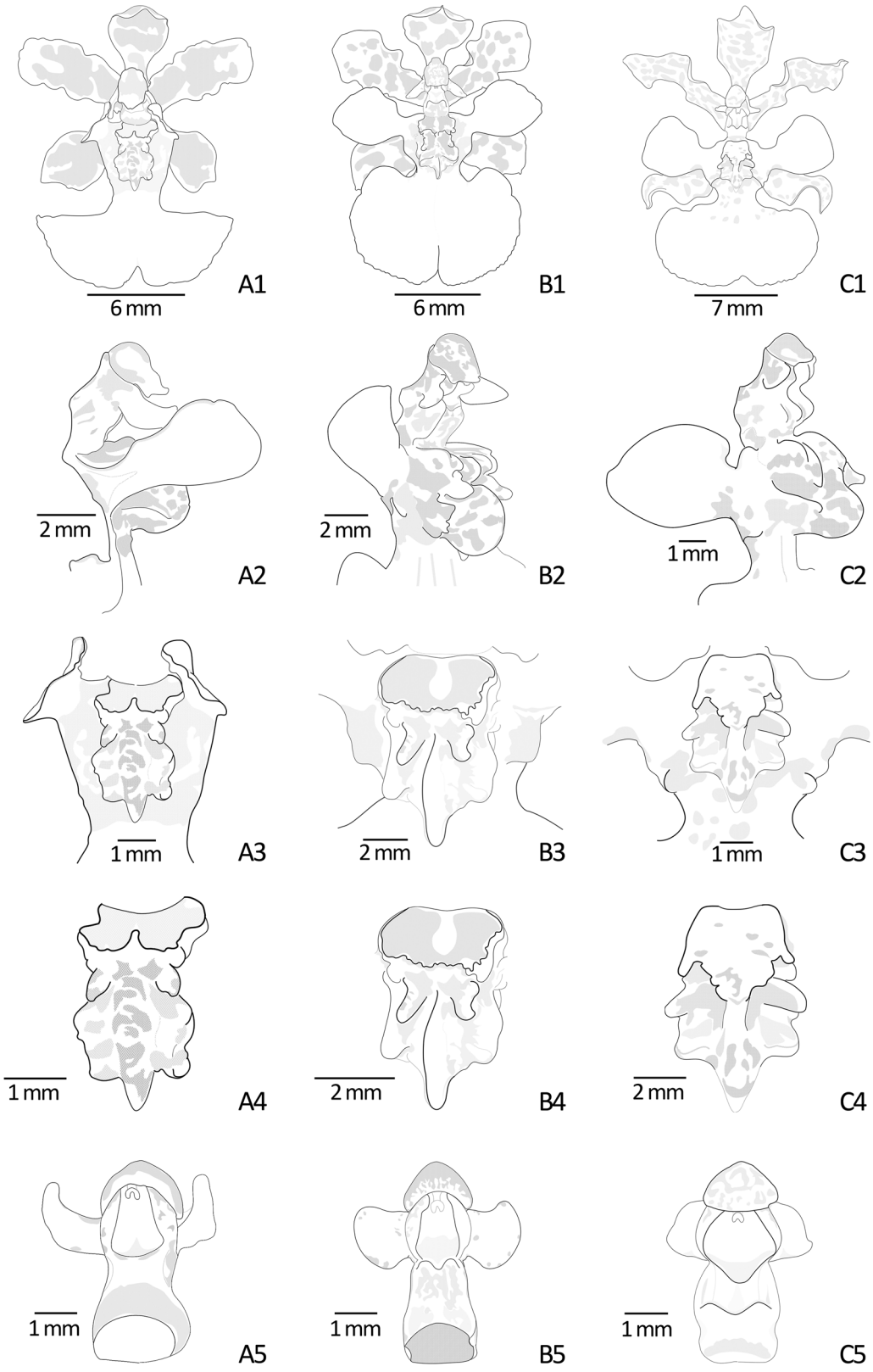

FIGURE 3. Morphological comparison of *Cohniella ×francoi* and putative parents. **A1–A5**. *Cohniella ascendens*. **B1–B5.** *Cohniella ×francoi*. **C1–C5.** *Cohniella brachyphylla*. **A1–C1.** Flowers. **A2–C2.** Column and base of labellum, lateral view. **A3–C3.** Disc and callus, front view. **A4–C4.** Callus. **A5–C5.** Column, ventral view. Drawing by W. Cetzal-Ix.

TABLE 2. Morphological comparison of *Cohniella ×francoi* and its putative parental species.

Characters	*Cohniella ascendens*	*Cohniella ×francoi*	*Cohniella brachyphylla*
Plant orientation	Semipendulous	Semipendulous	Erect to arching
Leaf length (cm)	(13–)15–86	(13.6–)17.8–52.0	(9–)12–42
Inflorescence length (cm)	(11–)14–65(–80)	9.7–21.0	(15–)24–110
Flower size (mm)	15–22	18–19	17–25
Central lobe of the labellum (mm)	5–7 × 8.5–13.0	7–8 × 12.0–12.5	4–14 × 4–18
Lateral lobes of the labellum (mm)	4–8 × 2–4	4.0–4.5 × 3.0–3.5	5–11 × 3–5
Lateral lobes of the labellum (position)	Erect, perpendicular to the central lobe	Spreading, in the same plane as the central lobe	Spreading, in the same plane as the central lobe
Lateral lobes of the labellum (shape)	Oblong to suborbicular	Oblong to subquadrate	Oblong to subquadrate
Disc of the labellum (shape)	Obovate	Rectangular	Rectangular
Lateral extension on the margins of the disc	Absent	Present	Present
Callus shape	*Cohniella ascendens* type	*Cohniella ascendens* type	*Cohniella brachyphylla* type
Callus (color)	Brown with yellow teeth	Brown with white teeth	White with yellow and pink teeth
Isthmus (mm)	0.5–4.0 × 1.3–3.0	2.0–3.0 × 1.0–1.5	1.0–2.0 × 1.2–3.5
Column base (shape)	Cylindrical	Cylindrical	Subquadrate
Column wings (shape)	Linear-oblong	Linear-oblong	Oblate
Column wings (color)	Yellow	Yellow with reddish points	Yellow
Stigmatic cavity (shape)	Obovate	Obovate	Rounded

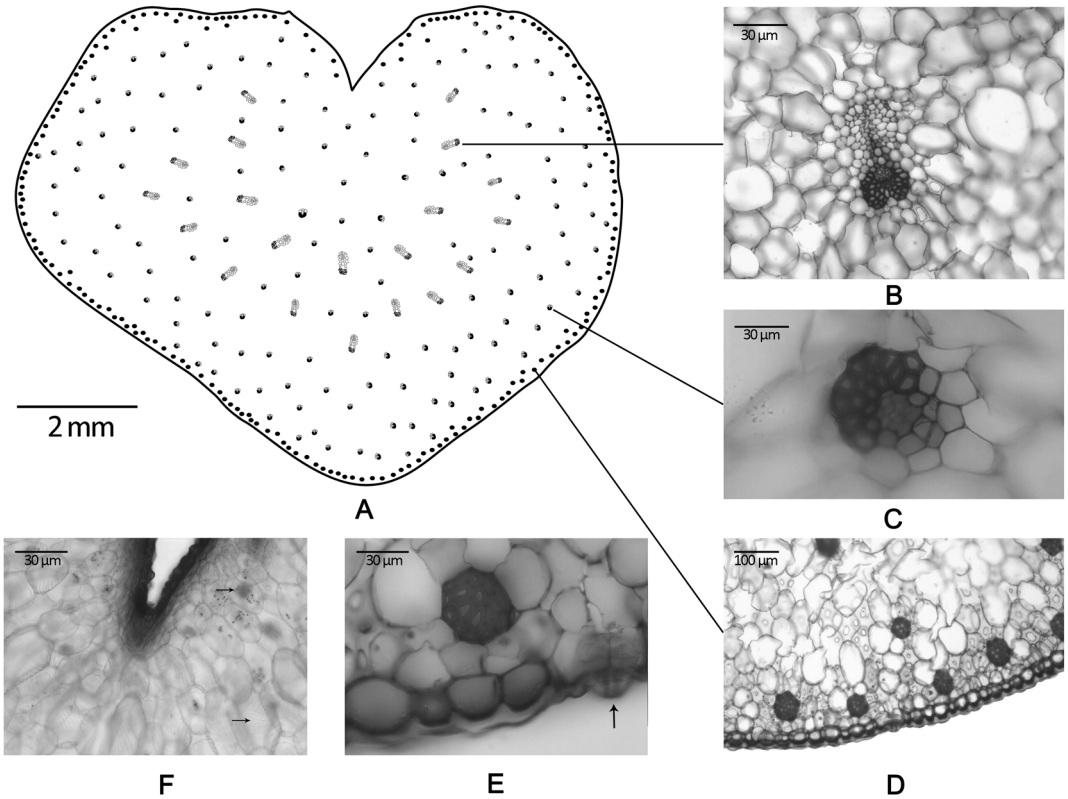

FIGURE 4. Leaf anatomy of *Cohniella ×francoi*, transverse sections. **A.** Schematic cross section near the middle of the leaf. **B.** Larger vascular bundles. **C.** Smaller vascular bundles. **D.** Extravascular fibers. **E.** Stoma and extravascular fibers, detail. **F.** View of the mesophyll, spiral cell wall thickenings and druses (indicated by arrows).

Cohniella ×francoi is further distinguished from *C. ascendens* and *C. brachyphylla* by the brown callus with white teeth whereas the combination of the *Cohniella ascendens* type callus with a rectangular disc bearing conical lateral extensions on the margins is unique to this nothospecies (Fig. 5).

FIGURE 5. Morphological comparison of *Cohniella ×francoi* and putative parents. A. *Cohniella ascendens* (Costa Rica, based on *Pupulin 5784*, JBL). B. *Cohniella ×francoi* (Costa Rica, *Pupulin s.n. sub Carnevali 7257*, CICY). C. *Cohniella brachyphylla* (Costa Rica, *Bogarin 6153*, JBL).

TABLE 3. Anatomical comparison of *Cohniella ×francoi* and its putative parental species.

Characters	*Cohniella ascendens*	*Cohniella ×francoi*	*Cohniella brachyphylla*
Dermal tissue system			
Cuticle	Smooth	Smooth	Papillose
External periclinal walls of the epidermal cells	Convex	Convex	Straight
Epidermal cell shape	Penta-septagonal	Hexagonal	Penta-hexagonal
Stomata type	Paracytic	Tetracytic	Paracytic
Stomata guard cell striations	Absent	Absent	Present
Fundamental tissue system			
Mesophyll cell wall thickenings	Spiral	Reticulate	Spiral
Starch	Absent	Absent	Present
Cellular inclusions type	Druses	Druses	Raphides
Vascular tissue system			
Arrangement of vascular bundles	One central arch	Two central arches	One central arch

Anatomical analysis:—*Cohniella ×francoi* has anatomical features intermediate between the putative parents (Table 3). It is similar *C. ascendens* by the smooth cuticle, convex external periclinal walls of the epidermal cells, the absence of striations in the stomatal guard cellls, the absence of starch in parenchyma cells of mature plants, and the presence of druses in parenchyma cells; it is similar to *C. brachyphylla* in the hexagonal epidermal cell shape. This combination of anatomical features renders this nothospecies most similar to *C. ascendens*. Otherwise, the putative hybrid is characterized anatomically by tetracytic stomata,

reticulate wall thickening walls of the mesophyll cells, and the vascular bundles arranged in two central arches. *Cohniella* species with smooth cuticle are usually found growing under more shady and humid conditions than those with a papillose cuticle (Cetzal-Ix 2012b). This nothospecies also has two concentric rings of vascular bundles in the mesophyll, a character found only in species of the *C. ascendens* complex (albeit absent from *C. ascendens* itself), a group of species restricted to humid, shady environments (Cetzal-Ix 2012b).

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