Nitidobulbon, a New Genus of Maxillariinae (Orchidaceae)

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Abstract. *Nitidobulbon* Ojeda, Carnevali & G. A. Romero, a new genus of the Maxillariinae (Orchidaceae), is described and illustrated. Its circumscription is supported by morphological, anatomical, and molecular evidence. The three species of *Nitidobulbon* are characterized by long flower peduncles, smooth, shiny pseudobulbs, and distinctive leaf anatomy. We present a taxonomic key to differentiate *Nitidobulbon* from related genera and also provide a key to the species within the genus. Three new combinations are established: *N. cymbidioides* (Dodson, J. T. Atwood & Carnevali) Ojeda & G. A. Romero, *N. nasutum* (Reichenbach f.) Ojeda & Carnevali, and *N. proboscideum* (Reichenbach f.) Ojeda & Carnevali. In synonymy to *N. nasutum*, the name *Maxillaria oxysepala* Schlechter is lectotypified.

Resumen. *Nitidobulbon* Ojeda, Carnevali & G. A. Romero, un nuevo género de Maxillariinae (Orchidaceae), es descrito e ilustrado. Su circunscripción se apoyada en evidencia morfológica, anatómica y molecular. Las tres especies de *Nitidobulbon* se caracterizan por largos pedúnculos florales, seudobulbos lisos y brillantes, y por una anatomía foliar distintiva. También presentamos una clave para diferenciar *Nitidobulbon* de géneros emparentados, otra para las especies del genero y proponemos tres nuevas combinaciones: *N. cymbidioides* (Dodson, J. T. Atwood & Carnevali) Ojeda & G. A. Romero, *N. nasutum* (Reichenbach f.) Ojeda & Carnevali y *N. proboscideum* (Reichenbach f.) Ojeda & Carnevali. En la sinonimia a *N. nasutum*, el nombre *Maxillaria oxysepala* Schlechter es lectotipificado.

Key words: Heterotaxis, *Maxillaria*, Maxillariinae, *Nitidobulbon*, Orchidaceae, *Ornithidium*.

As currently circumscribed, Maxillariinae (Orchidaceae) consists of two groups of genera. The first group is the complex of genera around *Lycaste* Lindley and *Bifrenaria* Lindley, which is composed of genera basal in the phylogenetic tree of the subtribe that feature (1) plicate or subcoriaceous leaves always with convolute vernation (Romero & Carnevali, 2001) and (2) racemose or 1-flowered inflorescences. The phylogenetic relationships within the *Lycaste* alliance (sensu Dressler, 1993) were studied by Ryan et al. (2000), while the relationships within the *Bifrenaria* alliance were analyzed by Koehler et al. (2002). Further into the phylogenetic tree, there is another large, internal clade (ca. 650 spp., Govaerts et al., 2005) corresponding to Maxillariinae sensu Dressler (1993). This clade is characterized by 1-flowered inflorescences and conduplicate leaves, and will hereafter be referred to as the Core Maxillariinae (sensu Whitten et al., 2007).

Past classification systems (Dressler, 1993) and floristic treatments (e.g., Atwood & Mora Retana, 1999; Carnevali & Ramírez, 2003) have traditionally recognized eight genera within Core Maxillariinae, although often admitting that generic boundaries were unsatisfactory, probably unnatural, and required phylogenetic research. These eight genera are *Anthosiphon* Schlechter, *Chrysocycnis* Linden & Reichenbach f., *Cryptocentrum* Bentham, *Cyrtidiorchis* Rauschert, *Maxillaria* Ruiz & Pavón, *Mormolyca* Fenzl, *Pityphyllum* Schlechter, and *Trigonidium* Lindley.

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Among these eight genera, *Maxillaria* has always been the largest, containing most of the species of the subtribe, while the remaining seven genera were defined by several floral apomorphies. A recent phylogenetic work using several DNA regions, both nuclear and plastid (Whitten et al., 2007), identifies 17 clades within Core Maxillariinae, which are deemed worthy of generic recognition due to morphological and geographical coherence and distinctness, as well as high bootstrap support. A first striking conclusion from the phylogenetic topologies recovered from this phylogenetic analysis is the fact that, as previously circumscribed, *Maxillaria* is grossly polyphyletic with all of the other genera traditionally recognized as embedded within it. A second conclusion is that generic concepts of past taxonomy had overemphasized homoplasious floral characters, leaving the genus *Maxillaria* as a catch-all taxonomic recipient for members of Core Maxillariinae lacking these floral apomorphies. It is obvious from this recent phylogeny that vegetative morphology and geography were as good (or better) predictors of relationships as floral morphology.

The phylogenetic structure revealed by Whitten et al. (2007) is reflected in a classification system proposed by Blanco et al. (2007). One of the clades, located in a basal position within Core Maxillariinae, will be referred to as the *Heterotaxis* clade and consists of three internal subclades. The *Heterotaxis* clade received 100% bootstrap support in the combined nuclear ribosomal ITS (nrITS), *matK* + *trnK*, and *atpB-rbcL* spacer analysis in Whitten et al. (2007). A five-region analysis performed by these same authors for a smaller sample of taxa using the plastid *rpoC1* region yielded a similar topology and level of support for the *Heterotaxis* clade (Whitten et al., 2007). The three internal subclades are less well supported (see below) but are morphologically distinctive. These subclades were earlier recovered in the morphology + anatomy + nrITS analyses by Ojeda (2003) and Ojeda et al. (2003). An alternative classification system would treat these three subclades as a single genus, but such a taxonomic aggregation would be morphologically undiagnosable. Because there are already generic names for two of these subclades, including the proper combinations for many of the species, we have chosen to treat the three subclades as different taxa at the generic level. These three clades are *Heterotaxis* Lindley (71% bootstrap support in the four-region analysis; 74% in the five-region analysis), *Ornithidium* Salisbury ex R. Brown (60% and 77% support, respectively), and the complex of species around *Maxillaria nasuta* Reichenbach f. (81% and 79% support, respectively) (Whitten et al., 2007: 1862). This last species group lacks a generic name and is herein proposed as such, as the new genus, *Nitidobulbon*. In the combined molecular analysis (Whitten et al., 2007), the relationships of the three clades are unresolved. However, in the combined morphology + anatomy + nrITS analysis (Ojeda, 2003: 67), *Nitidobulbon* is sister to *Heterotaxis* + *Ornithidium*, clades receiving 97% and 100% jackknife support, respectively. Thus, we feel confident that the hypothesis of relationships here proposed will be supported by further phylogenetic analyses. Furthermore, the fact that the three clades are morphologically distinct and easily diagnosable, both florally and vegetatively, warrants and supports the recognition of three distinct genera.

Heterotaxis comprises 11 orchid species of mainly sympodial growth, which are characterized by short rhizomes and laterally compressed, oblong, unifoliate pseudobulbs subtended by various leaf-bearing sheaths. The flowers are yellow to orange, although the labellum can rarely be purple and the calli vary in size and texture (Carnevali, 1991).

Within *Heterotaxis*, two major clades have been recovered (Ojeda, 2003), with one clustered around *H. sessilis* (Swartz) F. Barros (i.e., the Sessilis clade) and a second clustered around *H. discolor* (G. Loddiges ex Lindley) Ojeda & Carnevali (i.e., the Discolor clade). The Sessilis clade comprises species with small vegetative and floral parts, with pseudobulbs mostly hidden by the leaf sheaths, and the leaves succulent and typically deeply concave to triquetrous (Ojeda, 2003). In contrast, the Discolor clade contains robust, taller species exceeding 40 cm with large vegetative and floral parts, pseudobulbs that are well exposed, and leaves that are flat and coriaceous (Ojeda, 2003).

The *Maxillaria nasuta* clade, which includes *M. cymbidioides* Dodson, J. T. Atwood & Carnevali and *M. proboscidea* Reichenbach f. (Ojeda, 2003; Ojeda et al., 2005), has previously been included in the *Heterotaxis* alliance (Carnevali, 1991; Barros, 2002; Christenson, 2002). The three species in this clade are commonly misidentified and confused with those of the Discolor clade of *Heterotaxis*, especially when working with sterile specimens. However, current evidence from morphology and gross foliar anatomy can identify six synapomorphies in *M. nasuta* and relatives (see the key below): (1) bracts are large, wrapping the internodes of the peduncle, largely obscuring the peduncular axis; (2) the inflorescence peduncle is longer than the pseudobulb; (3) the floral bract covers the pedicel and part of the ovary; (4) the surface of the column is papillose; (5) the dorsal (adaxial) surface of the petals is papillose; and (6) the leaves exhibit a type IV vascular pattern, with three sizes of vascular bundles (large, usually occupying the

entire mesophyll from adaxial to abaxial epidermis; medium; and small, with medium and small bundles alternating several times between two larger vascular bundles) (Ojeda, 2003). We decided to include *M. nasuta*, *M. cymbidioides*, and *M. proboscidea* in a new genus rather than lumping *Heterotaxis*, *Ornithidium*, and the *M. nasuta* clade (where *Ornithidium* has nomenclatural priority). In our opinion, such a broad circumscription of *Ornithidium* would be morphologically too heterogeneous and therefore recognizable only on the basis of molecular evidence.

Nitidobulbon Ojeda, Carnevali & G. A. Romero, gen. nov. TYPE: *Nitidobulbon nasutum* (Reichenbach f.) Ojeda & Carnevali.

Hoc genus *Heterotaxidi* Lindley affinis, sed ab ea bracteis floralibus ovarium excedentibus atque pseudobulbis nitidis valde compressis recedit.

Plants caespitose epiphytes, more rarely lithophytes or subterrestrials, erect, ca. 20–40 cm tall; rhizomes with reduced internodes; pseudobulbs large, 6–9 cm tall × 3–5 cm wide, laterally compressed, without ridges, smooth, appearing varnished; generally unifoliate, rarely bifoliate. Leaves coriaceous, erect on the pseudobulb apex, basally attenuate and forming a 2–4 cm pseudopetiole, apex bilobed; 3 sizes of vascular bundles in a medial cross section of the leaves: (1) large (usually occupying the entire mesophyll from adaxial to abaxial epidermis), (2) medium, and (3) small, arranged as type IV (Ojeda, 2003). Inflorescence 1-flowered, borne on axils of pseudobulb-subtending leaves; peduncle fleshy, 12–14 cm, ca. twice as long as the pseudobulb, with 4 internodes, generally the 2 closest to the ovary shorter than the 2 distant from the ovary; covered by triangular bracts usually as long as the internodes; floral bract similar to peduncular bracts, membranous, triangular, acute, ca. 2 cm, similar in length to ovary. Flowers relatively large, 3–5 cm wide, resupinate, yellow to brown; lateral sepals similar to the dorsal sepal, oblanceolate to spatulate, acute, yellow to brown, externally papillose; petals ± similar to sepals, but shorter and narrower; labellum articulate to column foot, usually red to brown, surface shiny, lacking a raised pad of glandular hairs (as in *Heterotaxis*); pollinia 4, unequal, on a squarish to oblong tegula; column 8–10 mm, hemicylindric, papillose, arcuate and with a poorly defined foot. Fruit a capsule with lateral dehiscence.

Etymology. The new genus name is taken from the Latin "nitidus," meaning shiny, and "bulbus," meaning bulb, in reference to the shiny, varnished texture of the pseudobulbs.

KEY TO THE GENERA *NITIDOBULBON*, *HETEROTAXIS*, AND *ORNITHIDIUM*

1a. Caespitose, sympodial, or pseudomonopodial plants; internodes reduced, with a single 1-flowered inflorescence per leaf axil; column arcuate; labellum free, mostly flat to concave; fruits laterally dehiscent 2
1b. Caespitose, pseudomonopodial, or monopodial plants; internodes reduced to elongated, with 1 to many 1-flowered, simultaneous inflorescences per leaf axil; column sigmoid; labellum basally adnate to the column or free (if so, then ≤ 10 mm long, variously lobed, recurved to sigmoid, often ciliate or fimbriate), often saccate; fruits apically dehiscent . . . . . *Ornithidium*
2a. Floral peduncle almost always as long or longer than pseudobulb; pseudobulbs laterally compressed, without ridges and with a shiny varnished surface; petals without a subapical mucron; leaf cross section with 3 sizes of vascular bundles, the largest spanning the entire mesophyll. . . .*Nitidobulbon*
2b. Floral peduncle shorter than to equal in length to pseudobulbs; pseudobulbs (when present) laterally compressed, with longitudinal ridges and without shiny varnished surface; petals with a subapical mucron; leaf cross section with 2 sizes of vascular bundles, the largest not spanning the entire mesophyll . . . . . *Heterotaxis*

KEY TO THE SPECIES OF *NITIDOBULBON*

1a. Plants relatively small, pseudobulbs 4.5–5.5 cm long; leaves 20–24 mm wide; sepals 25–27 mm long; labellum 14–15 mm long . . . . . .*N. cymbidioides*
1b. Plants relatively large, pseudobulbs 8–12 cm long; leaves 25–50 mm wide; sepals 27–35 mm long; labellum 18–25 mm long 2
2a. Sepals widely spreading, apices obtuse or acute; labellum apically broadly obtuse to rounded, bracts of the inflorescence not inflated; floral bract shorter than the pedicellate ovary . . . . . *N. proboscideum*
2b. Sepals either ± parallel to the petals or reflexed, apices acuminate; labellum ± acuminate or acute; bracts of the inflorescence usually ± inflated; floral bract longer than or nearly equal to the pedicellate ovary. . . . . *N. nasutum*

1. Nitidobulbon cymbidioides (Dodson, J. T. Atwood & Carnevali) Ojeda & G. A. Romero, comb. nov. Basionym: *Maxillaria cymbidioides* Dodson, J. T. Atwood & Carnevali, Orquideología 20: 266. 1997. TYPE: Ecuador. Imbabura: Lita to Ibarra, Km 11; terrestrial on embankment, 700 m, 27 Mar. 1994 [specimen in flower prepared 10 Nov. 1994], *C. H. Dodson & G. Carnevali 19270* (holotype, MO).

Distribution. Nitidobulbon cymbidioides is currently known with certainty only from the western slopes of the Andes in northern Ecuador, although it may also occur in neighboring southwestern Colombia (Nariño Department).

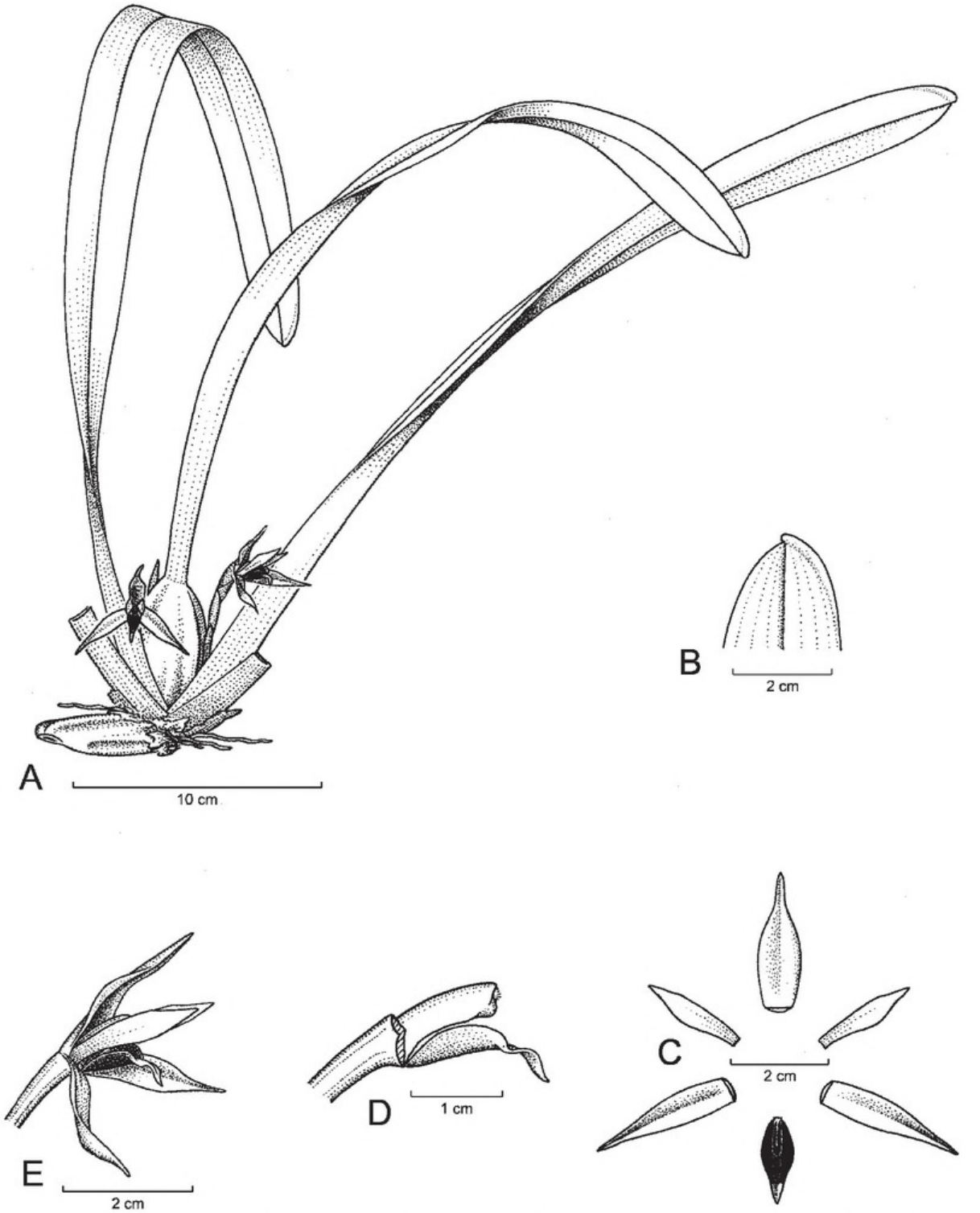

Figure 1. *Nitidobulbon nasutum* (Reichenbach f.) Ojeda & Carnevali. —A. Flowering plant. —B. Apex of leaf. —C. Floral segments. —D. Lateral view of column and lip (sepals and petals removed). —E. Lateral view of flower. Based on *G. C. K. & E. Dunsterville 298* (AMES), from Venezuela.

2. Nitidobulbon nasutum (Reichenbach f.) Ojeda & Carnevali, comb. nov. Basionym: *Maxillaria nasuta* Reichenbach f., Beitr. Orchid.-K. C. Amer. 104. 1866. TYPE: Novo Granada [Colombia]. Lajitas, s.d., *L. J. Schlim 9* (holotype, W [Reich. Hb. Orchid. 47880]; isotype, K). Figure 1.

Maxillaria nasalis Reichenbach f., Ref. Bot. 2: t. 102. 1872, nom. illeg. TYPE: Costa Rica, s.d., *A. R. Endress 266* (holotype, W).

Maxillaria glumacea Rolfe, Bull. Misc. Inform. Kew 210. 1892. Syn. nov. TYPE: Brazil. s.d., *Hort. Sander s.n.* (holotype, K).

Maxillaria brevipedunculata Ames & C. Schweinfurth, Sched. Orchid. 10: 91. 1930. TYPE: Costa Rica. Toro

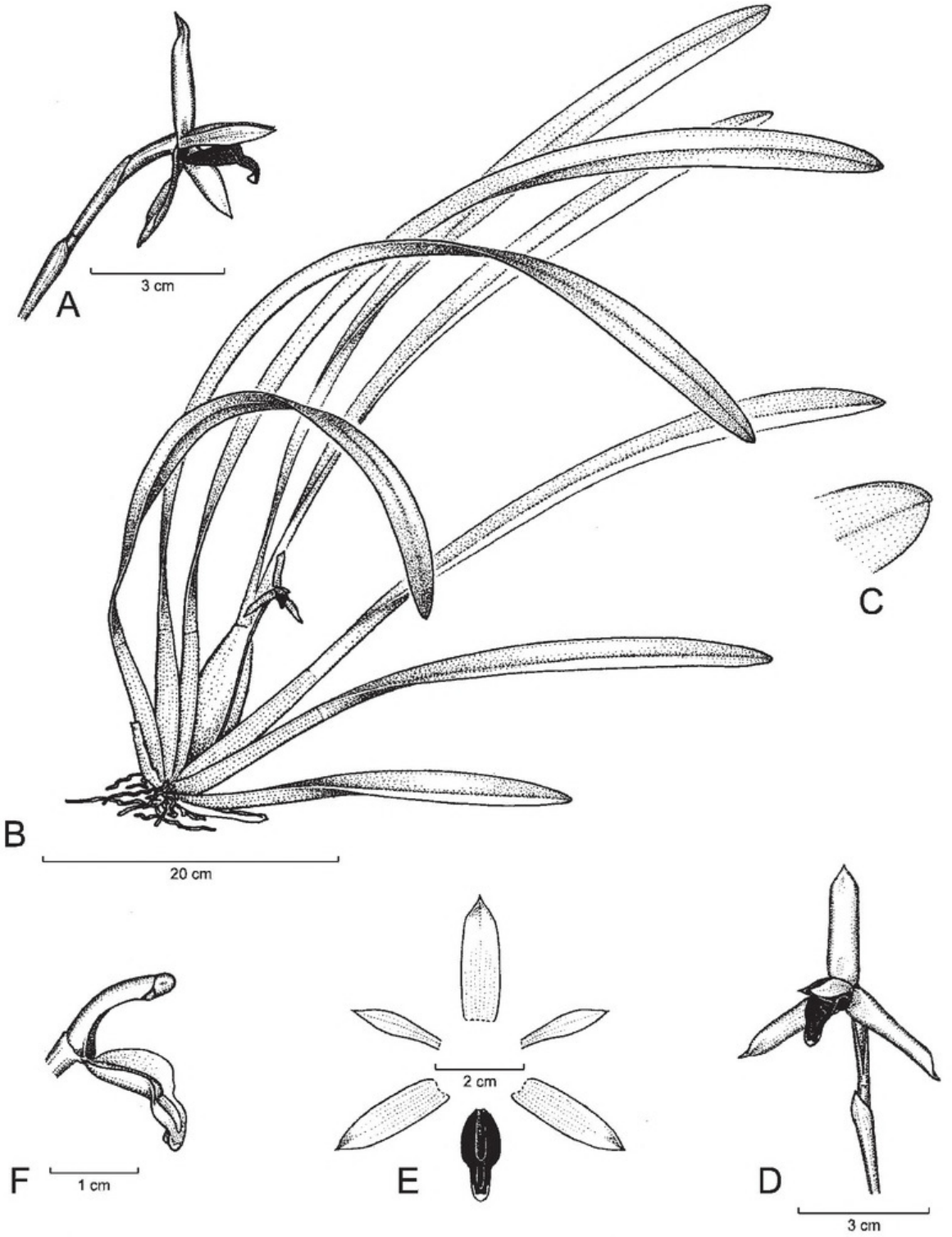

Figure 2. *Nitidobulbon proboscideum* (Reichenbach f.) Ojeda & Carnevali. —A. Back view of flower. —B. Flowering plant. —C. Apex of leaf. —D. Front view of flower. —E. Floral segments. —F. Side view of column and lip (sepals and petals removed). Based on *G. C. K. & E. Dunsterville 379* (AMES), from Venezuela.

Amarillo, 1600 m, 19 Sep. 1925, *A. Alfaro 190* (holotype, US).

Maxillaria oxysepala Schlechter, Repert. Spec. Nov. Regni Veg. 27: 73. 1929. TYPE: Bolivia. La Paz: Hacienda Simaco sobre el camino a Tipuani, 1400 m, Feb. 1920, *O. Buchtien 5003* (lectotype, designated here, AMES 25122; isotypes, AMES 26478, G, US).

Distribution. As currently circumscribed, *Nitidobulbon nasutum* ranges from southern Mexico, throughout Central America, and into Bolivia along the Andean Range, the Venezuelan Coastal Range, the Guianas, and the northern Amazon Basin.

Discussion. The holotype of *Maxillaria oxysepala*, originally at B, was destroyed. We have selected AMES 25122 as lectotype because it is the most representative specimen we examined.

3. Nitidobulbon proboscideum (Reichenbach f.) Ojeda & Carnevali, comb. nov. Basionym: *Maxillaria proboscidea* Reichenbach f., Bonplandia 2: 16. 1854. *Heterotaxis proboscidea* (Reichenbach f.) F. Barros, Hoehnea 29: 113. 2002. TYPE: Venezuela. Dist. Capital: Caracas, s.d., *H. Wagener s.n.* (holotype, W [Reich. Hb. Orchid. 47879]). Figure 2.

Distribution. Nitidobulbon proboscideum is likely restricted to northern Venezuela, possibly into the Guayana Region (Carnevali & Ramírez, 2003). Plants from outside this area that are referred to this species in floristic treatments may belong to *N. nasutum* or to other, possibly undescribed taxa.

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