SARCOGLOTTIS WOODSONII (ORCHIDACEAE: SPIRANTHINAE)—REDISCOVERED IN COSTA RICA AFTER 80 YEARS, WITH A PRELIMINARY SURVEY ON AQUATIC AND OTHER WETLAND ORCHIDS

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Abstract: Orchidaceae, a highly diverse family of angiosperms, exhibits remarkable ecological and morphological adaptations, with most of its species being epiphytic or terrestrial. Nonetheless, their occurrence in aquatic and wetland habitats in the tropics is relatively uncommon, with only a few species adapted to these environments. Consequently, our current understanding of orchids inhabiting wetland ecosystems is limited. This research focuses on *Sarcoglottis woodsonii*, an aquatic orchid species exclusively found in palustrine wetlands of southern Central America. Previously considered endemic to western Panama, our recent collections (the first since 1940) extend its known distribution to include southern Costa Rica. We provide an updated description, a modern illustration, a conservation assessment based on IUCN criteria, and novel ecological data that shed light on its aquatic habit. With this recent discovery, the number of known *Sarcoglottis* species in Costa Rica stands at six. We provide a preliminary survey of reported wetland and aquatic orchid species from the Neotropics and give novel definitions for both wetland and aquatic plants. We also present an inventory of the vascular plant species found in the Cañas Gordas/Valle Azul wetland in Costa Rica, where *S. woodsonii* occurs. This study enhances our understanding of orchid diversity in wetland ecosystems and emphasizes the importance of conserving these unique habitats, often inadequately protected and surrounded by heavily altered ecosystems.

Keywords: aquatic orchids, Flora of Costa Rica, Flora of Panama, new records, wetland habitats

Orchidaceae are among the most species-rich families of seed plants in the Americas (Ulloa-Ulloa et al., 2017). This is particularly evident in Mesoamerica (Dressler, 2023) and the tropical Andean countries (Ulloa-Ulloa et al., 2017; Pérez-Escobar et al., 2022). The remarkable diversity of orchids is reflected in their extensive ecological and morphological adaptations (Dressler, 1981; Stevens, 2001 onwards). Although most orchid species are epiphytic, approximately 20% are terrestrial, and an estimated 5% can grow facultatively as terrestrials or epiphytes (Dressler, 1981). Surprisingly, despite their vast diversity, the Orchidaceae have not extensively colonized aquatic and wetland habitats in the tropics. Only a limited number of species within the family have successfully adapted to thrive in these environments (e.g., Arber, 1920, and Cook et al., 1974, do not even mention Orchidaceae in their classic treatises on aquatic plants; Sculthorpe, 1967, does not include it in his table of families of aquatic vascular plants).

In this context, it is important to define what we mean by wetlands and to distinguish between aquatic and wetland plants. We adhere in general to the wetland definition agreed in the Ramsar Convention (1971): "wetlands are areas of marsh, fen, peatland or water, whether natural or artificial, permanent or temporary, with water that is static or flowing, fresh, brackish or salty, including areas of marine water the depth of which at low tide does not exceed six meters," however, we also include areas with waterlogged substrates, even if standing water is not visible to the human eye. Or, as Ervin (2023) defines them, wetlands are "areas where shallow surface waters or saturated soils are present during a biologically significant portion of the year."

Some authors (most notably den Hartog and Segal, 1964, and Ervin, 2023) have explored the complexities associated with defining aquatic and wetland plants. Our study defines *aquatic plants* as those that regularly complete their life cycle while growing in or on standing or flowing water, whether fully or partially submerged, and for most of their active growing period. It is worth noting that some authors (e.g., den Hartog and Segal 1964) exclude plants with emergent vegetative organs from this definition, even if their basal parts grow constantly in water. Additionally, we define *wetland plants* as those that regularly occur in wetland habitats,

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regardless of whether they are in direct contact with standing or running water. This includes epiphytes and plants that grow around bodies of water but not directly growing in the water. According to these definitions, almost all aquatic plants are wetland plants (except for rare cases of plants that regularly grow in phytotelmata in non-wetland habitats, e.g., *Anthurium bromelicola* Mayo & L.P.Felix, *Anthurium sterilispadix* K.M.Pimenta & Mayo, both Araceae, and *Utricularia humboldtii* R.H.Schomb., Lentibulariaceae, when they grow in the water impounded in bromeliad tanks away from wetlands), but at the same time, many wetland plants are not aquatic. Also, according to our definitions, plants growing on waterlogged substrates without open bodies of water (either standing or running water), are classified as wetland plants, not as aquatic plants. However, exceptions to this latter definition might arise when the substrate remains consistently saturated. Numerous plants, such as members of Alismataceae or *Heteranthera* Ruiz & Pav. (Pontederiaceae), typically deemed aquatic by our criteria, occasionally thrive in moist soils without visible surface water.

According to our definitions given above, most wetland orchids are not aquatic; they are either epiphytes or, lithophytes, or terrestrials that can grow on water-saturated soils, but normally not with standing water. Truly aquatic orchid species are rare in the family, and the occurrence of this habit has been either overlooked or received little attention from orchidologists. For example, the Identification Manual for Wetland Plant Species of Florida (Dressler et al. 1991), whose authors include two prominent orchid experts, includes a single aquatic orchid species. However, McCartney (1998) mentions three additional ones that meet our definition, which also occur in the state. According to Ervin´s (2023) classification of growth forms of aquatic plants, all aquatic orchid species are emergent (i.e., rooted in or on the submerged substrate, with stems and leaves that extend above the water surface). We do not know of any orchid species whose normal growth habit fits Ervin´s other categories of aquatic plants: floating-leafed (i.e., rooted in or on the substrate, with leaf blades that float on the water surface; e.g., *Nymphaea* L., Nymphaeaceae), submersed (i.e., rooted in or on the substrate, with stems and leaves beneath the water surface; e.g., Podostemaceae), or free-floating (i.e., not rooted in or on the substrate, with stems and leaves that float freely on or beneath the water surface; e.g., Araceae subfamily Lemnoideae).

A related plant habit category is that of rheophytes, i.e., those that are adapted to endure fast-moving water currents, either all or most of the time when they grow on riverbeds (therefore also aquatic, e.g., Podostemaceae), or occasionally when river levels rise seasonally or for brief periods during rainstorms (therefore not necessarily aquatic). The only (facultatively) rheophytic orchids from the Neotropics that we know of are a few species of *Phragmipedium* Rolfe, which belong in the second sub-category (see below). Vermeulen and Tsukaya (2011) enumerate some allegedly rheophytic orchids from southeast Asia.

In the Neotropics, *Habenaria* Willd. is probably the most likely orchid genus to be encountered in wetland habitats (Rolfe, 1901; Horich, 1983), with at least four widely distributed species (*H. gourlieana* Gillies ex Lindl., *H. pringlei* B.L. Rob., *H. repens* Nutt., and *H. sartor* Lindl.) frequently growing as aquatics. In Mexico, *Spiranthes graminea* Lindl. ex Benth. grows alongside *H. repens* amid floating vegetation mats. *Bletia purpurea* (Lam.) DC. and *H. pringlei* can thrive in flooded grasslands, or swampy regions called "popales," where the water level remains low (Hágsater et al., 2005). Plants of *Phragmipedium klotzschianum* (R.H. Schomb. ex Rchb.f.) Rolfe and *P. longifolium* (Warsz. & Rchb. f.) Rolfe often grow associated with running water, usually on seepages where the water flow is slow on its roots; however, they can also facultatively grow as rheophytes on riverbanks and around waterfalls (Dunsterville and Dunsterville, 1982; Díaz-Morales et al., 2021). The ecologically versatile *Epidendrum radicans* Pav. ex Lindl. and *Spathoglottis plicata* Blume (the latter native to southeast Asia and the western Pacific but naturalized in parts of the Neotropics), which inhabit primarily non-wetland habitats, are occasionally seen growing in wetlands (Horich, 1983). Records from other terrestrial genera, such as *Aspidogyne* Garay (*Aspidogyne tuerckheimii* (Schltr.) Garay, "Bosque lluvioso, pantanoso-yolilloso de Suerre y Dos Bocas," *P. Shank and A. Molina 4144* AMES [66497]); *Microchilus* C. Presl (*Microchilus tessellatus* Ormerod, "Terrestrial in low, swampy areas…," *M. Grayum et al. 8925* MO [713953/A:3709414]); and *Palmorchis* Barb. Rodr. (*Palmorchis paludicola* Dressler, "*Raphia taedigera* palm swamp," *S. Mori and R. Anderson 129* BM [000061071], F [1648825/F0076614F]), could indicate that some species of other, mostly terrestrial clades, can occasionally grow in wetland environments, possibly as facultatively aquatic plants. In tropical South America, besides some of the previously cited species, Kahn et al. (1993), Velásquez (1994), Pott and Pott (2000, 2021), Chocce et al. (2004), Batista and Bianchetti (2010), Batista et al. (2014), Lasso et al. (2014), Mereles et al. (2015), Madriñán et al. (2017), and Pansarin et al. (2020) report *Aspidogyne debilis* (Lindl.) Meneguzzo, *Cleistes rosea* Lindl., *Cyrtopodium paludicola* Hoehne, *Duckeella pauciflora* Garay, *Epistephium parviflorum* Lindl., *Eulophia alta* (L.) Fawc. & Rendle, *Galeandra styllomisantha* (Vell.) Hoehne, *Habenaria amambayensis* Schltr., *H. aricaensis* Hoehne, *H. bicornis* Lindl., *H. glazoviana* Kraenzl., *H. leprieurii* Rchb. f., *H. nabucoi* Ruschi, *H. orchiocalcar* Hoehne, *H. polycarpa* Hoehne, *H. pratensis* (Salzm. *ex* Lindl.) Rchb.f., *H. sartor* Lindl., *H. spathulifera* Cogn., *Liparis inundata* (Barbosa Rodrigues) A.W. Hill, *Otostylis paludosa* (Cogn.) Schltr. and three epiphytic species, *Catasetum roseo-album* (Hook.) Lindl., *Epidendrum lacustre* Lindl., and *Rodriguezia venusta* (Lindl.) Rchb. f., from wetland habitats. Most likely, most of those species (with the likely exception of some of the *Habenaria* species, *L. inundata* and *O. paludosa*) are not truly aquatic plants. At the tops of some tepuis in Venezuela, *Guanchezia maguirei* (C. Schweinf.) G.A.Romero & Carnevali grows on boggy soil (even with its pseudobulbs immersed in the wet substrate). However, at other sites, it grows terrestrially or as an epiphyte (Dunsterville and Dunsterville, 1973, 1976, as

Bifrenaria maguirei C. Schweinf.). Lot et al. (2013) and Les (2020) also list the genera *Arethusa* L., *Bletia* Ruiz & Pav., *Calopogon* R. Br., *Cypripedium* L., *Epipactis* Zinn, *Galearis* Raf., *Malaxis* Sol. ex Sw., *Platanthera* Rich., *Pogonia* Juss., *Ponthieva* R. Br., *Schiedeella* Schltr., *Spiranthes* Rich., and *Warrea* Lindl. as having wetland inhabiting representatives, but those genera are either mostly north temperate or have been only rarely recorded in wetlands south of Mexico. In Florida and other regions of North America, in addition to *H. repens*, species such as *Platanthera nivea* (Nutt.) Luer, *Spiranthes odorata* (Nutt.) Lindl., and *S. laciniata* (Small) Ames facultatively grow in aquatic environments (McCartney, 1998). *Spiranthes odorata* is occasionally sold as an aquarium plant (Salazar, 2003b). In southern Florida (but not in Cuba), the epiphytic *Dendrophylax lindenii* (Lindl.) Benth. ex Rolfe grows exclusively on trunks and branches that overhang standing water in swamps, apparently because of the protective thermal insulation against occasional freezing winter temperatures provided by the high relative humidity (Mújica et al. 2018).

Coastal lagoons and brackish river deltas with flooded forests dominated by mangroves can also be classified as wetlands. Though orchids are not commonly found in such habitats, a few epiphytic species that can tolerate certain salinity levels have been reported to grow on mangroves even when in occasional contact with brackish water or saline spray. Examples include *Brassavola nodosa* (L.) Lindl., *Encyclia alata* (Bateman) Schltr., *Myrmecophila brysiana* (Lem.) G.C. Kenn., *M. christinae* Carnevali & Gómez-Juárez, *M. tibicins* (Bateman) Rolfe, and *Prosthechea cochleata* (L.) W.E. Higgins, mostly found along the Caribbean coast of Mexico and Central America (Hágsater et al., 2005). According to our definitions above, these species can be classified as occasional wetland plants, but none are truly aquatic. A synopsis of the Neotropical and other New World orchid species previously reported as associated with wetlands (including aquatic and non-aquatic species) is provided in Table 1. No attempt has been made here to list wetland orchids from other parts of the world.

Sarcoglottis C. Presl., a primarily terrestrial genus of orchids, includes approximately 45–50 species distributed from Mexico to northern Argentina (Salazar, 2003a; POWO, 2022). The genus belongs to the subtribe Spiranthinae, the most species-rich clade of mainly terrestrial orchids in the Neotropics (Salazar et al., 2018). *Sarcoglottis* appears monophyletic and sister to a clade that includes most of *Brachystele* Schltr., polyphyletic *Odontorrhynchus* M.N. Correa, polyphyletic *Pelexia* Poit. ex Lindl., and *Sauroglossum corymbosum* (Lindl.) Garay (Salazar et al., 2018). Morphological characteristics of *Sarcoglottis* include its usually very abbreviated vegetative stem, usually clustered, fleshy roots, pseudopetiolate, non-plicate leaves, usually arranged in a rosette, commonly deciduous in anthesis, and inflorescences arranged as erect racemes, with relatively large flowers for the subtribe (Dressler, 2003). One of the most distinctive traits of the genus is the fusion of the proximal parts of the lateral sepals, which extend beneath the ovary, forming a nectary (Salazar, 2003a; Salazar et al., 2019).

Sarcoglottis woodsonii (L.O. Williams) Garay is one of the most peculiar species in the genus due to its elongated rhizome and its relatively short leaves that are persistent during anthesis (traits reminiscent of species in the subtribe Goodyerinae). Unlike most *Sarcoglottis* species, *S. woodsonii* is confined to palustrine wetland environments, distinguishing it as one of the few Mesoamerican orchids restricted to these habitats (Williams, 1946, as *Spiranthes woodsonii* L.O. Williams). As detailed below, *S. woodsonii* is a true aquatic orchid.

Bogarín et al. (2014) listed this species as endemic to Panama, with known specimens collected near Boquete in Chiriquí. Aside from our gatherings, the only other collections, to our knowledge, date back to 1918, 1938, and 1940. This work aims to update the description of *S. woodsonii* by incorporating our recent collections (the first ones from Costa Rica) and providing basic observations on its natural history and the flora associated with its habitat. With this new record, six species of *Sarcoglottis* are now known in Costa Rica (Pupulin et al., 2023).

Materials and Methods

Fieldwork was conducted on 16 June 2022 and 10 June 2023 between Cañas Gordas and Valle Azul in the Agua Buena district, Coto Brus county in Puntarenas province, Costa Rica. The study site is a wetland in a palustrine depression at ca. 8°45'19.2"N, 82°55'23.1"W, at 1130 m elevation, with its main longitudinal axis running from east to west (Fig. 1). The depression is situated approximately 100 meters from the international border with Panama at its easternmost point. It is drained by a small stream at its westernmost end. The area falls within the premontane wet-to-pluvial transition forest life zone (Tosi, 1969). Although municipal laws protect the local wetlands, they have suffered extensive degradation due to human activities, including trampling and waste from domesticated animals.

The vegetation in the study area is primarily composed of various species of grasses (Poaceae) and sedges (Cyperaceae) that emerge from the standing water and form a "floating mat," almost completely hiding the water surface from view. Woody plants are scarce in the wetland itself. Plant material was studied in situ, with specimens of *Anagallis pumila* Sw., *Bacopa salzmannii* (Benth.) Wettst. ex Edwall, *Sarcoglottis woodsonii*, and *Syngonanthus caulescens* (Poir.) Ruhland collected and transported to the greenhouses of the School of Biology or the Lankester Botanical Garden Research Center, both of which belong to the University of Costa Rica. Herbarium specimens were deposited in the JBL (spirit) and USJ herbaria. Specimens of the genus *Sarcoglottis* were physically examined in the CR, HLDG, JBL, PMA, UCH and USJ herbaria, and digital images were studied from AMES, MO, and US herbaria (acronyms according to Thiers, 2023).

Photographic documentation through a Lankester Composite Dissection Plate (LCDP) was conducted at the Lankester Botanic Garden's Photography Laboratory.

TABLE 1. Reported Neotropical and other New World orchid species associated with wetlands. Indication of habit as "aquatic" for some species follows our definition of aquatic plants given in the Introduction. References mentioned here are included in the Literature cited section. Suprageneric classification follows Chase et al. (2015).

SUBFAMILY TRIBE SUBTRIBE	SPECIES	HABIT	REFERENCE OR HERBARIUM VOUCHER
Vanilloideae Pogonieae	*Cleistes rosea* Lindl.	Terrestrial, facultatively on flooded terrain	Madriñán et al. (2017)
	Cleistes tenuis (Rchb.f.) Schltr.	Terrestrial, facultatively on seasonally flooded savannas	Chocce et al. (2004)
	Duckeella pauciflora Garay	Terrestrial, facultatively on flooded terrain	Madriñán et al. (2017)
Vanilleae	*Epistephium parviflorum* Lindl.	Terrestrial, facultatively on seasonally flooded savannas	Chocce et al. (2004), Madriñán et al. (2017)
	Vanilla bicolor Lindl.	Hemiepiphytic facultatively on wetlands dominated by the palm *Mauritia flexuosa* L.f.	Householder et al. (2010)
	Vanilla guianensis Splitg.	Hemiepiphytic facultatively on wetlands dominated by the palm *Mauritia flexuosa*	Householder et al. (2010)
	Vanilla karen-christianae Karremans & P. Lehm.	Hemiepiphytic facultatively on wetlands dominated by the palm *Mauritia flexuosa*	Householder et al. (2010, as *Vanilla ribeiroi* Hoehne)
	Vanilla marowynensis Pulle	Hemiepiphytic facultatively on wetlands dominated by the palm *Mauritia flexuosa*	Householder et al. (2010, as *Vanilla cristato-callosa* Hoehne)
	Vanilla palmarum (Salzm. ex Lindl.) Lindl.	Hemiepiphytic facultatively on wetlands dominated by the palm *Mauritia flexuosa*	Householder et al. (2010)
	Vanilla planifolia Andrews	Hemiepiphytic facultatively on wetlands	Own unpublished data
	Vanilla pompona Schiede	Hemiepiphytic facultatively on wetlands dominated by the palm *Mauritia flexuosa*	Householder et al. (2010)
Cypripedioideae	*Phragmipedium klotzschianum* (R.H. Schomb. ex Rchb. f.) Rolfe	Terrestrial or lithophyte, occasionally as a rheophyte	Dunsterville and Dunsterville (1982)
	Phragmipedium longifolium (Warsz. & Rchb. f.) Rolfe	Terrestrial or lithophyte, facultatively on flooded seepage terrain, occasionally as a rheophyte	Díaz-Morales et al. (2021)
	Phragmipedium vittatum (Vell.) Rolfe	Terrestrial or aquatic? on flooded terrain	Batista and Bianchetti (2010)
Orchidioideae Cranichideae Goodyerinae	*Aspidogyne debilis* (Lindl.) Meneguzzo	Terrestrial, facultatively on flooded terrain or floating vegetation	Pott and Pott (2000, as *Erythrodes* cf. *pumila*, 2021)
	Aspidogyne tuerckheimii (Schltr.) Garay	Apparently facultatively on flooded terrain	*P. Shank y A. Molina 4144* (AMES 66497)
	Microchilus tessellatus Ormerod	Apparently facultatively on flooded terrain	*M. Grayum et al. 8925* (MO-713953/A:3709414)

TABLE 1 CONT. Reported Neotropical and other New World orchid species associated with wetlands. Indication of habit as "aquatic" for some species follows our definition of aquatic plants given in the Introduction. References mentioned here are included in the Literature cited section. Suprageneric classification follows Chase et al. (2015).

SUBFAMILY TRIBE SUBTRIBE	SPECIES	HABIT	REFERENCE OR HERBARIUM VOUCHER
Spiranthinae	*Sarcoglottis simplex* (Griseb.) Schltr.	Terrestrial, facultatively on seasonally flooded savannas	Chocce et al. (2004)
	Sarcoglottis uliginosa (Barb.Rodr.) Barb.Rodr.	Aquatic? on flooded terrain	Batista and Bianchetti (2010)
	Sarcoglottis woodsonii (L.O. Williams) Garay	Aquatic, on floating vegetation	Woodson and Schery (1942), this study
	Schiedeella durangensis (Ames & C. Schweinf.) Burns-Bal.	Terrestrial?, on flooded terrain	Lot et al. (2013)
	Schiedeella tenella (L.O. Williams) Burns-Bal.	Terrestrial?, facultatively on flooded terrain	Lot et al. (2013)
	Spiranthes delitescens	Aquatic in marshy meadows	Hágsater et al. (2005), Gerardo Salazar, pers. comm.
	Spiranthes graminea Lindl. ex Benth.	Aquatic	Hágsater et al. (2005), Lot et al. (2013), McCartney 1998
	Spiranthes laciniata (Small) Ames	Terrestrial, facultatively on flooded terrain	McCartney (1998)
	Spiranthes nebulorum Catling & V.R. Catling	In *Sphagnum* sp. bogs	Hágsater et al. (2005)
	Spiranthes odorata (Nutt.) Lindl.	Terrestrial, facultatively on flooded terrain	McCartney (1998)
	Veyretia hassleri (Cogn.) Szlach.	Terrestrial, facultatively on flooded terrain	Pott and Pott (2000, as *Sarcoglottis hassler*i (Cogn.) Schltr.)
Orchidae Orchidinae	*Habenaria amambayensis* Schltr.	Terrestrial, facultatively on flooded terrain	Pott and Pott (2000, 2021)
	Habenaria anisitsii Kraenzl.	Terrestrial, facultatively on flooded terrain	Pott and Pott (2000)
	Habenaria aricaensis Hoehne	Aquatic	Pott and Pott (2000, 2021)
	Habenaria balansae Cogn.	Terrestrial on flooded terrain	Batista and Bianchetti (2010)
	Habenaria bicornis Lindl.	Terrestrial?, on permanently wet savannas	Batista et al. (2014)
	Habenaria bractescens Lindl.	Aquatic	Lot et al. (2013)
	Habenaria crucifera Rchb.f. & Warm. *var. brevidactyla* J.A.N. Bat. & Bianch.	Terrestrial on flooded terrain	Batista and Bianchetti (2010)
	Habenaria floribunda Lindl.	Aquatic or terrestrial	Lot et al. (2013)
	Habenaria edwallii Cogn.	Terrestrial on flooded terrain	Batista and Bianchetti (2010)
	Habenaria glazioviana Kraenzl. ex Cogn.	Terrestrial, facultatively on flooded terrain	Pott and Pott (2000, 2021)

TABLE 1 CONT. Reported Neotropical and other New World orchid species associated with wetlands. Indication of habit as "aquatic" for some species follows our definition of aquatic plants given in the Introduction. References mentioned here are included in the Literature cited section. Suprageneric classification follows Chase et al. (2015).

SUBFAMILY TRIBE SUBTRIBE	SPECIES	HABIT	REFERENCE OR HERBARIUM VOUCHER
Orchidae Orchidinae cont.	*Habenaria gourlieana* Gillies ex Lindl.	Aquatic	Batista and Bianchetti (2010), Madriñán et al. (2017), Mereles et al. (2015)
	Habenaria guaraensis J.A.N. Bat. & Bianch.	Aquatic on flooded terrain	Batista and Bianchetti (2010)
	Habenaria leprieurii Rchb. f.	Terrestrial, facultatively on seasonally flooded savannas	Chocce et a. (2004), Madriñán et al. (2017)
	Habenaria leucosantha Barb.Rodr.	Terrestrial on flooded terrain	Batista and Bianchetti (2010)
	Habenaria mesodactyla Griseb.	Terrestrial, facultatively on seasonally flooded savannas	Chocce et al. (2004)
	Habenaria montiswilhelminae Renz	Terrestrial, on seasonally or permanently humid grassy fields	Batista and Bianchetti (2010)
	Habenaria nabucoi Ruschi	Terrestrial, facultatively on flooded terrain or floating vegetation	Pott and Pott (2021)
	Habenaria nuda Lindl. var. *pygmaea* Hoehne	Terrestrial on flooded terrain	Batista and Bianchetti (2010)
	Habenaria orchiocalcar Hoehne	Terrestrial, facultatively on flooded terrain	Pott and Pott (2000, 2021)
	Habenaria polycarpa Hoehne	Terrestrial, facultatively on flooded terrain	Pott and Pott (2021)
	Habenaria pratensis (Salzm. ex Lindl.) Rchb. f.	Terrestrial, facultatively on flooded terrain	Pott and Pott (2000, 2021)
	Habenaria pringlei B.L Rob.	Aquatic or terrestrial, including floating vegetation	Aburto-Oropeza et al. (2021), Hágsater et al. (2005)
	Habenaria pubidactyla subsp. *brasiliensis* J.A.N. Bat. & Bianch.	Terrestrial on flooded terrain	Batista and Bianchetti (2010)
	Habenaria repens Nutt.	Aquatic or terrestrial, including floating vegetation	Aburto-Oropeza et al. (2021), Hágsater et al. (2005), Hawkes (1953), Horich (1979, 1983), Lasso et al. (2014), Lot et al. (2013), Madriñán et al. (2017), McCartney (1998), Mereles et al. (2015), Pott and Pott (2000, 2021), Velásquez (1994)
	Habenaria sartor Lindl.	Aquatic or terrestrial	Kahn et al. (1993), Madriñán et al. (2017), Velásquez (1994)
	Habenaria spathulifera Cogn.	Terrestial, facultatively on flooded terrain	Pott and Pott (2021)
	Platanthera brevifolia (Greene) Kraenzl.	Terrestrial, facultatively on flooded terrain	Hágsater et al. (2005), Gerardo Salazar, pers. comm

TABLE 1 CONT. Reported Neotropical and other New World orchid species associated with wetlands. Indication of habit as "aquatic" for some species follows our definition of aquatic plants given in the Introduction. References mentioned here are included in the Literature cited section. Suprageneric classification follows Chase et al. (2015).

SUBFAMILY TRIBE SUBTRIBE	SPECIES	HABIT	REFERENCE OR HERBARIUM VOUCHER
Orchidae Orchidinae cont.	*Platanthera calderoniae* López-Ferr. & Espejo	Aquatic	Gerardo Salazar, pers. comm.
	Platanthera limosa Lindl.	Aquatic	Lot et al. (2013)
	Platanthera nivea (Nutt.) Luer	Terrestrial, facultatively on flooded terrain	McCartney (1998)
Epidendroideae Neottieae	*Epipactis gigantea* Dougl. ex Hook.	Terrestrial, facultatively on flooded terrain	Lot et al. (2013)
	Palmorchis paludicola Dressler	Terrestrial?, apparently facultatively on flooded terrain	*S. Mori and R. Anderson 129* (BM 000061071, F 1648825/ F0076614F)
Malaxideae Malaxidinae	*Liparis inundata* (Barb.Rodr.) A.W. Hill	Aquatic	Pansarin et al. (2020)
	Malaxis aff. *abieticola*	Terrestrial, facultatively in flooded montane grasslands	Hágsater et al. (2005), Gerardo Salazar, pers. comm.
	Malaxis aff. *brachystachys*	Terrestrial, facultatively on flooded terrain	Hágsater et al. (2005), Gerardo Salazar, pers. comm.
	Malaxis aff. *mysurus*	Terrestrial, facultatively on flooded terrain	Hágsater et al. (2005), Gerardo Salazar, pers. comm.
	Malaxis zempoalensis López-Ferr. & Espejo	Aquatic	Hágsater et al. (2005, as *Malaxis palustris* Espejo & López-Ferrari) Lot et al. (2013)
Collabieae	*Calanthe calanthoides* (A. Rich. & Galeotti) Hamer & Garay	Terrestrial, facultatively on flooded terrain	Hágsater et al. (2005)
	Spathoglottis plicata Blume	Terrestrial, facultatively on flooded terrain	This study
Cymbidieae Catasetinae	*Catasetum bergoldianum* Foldats	Epilithic, facultatively on flooded rock cavities	Madriñán et al. (2017)
	Catasetum integerrimum Hook.	Epiphytic, on mangroves	Aburto-Oropeza et al. (2021)
	Catasetum kamatawara Damián, Mitidieri & Bonilla	Epiphytic, on "aguajales" dominated by the palm *Mauritia flexuosa*	Damián et al. (2021)
	Catasetum roseo-album (Hook.) Lindl.	Terrestrial or epilithic, facultatively on flooded terrain or epiphytic	Madriñán et al. (2017, as *Catasetum discolor* (Lindl.) Lindl.)
	Galeandra styllomisantha (Vell.) Hoehne	Terrestrial, facultatively on flooded terrain	Pott and Pott (2000, 2021)
Cyrtopodiinae	*Cyrtopodium paludicola* Hoehne	Terrestrial, facultatively aquatic? on flooded terrain	Batista and Bianchetti (2010), Pott and Pott (2021)
	Cyrtopodium parviflorum Lindl.	Terrestrial, facultatively on seasonally flooded savannas	Chocce et al. (2004)

TABLE 1 CONT. Reported Neotropical and other New World orchid species associated with wetlands. Indication of habit as "aquatic" for some species follows our definition of aquatic plants given in the Introduction. References mentioned here are included in the Literature cited section. Suprageneric classification follows Chase et al. (2015).

SUBFAMILY TRIBE SUBTRIBE	SPECIES	HABIT	REFERENCE OR HERBARIUM VOUCHER
Eulophiinae	*Eulophia alta* (L.) Fawc. & Rendle	Terrestrial, facultatively on flooded terrain, floating vegetation mats or epiphytic	Kahn et al. (1993), Lot et al. (2013), Madriñán et al. (2017), Mereles et al. (2015), Pott and Pott (2021)
Maxillariinae	*Guanchezia maguirei* (C. Schweinf.) G.A. Romero & Carnevali	Terrestrial or epiphytic, facultatively on boggy soil on tops of tepuis	Dunsterville and Dunsterville (1973, 1976), as *Bifrenaria maguirei* C. Schewinf.
	Maxillaria tenuifolia Lindl.	Epiphytic, on mangroves	Aburto-Oropeza et al. (2021)
Oncidiinae	*Gomesa hydrophila* (Barb.Rodr.) M.W. Chase & N.H. Williams	Terrestrial or aquatic? on flooded terrain	Batista and Bianchetti (2010, as *Oncidium hydrophilum* Barb.Rodr.)
	Macradenia brassavolae Rchb.f.	Epiphytic, in wetlands dominated by *Raphia taedigera*	Pupulin and Ossenbach (2016)
	Notylia orbicularis A.Rich. & Galeotti	Epiphytic, facultatively on wetland trees and mangroves	Aburto-Oropeza et al. (2021)
	Oncidium sphacelatum Lindl.	Epiphytic, facultatively on wetland trees and mangroves	Aburto-Oropeza et al. (2021)
	Rodriguezia venusta Rchb. f.	Epiphytic, facultatively on wetland savannas or trees	Madriñán et al. (2017)
	Trichocentrum lindenii (Brongn.) M.W. Chase & N.H. Williamsq	Epiphytic, facultatively on wetland trees and mangroves	Aburto-Oropeza et al. (2021)
Zygopetalinae	*Otostylis brachystalix* (Rchb. f.) Schltr.	Terrestrial, facultatively aquatic on seasonally flooded savannas	Chocce et al. (2004)
	Otostylis paludosa (Cogn.) Schltr.	Aquatic, on boggy "aguajales" dominated by the palm *Mauritia flexuosa*	Chocce et al. (2004)
	Warrea costaricensis Schltr.	Terrestrial, facultatively on flooded terrain	Lot et al. (2013)
Epidendreae Bletiinae	*Bletia catenulata* Ruiz & Pav.	Terrestrial or aquatic? on flooded terrain	Batista and Bianchetti (2010)
	Bletia purpurea (Lam.) D.C.	Terrestrial, facultatively on flooded terrain	Hágsater et al. (2005), Lot et al. (2013)
	Bletia tenuifolia Ames & C. Schweinf.	Terrestrial, facultatively on flooded terrain	Lot et al. (2013)
Laeliinae	*Brassavola nodosa* (L.) Lindl.	Epiphytic, on mangroves	Hágsater et al. (2005)
	Encyclia alata (Bateman) Schltr.	Epiphytic, on mangroves	Aburto-Oropeza et al. (2021), Hágsater et al. (2005)
	Epidendrum lacustre Lindl.	Epiphytic or epilithic, facultatively on partially submersed trunks?	Velásquez (1994)
	Epidendrum nocturnum Jacq.	Epiphytic, on mangroves	Aburto-Oropeza et al. (2021)
	Epidendrum radicans Pav. ex Lindl.	Terrestrial, facultatively on flooded terrain or adjacent floating vegetation	Horich (1983), this study
	Myrmecophila brysiana (Lem.) G.C. Kenn.	Epiphytic, on mangroves	Hágsater et al. (2005)

TABLE 1 CONT. Reported Neotropical and other New World orchid species associated with wetlands. Indication of habit as "aquatic" for some species follows our definition of aquatic plants given in the Introduction. References mentioned here are included in the Literature cited section. Suprageneric classification follows Chase et al. (2015).

SUBFAMILY TRIBE SUBTRIBE	SPECIES	HABIT	REFERENCE OR HERBARIUM VOUCHER
Laeliinae cont.	*Myrmecophila christinae* Carnevali & Gómez-Juárez	Epiphytic, on mangroves	Hágsater et al. (2005)
	Myrmecophila tibicinis (Bateman) Rolfe	Epiphytic, on mangroves	Aburto-Oropeza et al. (2021), Hágsater et al. (2005)
	Prosthechea cochleata (L.) W.E. Higgins	Epiphytic, on mangroves	Aburto-Oropeza et al. (2021), Hágsater et al. (2005)
Sobralieae	*Sobralia abel-arayae* Dressler, Mel. Fernández & Pupulin	Terrestrial, facultatively on flooded terrain	Dressler et al. (2014)
Vandeae Agraecinae	*Dendrophylax lindenii* (Lindl.) Benth. ex Rolfe	Epiphytic in swamps	Mújica et al. (2018)
Polystachyinae	*Polystachya caracasana* Rchb. f.	Epiphytic, on mangroves	Aburto-Oropeza et al. (2021)

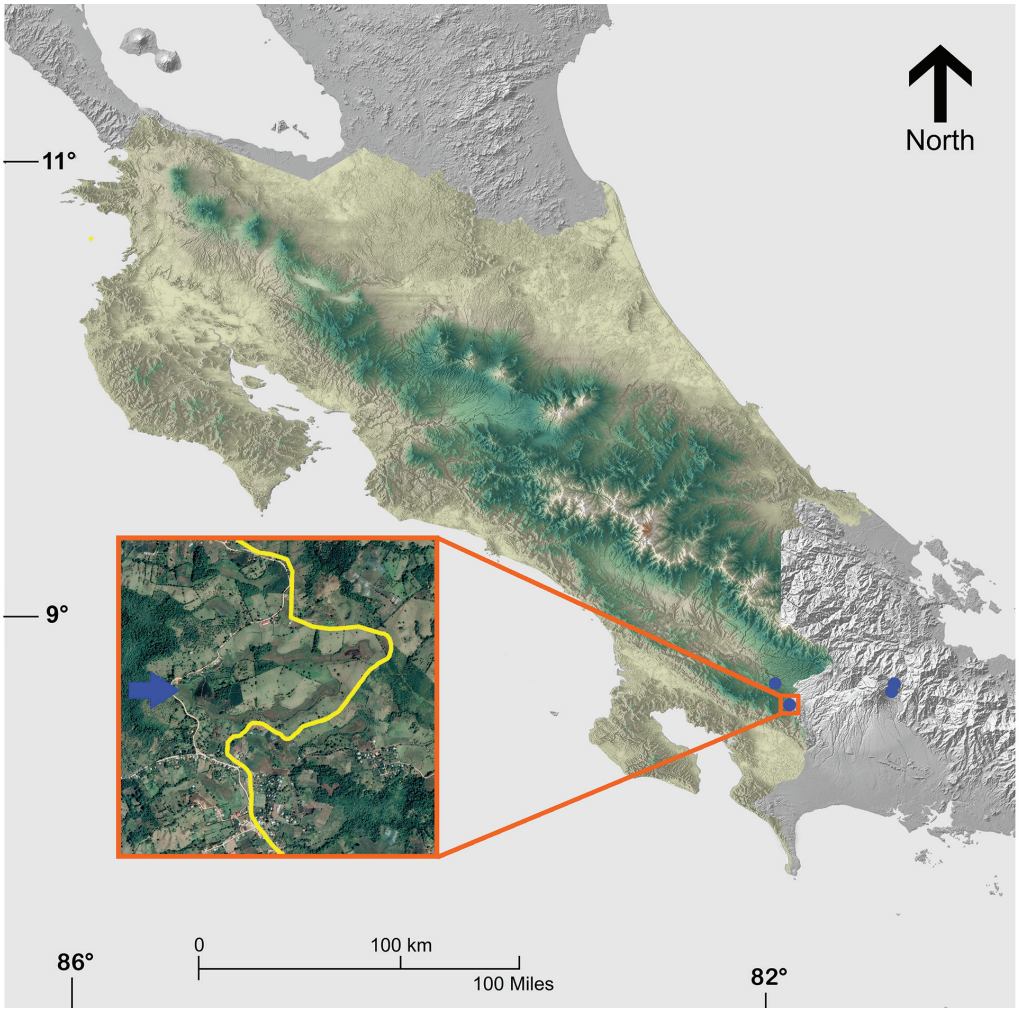

FIGURE 1. Study site and distribution map of *Sarcoglottis woodsonii* in Costa Rica and Panama. Inset: satellite image showing the study site with the wetland surrounded by highly altered habitat. The yellow line and blue arrow denote the Costa Rica-Panama border and sample collection site, respectively. Blue dots represent the localities of examined herbarium specimens and one iNaturalist report. The map was adapted from Guzmán Q., J. Antonio (2021). Costa Rica exaggerated relief map. https://doi.org/10.6084/m9.figshare.16613515.v1 by J. Antonio Guzmán Q. and GoogleEarth Pro 7.3 2022.

A Nikon D850 camera was employed with a Nikon AF-S DX NIKKOR 18–105mm f/3.5-5.6 G ED macro lens. For achieving optimal focus and depth of field, photo stacking was performed using a Nikon PB-6 bellows equipped with a Zeiss 40 mm 1:4.5 Luminar macro lens, along with the Cognysis StackShot automated macro rail for focus stacking and Broncolor Siros 800 S flashes. The resulting stack of individual images was aligned and blended using the Zerene Stacker software. The LCDP was diagrammed with Adobe Photoshop 2023.

A preliminary assessment of the conservation status of the species was made using the International Union for Conservation of Nature criteria (IUCN, 2017). The area of occupancy (AOO) and the extent of occurrence (EOO) were calculated using GeoCat (Bachman et al., 2011).

Results

Sarcoglottis woodsonii (L.O. Williams) Garay, Bot. Mus. Leafl. 28(4): 355. 1980 [1982].

Basionym: *Spiranthes woodsonii* L.O. Williams, Ann. Missouri Bot. Gard. 29(4): 337. 1942. TYPE: PANAMA. Chiriquí: Vicinity of Boquete, elev. 1200–1500 m, 24–26 July 1940, *R. E. Woodson Jr. and R. W. Schery 753* (holotype: AMES [59595]; isotypes: AMES [85462], MO [not seen]). (Fig. 2).

Palustrine *herb* of up to 180 cm in length. *Roots* up to 30 cm long, uniformly 3–5 mm in diameter, pubescent, arising from the rhizome nodes. *Stems* unbranched, or with few (2–3) branches arising from a horizontal rhizome, to 5 mm in diameter in the aerial portions, decumbent, the proximal part forming a long, creeping rhizome up to 80 cm long or longer, covered with scarious remnants of leaf sheaths, the distal, erect portion to 55 cm long (excluding the inflorescence). *Leaves* elliptic to oblong, 3.0–10.5 × 1.1–3.3 cm, acute to obtuse, pseudopetiolate, conduplicate, slightly concave, adaxially dark green, slightly glaucous, glossy, with the central vein paler and grooved, with a tubular, sheathing base of 2.2–4.0 cm long; up to 17 leaf blades present at flowering, spirally arranged, on the lower half of the erect portion of the stem, with progressively smaller blades distally, the most terminal leaves amplexicaul, bract-like, and adpressed to the stem; pseudopetiole 0.8 × 1.0 cm. *Inflorescence* an apical, erect, pedunculate raceme, pubescent with densely glandular hairs, stout, to 60 cm long, 6 mm in diameter, peduncle 30–45 cm long, with 5–6 tightly appressed tubular, ensiform, amplexicaul, acute to acuminate bracts to 8.0–9.0 × 0.8–1.0 cm, rachis 5–10 cm long, with 5–14 helically arranged (with up to 7 simultaneously open flowers), closely spaced flowers opening in succession, with widely ovate, acute to acuminate, not amplexicaul, bracts, basally glandular-pubescent, shorter or sometimes as long as the ovary, 3.6–6.5 × 1.2–1.6 cm. *Flowers* mildly fragrant, up to 5.2 cm long, densely white-pubescent on the ovary and outer part of the floral segments, resupinate, basally tubular, arcuate toward the apex; flower buds rostrate; ovary glandular-pubescent, cylindrical, with parietal placentation, to 2.5–3.5 × 0.6–0.8 cm; sepals dark green and covered with white hairs abaxially, white with faintly green longitudinal veins adaxially; petals white on both surfaces, with 2–3 conspicuous green lines adaxially; labellum greenish white on both surfaces, with ca. 7 conspicuous green lines adaxially. *Dorsal sepal* ovate to elliptic-lanceolate, acute or subacute, deeply concave over the lip and column, with the apex slightly pointing upwards, adherent but not adnate with the petals, 1.5–1.9 × 0.3–0.4 cm. *Lateral sepals* narrowly oblong, basally connate, and decurrent on the ovary for about 1.5 cm, forming a saccate mentum (nectary), subacute, the free portion falcate, reflexed, spreading (the tips sometimes crossing), and somewhat involute-navicular apically, 3.5–3.7 × 0.3–0.5 cm. *Petals* linear-ligulate, subfalcate, acute, pubescent along the lower margin, slightly reflexed apically and connivent with the dorsal sepal forming a hood (galea) over the column and labellum, 1.5–1.8 × 0.2–0.3 cm. *Labellum* clawed, strongly arcuate apically, adnate to the lateral sepals, with two basal, digitate, filiform, acute projections up to 7 mm long, canaliculate; blade linear-oblong, constricted basally and below the apex, the hypochile oblong-obovate or subpandurate, widened apically, the epichile reniform, emarginate, strongly reflexed, with 2 convergent oblique keels, each one running from each side of the apical constriction of the *hypochile* to the middle of the *epichile*, pubescent at the base of the projections, the *mesochile* and along keels of the *epichile*, 2.8–3.5 × 0.6–0.7 cm. *Nectary* to 1.6 cm long. *Column* subulate, abaxially pubescent, to 1.4 × 0.3 cm. *Pollinia* 2, narrowly ovoid to oblong, sulcate, puberulent with a short, rhombic greyish viscidium. *Stigma* ventral, bilobed, wet, shiny. *Anther cap* cucullate, oblong-elliptic, rostrate, with two cells (thecae). *Fruit* a fusiform capsule, erect, pubescent, longitudinally dehiscent, to 4 cm long.

Etymology: This species is named after Robert Everard Woodson Jr. (1904–1963), a prominent botanist from the Missouri Botanical Garden. He co-discovered the species and was a key contributor to the pioneering Flora of Panama Project.

Additional Specimens Examined: COSTA RICA. Puntarenas: Coto Brus, Distrito Agua Buena, palustrine depression between Cañas Gordas and Valle Azul, at 08°45'19.2"N, 82°55'23.1"W, 1130 m, 16 June 2022, *R. Acuña, M. Blanco, and M. Artavia 3282* (JBL spirit); same locality, 9 June 2023, *R. Acuña et al. s.n.* (USJ, JBL). PANAMA. Chiriquí: Finca Lérida to Boquete, elevation ca. 1300–1700 m, in swampy meadows; flowers pale yellowish-green, 8–10 July 1938, *R. E. Woodson Jr., P. H. Allen, and R. W. Siebert 1148* (AMES [55697, 58836, 58837, 58838]; MO [780400/accession 1172202]); Vicinity of El Boquete, woods near O'Donnell Hacienda, altitude 1000–1500 m, 14 February 1918, *L. R. Cornman 2050* (US [00017906]).

iNaturalist observation: COSTA RICA. Puntarenas: Coto Brus, Distrito San Vito at 8.795242 N, 82.961644 W, 31 October 2023, Marcel Esquivel (https://www.inaturalist.org/observations/189567668).

Distribution: This species has been documented from only three locations: the vicinity of Boquete in Chiriquí province, Panama (its type locality), between Valle Azul and Cañas Gordas (a few hundred meters from the border with Panama), and near Las Cruces Biological Station, both in Puntarenas province, Costa Rica (Fig. 1).

FIGURE 2. *Sarcoglottis woodsonii* (L.O.Williams) Garay. **A**, Plant (rhizome extended; in its natural orientation, the rhizome lays horizontally on top of other aquatic plants, at or just above the water level); **B**, Flower side, front, and oblique views; **C**, Perianth, dissected and flattened; **D**, Ovary, column and lip, side view; **E**, Ovary and column, abaxial, adaxial, and side views; **F**, Pollinarium and anther cap. LCDP from *R. Acuña et al. s.n.* (coll. date: 9 June 2023, USJ, JBL).

Habitat and Ecology: *Sarcoglottis woodsonii* appears restricted to freshwater wetlands at middle elevations (1000–1700 m) in southeastern Costa Rica and western Panama on the Pacific slopes of the Cordillera de Talamanca and Fila Costeña. In Costa Rica, we discovered a small population near the western edge of the wetland, where the specimens studied for this research were collected (Fig. 3). This wetland is a marsh that has water throughout the year. Long sections of the vegetative stems (up to 80 cm) of *Sarcoglottis woodsonii* were observed growing horizontally on semi-submerged vegetation, more or less at surface level. Evidently, the erect, leafy portions of the decumbent stems gradually become horizontal (turning into a "rhizome") as the stem apex continues elongating and producing new leaves; only the portion immediately below the apex stays erect. The bases of the plants were rooted on small emergent lumps of wet soil, the horizontal rhizomes produced roots into the water, and the distal part of the stems were erect (up to 1 m, including the inflorescence). Louis O. Williams (in Woodson and Schery, 1942) indicated that this species has a "creeping underground rhizome or stem," but this was likely a misinterpretation, based on his examination of the morphology of the dried herbarium specimens only, whose labels have a meager description of the plants and their habitat. The vascular plant wetland community growing alongside *S. woodsonii* comprises at least 71 species (Table 2). It is dominated by sedges and grasses (Figs. 4–5), a common pattern in many wetlands in Costa Rica (R. Acuña-Castillo et al., unpubl. data). Our observations and herbarium data indicate that Cyperaceae, with 18 recorded species, has the highest species richness in this locality, followed by Poaceae, with ten species, and

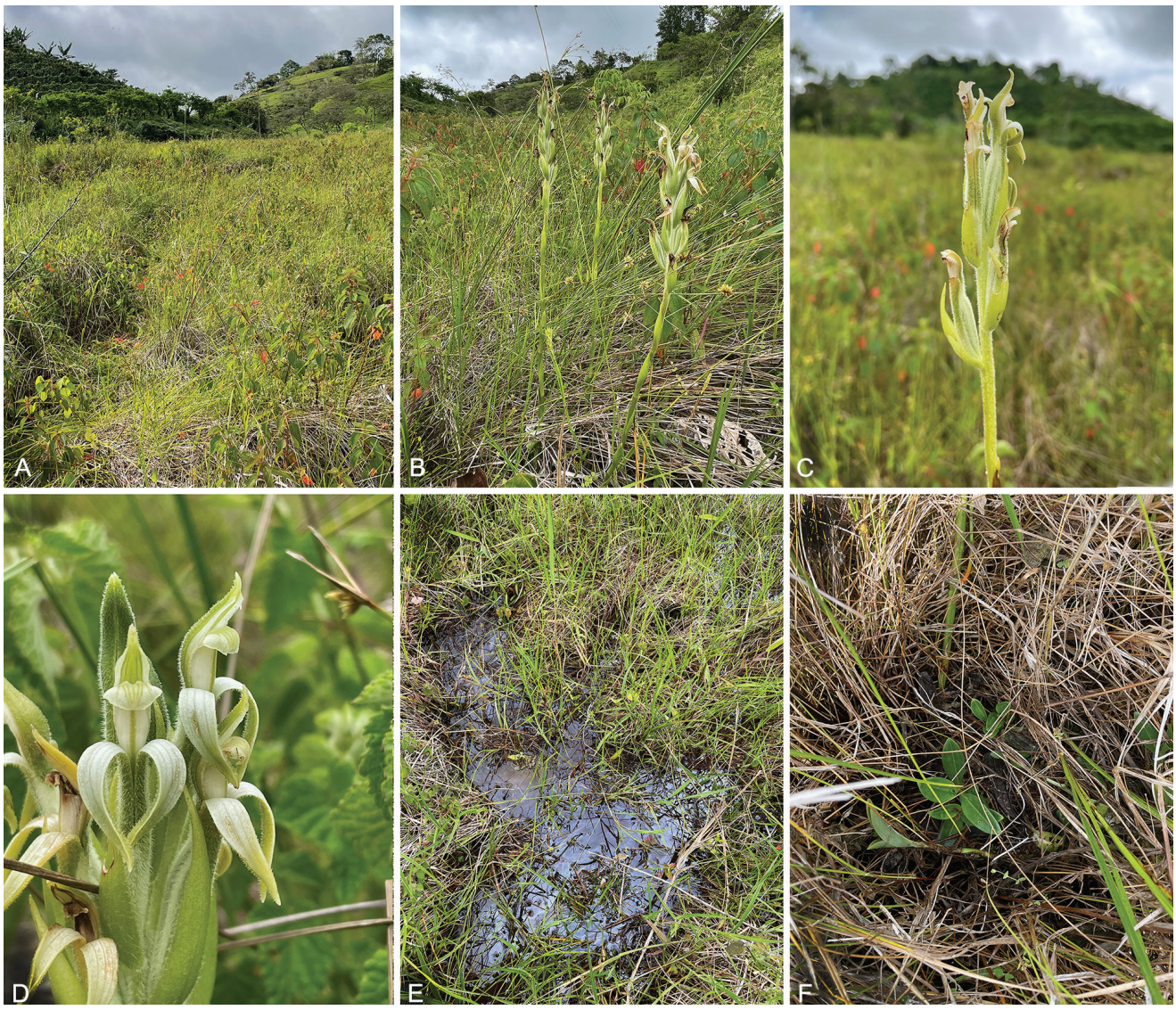

FIGURE 3. Natural habitat of *Sarcoglottis woodsonii* in Agua Buena, Costa Rica. **A**, View of the palustrine depression where *S. woodsonii* plants grow; **B**, Plants with flowers and fruits; **C**, Inflorescences with herbivore damage; **D**, Inflorescence with undamaged flowers of various ages, and a bud; **E–F**, Juveniles and seedlings growing in the water and among grasses and sedges.

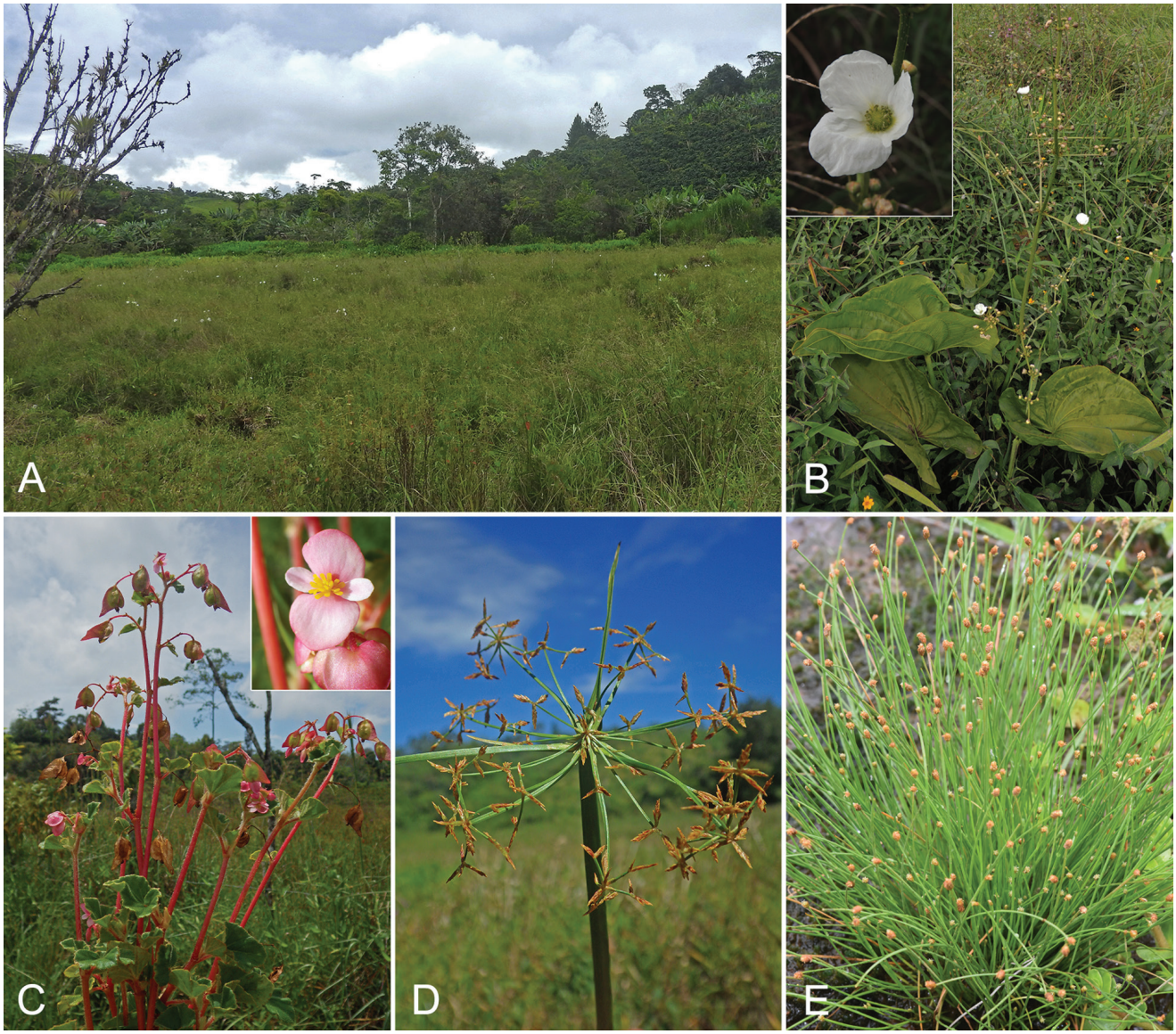

FIGURE 4. Palustrine depression in Agua Buena between Cañas Gordas and Valle Azul, Costa Rica, where **A**, *Sarcoglottis woodsonii* was found, as well as **B–E**, some representative species growing in sympatry; **B**, *Echinodorus floribundus* (Alismataceae); **C**, *Begonia fischeri* (Begoniaceae); **D**, *Cyperus haspan* (Cyperaceae); **E**, *Eleocharis filiculmis* (Cyperaceae).

Fabaceae, with four. Regarding genera, the most species-rich is *Eleocharis* R. Br., with seven species, followed by *Cyperus* L., *Hyptis* Jacq., *Ludwigia* L., *Persicaria* (L.) Mill., and *Rhynchospora* Vahl, with three species each. Some remarkable species growing in the same wetland but that are either rare or have not been collected in other localities in Costa Rica, include *Ageratum riparium* B.L. Rob., *Coelorachis aurita* (Steud.) A. Camus, *Echinodorus floribundus* (Seub.) Seub. (Fig. 4), *Eriochrysis cayanensis* P. Beauv. (Fig. 5), *Escobedia grandiflora* (L. f.) Kuntze (Fig. 5), *Fuirena incompleta* Nees (Fig. 5), *Rhynchospora velutina* (Kunth) Boeckeler (Fig. 5), and *Syngonanthus caulescens* (Poir.) Ruhland (Fig. 5), underlining that *S. woodsonii* is part of a very interesting wetland plant flora (Table 2).

Phenology: We found plants of *Sarcoglottis woodsonii* during June in anthetic and fruiting reproductive stages, with some capsules already open and dispersing seeds. Similarly, two collections from Panama (*Woodson and Schery 753*, *Woodson et al. 1148*) were collected in July and were fertile. The plants we have cultivated *ex-situ* since June 2022 are developing inflorescences for the first time as of June 2024. However, a specimen (*Cornman 2050*) was collected in flower in February (but see Discussion), and a recent record of a flowering plant (iNaturalist, see information above) was made in October.

Provisional Conservation Status: Based on a generous cell width of 3 km, the GeoCAT assessment tentatively considers *Sarcoglottis woodsonii* as Endangered (EN), under the IUCN categories and criteria B2ab(iii); D. The

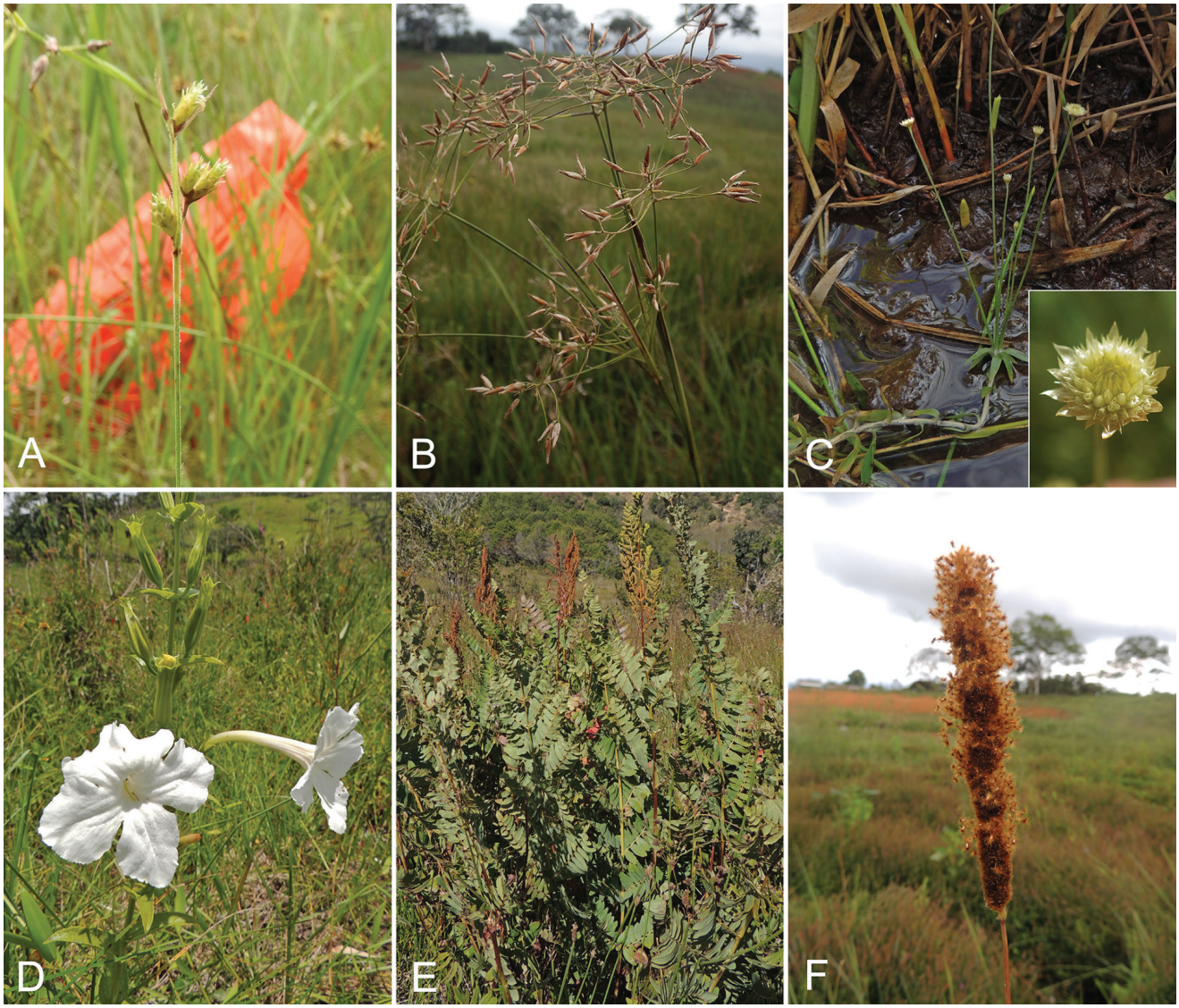

FIGURE 5. More representative species growing in the palustrine depression in Agua Buena, between Cañas Gordas and Valle Azul, Costa Rica; **A**, *Fuirena incompleta* (Cyperaceae); **B**, *Rhynchospora velutina* (Cyperaceae); **C**, *Syngonanthus caulescens* (Eriocaulaceae); **D**, *Escobedia grandiflora* (Orobanchaceae); **E**, *Osmunda regalis* (Osmundaceae); **F**, *Eriochrysis cayanensis* (Poaceae).

criterion B2 was selected because its Area of Occupancy is between 10 and 500 km^2 (36 km^2, the Extent of Occurrence of ca. 220 km^2 would also fall in the EN category range). The criterion "a" was selected because the species shows a fragmented distribution known only from three localities in a botanically well-inventoried area. The "b(iii)" criterion was chosen because there is a projected decline in the area, extent, and quality of the species' habitat, resulting from land use changes, overgrazing, siltation, and wetland drainage for agricultural, livestock grazing, or infrastructure development purposes. Wetlands are frequently perceived as "useless land" by farmers and developers in Panama and Costa Rica, and many wetlands near the area of study have been either highly altered or completely drained in the last two decades (J. Flores-Rojas, pers. comm.). The Cañas Gordas and Valle Azul wetlands are classified by the Costa Rican Wetlands Vulnerability Index as highly vulnerable (Jiménez, 2016; Veas-Ayala et al., 2022). In June 2023, three of the authors noticed that a large amount of lateritic soil from a nearby small landslide was moved very close to the margins of the wetland where *S. woodsonii* was studied in Costa Rica. This could pose an immediate and serious threat to this population of the species, as torrential rainfalls may cause material movement toward the wetland, which may cover some of the vegetation and cause siltation. Likewise, the Panamanian government has been pursuing an agenda to settle natural savannas and wetlands from middle elevations in Chiriquí province, which are viewed as suitable for human infrastructure development, with the mistaken belief that there would not be significant ecological

Table 2. Vascular plant species known from the wetland sampled in this study.

Family	Species	Voucher Specimen
Acanthaceae	*Lepidagathis alopecuroidea* (Vahl) R. Br. ex Griseb.	*J.E. Jiménez et al. 4206* (USJ)
Alismataceae	*Echinodorus floribundus* (Seub.) Seub.	*J.E. Jiménez et al. 4211* (USJ)
Alismataceae	*Limnocharis laforestii* Griseb.	*J.E. Jiménez et al. 4209* (USJ)
Araceae	*Spathiphyllum atrovirens* Schott	*R. Acuña et al. s.n.* 16.Ago.2019 (USJ)
Araliaceae	*Hydrocotyle umbellata* L.	*R. Acuña et al. s.n.* 16.Ago.2019 (USJ)
Asteraceae	*Ageratum riparium* B. L. Rob.	*J. Gómez-Laurito & R. Ortiz 13348* (USJ)
Asteraceae	*Wedelia filipes* Hemsl.	*J.E. Jiménez et al. 4201* (USJ)
Begoniaceae	*Begonia fischeri* Schrank	*R. Acuña 724* (USJ)
Caryophyllaceae	*Drymaria villosa* Schltdl. & Cham.	*J.E. Jiménez et al. 4210* (USJ)
Commelinaceae	*Floscopa glabrata* (Kunth) Hassk.	*J.E. Jiménez et al. 4198* (USJ)
Commelinaceae	*Tripogandra serrulata* (Vahl) Handlos	*J. Gómez-Laurito et al. 14942* (USJ)
Cyperaceae	*Cyperus haspan* L.	*J. Gómez-Laurito & R. Ortiz 13341* (USJ)
Cyperaceae	*Cyperus lanceolatus* Poir.	*R. Acuña 721* (USJ)
Cyperaceae	*Cyperus unioloides* R. Br.	*R. Acuña 739* (USJ)
Cyperaceae	*Eleocharis acutangula* (Roxb.) Schult.	*J. Gómez-Laurito et al. 14922* (USJ)
Cyperaceae	*Eleocharis elegans* (Kunth) Roem. & Schult.	*J.E. Jiménez et al. 4207* (USJ)
Cyperaceae	*Eleocharis filiculmis* Kunth	*R. Acuña 726* (USJ)
Cyperaceae	*Eleocharis montana* (Kunth) Roem. & Schult.	*R. Acuña et al. 2009* (USJ)
Cyperaceae	*Eleocharis pachystyla* (C. Wright) C.B. Clarke	*J. Gómez-Laurito 10722* (USJ)
Cyperaceae	*Eleocharis retroflexa* (Poir.) Urb.	*J.E. Jiménez et al. 4197* (USJ)
Cyperaceae	*Eleocharis sellowiana* Kunth	*J. Gómez-Laurito et al. 14966* (USJ)
Cyperaceae	*Fimbristylis dichotoma* (L.) Vahl	*R. Acuña et al. 2010* (USJ)
Cyperaceae	*Fuirena incompleta* Nees	*J. Gómez-Laurito et al. 14947* (USJ)
Cyperaceae	*Fuirena umbellata* Rottb.	*J.E. Jiménez et al. 4205* (USJ)
Cyperaceae	*Kyllinga pumila* Michx.	*R. Acuña 741* (USJ)
Cyperaceae	*Rhynchospora marisculus* Lindl. ex Nees	*J. Gómez-Laurito et al. 14968* (USJ)
Cyperaceae	*Rhynchospora radicans* (Schltdl. & Cham.) H. Pfeiff.	*J. Gómez-Laurito & R. Ortiz 13348* (USJ)
Cyperaceae	*Rhynchospora velutina* (Kunth) Boeckeler	*R. Acuña 723* (USJ)
Cyperaceae	*Scleria distans* Poir.	*J. Gómez-Laurito 10703* (USJ)
Equisetaceae	*Equisetum giganteum* L.	*J. Gómez-Laurito et al. 13744* (USJ)
Eriocaulaceae	*Syngonanthus caulescens* (Poir.) Ruhland	*J.E. Jiménez et al. 4199* (USJ)
Fabaceae	*Desmodium adscendens* (Sw.) DC.	*J. Gómez-Laurito et al. 14913* (USJ)
Fabaceae	*Mimosa debilis* Humb & Bonpl. ex Willd.	*R. Acuña et al. 2019* (USJ)
Fabaceae	*Senna cobanensis* (Britton) H.S. Irwin & Barneby	*J. Gómez-Laurito 10700* (USJ)
Fabaceae	*Vigna luteola* (Jacq.) Benth.	*R. Acuña et al. 2030* (USJ)
Lamiaceae	*Hyptis lantanifolia* Poit.	*J.E. Jiménez et al. 4204* (USJ)

Table 2 CONT. Vascular plant species known from the wetland sampled in this study.

FAMILY	SPECIES	VOUCHER SPECIMEN
Lamiaceae	*Hyptis recurvata* Poit.	*J. Gómez-Laurito et al. 13769* (USJ)
Lamiaceae	*Hyptis sinuata* Pohl ex Benth.	*J. Gómez-Laurito 10747* (USJ)
Lythraceae	*Cuphea carthagenensis* (Jacq.) J.F. Macbr.	*R. Acuña 719* (USJ)
Malvaceae	*Peltaea trinervis* (C. Presl) Krapov & Cristóbal	*R. Acuña et al. s.n.* 16.Ago.2019 (USJ)
Melastomataceae	*Graffenrieda galeottii* (Naudin) L.O. Williams	*J. Gómez-Laurito 10689* (USJ)
Melastomataceae	*Rhynchanthera paludicola* (Donn. Sm.) Gleason	*R. Acuña 733* (USJ)
Ochnaceae	*Sauvagesia erecta* L.	*J. Gómez-Laurito et al. 14914* (USJ)
Onagraceae	*Ludwigia leptocarpa* (Nutt.) H. Hara	*R. Acuña 743* (USJ)
Onagraceae	*Ludwigia peruviana* (L.) H. Hara	*R. Acuña et al. 2025* (USJ)
Onagraceae	*Ludwigia rigida* (Miq.) Sandwith	*J. Gómez-Laurito 10741* (USJ)
Orchidaceae	*Epidendrum radicans* Pav. ex Lindl.	*J. Gómez-Laurito 10714* (USJ)
Orchidaceae	*Sarcoglottis woodsonii* (L.O. Williams) Garay	*R. Acuña et al. 3282* (JBL)
Orobanchaceae	*Escobedia grandiflora* (L. f.) Kuntze	*J.E. Jiménez et al. 1325* (CR)
Osmundaceae	*Osmunda regalis* L.	*R. Acuña 737* (USJ)
Phyllanthaceae	*Phyllanthus stipulatus* (Raf.) G. L. Webster	*J.E. Jiménez et al. 4196* (USJ)
Plantaginaceae	*Bacopa salzmannii* (Benth.) Wettst. Ex Edwall	*R. Acuña 727* (USJ)
Poaceae	*Andropogon bicornis* L.	*R. Acuña et al. 2024*(USJ)
Poaceae	*Coelorachis aurita* (Steud.) A. Camus	*R. Acuña 722* (USJ)
Poaceae	*Echinochloa polystachya* (Kunth) Hitchc.	*J. Gómez-Laurito 10755* (USJ)
Poaceae	*Eriochrysis cayanensis* P. Beauv.	*J. Gómez-Laurito et al. 13778* (USJ)
Poaceae	*Homolepis glutinosa* (Sw.) Zuloaga & Soderstr.	*J. Gómez-Laurito 10733* (USJ)
Poaceae	*Isachne polygonoides* (Lam.) Döll	*J. Gómez-Laurito 10761* (USJ)
Poaceae	*Leersia hexandra* Sw.	*R. Acuña 742* (USJ)
Poaceae	*Paspalum boscianum* Flüggé	*R. Acuña et al. 2038* (USJ)
Poaceae	*Rugoloa polygonata* (Schrad.) Zuloaga	*R. Acuña 735* (USJ)
Poaceae	*Trichanthecium parvifolium* (Lam.) Zuloaga & Morrone	*R. Acuña 720* (USJ)
Polygalaceae	*Monnina sylvicola* Chodat	*J. Gómez-Laurito 10691* (USJ)
Polygalaceae	*Persicaria acuminata* (Kunth) M. Gómez	*J.E. Jiménez & J. Porras 4178* (USJ)
Polygalaceae	*Persicaria meisneriana* (Cham. & Schltdl.) M. Gómez	*R. Acuña et al. 2042* (USJ)
Polygonaceae	*Persicaria punctata* (Elliott) Small	*J.E. Jiménez & J. Porras 4180* (USJ)
Pontederiaceae	*Heteranthera reniformis* Ruiz & Pav.	*R. Acuña et al. 1999* (USJ)
Primulaceae	*Anagallis pumila* Sw.	*R. Acuña 731* (USJ)
Rubiaceae	*Galium hypocarpium* (L.) Endl. ex Griseb.	*J. Gómez-Laurito et al. 14955* (USJ)
Rubiaceae	*Palicourea padifolia* (Humb. & Bonpl. ex Roem. & Schult.) C.M. Taylor & Lorence	*J. Gómez-Laurito 10731* (USJ)
Rubiaceae	*Spermacoce prostrata* Aubl.	*J. Gómez-Laurito 10721* (USJ)
Xyridaceae	*Xyris laxifolia* Mart.	*R. Acuña 728* (USJ)

trade-offs derived from changes in land use (as opposed to the impact caused by forest clearing). This view ignores that these savannas and wetlands are habitats for many endemic or rare species (R. Flores pers. comm.). Furthermore, to our knowledge, the species has not been collected near its type locality in Panama for several decades.

The wetlands around Valle Azul and Cañas Gordas constitute a complex of small wetlands and lagoons. They have been listed in previous Costa Rican National Wetland Censuses: as Codes 826 and 827 in Windevoxhel et al. (1998) and as part of the Alta Talamanca Unit in Proyecto Humedales del SINAC-PNUD-GEF (2018b). However, only very condensed geographical location information is provided by those authors, offering no elaboration on other basic biotic and abiotic characteristics. In contrast, other wetlands in the same general area (Laguna Zoncho, Humedal Paraguas, Laguna El Campo, Laguna San Joaquín), albeit less biodiverse or in a more degraded condition, are described in greater detail by both Windevoxhel et al. (1998) and Proyecto Humedales del SINAC-PNUD-GEF (2018b), and for some of these, even very basic biotic inventories are provided by these authors. The relative lack of knowledge about the Valle Azul and Cañas Gordas wetlands could pose an additional risk factor for conserving *S. woodsonii* and other rare species. Despite documentation of some of the common taxa in these areas (Proyecto Humedales del SINAC-PNUD-GEF 2018a), a detailed list of their wetland flora was still lacking. It is important to note that this wetland is on the buffer zone of the UNESCO-declared Biosphere Reserve of La Amistad, recognized as part of a major global Center of Plant Diversity: the Costa Rica-Chocó Center, specifically in the Central Cordillera of Costa Rica and Panama Sub-center (Barthlott et al., 2005; Kappelle and Horn, 2016).

Discussion

Sarcoglottis woodsonii is easily distinguished from other species in the genus by its unique decumbent, elongated stems, which can reach lengths of up to 1.8 meters (including both rhizomes and aerial stems). In contrast, other *Sarcoglottis* species have stems and rhizomes with highly abbreviated internodes (the plants appear rosulate). Additionally, *S. woodsonii* produces uniformly long and slender roots (less than 5 mm in diameter) developed from the elongated internodes of the rhizome. The other species of this genus show thicker, succulent, fasciculate roots. Furthermore, the aerial stems of *S. woodsonii* exhibit leaves separated by very obvious, elongated internodes. This is unlike the very short internodes found in the stems of other species of *Sarcoglottis* (Salazar, 2003a).

The specimen *Cornman 2050* (determined as *Spiranthes woodsonii* by L. O. Williams in 1942 and cited as such by Allen, 1949) could not be determined with certainty by us because it consists of two incomplete plant fragments. One fragment includes the stem apex with two leaves and an inflorescence, while the other consists of only a single inflorescence. Since the specimen lacks stems and roots, we consider its affinities to *Sarcoglottis woodsonii* uncertain. While some characteristics, such as oblong leaves with elongated internodes, match *S. woodsonii*, disparities in the flowering date (February) and collection environment (in woods) exist when compared to our observations and protologue data. Conclusive identification would require a physical examination of the flowers, which was not possible at the time since we could only access a digital image of the specimen. Therefore, we have provisionally identified it as *S. woodsonii* based on L. O. Williams' identification (Allen, 1949).

Despite being described as a palustrine species in the protologue (Williams, 1946), this information has been overlooked due to the limited availability of data on *Sarcoglottis woodsonii*. This species is a truly aquatic orchid because of its shallowly submerged rhizomes and roots, and its microhabitat is restricted to grassy swamps with standing water. There is another known aquatic representative of the genus (*Sarcoglottis uliginosa* (Barb.Rodr.) Barb. Rodr.), which, according to Batista and Bianchetti (2010), can grow on water-saturated soils with water over the surface.

Our study contributes to a better understanding of orchid diversity in wetland ecosystems in the Neotropics and emphasizes the urgent need to inventory and conserve these unique habitats. Unfortunately, these areas are often unprotected, suffer from high human pressure, and are surrounded by fragmented landscapes.

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