

× *BENSTEINIA RAMONENSIS*, A NEW NATURAL HYBRID IN THE
ZYGOPETALINAE (ORCHIDACEAE)

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ABSTRACT. A new nothospecies in the subtribe Zygopetalinae (Orchidaceae), × *Bensteinia ramonensis*, is described and illustrated from Costa Rica, and its relationships are discussed. A summary of natural and artificial hybridization in the subtribe is offered.

Key words: Orchidaceae, Epidendroideae, Zygopetalinae, natural hybrids, *Bensteinia*, Costa Rica

The thousands of artificial orchid hybrids produced for horticultural purposes show that many members of the Orchidaceae are capable of developing viable seeds through intrageneric and intergeneric crosses, sometimes involving five or six different genera. In many advanced orchid groups, artificial hybridization has revealed low levels of genetic incompatibility among members of related genera, and it is likely this leaky barrier allows in the wild some gene exchange to add to the genetic pool. With a few notable exceptions, interfertility usually decreases with genetic divergence in more distantly related taxa and, as a general rule, is higher within subtribes.

Nevertheless, natural hybridization is relatively uncommon in the family. In natural populations, reproductive isolation is maintained through several distinct barriers, including pre-pollination mechanisms (mainly geographic, temporal, and dependent on floral structure and ethology) and sexual incompatibility. Among isolating mechanisms, pollination seems especially critical in the Orchidaceae. Hybrid unfitness, i.e., low viability and failures in attracting suitable pollinators, may also account for the scarcity of hybrids in nature. Natural hybrids are usually restricted to intrageneric crosses and crosses among closely related genera.

The subtribe Zygopetalinae encompasses 35 Neotropical genera and some 400 species, mainly characterized by the presence of four flattened, superposed pollinia, a narrow stigma, and a tissue extension on the ventral surface of the column. Dressler (1981) recorded 22 intergeneric hybrids in the subtribe, mostly artificially produced with horticulturally relevant species of *Zygopetalum* Hook. A review of novel hybrids in the Zygopetalinae was recently done by Shaw (2005), who recorded both intergeneric hybrids with members of the allied subtribe Lycastinae (*Lycabstia* = *Lycaste* × *Pabstia*, and the tri-generic *Takakiara* = *Lycaste* × *Pabstia* × *Zygo-*

petalum), and new bi- and tri-generic hybrid genera within the subtribe like *Propetalum* (= *Promenaea* × *Zygopetalum*), *Cochlepetalum* [= *Cochleanthes* (actually *Warscewiczella*) × *Zygopetalum*], and *Propabstopetalum* (= *Propetalum* × *Zygopabstia*).

Among the usually pseudobulbless, conduplicate-leaved, one-flowered genera of the *Huntleya* clade (Whitten et al. 2005), 9 intergeneric hybrids have been recorded (Dressler 1981, Shaw 2005). Of these, only the hybrids between *Benzingia* sp. and *Kefersteinia* sp., and between *Cochleanthes aromatica* (Rchb.f.) R.E.Schult. & Garay and *Warscewiczella discolor* (Lindl.) Rchb.f., occur naturally. The first was found only once in the Amazonian region of Ecuador, along the Río Pastaza (Neudecker 1994, Dodson & Luer 2005), while the latter is an infrequent epiphyte recorded from the Caribbean watershed of the Costa Rican mountain chains (Dressler 2003). Another natural hybrid had been recorded in the *Huntleya* clade between *Pescatorea* Rchb.f. and *Bollea* Rchb.f., but recent molecular analyses (Whitten et al. 2005) reveal that the two taxa are congeneric.

The occurrence of a natural hybrid between the genera *Benzingia* (as *Ackermania* Dodson) and *Kefersteinia* was first recorded by Neudecker (1994) on the basis of a plant growing among mixed populations of *Benzingia caudata* (Ackerman) Dressler, *Kefersteinia sanguinolenta* Rchb.f., and *K. vollesii* Jenny (= *K. pusilla* C. Schweinf.). More recently, Dodson & Luer (2005) suggested as the putative parents *Ackermania palorae* (Dodson & Hirtz) Dodson & Escobar [= *Benzingia palorae* (Dodson & Hirtz) Dressler] and *Kefersteinia lojiae* Schltr. Although the flower of the natural hybrid is strongly reminiscent of *Benzingia* in gross morphology, the red-purple spotting on the petals and the lip, and the finely undulate margins of the lip midlobe, show a genetic influence of *Kefersteinia*. Neu-

decker (1994) intended to publish the new nothogenus with the name of *Ackersteinia* but, probably because of a typographical error, the protologue described the new taxon as an intrageneric hybrid of *Ackermania*; moreover, due to the lack of reference to the location of the holotype, the publication of the new nothospecies was invalid, and the name × *Ackersteinia dodsonii* was validated by Dodson & Luer only in 2005. The same orchid genus *Ackermania* was published without explicit indication of the type, and it is therefore invalid; furthermore, the generic name *Ackermania* in the Orchidaceae is likely predated by the fungal genus *Ackermania* Pat.

Molecular data show a close relationship between *Ackermania*, *Benzingia*, and *Chondrorhyncha reichenbachiana*, which form a highly supported clade and should be treated as a single genus (Whitten et al. 2005). Although these taxa are diverse in flower morphology (probably as a result of different pollination systems), they are vegetatively very similar, with pendent, glaucous grey-green leaves, provided with papillose leaf cells in the upper epidermis. *Benzingia* having priority over the illegitimate name *Ackermania*, the two species of the latter genus were recently transferred by Dressler to a broadened concept of *Benzingia* (in Whitten et al. 2005). The generic name *Benzingia*, originally published without explicitly indicating the type (Dodson 1989), was revalidated by Dodson and Romero (1995), together with the two species at that time assigned to the genus. In consideration of the new generic alignments of the taxa in the group, Christenson (2006) renamed the hybrid between *Ackermania* [= *Benzingia*] and *Kefersteinia* as × *Bensteinia*, making the new combination × *Bensteinia dodsonii* (Neudecker) Christenson.

During the systematic collections aimed toward the preparation of a treatment of the subtribe Zygopetalinae for the *Flora Costaricensis* (Pupulin in prep.), a plant native from the wet forest of the Cordillera de Tilarán in Costa Rica appeared, with flowers that exhibit intermediate characters between *Kefersteinia* and *Benzingia*. It is described here as a new natural hybrid:

× *Bensteinia ramonensis* Pupulin, *nothosp. nov.* Type: Costa Rica—Alajuela: San Ramón, Angeles, Reserva Biológica Alberto M. Brenes, 10°13'08.5"N, 84°35'48.4"W, 900–1000 m, Saino trail, tropical wet, transition to premontane wet forest, 25 September 2005, flowered in cultivation at Jardín Botánico Lankester, 7 October 2005, *D. Bogarín 1923* (holotype, CR-Spirit).

FIGURES 1, 2.

Herba epiphytica caule abbreviato foliis conduplicatis petiolatis anguste elliptico-oblanco-latis acuminatis ad 15 cm longis, floribus intermediis inter *Kefersteiniam* excentricam Dressler & Mora-Ret. et *Benzingiam* reichenbachianam (Schltr.) Dressler, sepalis lateralibus patentibus, labello excentrico albo maculis purpureis notato, columnae facie abaxialis carina humilis instructa, pollinarii stipite lanceolato-elliptico abbreviato viscidioque subquadrato parvo munito (atque *K. excentricam*), floris amplitudine, labello integro, callo humili labelli pars media attingens, columna elongata (atque *B. reichenbachianam*). Typus: Costa Rica, *D. Bogarín 1923* (holotypus, CR-Spirit).

Plant epiphytic, caespitose, without pseudobulbs, the abbreviated stem enclosed by 4–5 imbricating sheaths, the upper ones foliaceous. **Leaf** petiolate, conduplicate, narrowly elliptic-oblanco-late, acuminate, dark green, 8.5–20 × 0.9–1.5 cm. **Inflorescence** lateral, from the axil of the lower sheaths, 1-flowered; peduncle terete, patent to pendent, to 3 cm long, provided with an ovate, conduplicate bract, 5 mm long, near the base. **Floral bract** double, conduplicate, the external one widely ovate, 4 mm long, the internal bractlet ligulate, 5 mm long. **Ovary** pedicellate, to 1.5 cm long including the pedicel. **Flower** proportionately large, the sepals pale creamish white, flecked reddish-purple, the petals creamish white, heavily spotted and blotched with purple, the lip creamish white, spotted purple, the spots forming 5–7 nectar guides toward the apex of callus; the callus spotted purple. **Dorsal sepal** narrowly elliptic, acuminate, concave, hooked at apex, 16 × 6 mm. **Lateral sepals** narrowly elliptic-lanceolate, subacute, spreading, concave, conduplicate-folded toward the base, 20 × 5 mm. **Petals** elliptic, rounded, apiculate, 14 × 8 mm. **Lip** excentric, slightly twisted toward the right side, elliptic-obovate, obscurely 3-lobed, obtuse, the apical margin crenulate, the basal margins erect toward the column, 18 × 15 mm; disc with a low, bilobed, irregularly toothed callus, born toward the middle of the lip lamina, ca. 2 × 8 mm. **Column** straight, clavate, footed, 15 mm long, the ventral surface sparsely woolly toward the margins, provided with a low, glabrous, substigmatic keel; the stigma transversal, narrow. **Anther cap** ovate-elliptic, cucullate, 2-celled. **Pollinia** 4, subsigmoid, in 2 pairs of different size, on an elliptic-ovate, hyaline stipe, ventrally provided with an indistinct, subquadrate, hyaline viscidium.

HABITAT: Epiphytic in shade in extremely wet premontane forest, at about 1000 m elevations, along the Caribbean watershed of the Tilarán mountain range in northern Costa Rica. Flowering occurs at least in September–October.

DISTRIBUTION: Known only from Costa Rica.

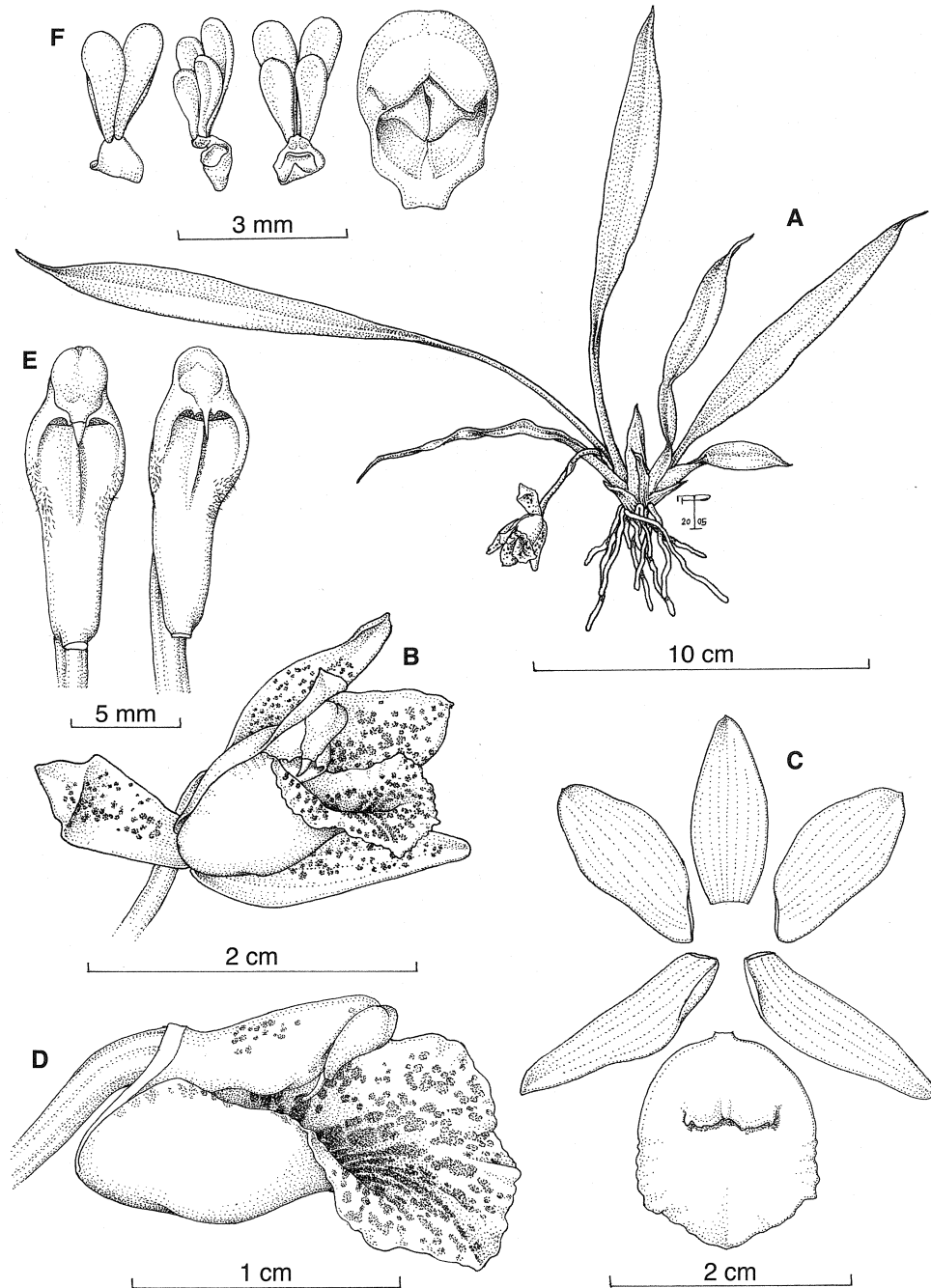


FIGURE 1. \times *Bensteinia ramonensis*. A. habit. B. flower. C. dissected perianth. D. column and lip, lateral view. E. column, ventral and three quarter views. F. pollinarium (three views) and anther cap. Drawn by the author from the holotype.

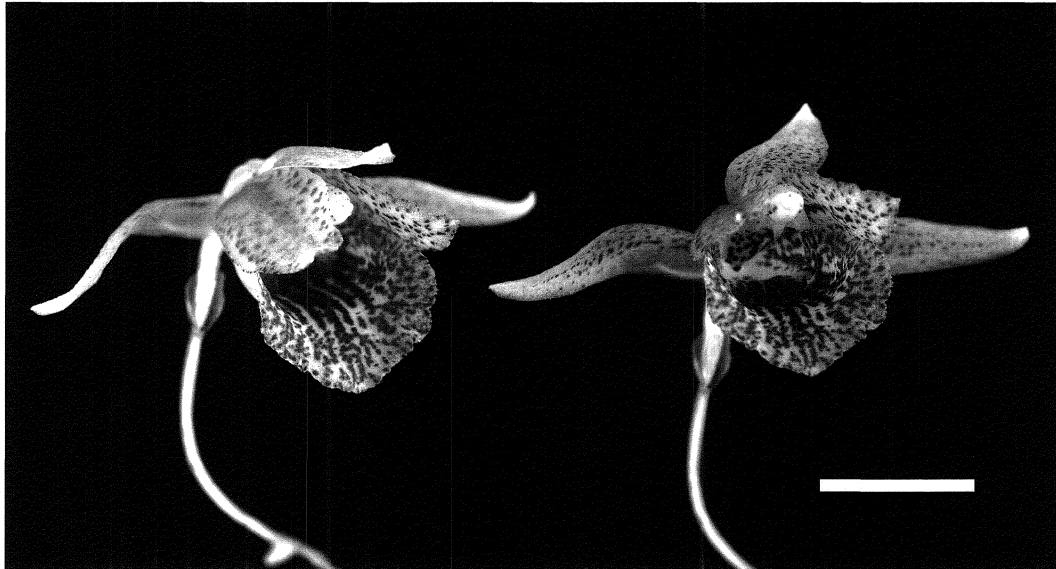


FIGURE 2. Flower of × *Bensteinia ramonensis*. Scale bar = 1 cm. Photograph by D. Bogarín of the flower that served as the holotype.

ETYMOLOGY: Named from the orchid rich region of San Ramón in Costa Rica, where the natural hybrid was found.

A single plant of *Bensteinia* appeared within a mixed collection of *Zygopetalinae* from the Alberto M. Brenes Biological Reserve, in northern Costa Rica. The plant habit was reminiscent of that of *Benzingia*, with long-petiolate, narrow, dark grey-green and somewhat glaucous leaves. The upper epidermal leaf cells are papillose in *Benzingia*, whereas they are smooth in the other genera of the *Huntleya* clade. *Benzingia reichenbachiana* (formerly *Chondrorhyncha*) is a common epiphyte at A.M. Brenes Reserve (Gómez-Laurito & Ortiz 2004; photograph in Pupulin 2005a: 104) and all along the Caribbean watershed of the Tilarán and Central Volcanic ranges in Costa Rica, where it grows on shaded spots at elevations of 1000–1500 meters.

However, the flower of *Bensteinia* markedly differs from that of *Benzingia*. The lip is excentric with respect to the bilateral symmetry of the flower, slightly twisting toward the right side. Moreover, the lateral sepals do not turn back and are not hooked as in *B. reichenbachiana*, and the dorsal sepal is subequal to the lateral sepals, whereas in *B. reichenbachiana* it is distinctly smaller. In *Bensteinia ramonensis* the sepals and petals are flecked, spotted, and blotched with purple, contrasting with the uniform pale cream color of the flower segments in *B. reichenbachiana*, and the lip is almost completely covered by purple blotches, whereas in *B. reichenbachiana*

the blotches of this color are usually restricted to the central portion of the lip, where they form five to seven distinct nectar guides. Finally, the pollinarium of *Bensteinia* present two sets of subsigmoid pollinia on a small lanceolate stipe, adaxially provided with a subquadrate, indistinct viscidium; in *B. reichenbachiana* the pollinia are straight and the stipe is subequal to the pollinia.

This last set of characters is consistent with the shape and color of *Kefersteinia excentrica* flowers. This species was originally described from the wet forests of the Talamanca mountain chain in Costa Rica, but Pupulin (2001) and Gómez-Laurito & Ortiz (2004) also recorded it from the A.M. Brenes Reserve. In Costa Rica it is an uncommon epiphyte in premontane wet forests, where it usually establishes on mossy tree trunks in shady sites, at elevations of 1000–1500 meters. The lip of *K. excentrica* is distinctly “off-center” when observed from the front (hence the specific epithet), and this character is probably designed to drive the pollinator along the margin of the lip, in order to place the pollinarium on the basal segment of its antenna (Dressler 1981: 248). Also, the lip of *K. excentrica* presents two small apical lobes, and a remnant of these lobes can be observed on the distal portion of the lip of *Bensteinia ramonensis*. Nevertheless, the morphology of the callus on the lip of *B. ramonensis* markedly differs from that of *K. excentrica*. The latter has been assigned to the Sect. *Umbonatae* by Senghas and

Gerlach (1993) due to characteristic stipitate calyx, and Szlachetko (2003) elevated it to the generic rank with the name *Senghasia*. The section includes three species in Costa Rica (Pupulin 2001, 2005b), but none of the other two species has never been recorded from the Preserve. The general morphology of the column of *Bensteinia* agrees with that of *Benzingia*, lacking the subquadrate plate on the ventral surface that is characteristic of *Kefersteinia*; nevertheless, it bears a low ventral keel, probably analogous to the weak median keel on the plate of *K. excentrica*.

ACKNOWLEDGMENTS

I am deeply indebted to my colleague Diego Bogarín, of Lankester Botanical Garden, for collecting and photographing the plant used for this study, and for the useful discussions on its generic placement. Wild specimens intended for this study were obtained through scientific collection permits No. 36702 and 36891 issued by the Costa Rican Ministry of Environment and Energy (MINAE) and National System of Conservation Areas (SINAC), whose cooperation I sincerely acknowledge. Part of this study has been sponsored by the Darwin Initiative, UK, in the framework of the project "Conservation and Monitoring of Meso-American Orchids."

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