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The world upside down: the first *Kefersteinia* (Orchidaceae: Zygopetalinae) with non-resupinate flowers

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Abstract

A new species of *Kefersteinia* (Orchidaceae, Zygopetalinae), *K. carolorum*, from the state of Táchira, Venezuela, is herein described, illustrated, and characterized based on morphological features. *Kefersteinia carolorum* is similar to *K. lactea* from Costa Rica, but it differs in the non-resupinate flowers and the longer callus. The labellum in the upper-most position that distinguishes this species is unique in the genus but has evolved independently in Zygopetalinae at least three times. Evolutionary, ecological, and functional implications of this character are explored. The conservation status of the new taxon is assessed as DD according to IUCN (International Union for Conservation of Nature) criteria. We also provide a key to identify the genera of the Zygopetalinae with labellum in an upper-most position. In addition, we offer a key for the *Kefersteinia* species from Venezuela, a figure, and a map showing their geographical distributions.

Key words: resupination, pollination, Orchidaceae, Táchira, Venezuela

Introduction

Kefersteinia Reichenbach (1852: 633) encompasses about 60–70 species found from southern Mexico to Bolivia (Harding 2008; Pupulin 2009; Plant List 2013). The genus is most diverse in humid forests at low and intermediate elevations along the Andes of Ecuador (21 species known), Peru (17 species recorded), and in the mountains of Panama and Costa Rica, where eleven species have been recorded (Pupulin & Merino 2008). Species diversity rapidly diminishes toward the north, where a single species (*K. tinschertiana* Pupulin (2004: 166)) is known from Guatemala to southern Mexico (Pupulin & Merino 2008). The Amazonian lowlands and the Guayana region are also poorly represented (Carnevali *et al*. 2007).

Based on labellum and callus morphology, two groups of species may be identified, albeit still excluding several aberrant species, e.g. *Kefersteinia endresii* Pupulin (2001: 543–545). An Andean group of taxa, centered around *Kefersteinia graminea* (Lindley 1844: 101) Reichenbach (1852: 634, the type of the genus) is characterized by a labellum the lamina of which folds back abruptly at the middle, also having a sessile, low-laminar callus (Pupulin 2009). A second morphological group, mainly occurring in Panama and Costa Rica but with species along the Pacific watershed of Colombia and Ecuador and in western Venezuela, is similar to *K. wercklei* Schlechter (1923: 53) and the flowers feature a labellum with a straight lamina; the thickly fleshy callus is supported by a distinct stalk (Pupulin 2009). These two groups of taxa are not monophyletic entities (Whitten *et al*. 2005), thus precluding them to be formally recognized, as attempted by Senghas & Gerlach (1992: 1641), as *Kefersteinia* sect. *Umbonatae*, and later by Szlachetko (2003: 335), who proposed the genus *Senghasia*.

Subtribe Zygopetalinae Schlechter (1926: 577), consists of 35 Neotropical genera. All, with the exception of *Chaubardiella* Garay (1969: 146) (ca. 8–9 species) and a single species of *Benzingia* Dodson ex Dodson in Romero-González & Dodson (2010: 526) (*B. hirtzii* Dodson in Romero-González & Dodson (2010: 527)) are characterized by resupinate flowers. Furthermore, the flowers of *Aetheorhyncha andreettae* (Jenny 1989: 92) Dressler (in Whitten *et al*. 2005: 95) are described as "resupinate, almost erect in natural position" (Pupulin (2009: 460), also see

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photograph by Madame Popow at http://www.orchidspecies.com/chondandreettae.htm), although in some cultivars the labellum may appear to be held uppermost (see, for example, photo by K. Senghas at https://orchid.unibas.ch/phpMyHerbarium/602042/1/Aetheorhyncha/andreettae/Jenny_Rudolf/Dressler_Robert_Louis/specimen.php). As the available evidence strongly suggests that plants of *A. andreettae* normally bear resupinate flowers, we do not include it in our discussion below.

Here we report the finding of non-resupinate flowers in a species of yet an additional genus of Zygopetalinae, *Kefersteinia*, which is here described and illustrated.

Materials and Methods

The description of the new species was prepared from measurements, photographs and scans, and other data sent to the authors by Carlos García Esquivel and prepared from plants he and Carlos Bello (from San Cristóbal, State of Táchira, Venezuela) collected in the field. Also, one of us (GC) had the opportunity to dissect and photograph flowers in spirit furnished by the collectors during a short research stay at VEN in 2009. Unfortunately, no pollinaria were available. A distributional map was produced by plotting the locality data cited in herbarium specimens on an image data "shaded and colored SRTM elevation model" (NASA/JPL/NIMA 2002) using ArcView 3.2 (ESRI 1999).

We should point out that our research was constrained by CITES, which can limit the shipping of material of Orchidaceae even between research institutions.

Taxonomy

Kefersteinia carolorum Carnevali & Cetzal, ***sp. nov.*** (Figs. 1–2)

A species similar to *Kefersteinia lactea* (Reichenbach 1872: 1290) Schlechter (1923: 228–229) but bearing non-resupinate flowers with a proportionately longer callus on the labellum; also, the broadest section of the column is above the middle as opposed to broadest below the middle in *K. lactea*.

Type:—VENEZUELA. Táchira: Río Chiquito, 7° 34' 9" N, 72° 20' 48" W, approx. 1,440–1,500 m, 4 July 2013, *C. García Esquivel & C. Bello s.n.* (holotype, VEN!; photographs at CICY, AMES).

Plant to 10–11 cm tall, epiphytic, erect, caespitose, stems very short and totally enveloped by leaf-sheaths, each shoot provided with 2–3 leaves and 2–3 acute basal sheaths. Roots terete, thick, white. Leaves 3–9 x 0.6–1.3 cm, narrowly oblanceolate-elliptic, acute to abruptly acuminate, narrowing at base to a conduplicate petiole ca. 1 cm long. Inflorescence 14.5 mm long, 1-flowered, slender, suberect to arcuate-pendent, peduncle terete, green, with 2-internodes and with one peduncle bract at base 4 x 4 mm, a more distal one of 3.5 x 3 mm; floral bract double, the outer one broadly ovate, shortly acuminate, 4.0 x 3.0 mm, the subopposite internal bractlet smaller, narrowly lanceolate, acute, 3.0 x 1.6 mm. Ovary terete-subclavate, rounded in section, to 5 mm long including the pedicel. Flowers white or pale green (a few, if any, purple dots occasionally found at the very base of the petals), non-resupinate, the labellum marked with small, dispersed purple blotches, the callus white spotted purple, the column white. Dorsal sepal 10 x 4.1 mm, oblong-elliptic, acute, slightly incurved toward the column, concave distally, abaxially subcarinate. Lateral sepals 11 x 4.2 mm, inserted along the margins of the column foot, oblong-elliptic, obtuse to subacute, minutely apiculate, concave apically, dorsally slightly carinate along the mid-nerve. Petals 11 x 4.2 mm, elliptic, acute or subobtuse, dorsally slightly carinate along the mid-vein. Labellum 10 x 12 mm upon flattening, deeply concave and with the apical half geniculate in natural position, transversely broad elliptic to subcircular upon flattening, shallowly 3-lobed, the central lobe shallowly emarginate, with a triangular, subapical apicule at the apex of the emargination, the apical margins slightly undulate; callus 5.2 x 2.0 mm, emerging directly from the base of the labellum, oblong in general outline, slightly pandurate when viewed from above, with a concave longitudinal channel and two apical, slightly flattened, acute, porrect teeth, ca. 1.5 mm long, also provided with two additional, smaller teeth about midlength. Column 8.4 x ca. 2.8 mm at the middle of the foot, oblong, stout, with a distinct foot 0.5 mm long, the lateral margins projecting midlength in 2 broadly semi-rounded wings, the abaxial surface displays a short infrastigmatic, apparently rounded, subancipitous keel, the ventral surface glabrous, the dorsal surface papillose. Anther cap cucullate, ovate, flattened, 2-celled. Pollinia not seen but presumably 4 in two pairs of different size, linear-oblong, on a triangular, folded stipe; viscidium hyaline, indistinct.

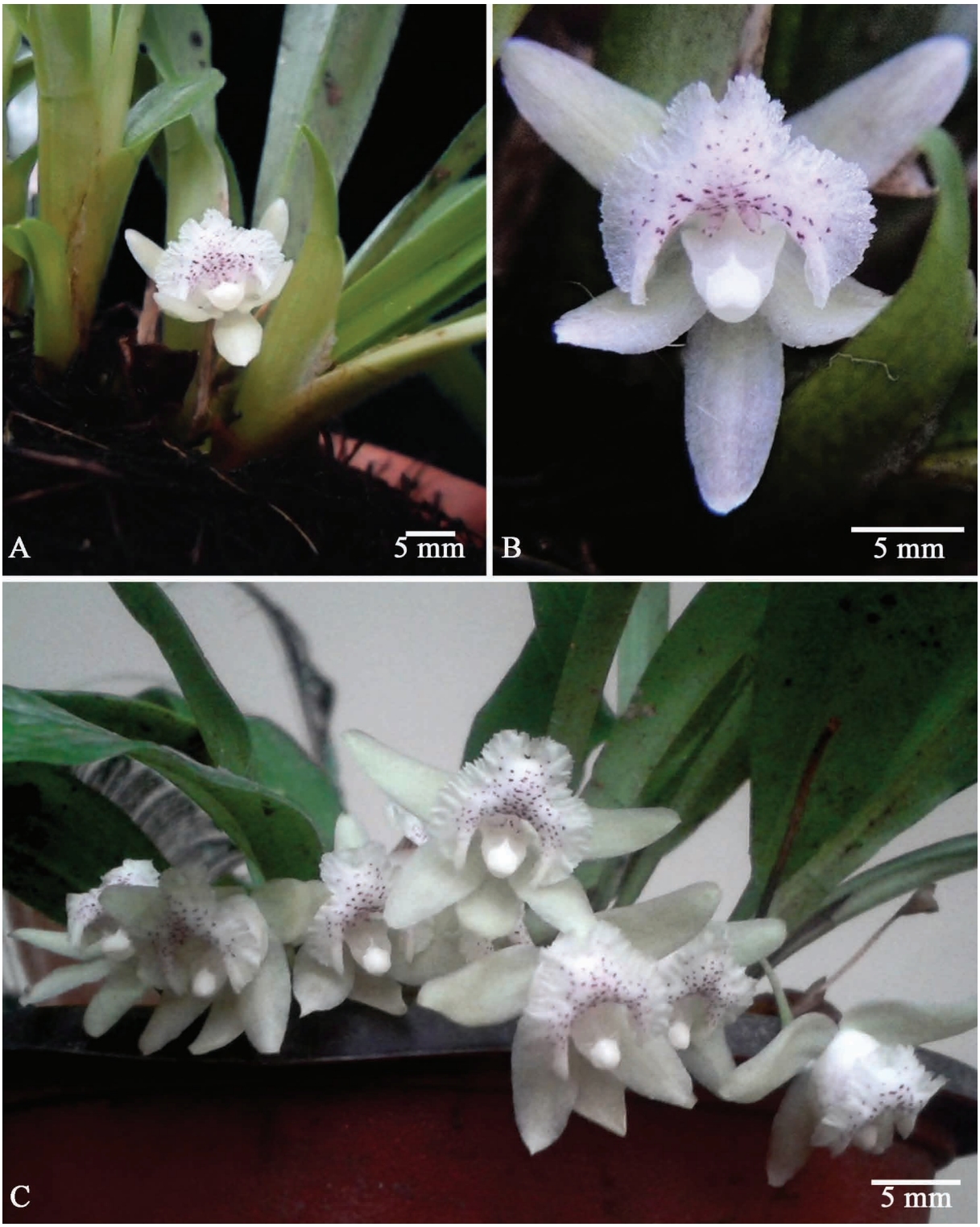

FIGURE 1. *Kefersteinia carolorum* Carnevali & Cetzal. **A.** Habit. **B.** Close up of the flower in natural position. **C.** Habit and mature plant in full bloom. [*C. García Esquivel & C. Bello s.n.* (VEN)].

Eponymy:—This new species honors Carlos García Esquivel, from Caracas, Venezuela, and Carlos Bello (from San Cristóbal, Táchira State, Venezuela), thus *Kefersteinia carolorum*, of the "Carloses", who together collected the plants on which the type of the species is based.

Distribution and ecology:—This species is known only from the type material collected in Táchira State, Venezuela, in tropical rain to cloud forest at 1,400–1,500 m near the village of Río Chiquito, Táchira, which is ca. 11 km SW in straight line from Santa Ana del Táchira (approx. 15 km south of the city of Rubio). The type locality is close to the Colombian-Venezuelan border (Fig. 3) and it is entirely possible that the species will be eventually

found in Colombia. The collectors of the type specimen recently sent pictures of flowering plants of the same species coming from a second locality, presumably close to where the type was collected, indicating that there are at least two populations of the new species.

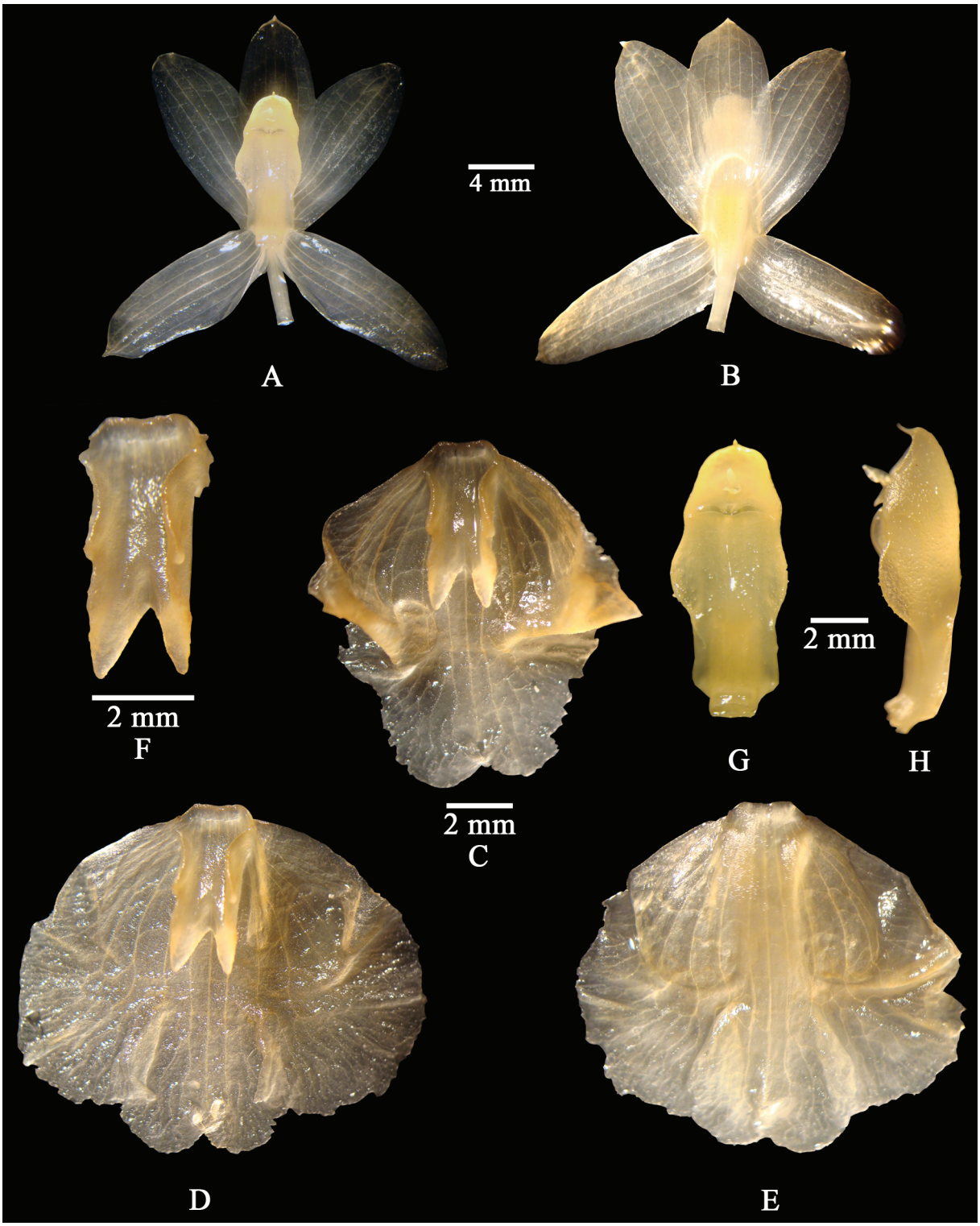

FIGURE 2. *Kefersteinia carolorum* Carnevali & Cetzal (based on pickled material). **A.** Sepals and petals with column, front view. **B.** Sepals and petals with column, back view. **C.** Labellum, front view. **D.** Labellum spread, front view. **E.** labellum spread, back view. **F.** column, front view. **G.** column, lateral view. [*C. García Esquivel & C. Bello s.n.* (VEN)].

Discussion:—*Kefersteinia carolorum* is easily distinguished from *K. lactea* and its close relatives by the non-resupinate flowers of uniform white, faintly pink, or greenish white color with purple spots on the labellum, by its relatively long, oblong callus ending in two relatively long teeth, themselves having, along the middle, another pair of teeth, and by the column that is broadest above the middle (versus broadest below the middle in *K. lactea*). It may

be confused with *K. microcharis* Schlechter (1923: 300), another close relative from Costa Rica, but in the latter the callus is proportionally much shorter, broader, and ending in two divergent, rounded, blunt teeth. It is further similar to *K. alba* Schlechter (1923: 228), but this species has no keel on the underside of the column.

Kefersteinia species are pollinated by male euglossine bees (Pupulin 2009 and references therein) and *K. carolorum*, due to its relatively reduced size, is most likely pollinated by one or more species of small *Euglossa* Latreille (1802: 436). Based on field observations of orchid pollination by the authors, some non-resupinate flowers appear to pose a challenge to pollinators when compared to resupinate flowers.

In the latter, bees simply land on the labellum right-side-up and penetrate the flower to collect floral fragrances (apparently in a convoluted way in previously known species of *Kefersteinia*, where the shape of the column ventrum and the callus beneath force bees to twist their body as they enter the flower "... so that the pollinarium is placed on the basal segment of [one of] the antennae"; Pupulin 2009).

Bees have two options when pollinating non-resupinate flowers. They can enter and exit the flower upside down, in which case the pollinarium is placed on the dorsum of the bee. Individual pollinators can easily be divided into two groups: "naive" bees that have to learn this complex maneuver (i.e., to enter and exit the flower upside down) and have at first difficulty performing it, and those that apparently have learned it before and can easily perform it (as when male euglossine bees visit all female and some male flowers of *Catasetum* Kunth (1822: 330) and flowers of *Gongora* Ruiz & Pavón (1794: 117). Bees can also enter non-resupinate flowers right side up, moving back and forth on the ventral face of the column as they gather fragrances, in which case the pollinarium is placed on the ventrum of the bee, as in the male flowers of *Catasetum discolor* (Lindley 1835: t. 1735) Lindley (1835: t. 1735), *C. longifolium* Lindley (1839: Misc. 94), and in *Chaubardiella* (with the possible exception of some populations of *C. tigrina* (Garay & Dunsterville *in* Dunsterville & Garay 1961: 72) Garay (1969: 146) with resupinate flowers, see, for example Dunsterville & Garay 1961: 14, 72), and *Benzingia* (*B. hirtzii*).

In *Chaubardiella*, the pollinarium has a strongly hooked viscidium that attaches to one of the legs of the pollinator (Dressler 2000; Whitten *et al*. 2005); in *Benzingia hirtzii*, where the uppermost position of the labellum is achieved by means of a strongly geniculate pedicel, apparently the viscidium strongly and quickly curls diagonally after removal (anonymous reviewer 2015), apparently another "way" to attach the pollinarium to one of the legs of the pollinator.

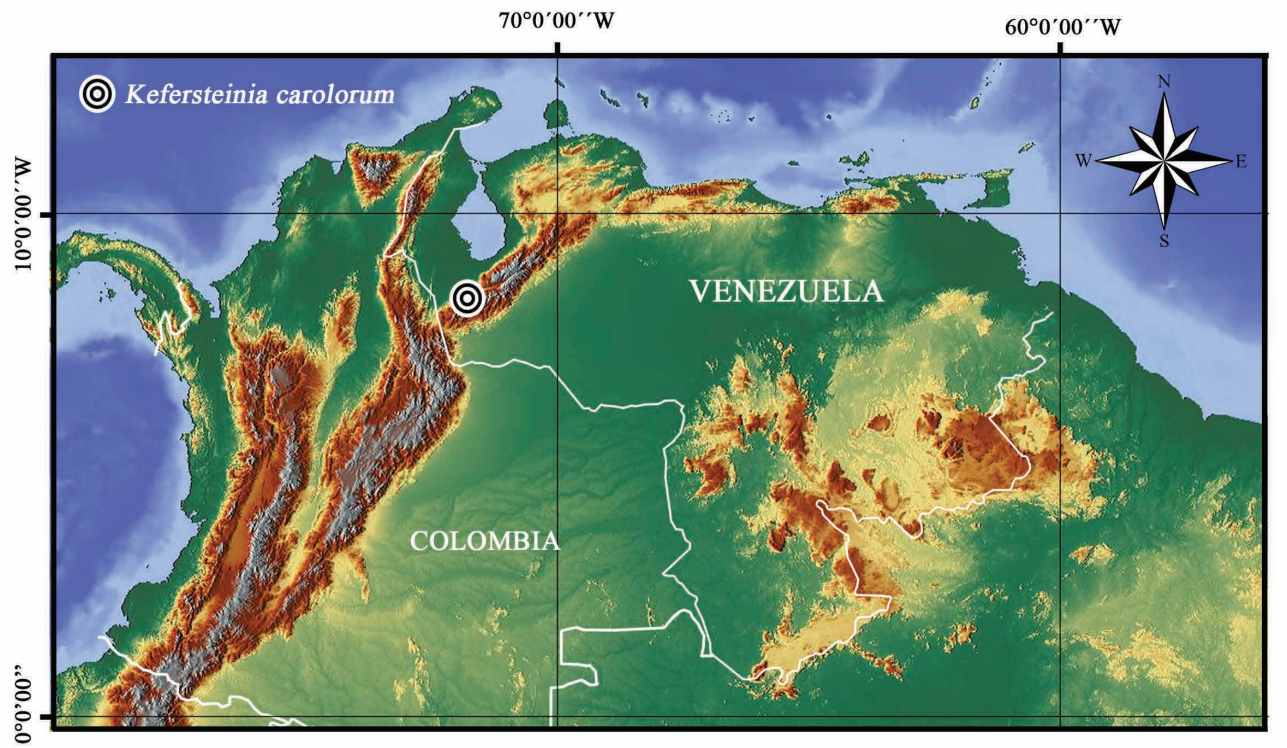

FIGURE 3. Distribution of *Kefersteinia carolorum*.

It is noteworthy that in the previous two known instances where non-resupination evolved in the Zygopetalinae, flowers function asymmetrically relative to the place of pollinaria attachment on the bee, i.e., the pollinarium is placed on the legs instead of the more common basically symmetrical attachment on the head, thorax, or abdomen of the bee.

Thus, it seems apparent that at least in the Zygopetalinae, the asymmetrical placement of pollinaria on the bee may be an exaptation for the evolution of successful species bearing non-resupinate flowers.

As cited above, in *Kefersteinia* the column is appressed against the callus of the labellum, forcing the pollinator to enter the flower in a contorted way (Pupulin 2009), and the pollinarium attaches itself to the basal segment of an antennae. This system functions in species of the genus with resupinate flowers. Would it work the same way in *K. carolorum*?

We have not examined the pollinarium of this species and how pollination of the new species takes place is uncertain. However, judging from the images we have seen of flowers of the species with anthers, the viscidium of *K. carolorum* appears to resemble those of its congeners (i.e., a hooked viscidium). Therefore, if bees approach the flower as they do in *Benzingia hirtzii* and *Chaubardiella* spp. (moving back and forth on the ventral side of the column), we hypothesize that the viscidium in this case may also curl around one of the legs rather than around one the antennae.

Non-resupinate flowers, thus, have evolved independently at least three times within Zygopetalinae: once in *Chaubardiella* placed in a clade that includes genera such as *Warscewiczella* Reichenbach (1852: 635) and *Chondrorhyncha* Lindley (1846: 12) with vegetatively large plants (Whitten *et al*. 2005) and again in the *Echinorrhyncha-Kefersteinia-Euryblema-Benzingia-Daiotyla* clade with small plants and deeply saccate labella (Fig. 4).

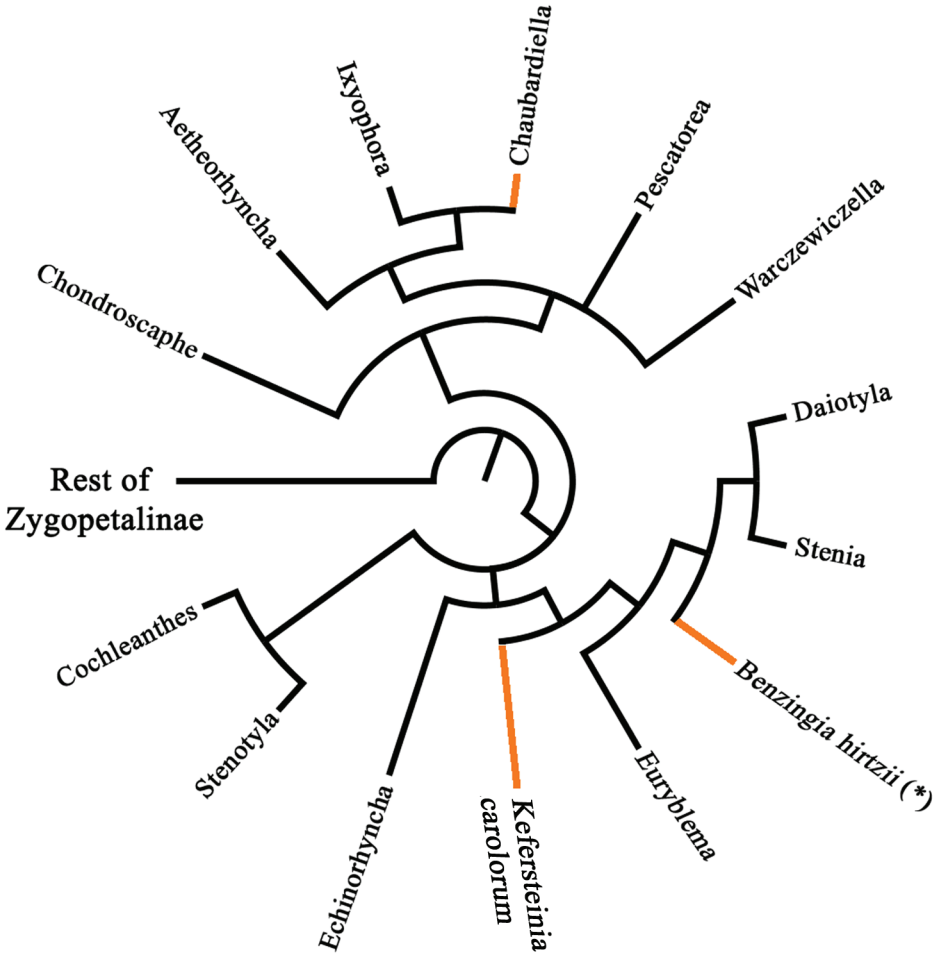

FIGURE 4. Phylogenetic relationships of Zygopetalinae genera with species (orange bars) bearing labella in an upward position. (Asterisk indicates labella in upward position due to geniculate ovary). Modified from Whitten *et al.* (2005).

The ontogenetic homologies of this syndrome (i.e., the labellum in an upper position) in Zygopetalinae are uncertain. *Benzingia hirtzii* seems to have achieved this condition *via* geniculation of the ovary and pedicel whereas in *K. carolorum* and in species of *Chaubardiella* flowers seem to be truly non-resupinate (e.g., ovary not twisting during floral development). Genera of the Zygopetalinae with the labellum held uppermost can be distinguished using the following key:

1. Margin of the labellum entire; callus broadly flabellate, flat ..... *Chaubardiella spp.*
- Margin of the labellum erose; callus non flabellate, either peltate, bilobed, laminar or composed of several teeth 2

2. Plants pendulous; flowers with labellum in upward position due to a geniculate ovary; column foot at least 1/3 the length of labellum blade; callus orange, oblong, flat; labellum yellow, densely maroon-spotted ..... *Benzingia hirtzii*
- Plants erect; flowers with labellum in upward position due to lack of torsion of ovary; column foot almost absent; callus white with lax pink spots, composed of two acute, flat keels separated by a concave longitudinal channel, each keel provided with middle and apical teeth; labellum white with lax pink spots ..... *Kefersteinia carolorum*

IUCN Red List category:—According to IUCN (2010), *K. carolorum* would be considered as Data Deficient (DD). Most likely, it is a rare, local taxon, whose conservation status requires assessment. The species in known from one, possibly two localities in the Táchira state of western Venezuela (Fig. 3).

Additional species of *Kefersteinia* with non-resupinate flowers

At the website of the Swiss Orchid Foundation at the Herbarium Jany Renz (https://orchid.unibas.ch/index.php/en/) there are two images (2063505, 2063506, photographs taken August 1983) that represent a second *Kefersteinia* species bearing non- resupinate flowers. One of us (GAR) had the opportunity to study pickled material obtained from the plants depicted in the photographs (*R. Jenny 41/83*, in his personal collection). The flowers are somewhat smaller and the callus is proportionally shorter and differently shaped. We have refrained to formally propose a new species for these plants because they are of unknown provenance.

Harding (2009) depicted images of a *Kefersteinia* species, from Urabá, Colombia, bearing conspicuously non-resupinate flowers that she referred to *K. klabochii* (Reichenbach 1885: 391) Schlechter (1920: 267). A careful examination of the detailed description of *Zygopetalum klabochii* Reichenbach (1885: 391) prepared by Professor Reichenbach and of the illustration accompanying the type material failed to detect any mention of a non-resupinate flower. This is unusual considering that Reichenbach meticulously prepared his diagnoses based upon live material and we are hard pressed to believe that he would have failed to observe such an unusual feature in a member of the Zygopetaliinae where non-resupinate flowers were unknown at the time (the description of all *Chaubardiella* species and of the lone species of *Benzingia* with this kind of flowers lied several decades into the future). In her extensive discussion of *K. klabochii*, Harding did not mention the non-resupination of the flowers of her plants from Colombia and we are forced to assume that she thought of resupination as an inconsequential feature of *Keferesteinia* flowers, a view we strongly disagree with. At first, Harding intended to propose a new species, *Kefersteinia urabaensis* Aguirre & Harding (*nomem nudum*), for these plants based upon a suite of morphological features other than flower resupination that supposedly differentiated her material from Reichenbach's species but eventually refrained from doing so in considering *K. klabochii* a variable species. We now think that Aguirre and Harding were initially right and that their Urabá material actually belongs to a species that has remained undescribed to the moment. The Urabá material differs from *K. carolorum* in its broader petals and sepals and a much more densely purple-spotted labellum that is obovate upon flattening.

Thus, there is now conclusive evidence that non-resupination in *Kefersteinia* is a phenomenon that, albeit uncommon, is not entirely unknown in the genus. It remains to be established whether non-resupination evolved once in the genus as all three known species seem fairly closely related based upon phenetic similarities, but a formal phylogenetic analysis is required to address this question.

Kefersteinia in Venezuela

Including the species described herein, there are six taxa of *Kefersteinia* in Venezuela, all part of the *K. graminea* morphological group (with the exception of *K. guacamayoana* Dodson & Hirtz (1989: pl. 505) and they can be identified using the following key:

1. Sepals reflexed; petals and sepals at least 3.5 times longer than wide; labellum subquadrate, apically truncate, yellow with 7 longitudinal lines of minute purple dots; callus solid, stalked, associated with a pair of united swollen globular structures ..... *K. guacamayoana*
- Sepals patently spreading; petals and sepals at most 3 times longer than wide; labellum ovate or suborbicular, apically rounded, white or pale green, often purple tinged, with purple or red-purple spots randomly distributed over its surface; callus laminar not associated with swollen globular structures 2
2. Labellum 9–12 mm long 3

- Labellum 17–21 mm long 5
3. Flowers non-resupinate, perianth uniformly white or green ..... *K. carolorum*
- Flowers resupinate, perianth green or yellow with purple blotches at the base or entire blade 4
4. Labellum cuneate-flabellate or obovate, 9–10 mm wide, dorsal sepal 10 × 4.4–4.5 mm, column 9 mm long ..... *K. sanguinolenta* Reichenbach (1852: 635)
- Labellum widely ovate or sub-rotund, 18 mm wide, dorsal sepal 15 × 7 mm, column 5 mm long ..... *K. gemma* Reichenbach (1874: 406)
5. Labellum broadly ovate or sub-rotund, sepals and petals lanceolate, oblong-lanceolate or elliptic-ovate, disc at base with two ascendant plates ..... *K. graminea*
- Labellum sub-rotund, square-sub-rotund or transversely elliptical, sepals and petals elliptic-ovate or oblong-elliptic; disc at base with two erect plates ..... *K. tolimensis* Schlechter (1920: 161)

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