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Natural history of the often-misunderstood *Govenia utriculata* (Orchidaceae): discovery of a Mexican population upsets West Indies endemism

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Abstract

Govenia utriculata (Sw.) Lindl. has been pervasively confused in herbaria and the literature, despite showing both vegetative and florally distinctive attributes. Here we document for the first time its presence in Mexico, provide a description, a detailed drawing and color photographs from live flowering plants, and compare it with its congeners. All verifiable records indicate that *G. utriculata* is restricted to the Bahamas, the Greater Antilles, and now also Mexico; literature reports from elsewhere were based on misidentifications. *Govenia utriculata* is distinguished by the large inflated sheath enclosing the leaf petioles, which in living condition is circular in cross section and partially filled with rainwater; such ample sheath is evident in herbarium specimens and shared only by Mexican endemic *G. lagenophora* Lindl. Florally, *G. utriculata* is recognized by its small, white flowers, narrowly elliptic, falcate, acute petals with transverse magenta bars above the middle of their inner surface, and narrowly ovate, acuminate labellum with longitudinal keels only below the middle. The single known Mexican population of *G. utriculata* occurs in a tropical deciduous forest nature reserve (Sierra Montenegro) in the state of Morelos, and thus is under nominal protection; moderate disturbance from trampling and nearby agriculture and cattle ranching was observed in the location but the population seems to be tolerant to such disturbance and all reproductive individuals were found in partially open areas and forest edges. All Mexican plants examined had auto-pollinating flowers; auto-pollination resulted from germination of the pollen on the rostellum briefly before anthesis, apparently precluding cross-pollination as the pollinia are stuck to the rostellum when the flowers open.

Keywords: Auto-pollination, biogeography, rainwater-collecting sheath, range extension, West Indies

Introduction

The genus *Govenia* Lindley (1830−40: 153) encompasses about 25 species of forest-dwelling, terrestrial orchids restricted to the Neotropics. Taxonomy of *Govenia* is challenging because of the relatively homogenous floral morphology among the species and the loss or distortion of some diagnostic characters, such as the species-specific patterns of floral colouration and the three-dimensional folding of the labellum, upon pressing and drying (Lindley 1835, Correll 1947, Dressler 1965, Greenwood 1981). For instance, Greenwood (1992a, b) showed that the presence/absence of magenta barring on the inner surface of the petals and whether there are brown dots on one or both labellum surfaces are consistent attributes allowing for the distinction between two previously much confused species, namely *G. capitata*

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Lindley (1835: sub. t. 1795; unmarked petals, brown spots on both the underside and the upper surface of the labellum) and *G. liliacea* (Lexarza in de la Llave & Lexarza 1825: 12−13) Lindley (1835: sub. t. 1795; barred petals, spots only on the labellum underside). Moreover, in its natural state the labellum of all *Govenia* species is convex, recurved and often has two longitudinal keels on its upper surface. Trying to spread out flat the three-dimensionally complex labellum out of a boiled flower inevitably results, in Correll's (1947: 218) words, in "folds, overlapping, pleating, and undulations" which make it difficult to interpret its shape and dimensions. Hence, taxonomic study of *Govenia* ideally requires examination of live specimens to achieve a familiarity with the distinguishing characters of the species; then, identification of herbarium specimens may be attempted using a combination of morphological characteristics and, in some instances, distributional/ecological data. Regrettably, purportedly new species continue to be described solely based on ill-defined outlines of boiled labella from herbarium specimens (Szlachetko & Kolanowska 2014), which adds to taxonomic confusion.

Here we present the results of our field and herbarium studies aimed at clarifying the identity *G. utriculata* (Swartz 1788: 119) Lindley (1839: Misc. 46−47), one of the species of this genus more pervasively confused both in literature and herbaria. We synthesize what is known about its geographical distribution and reproductive biology, provide a detailed drawing, color photographs and a description based on live flowering plants to aid in its identification, and discuss the characters that permit its recognition in both, fresh condition and herbarium specimens.

Material and methods

Morphological observations. We studied *ca*. 20 live flowering plants of *G. utriculata in situ* in Morelos, Mexico (see Representative specimens), and took for further examination in the laboratory flower buds, newly open flowers and older flowers in which the ovaries had started to develop into fruits from five such plants. Photographs were taken with a digital camera (Nikon D7100, Nikon Corporation, Tokyo, Japan) provided with a 60 mm AF Micro Nikkor lens (Nikon) and with a cell phone (iPhone 7, Apple Inc., California, USA) adapted on a stereomicroscope (Stemi SV 6, Karl Zeiss Mikroskopie). Our morphological description and line drawing were prepared from the Morelos plants. The latter were compared with live flowering plants of *G. utriculata* collected by several of us (GAS, IF-M, TC) in the Dominican Republic and in Puerto Rico (JDA), as well as with numerous specimens of *Govenia* species (including *G. utriculata*) housed in the herbaria AMES, AMO, ARIZ, ASU, BM, BR, CAS, CHAPA, COL, CORU, ENCB, F, FCME, GH, HOXA, IBUG, IEB, JBSD, K, LL, M, MEXU, MO, NY, P, QCA, QCNE, SERO, SLPM, TEX, UPRRP, UPS, US, USM, XAL and W.

Taxonomy

Govenia utriculata (Sw.) Lindley (1839: Misc. p. 46−47).
Limodorum utriculatum Swartz (1788: 119). TYPE:—JAMAICA. Swartz s.n. (lectotype selected by Ackerman in Ackerman et al. 2014: BM!, isolectotypes UPS!, W photograph!).
Cymbidium utriculatum (Sw.) Swartz (1799: 75).

Terrestrial *herb* 45−60 cm in height including the inflorescence. *Roots* several, arising from the base of the corm, terete, to 150 × 1.5–2.5 mm. *Corms* asymmetrically globose, dorsiventrally depressed, made up of 3–4 nodes, 2.5–3.5 × 4–5.5 cm, when young covered by 3–4 loose, membranaceous leaf sheaths. *Leaves* 5–6, lowermost 3–4 of them being bladeless sheaths, obtuse to rounded, 3–10 cm long, the uppermost one much longer, tubular, inflated, greyish-green with purplish-red suffusion, 19–25 × 3–4 cm, usually filled with rainwater; the upper 2 leaves with elongate petioles fully enclosed by the uppermost bladeless sheath, subquadrate in transverse section, 20–25 × 0.5–1 cm; blades elliptic, acuminate, deep green, plicate, 20−30 × 6–10 cm. *Inflorescence* racemose; peduncle terete, pale green, 38–42 × 0.4–0.5 cm, with 1–2 membranaceous, tubular, acute to obtuse bracts 3–4 cm long; raceme moderately loose, rachis 5−15 cm long, with 10−25 flowers which open successively. *Floral bracts* spreading, narrowly lanceolate, attenuate, 10−20 × 2−4 mm. *Flowers* resupinate, slightly ascending, perianth background colour white, the petals bearing faint, somewhat irregular transverse magenta bars on the distal 2/3 of their inner surface, the labellum with two lanceolate yellow areas on the inner surface extending about 2/3 of its length, three yellowish-brown to dark reddish-brown spots at the apex, sometimes with a less conspicuous additional brownish dot at the tip of each yellow area. *Ovary* slightly arcuate, subterete, with three rounded longitudinal keels, 7–15 × 1.5–2 mm. *Dorsal sepal* oblong-lanceolate, subacute, 18–19 × 3.9–4 mm. *Lateral sepals* oblong, falcate, acute, 12–14 × 4.3–5 mm. *Petals* narrowly elliptic, falcate, acute,

15–16 × 5.5–6 mm. *Labellum* versatile (*i.e.* motile with the union to the column foot acting as a hinge), in natural position ascending and approaching the column, but with weak pressure tipping down and then bouncing back upwards; shortly clawed, then abruptly expanded into a narrowly ovate, acuminate, arching lamina, with a central longitudinal channel bordered by two inconspicuous, rounded keels (which consist of folds that are convex on the upper surface and concave on the lower surface of the labellum), apex shortly acuminate; claw 0.5–1 × ca. 1.2 mm, lamina 9–10.3 × 6–6.5 mm. *Column* arcuate, truncate at apex, expanded into a broadly triangular, rounded wing at each side above the middle, channeled ventrally, 8–8.5 × 2–3 mm. *Anther* yellow, galeate, rostrate, ca. 2.5 × 2 mm. *Pollinarium* ca. 1 × 1 mm, consisting of four yellow, obliquely ovoid pollinia joined through pale yellow, granular caudicles to a short hamular stipe ending into a pointed, whitish viscidium. *Rostellum* a narrow transverse strip of tissue bearing a small, rounded remnant upon removal of the pollinarium, which is possible to do only shortly before anthesis; when the flowers open the pollinia are already germinating and stuck on the rostellar tissue. *Stigma* trapezoid, slightly concave, shiny, ca. 1 × 2 mm. *Capsules* ellipsoidal, pendulous, with six low longitudinal ribs, 2−3 × 0.5−1 cm. Fig. 1–5.

Phenology:—Flowering from August to December. Well-developed fruits recorded from November to February.

Distribution and habitat:—Bahamas, the Greater Antilles (Cuba, Dominican Republic, Jamaica, Puerto Rico) and Mexico (Morelos). Terrestrial, with the corms and roots immersed in leaf mould without penetrating the underlying soil. In the Caribbean it inhabits *Pinus occidentalis* forests and wet broad-leafed tropical forests at 0–1100 m elevation. In Mexico it dwells in partially disturbed tropical deciduous forest at 1350 m elevation. Salazar (2009) speculated that rainwater that accumulates in the sheaths of *G. lagenophora* Lindley (1839: Misc. 46–47), the only other species with an inflated sheath similar to that of *G. utriculata* (see Discussion), may represent a reserve of the liquid in the seasonally dry environments the former dwells in. A similar reasoning may apply to *G. utriculata* as it concerns its habitat in Mexico (tropical deciduous forest), although the value of such potential adaptation would be less obvious in the moister habitats that the latter occupies in the Greater Antilles (Ackerman *et al.* 2014).

Conservation status:—The single population of *G. utriculata* so far known in Mexico occurs on the edge of the buffer area of the Sierra de Montenegro state reserve, which is about 20 km long and encompasses ca. 7,500 ha of tropical deciduous forest on calcareous terrain at 1000−1775 m elevation, surrounded by valleys where natural vegetation has been eliminated as a result of agriculture and urban expansion, just a few kilometres southeast of the outskirts of the state capital, Cuernavaca (see https://sustentable.morelos.gob.mx/anp/sierra-montenegro). The *Govenia* population there is subject to occasional disturbance from trampling, as most plants, including all the reproductive individuals observed, grow at the forest edge on the sides of a dirt road and the trails used frequently by farmers from the nearby town on their way to their crop fields and pasturelands (which is often the case in the Greater Antilles; J. D. Ackerman pers. obs.). It is apparent that this species is tolerant to, and perhaps favored by, moderate disturbance. No obvious immediate threats to the Mexican population were noted.

According to the method for assessing risk of extinction for plants of the Mexican norm (MER-Plantas; SEMARNAT 2010), this species qualifies as "Endangered" since it attained a score >2 (2.04), with each of the four criteria rated as follows (maximum value for each = 1): A (characteristics of its geographical distribution) = 1; B (characteristics of its habitat) = 0.78; C (intrinsic vulnerability) = 0.26; and D (impact from human activities) = 0.0. Moreover, this species also qualified as Endangered by two "shortcut" MER-Plantas criteria: (I) Its known area of distribution in Mexico is under 1 km^2 and (II) the number of individuals recorded is less than 500. Likewise, according to the IUCN Red List criteria (IUCN 2012), at the regional level it qualifies as Endangered by Criterion D (population size estimated to number less than 250 mature individuals). Formal assessments of its risk status in the Bahamas and the Greater Antilles are lacking due to the paucity of information on its distribution, abundance and potential threats (Ackerman *et al.* 2014).

Reproductive biology:—Little is known on the reproductive biology of *Govenia*. The only formal study on the topic published so far is the one by Pansarin (2008). He reported pollination of Brazilian plants attributable to *G. gardneri* (identified as *G. utriculata*) by two species of hoverflies of the genus *Salpingogaster* (Syrphidae), which appeared to be deceived by the brown to orange spots on the labellum apex and the column base mimicking pollen clusters. The same fly species were observed visiting flowers of plants belonging to other families that offer pollen as reward. The finding that flowers of *G. gardneri* do not produce a reward is consistent with our observation of absence of nectar in fresh flowers of *G. praecox* Salazar & Greenwood (1993: 113–118), *G. lagenophora* (Salazar 2009), *G. polychroma* Salazar, Fernández-Díaz & Huerta-Alvízar (2018: 84–84), *G. utriculat*a (this work), as well as *G. bella* Greenwood (1987: 230–232), *G. capitata*, *G. gardneri*, *G. liliacea*, *G. mutica* Reichenbach (1852: 856), *G. superba* (Lexarza in de la Llave & Lexarza 1825: 13) Lindley (1830–1840: 153) and *G. tingens* Poeppig & Endlicher (1837: 5, t. 107; G. A. Salazar pers. obs.). Hence, the report of nectar for two Venezuelan *Govenia* species, including one identified there as *G. utriculata* (Seres & Ramírez 1995), should be taken with caution until it can be verified.

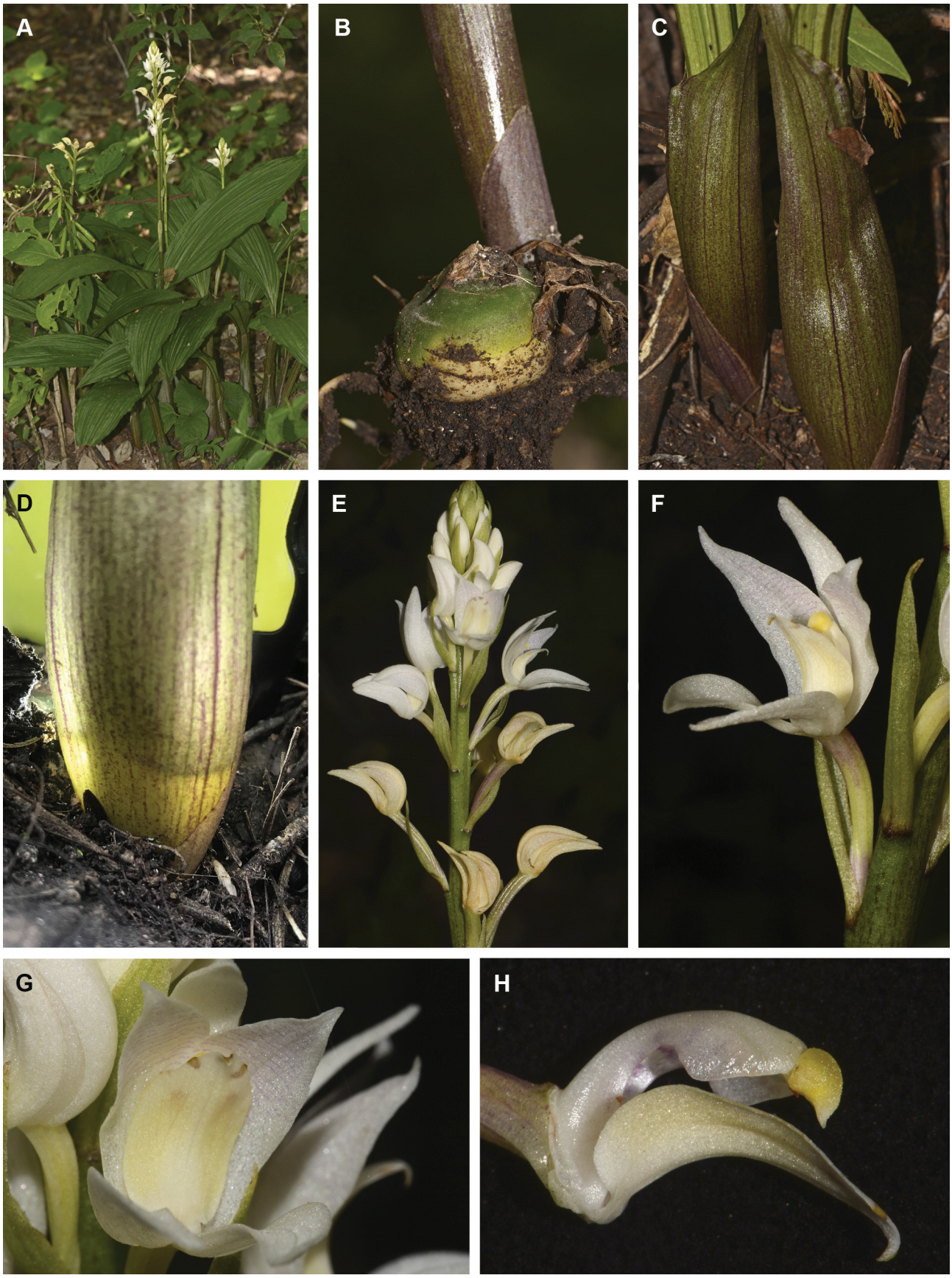

FIGURE 1. *Govenia utriculata*. A. Clump of plants *in situ*. B. Base of a plant removed from leaf litter to show the depressed corm from the previous year's growth and the developing corm enclosed by the sheath bases. C. Inflated sheaths of two adjacent plants. D. One such sheath illuminated from behind to show the accumulation of rainwater. E. Inflorescence. F. Flower, oblique view. G. Flower, front view. H. Labellum and column in natural position, side view. All from *Salazar* & *Octaviano-Landa 10282*. Photographs by Gerardo A. Salazar.

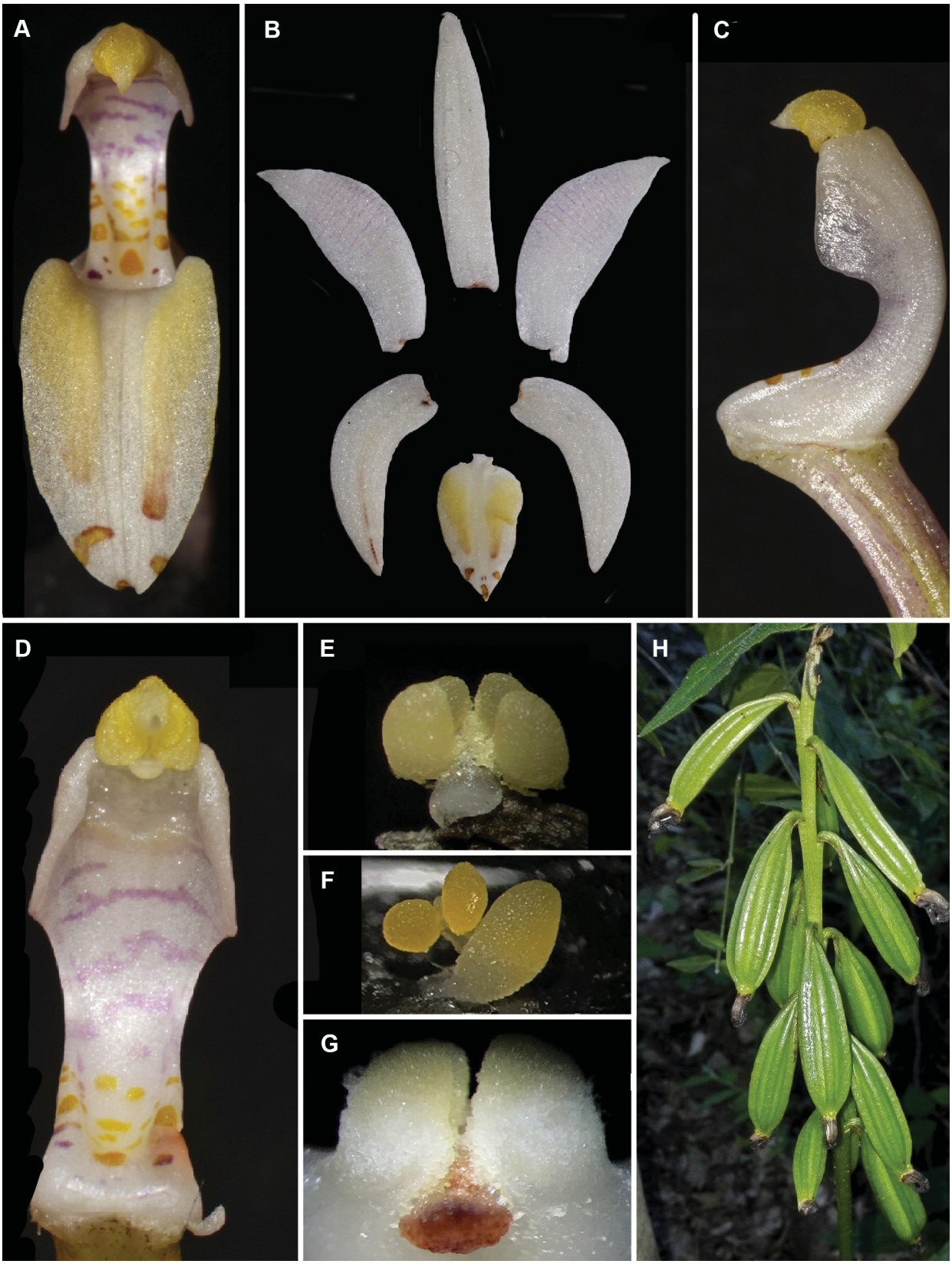

FIGURE 2. *Govenia utriculata*. A. Labellum and column from front after tipping the labellum downwards. B. Perianth dissection, segments flattened. C. Column, side view. D. Column, front view. E. Pollinarium removed from a flower bud just before anthesis, front view. F. Part of a pollinarium of a self-pollinating flower at anthesis; the large pollinium on the right-hand side is swollen because of germination of the pollen tubes. G. Pollinarium of a post-anthetic, self-pollinating flower showing the dried viscidium and the pollinia fussed to the rostellar tissue caused by pollen germination. H. Near-mature capsules. All from *Salazar* & *Octaviano-Landa 10282*. Photographs by Gerardo A. Salazar (A−G) and Víctor I. Octaviano-Landa (H).

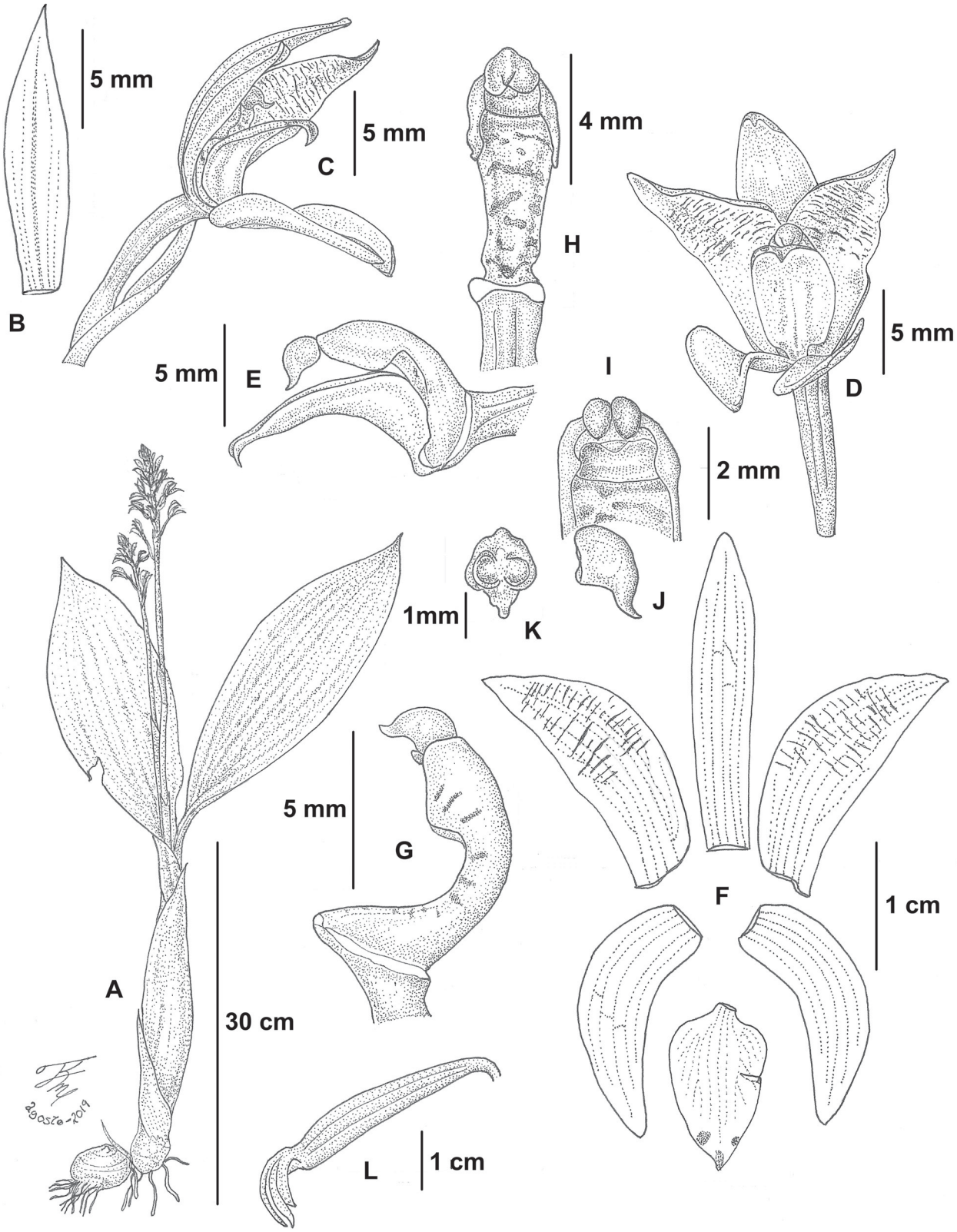

FIGURE 3. *Govenia utriculata*. A. Flowering plant. B. Floral bract, flattened. C. Flower, side view. D. Flower, front view. E. Labellum and column in natural position, side view. F. Perianth dissection, segments flattened. G. Column, side view. H. Column, front view. I. Column apex with anther removed, showing the pollinia, front view. J. Anther, side view. K. Anther, bottom view. L. Developing capsule. All from *Salazar* & *Octaviano-Landa 10282*. Drawn by Rolando Jiménez-Machorro.

FIGURE 4. Previously published illustrations of *bona fide Govenia utriculata*. A. Illustration from Fragmenta Botanica (Jacquin 1809: t. 32, fig. 4). B. Illustration from Botanical Magazine (Hooker 1845: t. 4151). C. Illustration from Flora of Jamaica (Fawcett and Rendle 1910: t. 22, fig. 1−3). D. Illustration by B. Angell. Reproduced with permission of the publisher and illustrator from: James D. Ackerman and Collaborators, Orchid Flora of the Greater Antilles, pg. 202, fig. 54. © 2014, The New York Botanical Garden, Bronx, New York.

All post-anthetic flowers of the Morelos population of *G. utriculata* we examined underwent self-pollination, showing at anthesis at least some (often all) of the four pollinia stuck to the underlying rostellum tissue because of the apparent germination of the pollen (Fig. F–G). Moreover, all open flowers were at various stages of capsule formation, and in no instance was it possible for us to remove an intact pollinarium once the flower had opened. Thus, that population apparently relies entirely on selfing for sexual reproduction, which may explain the large number of fruits that often form (Fig. 2H). Similarly, all the open flowers of the live plant we studied in the Dominican Republic were in various stages of capsule development, although in this case we were unable to verify whether this was the result of auto-pollination. Further studies are required to determine whether cross-pollination occurs at least occasionally in this species or it is fully dependent on auto-pollination.

Vernacular name:—Dominican Republic: *Botellitas* (Spanish for little bottles). No vernacular names have been recorded elsewhere.

Uses:—In the Dominican Republic, the rainwater that accumulates in the inflated sheath is used locally to refresh the eyes in case of infection (T. Clase pers. obs.).

Taxonomic discussion:—*Govenia utriculata* is distinguished by the inflated bladeless leaf sheaths, the uppermost of which completely encloses the leaf petioles and, in living condition, is circular in cross section and partially filled with rainwater (Fig. 1C−D, 3B, 4A, 5A−D). Such inflated sheath was literally described in Swartz's protologue of *Limodorum utriculatum* ("*vagina radicalia inflata*;" Swartz 1788: 120) and reflected in the specific epithet (from Latin *utriculatus*, bladder-like, inflated). Subsequent *bona fide* reports of *G. utriculata* have also described and illustrated the unmistakeable sheath. Jacquin (1809: 29, Pl. 32, Fig. 4; reproduced here as Fig. 5A) faithfully portrayed the plant and stated that the base of the sheath ("spathe") contains water, which is evident from the outside up to a height he marked on his figure. Likewise, Hooker (1845: t. 4151) referred to "the bladdery sheath surrounding its scape and the lower part of the leaves," which was clearly shown in the coloured plate (our Fig. 5B). Further illustrations and descriptions stressing such diagnostic character can be found in Flora of Jamaica (Fawcett & Rendle 1910: 113−114, Pl. 22, Fig. 1; our Fig. 5C) and the Orchid Flora of the Greater Antilles (Ackerman *et al.* 2014: 203, Fig. 54; reproduced here as Fig. 5D). Florally, *G. utriculata* is recognized by its relatively small, white flowers with narrowly elliptic, acute petals bearing faint transverse magenta bars above the middle on their inner surface, and the narrowly ovate, acuminate labellum with inconspicuous longitudinal keels below the middle (Fig. 1F–G, 2A−B, 3D–E, 4G−I).

The only other species of *Govenia* possessing a similarly inflated sheath containing rainwater is *G. lagenophora*, a Mexican endemic that dwells in seasonally dry montane oak forest and xerophilous scrub (Salazar 2009). *Govenia lagenophora* differs from *G. utriculata* in its long, cylindrical raceme with 30−50 flowers, these yellow to yellowish green with the sepals and petals densely spotted and tinged with brown, and the cream-yellow labellum tinged with brown below the middle, which is obtuse to emarginate at apex (see Dressler 1965).

Govenia capitata, a distinctive, large-flowered species from high-elevation conifer-oak forests endemic to the high Mexican cordilleras (see Greenwood 1992b), is still listed in some online compilations as a synonym of *G. utriculata* (e.g. Govaerts 2021), which likely represents a "relic" of Correll's (1947) treatment of *Govenia*. In that work, "offered more for convenience in dealing tentatively with the plants comprising the genus rather than as a final monographic treatment of the genus" on account of the difficulties inherent to its herbarium based taxonomy (Correll 1947: 219), over 25 nominal species were reduced to five species and two varieties. However, as pointed out by Garay & Romero-González (1999: 483), while herbarium specimens of *Govenia* are notoriously difficult to determine, difficulties do not mandate wholesale reduction of species to a few names.

Plants of *G. gardneri*, a widespread South American species originally described from a plant from the Serra dos Órgãos (Organ Mountains), southern Brazil, are often confused in literature with *G. utriculata* (e.g. Pansarín 2008; Pansarin & Pansarin 2010; Schinini 2010; Zuloaga *et al.* 2019). *Govenia gardneri* differs from *G. utriculata* in its narrow bladeless leaf sheaths 1.5−2 cm in diameter (vs. 3−4 cm), internally spotted (not barred), proportionately short and wide petals 1.8−2 times longer than broad (vs. 2.8−3.2 times longer than broad), and broadly ovate, obtuse labellum with prominent keels over most of its length (vs. keels only on the basal half). Botanical illustrations and descriptions of *G. gardneri* can be found in Hooker (1839), Cogniaux (1898–1902) and Hoehne (1942). High-quality colour photographs showing the narrow, tight bladeless sheaths and the characteristic flower colouration of *G. gardneri* were published by Pansarin & Pansarin (2010, as *G. utriculata*).

Representative specimens:—BAHAMAS. Andros: North Andros, Maidenhair Coppice no. 1, ca. 8 miles NW of Fresh Creek, 5 Jan. 1978, *Correll et al. 49372* (NY!). CUBA. Oriente: Monte Verde, 13 Feb. 1911, *Shafer 8678* (NY!). DOMINICAN REPUBLIC. San José de Ocoa: municipio Ocoa, La Ciénega, localidad La Laguna, 14.3 km al E de Ocoa, 1232 elev., 28 Nov. 2016, *Fragoso-Martínez et al. 543* (JBSD!). JAMAICA. without date or collector, donated in 1855 by *Hooker* [*s.n.*] (P!). MEXICO. Morelos: Sierra Montenegro, municipio Emiliano Zapata, Tetecalita,

subiendo del poblado hacia el paraje Las Peñas, 23 Aug. 2019, *Salazar & Octaviano-Landa 10282* (HUMO! MEXU!). PUERTO RICO. Utuado: Cerro Morales, 700−950 m, near summit, 5 Nov. 1984, *Ackerman & Montero-Oliver 2042* (UPRRP!).

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