

× COCHLEZELLA COSTARICENSIS, A NAME FOR A RARE NATURAL HYBRID IN THE ZYGOPETALINAE (ORCHIDACEAE)

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Abstract. A new nothospecies in the subtribe Zygotetalinae (Orchidaceae), × *Cochlezella costaricensis*, representing a cross between *Cochleanthes aromatica* and *Warczewiczella discolor*, is described and illustrated from Costa Rica, and its relationships are discussed.

Keywords: Orchidaceae, Epidendroideae, Zygotetalinae, natural hybrids, *Cochleanthes*, *Warczewiczella*, *Cochlezella*, Costa Rica

The literature reports some thirty artificial intergeneric hybrids in the Zygotetalinae Schltr. (Orchidaceae), mostly involving horticulturally relevant species of *Zygotetalum* Hook., but natural hybridization in the subtribe is infrequent, and still less common is the occurrence of natural hybrids involving two different genera. Among the pseudobulbless, conduplicate-leaved, one-flowered genera of the *Huntleya* Bateman ex Lindl. clade (Whitten et al. 2005, Pupulin 2009a), only 9 intergeneric hybrids have been recorded (Dressler 1981, Shaw 2005). Of these, only the nothogenera *Pescatobollea* Rolfe (*Pescatoria* Rchb.f. × *Bollea* Rchb.f.) and *Bensteinia* Christenson (*Benzingia* Dodson ex Dodson × *Kefersteinia* Rchb.f.) have been formally described as occurring naturally. After the reduction of *Bollea* Rchb.f. under *Pescatoria* Rchb.f. (Whitten et al. 2005), the natural crosses recorded in literature between species of these two groups [e.g., × *Pescatobollea gairiana* (Rchb.f.) Fowlie, × *Psbol. pallens* (Rchb.f.) Fowlie, *Psbol. bella* Rolfe] must now be considered as infra-generic hybrids. Therefore, with two nothospecies recorded from Ecuador (Neudecker 1994) and Costa Rica (Pupulin 2007, 2010), *Bensteinia* is so far the unique natural intergeneric hybrid genus recognized among the Zygotetalinae of the *Chondrorhyncha* Lindl. complex (Pupulin 2009a).

Natural hybridization is of particular interest as it is uncommon evidence that the biological barriers designed to maintain species integrity might be circumvented. In the case of the Orchidaceae, the tens of thousands of artificial hybrids produced by humans clearly show that genetic incompatibility does not play a major role in preventing the interchange of genetic material either among species of the same genus or between genera that are phylogenetically related (Adams & Anderson 1958, Garay & Sweet 1966, Dressler 1981, Arditti 2008). Most of the effective barriers that impede the transfer of genes between different species rely therefore on pre-pollination as well as geographical such as temporal, mechanical, and chemical mechanisms, which effectively prevent the right pollen from reaching the wrong stigma (Paulus & Gack 1990, Ayasse et al.

2003, Schiestl & Peakall 2005, Pansarin & Amaral 2007, Salzmann et al. 2007, Pinheiro et al. 2010). When a natural hybrid occurs, and especially if it occurs more than once, it implies that most of these barriers have become weak, and in some way are promoting the “wrong” pollen transfer. In terms of evolutionary consequences, the “faux pas” leading to the unusual combination of genes could be more than a simple mistake (Ellis & Johnson 1999, Cozzolino & Widmer 2005, Peakall 2007, Scopel et al. 2008, Steiner & Cruz 2009, Bellusci et al. 2010).

It was unfortunate that the supposed hybrid between *Cochleanthes aromatica* (Rchb.f.) R.E. Schult. & Garay (Fig. 1) and *Warczewiczella discolor* (Lindl.) Rchb.f. (Fig. 2), which was originally collected in the wild in Costa Rica by Clarence Horich and studied by Jack Fowlie, was never formally described nor was any material preserved for future reference. Nonetheless, Fowlie took a color photograph showing a large flower with spreading petals and an open and wide lip, wine-red in color, that was eventually published in an article dedicated to *C. aromatica* and *W. discolor*, two “blue orchids” from Costa Rica, and their natural hybrid (Horich, 1977). Horich was quite unclear about the locality where he collected the hybrid plant, referring simply to it as “a place in the mountains where both species occurred,” but he was emphatic in noting that he never found another plant of the natural hybrid, “in spite of there being other places where the two species grow together” (Horich 1977). Robert Dressler referred to this natural hybrid in 2003 in his treatment of *Cochleanthes aromatica* for the *Manual de Plantas de Costa Rica* (Dressler 2003: 53) but, again, he did not cite any voucher for this record. According to Dressler, the infrequent natural hybrid has a spreading lip that is dark red or purple-red in color, and this may suggest that Dressler also used Horich’s photographs as the main visual guide for his concept of the nothospecies. Of course, with just a photograph at hand, he could not prepare any specimens for the typification of the natural hybrid.

Indeed, the possibility that *C. aromatica* and *W. discolor* could erratically cross in nature is quite real, as the inter-

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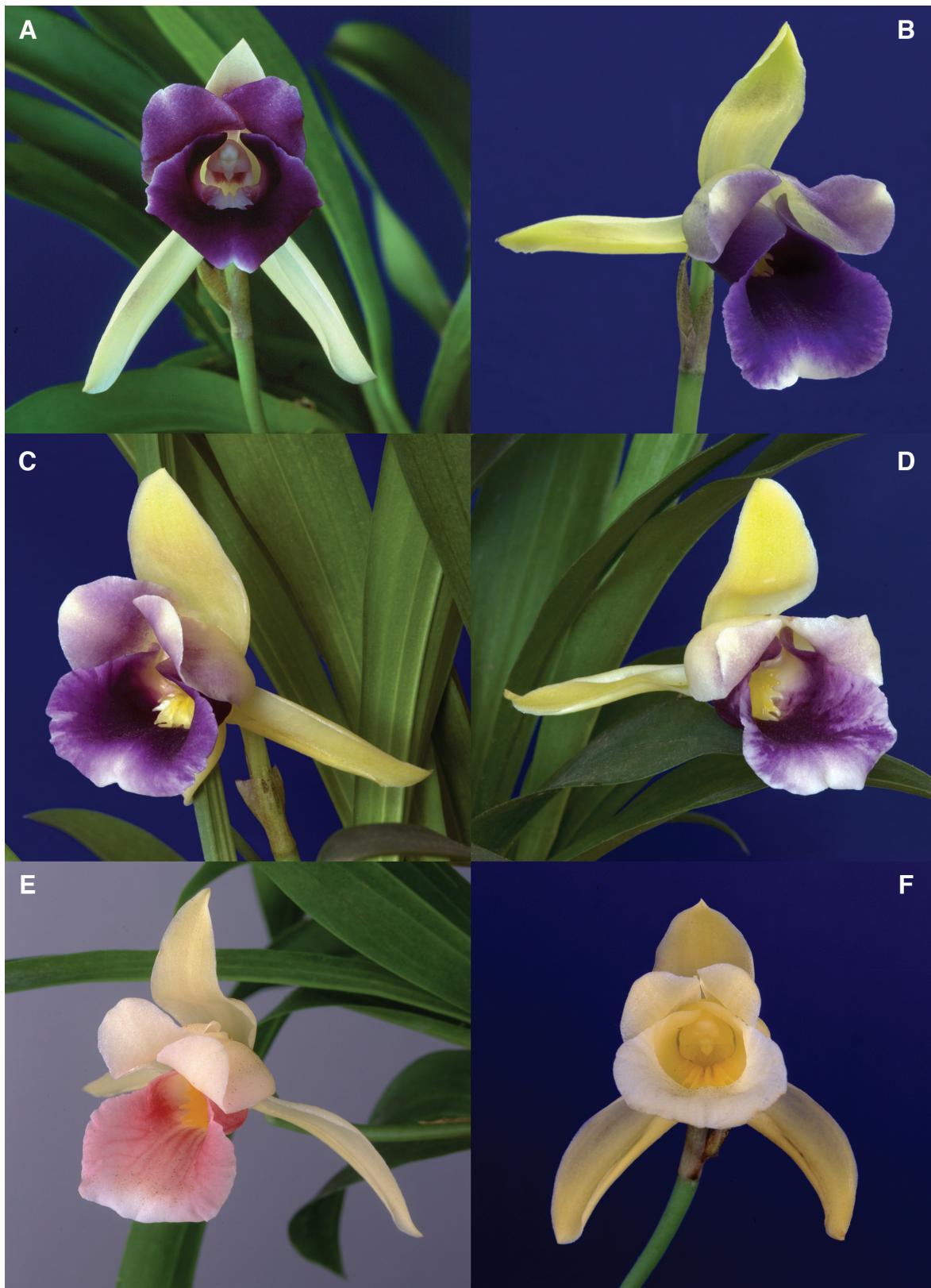


FIGURE 1. Flowers of *Warczewiczella discolor*, showing variations in lip color. **A**, *Pupulin* 1733 (JBL); **B**, *Karremans* 2292 (JBL); **C**, JBL-s.n. (JBL); **D**, *Pupulin* 5994 (JBL); **E**, without collecting data (JBL); **F**, *Víquez* s.n. (JBL). All the photos by the author.

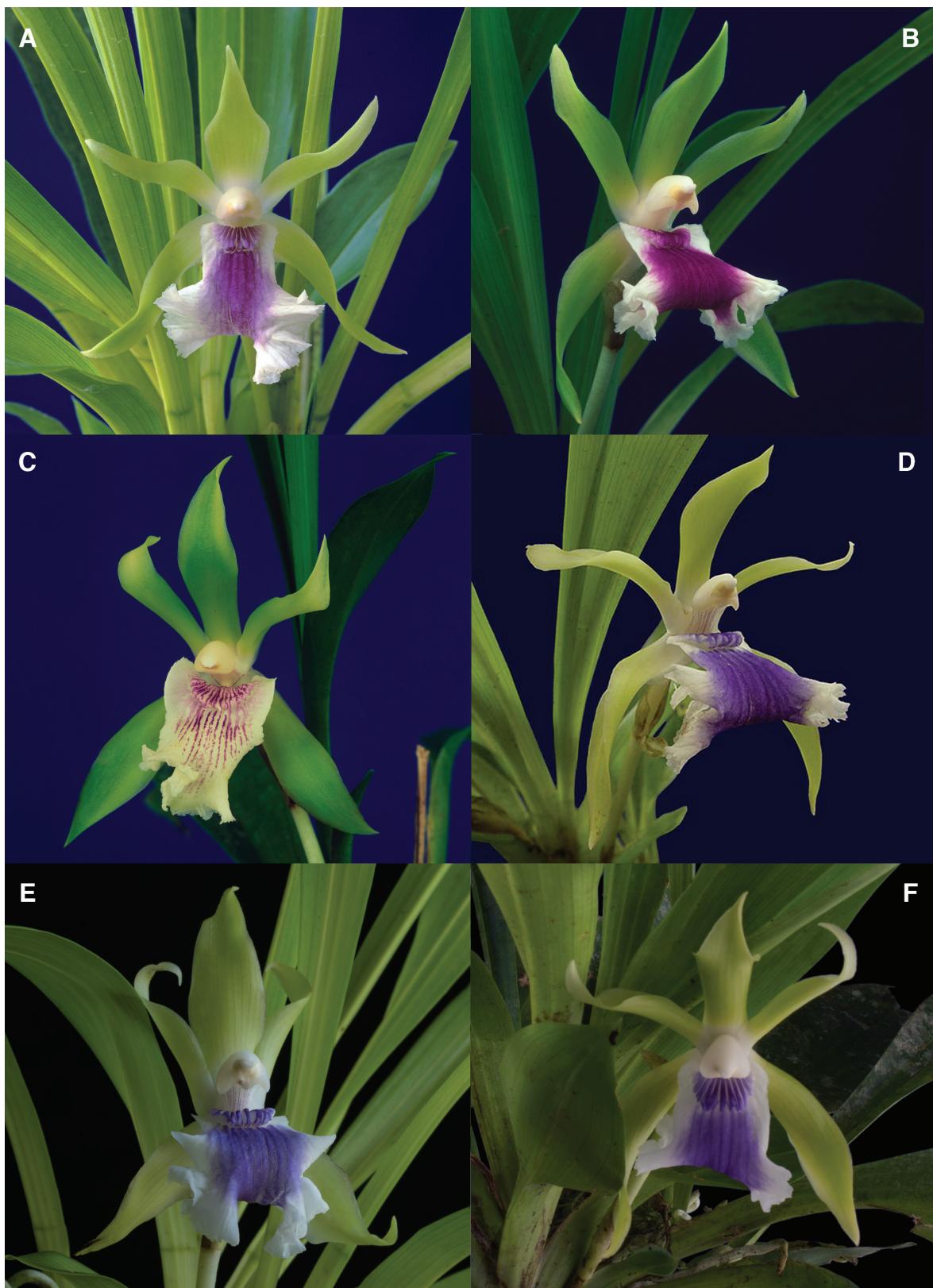


FIGURE 2. Variations in shape and color among flowers of *Cochleanthes aromatica*. **A**, Pupulin 2092 (JBL); **B**, Pupulin 6383 (JBL); **C**, JBL-01987 (JBL); **D**, JBL-03932 (JBL); **E**, Bogarín 1329 (JBL); **F**, Karremans 6665 (JBL). All the photos by the author.

fertility of the two genera has been proven artificially in four different hybrids, at least two of which are fertile [the aforementioned \times *Cochlezella* Overborook; \times *Czl.* Amazing (*C. flabelliformis* \times *W. amazonica*); \times *Czl.* Perfume (*C. aromatica* \times *W. marginata*); and \times *Czl.* Wildmoor, resulting from the cross of two *Cochlezella* hybrids, Amazing \times Overbrook] (Royal Horticultural Society 2015). According to van der Pijl and Dodson (1966), *C. aromatica* is pollinated by male bees of the genera *Euglossa* Latreille and *Eulaema* Lepeletier, which receive the pollinarium behind the head. Even though the specific pollinator of *W. discolor* has not been recorded yet, in most of the documented records in the Zygotetalinae of the *Huntleya* clade, the flowers attract male euglossine bees searching for perfume compounds, and *Eulaema meriana* Olivier is known to pollinate *Warczewiczella lipscomiae* (Rolfe) Garay in Panama (Croat 1978: 281). In the same species of *Warczewiczella*, the strongly reflexed lateral sepals with the margins infolded at the base mimic nectariferous spurs like those of a sympatric legume, *Clitoria javitensis* (Kunth) Benth. (Fig. 3), and also attracts female euglossine looking for food resources extending their tongue into the backswept lateral sepals in search of nectar (Ackerman 1983). This morphology driven by deceit, characterized by swept back lateral sepals that form a tubular false spur enclosing the notch on either side of the lip, allowing the passage of a bee's tongue, is scattered in the *Chondrorhyncha* complex and it is also present, although to a lesser degree, in *Cochleanthes* (Pupulin 2006, 2009b,

2009c). As both the putative parental species produce gullet flowers that show a mixture of fragrance reward and nectar-deceit pollination for long-tongued pollinators, the chances of an “erratic pollinator visit” to the “wrong” flower are greater. The fact that *C. aromatica* and *W. discolor* are not only sympatric in several areas across their distributional range (most notably along the eastern slopes of the Irazú and Turrialba volcanoes and along the low passes between the two watersheds of the Central Cordillera) (Fig. 4), but also partially overlap in their phenology, increase the chances of hybridization. *Cochleanthes aromatica* and *W. discolor* do have two different flowering peaks, in April–June and July–September, respectively (according to phenologic records maintained at the Lankester Botanical Garden based on 68 specimens of *C. aromatica* and 106 specimens of *W. discolor*), but almost 30% of the specimens of both species flower simultaneously in June and July (Fig. 5).

The hybrid genus between *Cochleanthes* and *Warczewiczella* already has a valid botanical name. According to the International Orchid Register (Royal Horticultural Society 2015), it was artificially created by William W. Wilson (1917–2014) crossing exactly *Cochleanthes aromatica* and *Cochleanthes* (now *Warczewiczella*) *discolor*. The resulting hybrid was registered as *Cochleanthes* Overbrook in 1964, and it remained undisturbed in that genus until Julian Mark Hugh Shaw coined \times *Cochlezella* in 2010 to give recognition to the separation of *Cochleanthes discolor* in his own genus



FIGURE 3. The flowers of *Warczewiczella lipscomiae* (A) are supposed to effectively mimic those of *Clitoria javitensis* (Fabaceae) (B). A: photo by the author. B: photo by S. Paton, from the Smithsonian Tropical Research Institute's Herbarium in Panama.

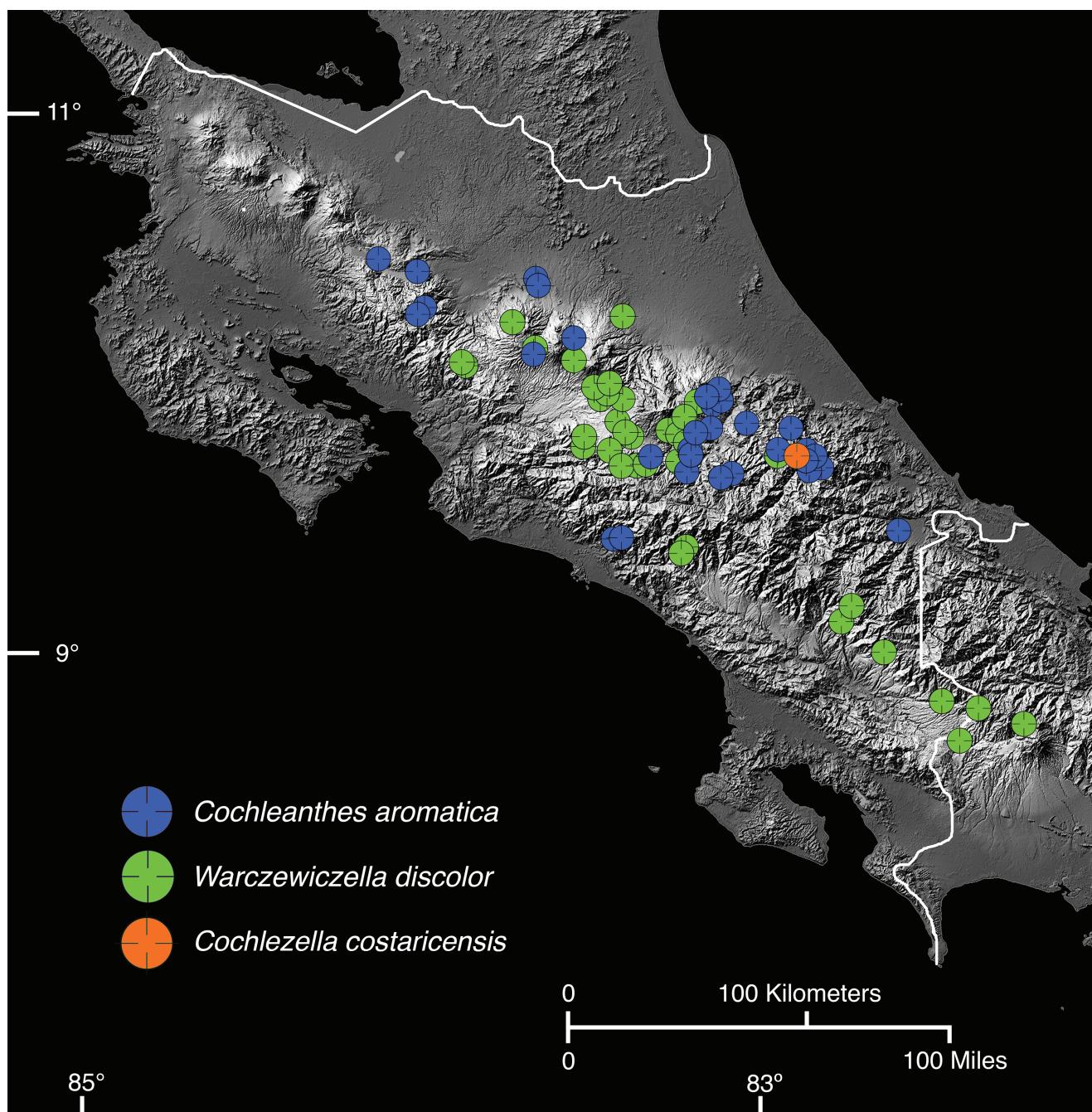


FIGURE 4. Distribution in Costa Rica of *Cochleanthes aromatica* (blue dots) and *Warczewiczella discolor* (green). The orange dot shows the putative collecting locality of the natural hybrid described here.

Warczewiczella (Shaw 2010: 79), where it originally was placed by Reichenbach (1852), a placement later confirmed by Fowlie (1969), eventually supported by contemporary molecular analyses (Whitten et al. 2005), and finally accepted in the treatment of the subtribe Zygopetalinae for *Genera Orchidacearum* (Pupulin 2009a).

Instead, what was still lacking a proper name, as well as a type and a formal description, was the natural hybrid that was found by Horich in the Costa Rican mountains, flowered with Fowlie in California, and was informally cited by Dressler in his monumental treatment of the Costa Rican Orchidaceae. For years, during the preparation of

my treatment of the subtribe Zygopetalinae for the flora of Costa Rica (Pupulin 2010), I actively looked for this elusive hybrid, visiting all the major orchid collections and the largest orchid shows in the country, but the search proved unsuccessful. Likewise, searching in the forests of Costa Rica for the hybrid between *Cochleanthes aromatica* and *Warczewiczella discolor* was and continues to be almost a nonsensical effort. The geographic distribution of the two species overlaps, both horizontally (see Fig. 4) and vertically, as *C. aromatica* has been recorded from 800 to 1,600 meters of elevation and populations of *W. discolor* are known at elevations between 700 and over 2,000 meters.

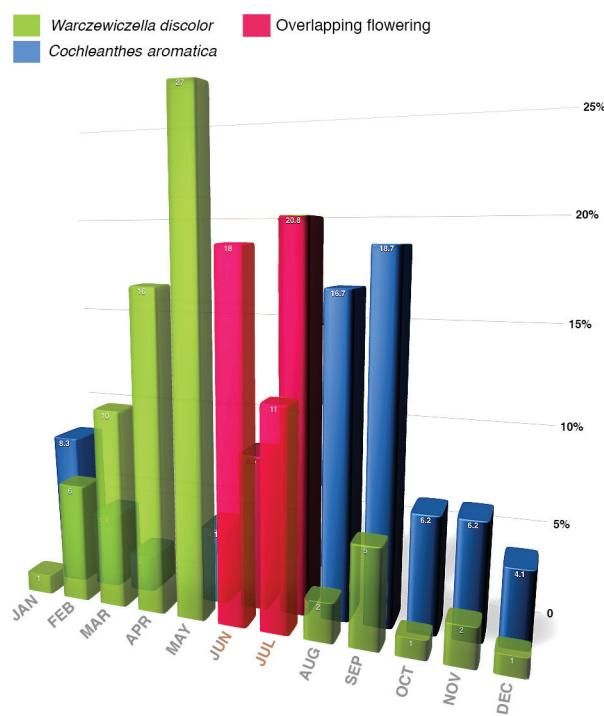


FIGURE 5. Graphic of the phenology of *Warczewiczella discolor* and *Cochleanthes aromatica*, showing distinct overlap in the months of June-July. Front row (green): *W. discolor*. Back row (blue): *C. aromatica*. Red columns: overlapping flowering period.

As the plants of *Cochleanthes* and *Warczewiczella* are almost indistinguishable in habit, and with no cues about the flowering time of the hybrid plants, the possibility of being in the right place at the right time to observe the flowering of a hybrid individual is virtually nonexistent.

I eventually had a chance to find a cultivated plant of wild origin at an orchid show recently held in Cartago, the ancient capital city of Costa Rica, which I describe herein.

× Cochlezella costaricensis Pupulin, nothosp. nov.

TYPE: Costa Rica. Cartago: Turrialba, collected by Marcos Brenes, probably in the region of Bajo Chirripó (*fide* collector), cultivated by Gerardo Víquez at Tierra Blanca, flowered 30 April 2015, F. Pupulin 8809 (holotype, JBL; isotype, JBL). Fig. 6–8.

Herba epiphytica caule abbreviato foliis conduplicatis petiolatis anguste oblanceolatis acutis vel subacuminatis ad 30 cm longis, floribus intermediis inter Cochleanthem aromaticam Reichenbachii filii et Warczewiczellam discolorum Reichenbachii filii, floris amplitudine, sepals lateralis lobus valde involutus, petalis anguste linear-ellipticis acutis patentibus, labello trilobato-pandurato angustiore inter lobulos laterales quam ad lobum medium, columna alis stigmaticis prominentis instructa (atque C. aromaticam), labello atrovirens lobulis lateribus erectis ad columnam pervenientis, callo albescente multiseriato apice digitato munito, columnae facie abaxialis pubescenti-lanuginosa in basi, odore capsico vel cedrino-lignaceo (atque W. discolorum).

Epiphytic, caespitose herbs without pseudobulbs, the leaves arranged like a fan. Roots terete, produced from

the rhizome at the base of the new vegetative shoots, ca 2 mm in diameter. Stem abbreviated, enclosed by six or seven imbricating sheaths, provided with hyaline margins, the upper ones foliaceous. Leaves conduplicate, articulate, membranaceous, oblanceolate-oblong, acute to subacuminate, abaxially carinate, 16–27 × 2.0–3.3 cm, strongly conduplicate at the base, grass green. Inflorescences 1–3, lateral, single-flowered, produced from the axils of lower sheaths, 7–10 cm long; peduncle terete, stout, spreading to suberect, provided with a conduplicate, papyraceous bract near the base; floral bract double, conduplicate, glumaceous-papyraceous, shorter than to subequal to the ovary, the external widely ovate, with hyaline-chartaceous margins, 20 × 14 mm, the subopposite internal bractlet narrowly lanceolate to ligulate, 17 × 6 mm. Flowers resupinate, large, spreading, with pale greenish white sepals and petals, the petals apically lightly flushed with purple, and solid violet lip, provided with a cream-coloured callus, boldly scented in the morning, the scent spicy. Dorsal sepal free, narrowly elliptic, acute, the apical portion gently reflexed-outrolled, 4.0 × 1.3 cm. Lateral sepals basally adnate to column foot, narrowly elliptic-lanceolate, acute, 4.3 × 1.2 cm, inrolled-folded toward base, strongly carinate abaxially, the keel somewhat protruding at the apex. Petals elliptic-oblanceolate, acute, the apex slightly reflexed, the apical margins wavy, 3.9 × 1.2 cm. Lip with a short claw, articulate with column foot, trilobed, obovate-flabellate in natural position, pandurate when spread, the base cordiform, 3.9 × 3.4 cm, the basal lobes erect, transversely elliptic, rounded, ca. 1.2 × 0.8 cm, the midlobe transversely elliptic, notched-bilobed at apex, 2.4 × 3.4 cm, the apical margins undulate; disc with a high ovate, multiseriate callus, 1.1 × 1.1 cm, composed of many low, rounded ridges, the upper margins angular, protruding apically into linear teeth, the central ones longer. Column straight, stout, hemiterete, 10 × 4.5 mm, dilated at apex into rounded stigmatic wings that converge toward the rostellum, the stigma transverse, slit-like, the base of the column extending into a velutine to sparsely hirsute foot, the apex of the foot with a low, conic-rounded callus. Anther cap shallowly cucullate, trapezoidal, two-celled. Pollinia 4, ovate-complanate, in two subequal pairs dorso-ventrally superposed, on a triangular stipe curling after removal, scarcely distinct from the ventral, elliptic, hyaline viscidium.

Etymology: The specific epithet is chosen in reference to Costa Rica, the country where the hybrid, as well as both the putative parents, are found.

A single plant of *Cochlezella* appeared within a mixed collection of *Warczewiczella* plants from the Caribbean watershed of the Talamanca mountain range, in central Costa Rica. The plant, believed to be a specimen of *Warczewiczella discolor*, was exhibited under that name at the Orchid Show of Cartago, on 30 April 2015. Its habit is indistinguishable from a plant of the true *W. discolor*, even though tending toward the largest size samples of that species. The flowers, however, are unmistakably different from those of *W. discolor*, and show several intermediate characters tending toward those of *C. aromatica* instead. Compared with typical flowers of *W. discolor*, the putative hybrid has larger flowers, with mostly spreading parts (vs. the lateral

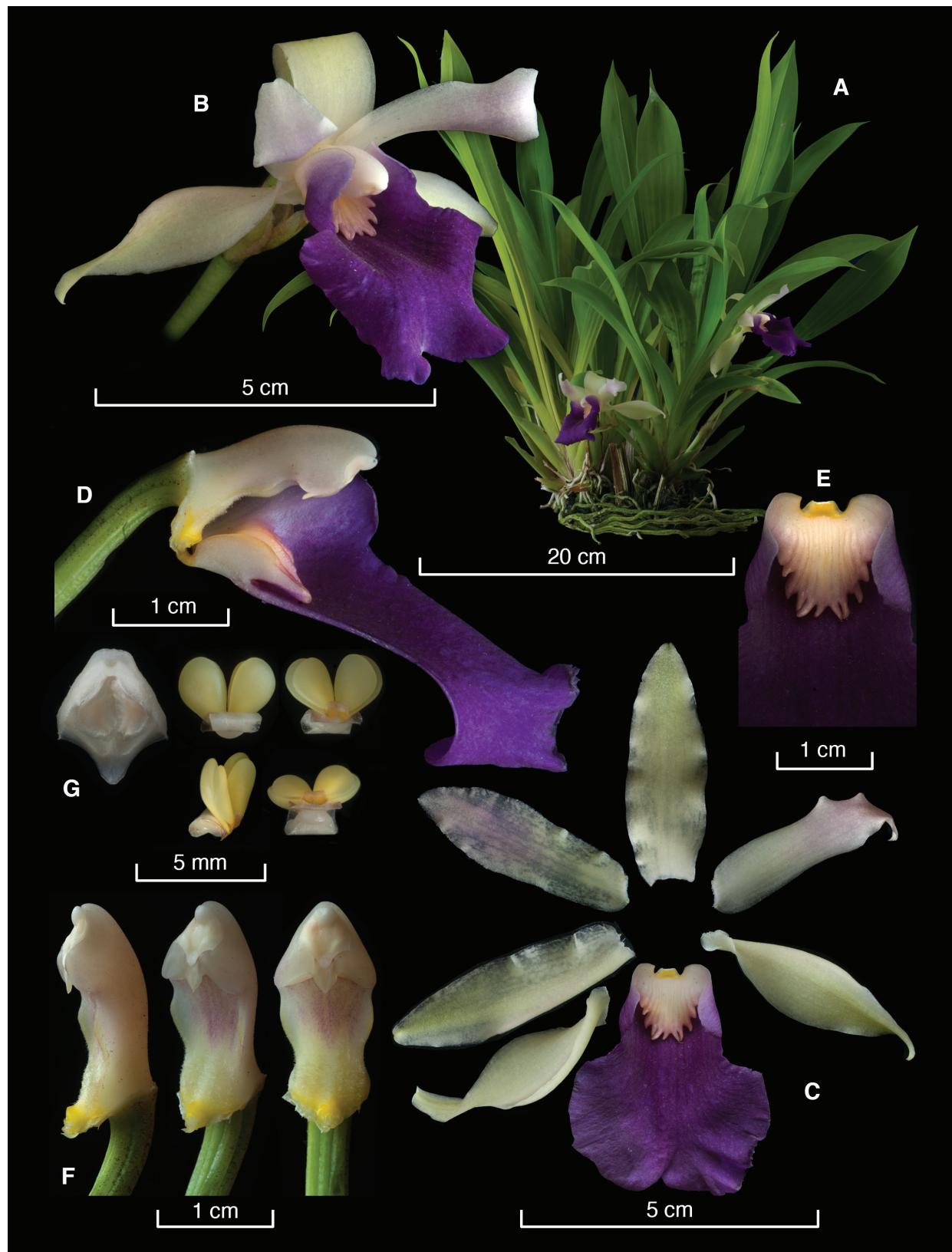


FIGURE 6. Lankester Digital Composite Plate of *× Cochlezella costaricensis*. **A**, habit; **B**, flower; **C**, dissected perianth; **D**, column and lip in lateral view (the lip longitudinally sectioned); **E**, callus; **F**, three views of the column; **G**, anther cap and pollinarium (four views). Prepared by the author.



FIGURE 7. The flower of *× Cochlezella costaricensis* that served as the holotype. Photo by the author.



FIGURE 8. The flower of *× Cochlezella costaricensis*. Three-quarter and frontal views of the flower that served as the holotype. Photos by the author.

sepals swept back and the petals almost porrect), the lateral sepals just slightly enrolled in the basal labellar portion (vs. with involute margins almost to the apex), narrowly linear-elliptic, acute petals (vs. broadly elliptic, obtuse-rounded), a lip that is wider across the midlobe than across the lateral lobes (vs. broadest at the base), and the column provided with prominent stigmatic wings, reminiscent of the column of *C. aromatica* (the column has no wings in *W. discolor*). On the other side, the flower of the hybrid also differs from those of *C. aromatica* by the completely deep violet lip (vs. white with a central lilac to violet blotch), with the lateral lobes erect to flank the column (vs. flat), the callus of the lip made up of several ridges ending in distinct teeth, and the pubescent-lanuginose ventral base of the column (vs. glabrous).

The flowers of *× C. costaricensis* emit a strong, spicy scent in the morning. The perfume also seems to show

intermediate characteristics between the powerful, sweet, lilac-hyacinth smell with notes of chocolate of *C. aromatica*, and the faint, camphoraceous, spicy, cedar-wood and black peppery fragrance of *W. discolor*.

To my knowledge, both the artificial (a few photographs of which are available through the Internet) and the natural hybrid presented here have a deep violet lip, a clear genetic legacy of the dark violet lip of *W. discolor*. Even though the form with deep violet labellum is the most frequent among populations of *W. discolor*, several individual variations occur in lip color (see Fig. 1), which may perhaps account for the unusual reddish coloration of the hybrid flower photographed by Horich. On the other side, whilst *C. aromatica* usually presents a white lip, longitudinally blotched and flecked with violet, individuals of this species with almost solid violet lip have also been documented (Fig. 9).

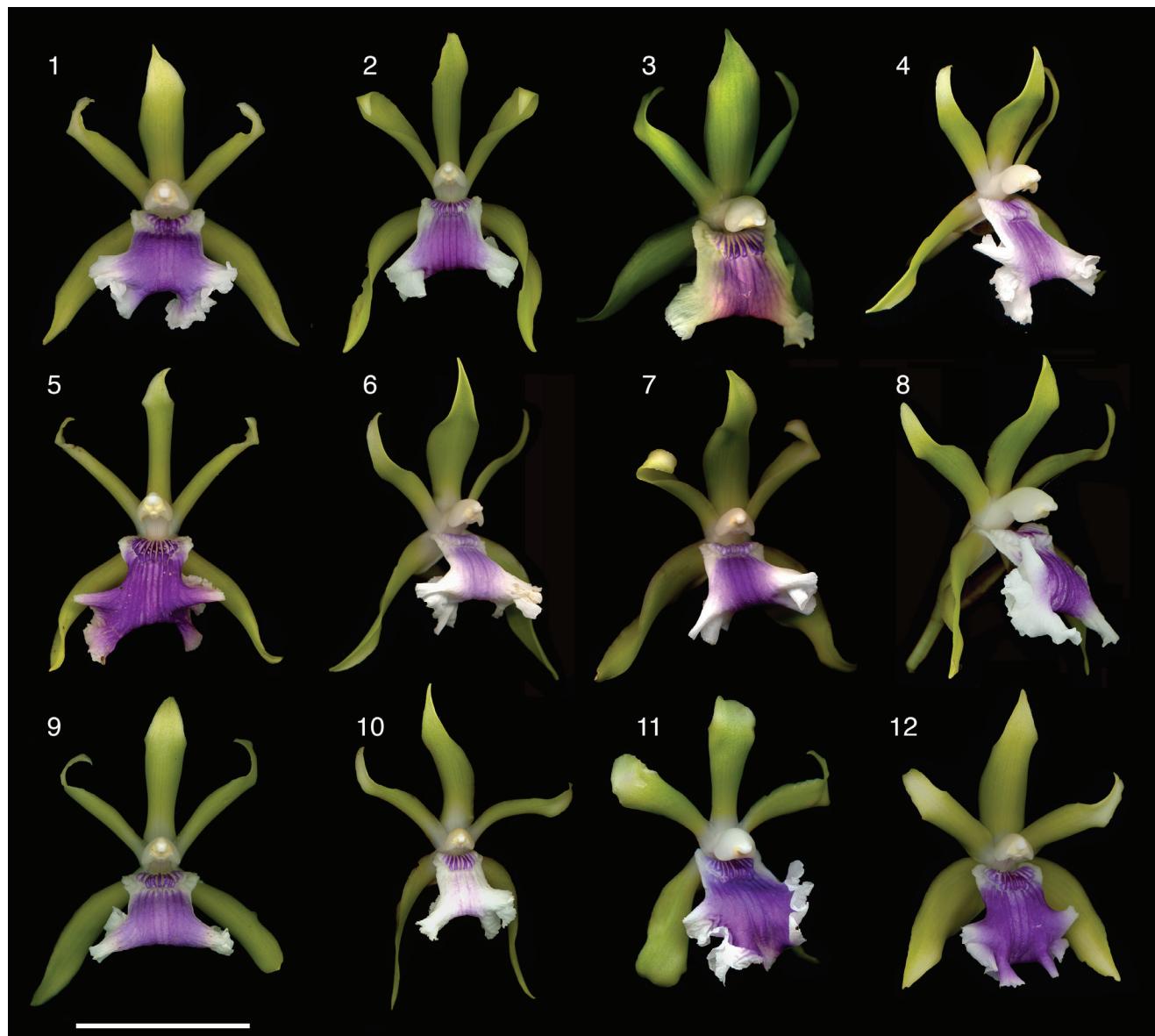


FIGURE 9. Variations in flower color among individuals of *Cochleanthes aromatica*. **1**, Blanco 1904; **2**, Pupulin 6363; **3**, Bogarín 9258; **4**, JBL-03932; **5**, JBL-s.n.; **6**, JBL-03932; **7**, Gómez 59; **8**, Pupulin 3058; **9**, Blanco 1904; **10**, JBL-01987; **11**, Bogarín 1635; **12**, Pupulin 6383. Scale bar = 5 cm. All the vouchers at JBL. Composite illustration by the author from images by F. Pupulin & D. Bogarín.

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