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GASTROCHILUS PECHEI (ORCHIDACEAE), A NEW ADDITION TO THE FLORA OF INDIA

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Abstract. *Gastrochilus pechei* was recently documented in Vijoynagar, Changlang district, Arunachal Pradesh, India. Identification was based on the spathulate sepals and petals; the acute, sub-triangular, slightly irregularly erose margin of the epichile with a central cushion, and the subglobose hypochile. The species belongs to the section *Brachycaules*. This report represents a new distribution record for India. An updated description and detailed photographs based on Indian material are provided.

Keywords/Palabras clave: Aeridinae, Arunachal Pradesh, *Gastrochilus*, new record, nuevo registro, Vijoynagar

Introduction.The genus *Gastrochilus* was established by D.Don in 1825 (Don, 1825). It is a monopodial orchid genus comprising 72 to 77 species (POWO, 2024; Zhang *et al*., 2024) widely distributed in tropical, subtropical and temperate Asia. This genus is characterised by a short axillary inflorescence, often with brightly coloured flowers, a distinct epichile on the front of the saccate hypochile, and two porate, globose pollinia that are borne on a slender stipe (Christenson, 1985; Seidenfaden, 1988; Tsi, 1996).

According to Pridgeon *et al.* (2014) this genus belongs to the subtribe Aeridinae because of its high species richness in East Asia and the Himalayas (Tsi, 1996). So far, 22 species have been recorded from India (Misra, 2019) of which 14 species viz. *Gastrochilus acutifolius* (Lindl.) Kuntze; *G. affinis* (King & Pantl.) Schltr.; *G. arunachalensis* A.N.Rao; *G. calceolaris* (Buch-Ham ex J.E.Sm.) D.Don; *G. changjiangensis* Q.Liu & M.Z.Huang; *G. dasypogon* (Sm.) Kuntze; *G. distichus* (Lindl.) Kuntze; *G. inconspicuus* (Hook.f.) King & Pantl.; *G. intermedius* (Griff. ex Lindl.) Kuntze; *G. obliquus* (Lindl.) Kuntze; *G. platycalcaratus* (Rolfe) Schltr.; *G. pseudodistichus* (King & Pantl.) Schltr.; *G. rutilans* Seidenf.; *G. sessanicus* A.N.Rao are found in Arunachal Pradesh (Nyorak, 2023).

During a field trip to Vijoynagar, in the Changlang district of Arunachal Pradesh on 11 September 2024, the first author collected an unidentified epiphytic orchid with its flower. After critical examination of the flowers and based on available literature (Chen *et al.*, 2009; Chowdhery, 1998; Gogoi, 2017, 2019; King & Pantling, 1898; Liu *et al*., 2020; Lucksom, 2007; Nyorak, 2023; Pearce & Cribb, 2002; Pradhan, 1979; Rao, 2009, 2010; Singh *et al.*, 2019; Swami, 2017) and, it was identified as *Gastrochilus pechei* (Rchb.f.) Kuntze based on yellow sepals and petals and white labellum, all densely covered with purplish spots, spathulate; epichile sub-triangular, slightly irregularly erose margin, apex acute; hypochile subglobose, with central cushion. It is known only from Myanmar in the Naungmeng town, Putao County, Kachin state (Liu *et al.*, 2020). Therefore, the present report of its occurrence from Arunachal Pradesh forms a new distributional record for India. A detailed description, illustration, and information on habitat and distribution have been provided in the present manuscript.

This species belongs to *Gastrochilus* D.Don, characterized by its epiphytic habit, monopodial growth with a short stem. It has many leathery, flat leaves that sheathe at the base, with an unequally bilobed apex. The inflorescence is lateral, relatively short, sub-umbellate, and bears a few to many flowers. The flowers are small to medium-sized and fleshy. Sepals and

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petals are free, similar, and spreading. The lip features a subglobose, saccate hypochile; the epichile is fan-shaped with fimbriate margins. The column is short and thick; there are 2 pollinia that are subglobose.

Materials and methods. Fresh plant material was collected during a botanical excursion on 11 September 2024 in the Vijoynagar of Changlang district of Arunachal Pradesh, India. It was identified based on available literature and critical examination of the flowers and the type specimens accessed from K and W. The measurements and species descriptions of vegetative and reproductive characters were made from living plants following the terminology for morphological descriptions by Beentje (2012). All the photos were taken with a Canon EOS 700D fitted with an EF 100 mm f/2.8L Macro USM lens. The voucher specimen has been deposited at the TOSEHIM (Herbarium of The Orchid Society of Eastern Himalaya), Regional Orchid Germplasm Conservation and Propagation Centre (Assam Circle), Assam.

Taxonomic treatment

Gastrochilus pechei (Rchb.f.) Kuntze in Revis. Gen. Pl. 2: 661. 1891; *Saccolabium pechei* Rchb.f. in Gard. Chron., ser. 3, 5: 447. 1889. (Fig. 1, 2).

TYPE: Myanmar, Moulmein. Rchb.f., 40811(W!), W0021485 (holotype); s.coll. s.n. (K!), K000891600 (isotype).

Plant epiphytic, pendent; roots clustered. *Stem* 1.0–1.5 cm long, erect or pendent, covered with overlapping leaf sheaths, stout, with 4–5 leaves. *Leaves* 15–20 × 3–5 cm, nearly basal, distichous, oblong, dark green above, pale green below, fleshy, apex obtuse and unequally 2-lobed, shortly sheathed at base. *Inflorescence* leaf opposed, umbel or sub-umbellate, 1–4, from the base of stem; peduncle 1.5–2.5 cm, straight, terete, stout, glabrous, with 2 cupular sheaths; rachis 0.5–0.8 cm long, with 4–12 pedicellate flowers; pedicellate-ovary 1.0–1.5 cm long, slightly ribbed, glabrous; floral bracts broad, obtuse, 0.5–0.5 × 0.2–0.3 cm. *Flower* 1.2–1.5 cm across, sepals and petals yellow with white lip, all densely covered with dark purplish spots; pedicel and ovary slender, 1.2–1.4 cm long. *Sepals* 1.2–1.3 × 0.4–0.5 cm, similar, spatulate, base contracted, obtuse, glabrous. *Petals* 1.1–1.1 × 0.3–0.4 cm, spatulate, obtuse. *Lip* with an epichile and a saccate hypochile; epichile 0.5–0.6 × 1.5–1.6 cm, subtriangular, fleshy on the center, adaxially glabrous, with a central cushion with a yellow blotch, margin irregularly fimbriate and erose, acute; hypochile 0.8–0.9 × 0.8–0.9 cm, subglobose, white tinged with yellow at bottom, outside with 5 ridges. *Column* 0.25–0.30 cm long, stout; rostellum deeply 2–lobed; pollinia 2, 0.08–0.12 cm across, grooved, ovoid, yellow; caudicle *ca.* 0.15 cm long, elongate; viscidium *ca.* 0.07 cm, oblong, grooved, apex bilobed; anther cap nearly subglobose, apex narrowed into a beak. *Fruit* 5–6 × 0.8–1.0 cm, cylindric, ridged, distinctly ribbed, pale green, glabrous, sparsely spotted with dark purple.

Specimen examined: India. Arunachal Pradesh: Changlang district, Vijoynagar, 11 September 2024, *V.K. Sahani 0001* (TOSEHIM!).

Flowering: September–October.

Habitat: Epiphytic in moist, evergreen rainforest on small trees near riverbanks at an elevation of 1200 m.

Distribution: Myanmar, and India (Arunachal Pradesh).

Discussion. According to recent molecular and morphological data, *Gastrochilus pechei* belongs to the sect. *Brachycaules* Q.Liu & J.Y.Gao ex Jun Y.Zhang & H.He (Zhang *et al*., 2024). Ten species are included in this section are distributed mainly in India, S and SW China, Nepal, Bhutan, Myanmar, Laos, Vietnam, and Thailand (Zhang *et al*., 2024). Out of 10 species, six species are documented from India, including: *Gastrochilus acaulis* (Hook.f.) Kuntze, *G. bigibbus* (Rchb.f. ex Hook.f.) Kuntze, *G. dasypogon* (Lindl.) Kuntze, *G. flabelliformis*, *G. obliquus* and *G. suavis* Seidenf. (Misra, 2019; Singh *et al*., 2019). As a result, with the present collection of *Gastrochilus pechei,* there are now seven species in this section within India, and there are now 23 species found in India, including 16 species from Arunachal Pradesh.

Morphologically, this species is closely similar to *G. arunachalensis, G. obliquus* and *G. somai*

FIGURE 1. *Gastrochilus pechei*. **A**. Plants in natural habitat. **B**. Close-up of the inflorescence in its natural habitat. **C**. Plants with fruits. Photographs and plate by Vinay Kumar Sahani and Khyanjeet Gogoi.

(Hayata) Hayata, but distinct from these having the spathulate, yellow sepals and petals and white lip, all densely covered with purplish spots; epichile sub-triangular, slightly irregularly erose margin, apex acute; hypochile subglobose, with central cushion. The differences between *Gastrochilus arunachalensis, G. obliquus, G. pechei* and *G. somai* are shown in Table 1.

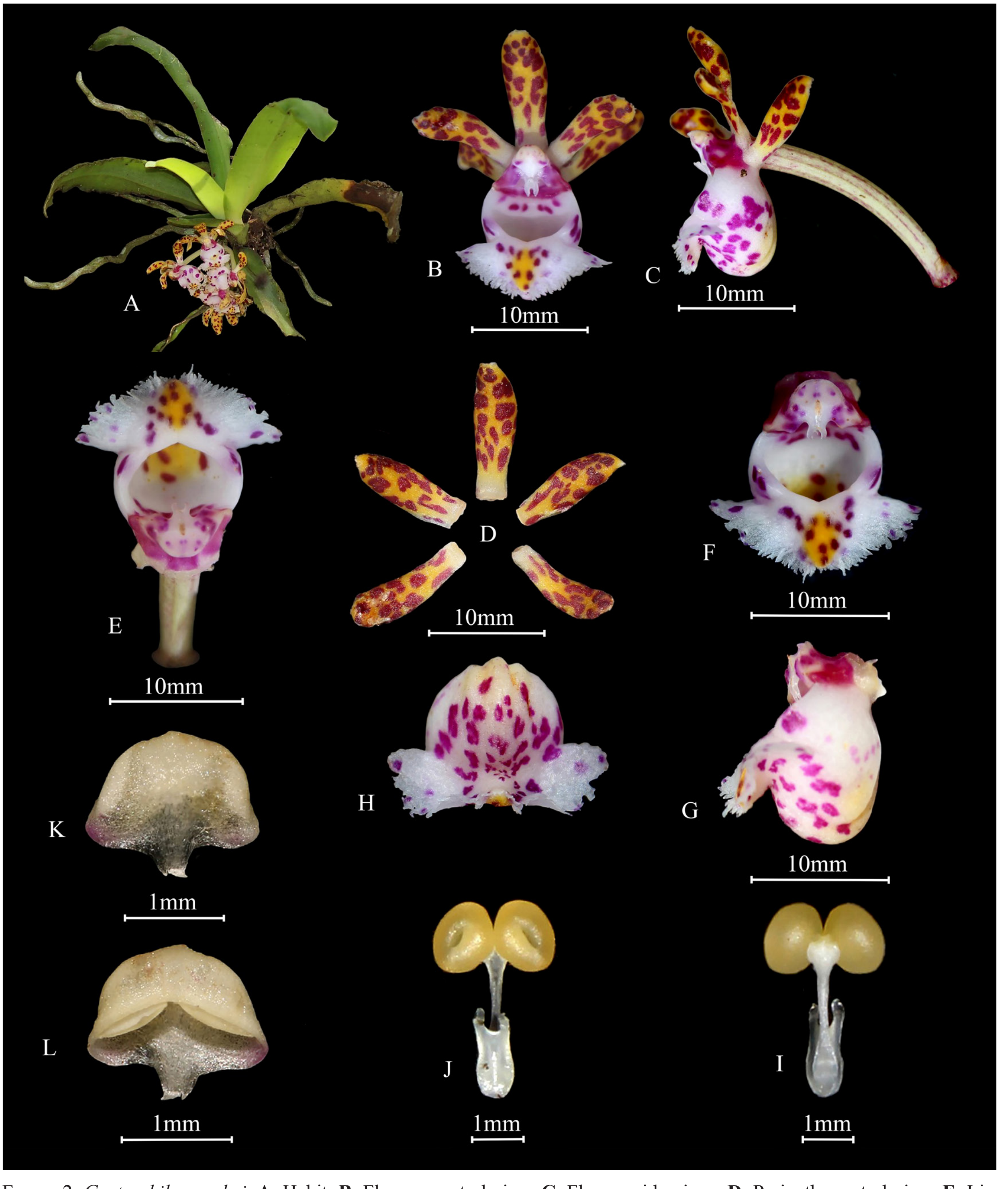

FIGURE 2. *Gastrochilus pechei*. **A**. Habit. **B**. Flower, ventral view. **C**. Flower, side view. **D**. Perianth, ventral view. **E**. Lip with ovary and column. **F**. Lip, ventral view. **G**. Lip, side view. **H**. Lip, dorsal view. **I**. Pollinarium, ventral view. **J**. Pollinarium, dorsal view. **K**. Anther cap, dorsal view. **L**. Anther cap, ventral view. Photographs and plate by Vinay Kumar Sahani and Khyanjeet Gogoi.

Conclusions. *Gastrochilus* is a small genus, but it is easy to be confused with other *Aeridinae* taxa without flowers. So, many species may be misidentified as other taxa. The record of *Gastrochilus pechei* in Arunachal Pradesh provides significant evidence that the two regions Myanmar and

Table 1. Differences between *Gastrochilus arunachalensis, G. obliquus, G. pechei,* and *G. somai.*

Character	***G. arunachalensis* (Rao, 1992)**	***G. obliquus* (Chen *et al.*, 2009)**	***G. pechei***	***G. somai* (Jin *et al.*, 2010)**
Stem	1–4 cm, with 3–4 leaves.	1–2 cm, stout, with 3–5 leaves.	1.0–1.5 cm, stout, with 4–5 leaves.	2–5 cm with 3–5 leaves.
Leaves	8–15 × 1.7–2.3 cm. oblong.	8–20 × 1.7–6.0 cm, oblong to oblong-lanceolate.	15–20 × 3–5 cm, oblong.	5–16 × 1.0–2.5 cm, linear, falcate or linear-lanceolate.
Inflorescence	8–10-flowered.	5–8-flowered.	4–12-flowered.	4–7-flowered.
Flowers	Yellow or yellow-green, with dark brown or purplish spots.	Sepals and petals yellow with white lip, all with brownish-purplish spots.	Sepals and petals yellow with white lip, all densely covered with dark purplish spots.	Sepals and petals yellowish green without purplish spots.
Sepal	Oblanceolate, 0.68–7 × 0.32–0.35 cm.	Subelliptic, 0.6–1.2 × 0.4–0.6 cm.	Spatulate, 1.2–1.3 × 0.4–0.5 cm.	Elliptic-obovate, 0.7–0.9 × 0.3–0.5 cm.
Petals	Oblanceolate, 0.62–0.65 × 0.23–0.25 cm.	spatulate, smaller than sepals.	Spatulate, 1.1–1.1 × 0.4 cm.	Similar to sepals or narrower.
Lip	Epichile 0.25–0.30 × 0.54–0.60 cm; hypochile cupular, 0.6 × 0.4 cm.	Epichile 0.5 × 0.8–1.0 cm; hypochile nearly subglobose-cucullate, 0.5–0.6 × 0.6–0.7 cm.	Epichile 0.5 × 1.5–1.6 cm; hypochile subglobose, ca. 0.80 × 0.84 cm.	Epichile 0.2–0.4 × 0.5–0.8 cm; hypochile laterally compressed, 0.5–0.7 × 0.4–0.6 cm.

Arunachal Pradesh are linked due to floristic similarities. Therefore, we believe that more species of *Gastrochilus* as well as other orchid species should be found if we undertake further field investigations and systematic studies.

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Author contributions. KG: Conceptualization (equal); Investigation (equal); Writing – original draft preparation (equal); MP: Data curation (equal); Writing – reviewing and editing (equal); Investigation (equal); VKS: Conceptualization (equal); Data curation (equal); Investigation (equal).

Conflict of interest. No conflict of interest to declare.

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DARWIN'S PRESCIENT LETTER REGARDING ORCHID MYCORRHIZA

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Abstract. On March 26, 1863, Charles Darwin wrote a letter to Joseph Dalton Hooker, describing his attempts to germinate orchid seeds. In this letter, he mentioned his hope to observe orchid seedlings and expressed a "notion that [the seeds]. . . are parasites in early youth on cryptogams!!". This statement appears to predict Noël Bernard's 1899 discovery that orchid seeds require fungal colonization for successful germination. However, there is some uncertainty regarding Darwin's exact meaning. The term "cryptogams" in his time commonly included fungi but also encompassed bryophytes, pteridophytes, and other non-vascular plants. Since Darwin mentioned sphagnum in his experiments, it is possible to suggest that he may have considered mosses as potential hosts rather than fungi. But, since this was a personal letter to Joseph D. Hooker rather than a formal publication, Darwin may have been less precise in his terminology. Nevertheless, considering Darwin's broader interest in plant-fungal interactions, it is very plausible that he regarded fungi as possible symbiotic partners in orchid germination. The extent of Darwin's prescience on the orchid-fungal relationship may be debatable terminologically (did he mean fungi by using "cryptogams"?). However, his speculation was remarkably intuitive, questioning whether orchids required an external biological partner for germination. Darwin's letter demonstrates his foresight, but it does not diminish Noël Bernard's monumental achievement. Bernard made his discovery independently, without knowledge of Darwin's observations, relying solely on his extraordinary scientific talent. His work remains a cornerstone of orchid science. Unfortunately, Darwin's prescient letter seems not to have been noticed, appreciated, or cited often enough in the orchid literature during its 162 years of existence.

Resumen. El 26 de marzo de 1863, Charles Darwin escribió una carta a Joseph Dalton Hooker, describiendo sus intentos de germinar semillas de orquídeas. En esta carta, mencionaba su esperanza de observar plántulas de orquídeas y expresaba una "noción de que [las semillas]... ¡en su juventud temprana son parásitas de criptógamas!". Si bien esta afirmación parece predecir el descubrimiento de Noël Bernard en 1899 de que las semillas de orquídea requieren colonización fúngica para germinar con éxito, existe cierta incertidumbre sobre el significado exacto de Darwin. En su época, el término "criptógamas" incluía comúnmente a los hongos, pero también abarcaba briofitas, pteridofitas y otras plantas no vasculares. Dado que Darwin mencionó *Sphagnum* en sus experimentos, es posible sugerir que estuviera considerando los musgos como hospederos potenciales en lugar de los hongos específicamente. Además, al tratarse de una carta personal a Joseph D. Hooker y no de una publicación formal, es probable que Darwin no fuera del todo preciso en su terminología. No obstante, considerando el interés más amplio de Darwin en las interacciones planta-hongo, es plausible que al menos haya considerado a los hongos como posibles socios simbióticos en la germinación de las orquídeas. Aunque el grado de su predicción sobre la relación orquídea-hongo puede ser debatible en cuanto a la terminología (¿se refería a los hongos al usar "criptógamas"?), su especulación fue notablemente intuitiva, cuestionando si las orquídeas necesitaban un socio biológico externo para la germinación de las semillas de orquídeas. La carta de Darwin demuestra su capacidad de visionaria, pero no resta mérito al logro monumental de Noël Bernard. Bernard hizo su descubrimiento de manera independiente, sin conocimiento de las observaciones de Darwin, basándose únicamente en su extraordinario talento científico. Su trabajo sigue siendo un pilar fundamental en la ciencia de las orquídeas. Lamentablemente, la carta premonitoria de Darwin parece no haber sido notada, apreciada o citada con la frecuencia que merece en la literatura sobre orquídeas hasta ahora, 162 años después de haber sido escrita.

Keywords/Palabras clave: cápsula, capsule, fungi, germinación, germination, hongo, seeds, semillas, substrate, sustrato, simbiosis, symbiosis

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Introduction. Orchids were appreciated, cultivated, written about, and illustrated in ancient China (Table 1) approximately 3000 years ago (Hew & Wong, 2024). The ancient Chinese probably did not recognize orchid seeds for what they are, observe their germination, or notice seedlings.

Or, if they did, they either did not document this or their writings on this subject have yet to be discovered. Possibly, they suspected that substrates, which support orchids in nature, contain factors beneficial to plants. Ancient Chinese cultivation practices recommended adding soil, which supports plants in the wild, to new potting mixes or locations (Hew & Wong, 2024). Unknowingly, they were adding mycorrhizal fungi along with the original substrate.

The Ebers papyrus (*ca.* 1500 BCE), Assyrian writings of the Ashurbanipal period (668–627 BCE), Theophrastus (370–285 BCE), Dioscorides (*ca.* 20–70 A. D.), Pliny the Elder (24–79 A. D.), the Bible, and writings from the old Turkish Empire do not mention orchid seeds (Table 1), their germination, or seedlings (Arditti, 1984, 1992; Dunn & Arditti, 2009; Jacquet, 1994; Lashley & Arditti, 1982; Lawler, 1984; Sezik, 1967, 1984; Yam *et al.*, 2002). If there are descriptions of orchid seeds and/or seedlings in very early writings or incunabula, they have yet to be found.

Information presented here about the properties, biology, and germination of orchid seeds and seedlings, along with mycorrhizal associations, is intentionally limited. Its sole purpose is to provide context for Charles Darwin's (Fig. 1A; 1809–1882) prescient letter dated March 26, 1863 (Table 1). Over its 161 years of existence, this letter, which clearly predicted the requirements orchids have during a critical phase of their life cycle, was likely: a) read by few others than Sir Joseph Dalton Hooker (Fig. 1B; 1817–1911; Director of the Royal Botanic Gardens, Kew, 1865–1885), and the editors of Darwin's letters; or b) cited only a few times in the orchid literature (Fay & Chase, 2009; Yam *et al*., 2009).

It is important to note that Darwin's prediction does not diminish the significance of Bernard's discovery (Bernard, 1899, 1990; Table 1). It remains a significant and important contribution to our understanding of orchids.

This paper documents early reports regarding orchid seed germination and development, leading to the discovery of mycorrhizal symbiosis by Noël Bernard (Bernard, 1899, 1902). The text is profusely illustrated, with many historical images, some seldom seen and a few modern ones. Together, these illustrations offer visual insights into subjects, processes, and individuals that are rarely encountered, even by experts. Table 1 summarizes key dates and events, illustrating the historical progression of seed germination.

Orchid seeds. Orchid seeds (Fig. 2, 3C–D, 4D, 7A) are often referred to as "dust seeds" due to their tiny size and low weight. They can range from 0.05 mm to 6 mm in length and 0.01 mm to 0.9 mm in width (which is actually their diameter). Their weight can range from 0.31 µg to 24 µg. The volume within the seed coats can range from as small as 0.12 mm^3 to as large as 38 mm^3. Seed coats tend to be water-repellent and hard to wet (for a review, see Arditti & Abdul Ghani, 2000). Their embryos (Fig. 2, 3D, 4D, 7A) are even smaller, measuring approximately 0.14 mm in length and 0.09 mm in width, with a minuscule volume of just 0.45 mm^3.

The free air space inside orchid seeds is created by the collapse of inner seed coat cells during seed enlargement (Lee & Yeung, 2023). This space can comprise up to 97% of the seed volume (Arditti & Abdul Ghani, 2000). Consequently, orchid seeds behave like tiny balloons, which can be suspended in air or float in water for extended periods (Arditti & Abdul Ghani, 2000).

When fruits (capsules) ripen, they split open and release the seeds, which are dispersed over long distances by air or water (Arditti & Abdul Ghani, 2000). On landing, the seeds settle on the ground, rocks, bark, cracks, and crevices or mix with soil, debris, and various particles, making them nearly impossible to see or monitor. There are a few exceptions to this. These exceptions produce fleshy fruits containing hard, rounded, and dark seeds, which are dispersed by animals (Karremans *et al.*, 2023). include certain species in the genera *Apostasia* Blume and *Neuwiedia* Blume (both of the subfamily Apostasioideae), *Selenipedium* Rchb.f. (Cypripedioideae), *Cyrtosia* Blume and *Vanilla* Plumier ex Mill. (Vanilloideae), *Rhizanthella* R.S.Rogers (Orchidoideae), *Palmorchis* Barb.Rodr. (Epidendroideae).

Nonetheless, all orchids depend on fungal symbionts for germination.

TABLE 1. Chronology of orchid mycorrhiza events.

Biology/Characteristic/Event/ Part of plant	Location/People/Culture	Period/Time/Date	Reference
Appreciation of orchids	China	*ca.* 1000 BCE	Hew & Wong, 2024.
Bernard's work translated into English	France	2007, 2011, 2017	Jacquet, 2007; Sellosse *et al.*, 2011, 2017.
Cultivation of orchids	China	*ca.* 1000 BCE	Hew & Wong, 2024.
Darwin's prescient letter about the role of fungi (mycorrhiza) in seed germination			
Written	UK	26 March 1863	Darwin, 1863.
Read	UK	1863	
Read	UK	2009	Fry & Chase, 2009.
Read	US, Singapore	2009	Yam *et al.*, 2009.
Read	Other	Unknown	
Discovery of role of mycorrhiza in orchid seed germination	France	1899	Bernard, 1899.
Embryo size, volume	USA, Malaysia	2000	Review by Arditti & Abdul Ghani, 2000.
Endophyte, orchid, 1st identification as fungus	Germany	1847	Reissek, 1847.
Fruit, orchid, formation of first description	Indonesia	*ca.* 1654–1670	Rumphius, 1741–1670.
Horticultural hybrid, orchid, 1st *Calanthe* Dominyi	UK	1856	Reviews by Arditti, 1985; Yam *et al.*, 2002.
Horticultural hybrid, orchid, 1st *Cattleya*	UK	1856	Reviews by Arditti, 1985.
	UK	1859	Yam *et al.* 2002.
Horticultural hybrid, orchid, 1st *Paphiopedilum* Dominyi	UK	1856	Reviews by Arditti, 1985; Yam *et al.*, 2002.
Horticultural hybrid, orchid, 1st, Singapore *Spathoglottis* Primrose	Singapore	1932	Arditti & Hew, 2007.
Illustrations of orchids	China	*ca.* 1000 BCE	Hew & Wong, 2024.
Mycorrhiza, orchids, role of, discovery	France	1899, 1902	Bernard, 1899, 1902.
Mycorrhiza, orchid, illustration, 1st	Germany	1824–1849	Link, 1840.
Mycorrhiza, orchid not known	China	*ca.* 1000 BCE	Hew & Wong, 2024.
Mycorrhiza term coined	Germany	1885	Frank, 1985 (translation).
Protocorm term proposed (as protocorme)	Netherlands, Indonesia	1890	Treub, 1890.
Protocorm term first used for orchids	France	1899, 1902	Bernard, 1899, 1902.
Protocorm term wrongly attributed to Bernard	UK	1999	Cribb, 1999.
Seed, orchids of, dispersal of	USA, Malaysia	2000	Reviews by Arditti & Abdul Ghani, 2000.

Table 1. *continues...*

Seed, orchid of, asymbiotic germination, 1st	USA	1921, 1922	Knudson, 1921, 1922.
Seed, orchid of, horticultural, 1st			Moore, 1849.
Seed, orchids of, illustration of	Switzerland	*ca.* 1550, 1654–1670	Gesner, 1751; Rumphius, 1741–1750, reviews by Arditti, 2024; Beckman, 2003; Soediono *et al.*, 1983; Wehner *et al.*, 2002; de Wit, 1959, 1977.
Seed, orchids of, size, volume, air space	USA, Malaysia	2000	Review by Arditti & Abdul Ghani, 2000.
Seedlings, orchids of, first description of	UK	1802, 1804	Salisbury, 1804.
Seeds, orchid of, germinating earliest illustrating of	UK	1802, 1804	Salisbury, 1804.
Seeds, orchids of, not mentioned/observed	Assyrian writings,		Hew & Wong, 2024.
and/recognized for what they are;	Ashurbanipal period	668–627 BCE	Arditti, 1984, 1992.
germination not observed;	Bible	1400–425 BCE	Jacquet, 1994; Lashley & Arditti, 1982; Lawler, 1984; Sezik, 1967, 1984; Yam *et al.*, 2002.
seedlings not noticed	China	*ca.* 1000 BCE	
	Dioscorides	20	
	Ebers Papyrus	1500 BCE	
	Plliny the Elder	24–79	
	Theophrastus	370-285 BCE	
	Turkish (Ottoman) empire	14–17th century	
Substrate perhaps suspected to contain beneficial factor(s)	China ca 1000 BCE		Hew & Wong, 2024.
Writing about	China	*ca.* 1000 BCE	Hew & Wong, 2024.

Conrad Gesner (1516–1565, Fig. 3A), the Swiss polymath, was the first to draw orchid seeds, specifically those of *Epipactis helleborine* (L.) Crantz (Fig. 3B; Table 1). He initially depicted them as mere dots (Fig. 3C) before creating magnified drawings that revealed the embryos and the space inside the seed coat (Fig. 3D; for reviews, see Arditti, 2024; Wehner *et al*., 2002). Gesner's orchid paintings and drawings were published in 1751 and 1771, over 200 years after he painted or drew them, in the second volume of his *Opera Botanica* (Gesner, 1751).

Georgius Everhardus Rumphius (1627–1702, Fig. 4A) studied orchids in Ambon, Indonesia (Beekman, 2003), including *Grammatophyllum scriptum* (L.) Blume (Fig. 4B; Table 1). He was the second person to describe orchid seeds, doing so between 1654 and 1670 (for reviews, see Beekman, 2003; Soediono *et al*., 1983; Wehner *et al.*, 2002; de Wit, 1959, 1977). He observed the formation of fruit [Fig. 4B (A–D in original smaller caps), and 4C].

Upon splitting ripe orchid fruits, Rumphius initially described the contents as flour and sand, later recognizing it as seeds (Rumphius, 1741–1750). Thus, due to a twist of fate, Rumphius' observation (the second) was published before Gesner's (the first). Rumphius did not paint or draw seeds (Fig. 4D is recent), likely because of his failing eyesight and eventual blindness. It is also possible that he did not have access to magnifying glasses in Ambon. However, this is unlikely, given that Roger Bacon (1220–1292) invented them in 1250 at the University of Oxford.

Orchid seed germination and seedlings. In the process of orchid seed germination, the first stage involves

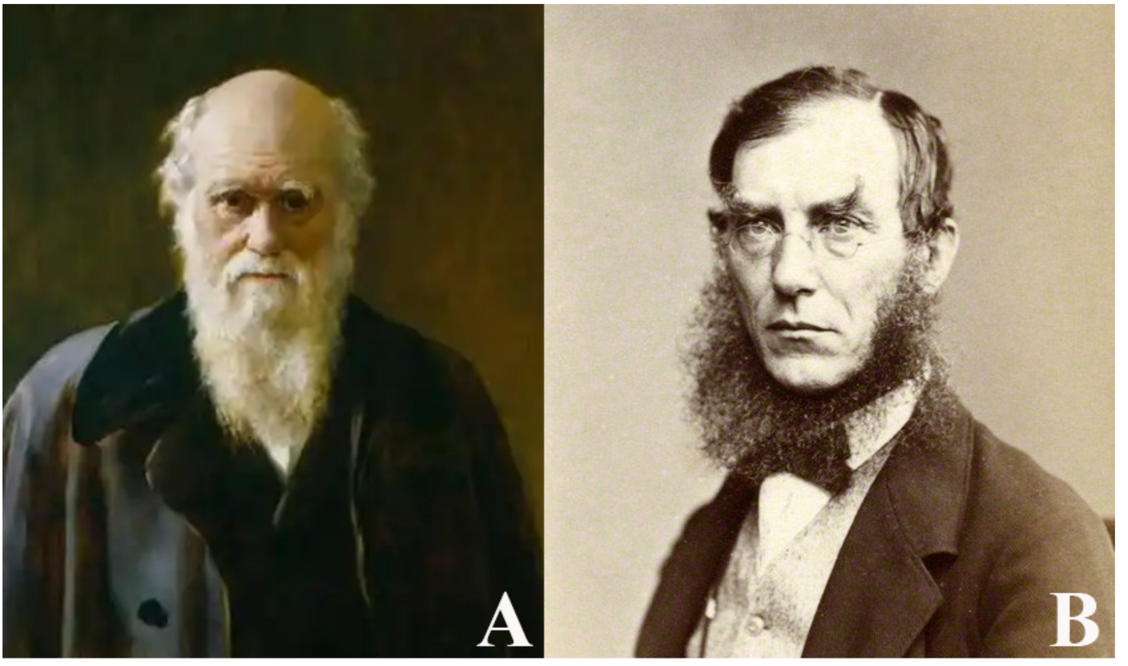

Figure 1. **A**. Charles Robert Darwin (1809–1982). **B**. Joseph Dalton Hooker (1817–1911). Sources: A, B, Wikipedia.

a small structure known as a protocorm. The term "protocorm" was first proposed in 1890 as "*protocome*" (Treub, 1890) by Melchior Treub (1851–1910), Director of the Bogor Botanical Gardens in Indonesia from 1880 to 1909, to describe an early stage of Lycopod germination. It is important to note that Bernard did not coin this term, as stated erroneously (Cribb, 1999; Table 1). Noël Bernard adopted the term for orchids in 1899 (Bernard, 1899; translated into English by Jacquet, 2007; reviewed and translated by Sellosse *et al.*, 2011, 2017). Today, "protocorm" is (almost) strictly associated with orchids.

The earliest known illustrations of germinating orchid seeds are Figures 5 and 6, as well as in the next section of the text. In recent years, many researchers have provided detailed descriptions and illustrations of protocorms and seedlings (Rasmussen, 1995; Yeung & Lee, 2024). The primary structure of protocorms is established during embryo development (Yeung, 2022). As germination proceeds, the embryos expand and transform into protocorms, which increase in size and emerge from the seed coat (testa).

A cell size gradient develops within protocorms, with smaller cells at the apical (top) end and larger cells at the basal (micropylar) end. The smaller cells at the apical end will eventually form the first leaf of protocorms and the shoot apical meristem. Meanwhile, the larger basal cells will grow and eventually accommodate the mycorrhizal fungi that play a role in symbiotic seed germination. Additionally, rhizoids emerge on the surface of the protocorm, with a greater abundance found at the basal end (Yeung, 2024).

After forming an initial small leaf, protocorms develop a shoot with leaves (Fig. 5–6). During orchid seed germination, a radicle is absent, and roots form later, typically at the base of the developing shoot. With the formation of roots, protocorms become seedlings. Morphological changes during asymbiotic seed germination are evident in a Brazilian orchid (Fig. 5 top; Hunhoff *et al.*, 2018). Changes also occur during symbiotic seed germination of a *Phalaenopsis* species (Fig. 5, bottom; Veitch, 1986). Because protocorms and early seedlings are very small and occur in limited numbers, they were not detected for a long time.

Features of seedlings were documented early in the study of seed germination. On January 5, 1802, the British botanist Richard Anthony Salisbury (1761–1879; Fig. 6C, Table 1) presented a paper at the Linnean Society of London, in which he described and

FIGURE 2. Orchid seeds painted by Joseph Georg Beer at 100× magnification. Size relationships are as shown. Scale: The long, narrow seed (red wedge, bottom center) is 1.46 mm long and 0.1 mm wide at the center of the (green, drop-shaped) embryo. Source: Beer, 1863.

FIGURE 3. RIGHT. Conrad Gesner and the first known drawings of orchid seeds. **A**. Conrad Gesner (1516–1565). **B**. *Epipactis helleborine* (L.) Crantz, flower. **C**. Seeds drawn as dots. **D**. Seed showing embryos in their centers. Handwritten numerals 2, 11 and 12 are in the original Painting, probably in Gesner's hand. The original illustrations did not contain size bars. They are nearly 500 years old and were published 200 years after Gesner drew them. Because publication was not on acid-free paper, A–D were post-produced with Photoshop to increase clarity. Sources: A, Wikipedia; B–D, Gesner, 1751.

illustrated germinating seeds of *Orchis morio* L. (=*Anacamptis morio* (L.) R.M.Bateman, A.M.Pridgeon, and M.W.Chase; Fig. 6A) and *Limodorum verecundum* Salisb. (=*Bletia purpurea* (Lam.) A.DC; Fig. 6C). Salisbury's work included the first descriptions and illustrations of orchid seedlings. His talk was published two years later (Salisbury, 1804). Other descriptions and illustrations of germinating orchid seeds and seedlings from Europe were published subsequently (for reviews, see Arditti, 1984, 1990; Yam *et al.*, 2002).

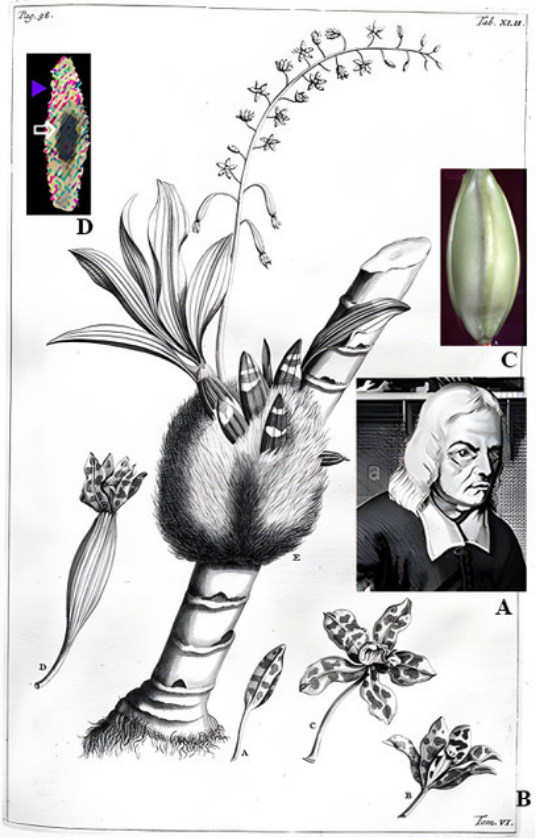

FIGURE 4. Georgius Everhardus Rumphius and his drawings of *Grammatophyllum scriptum* (L.) Blume. **A**. *Georgius Everhardus Rumphius* (1627–1702). **B**. *Grammatophyllum scriptum*, small capitals A–E in small non-bold face capital letters are as in the original. A. Unopened bud. B. Flower in the process of anthesis. C. Fully open flower. D. Young fruit with remnants of the perianth on top. E. Plant on a tree trunk, with leaves, root ball called trash basket and inflorescence with buds, opening flowers, fully open flowers and fruits**.** **C**. Fruit. **D**. Seed. Blue arrow, seed coat. Open arrow, embryo. Sources: A, B, Rumphius, 1741–1750; C, Joseph Arditti; D, courtesy B. Abbas, F. H. Listyorini, and B. Amriati. From their. *In vitro* seeds germination and plantlet development of *Development scriptum* Lindl. (Orchidaceae). *International Research Journal of Plant Science,* 2, 154–159, 2011.

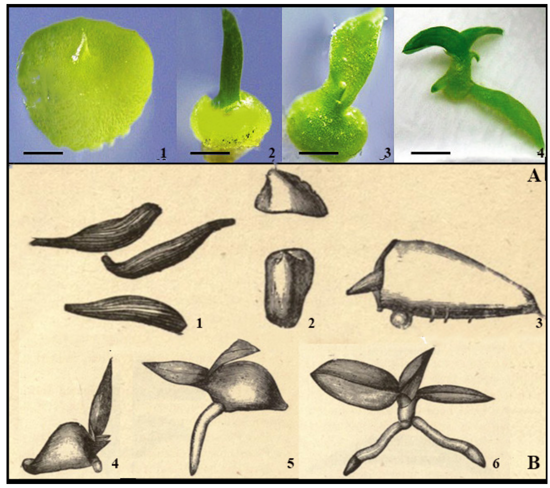

FIGURE 5. Seed germination and seedling development. **A**. Development of a Brazilian orchid from protocorm to plant. 1. Early protocorm. 2. First leaves. 3. Expansion of the first leaf and appearance of the second leaf. 4. Seedling with leaves and roots. Bars: 1–3, 1 mm; 4, 1 cm. **B**. Symbiotic seed germination drawings of *Phalaenopsis* (exact and specific dimensions and size bars are not available): 1. Seeds [*Phalaenopsis* seeds are 0.35±0.05 mm long and 0.08±0.01 mm wide (Arditti & Abdul Ghani, 2000]. 2. Four months old seedling. 3. Nine months old protocorm with a leaf primordium. 4. Leaf-bearing 15-month-old seedling with emerging root. 5. Seedling with two leaves and one root, 22 months old. 6. A seedling with three leaves and two roots, 2.5 years old. Sources: A, Hunhoff. V. L., L. A. Lage, E. G. Palu, W.Krause, and C. A. Silva. 2018. Nutritional requirements for germination and in vitro development of three Orchidaceae species in the southern Brazilian Amazon. *Ornamental Horticulture,* 24, 87–94. Reproduced with permission from Fernanda Carlota Nery, Editor-in-Chief; B. Veitch, 1986.

The first orchid seedlings in a horticultural establishment were those of *Prescottia plantaginea* Hook. (=*Prescottia plantaginifolia* Lindl. ex Hook.), which are believed to have arisen spontaneously in 1822 or 1832. They drew limited attention (for reviews, see Arditti, 1984; Yam *et al*., 2002). Attempts to germinate orchid seeds in France around the same time were unsuccessful, leading to the misconception that orchid seeds were incapable of germination (Arditti, 1984; Yam *et al*., 2002).

Efforts to germinate orchid seeds in the United Kingdom continued, and three successful germinations were reported in the same year (Cole, 1849; Gallier, 1849; Moore, 1849; for reviews, see Arditti, 1984, 1990; Yam *et al*., 2002; Table 1). In retrospect, it is clear that these germinations occurred because the seeds were inadvertently placed in locations or on

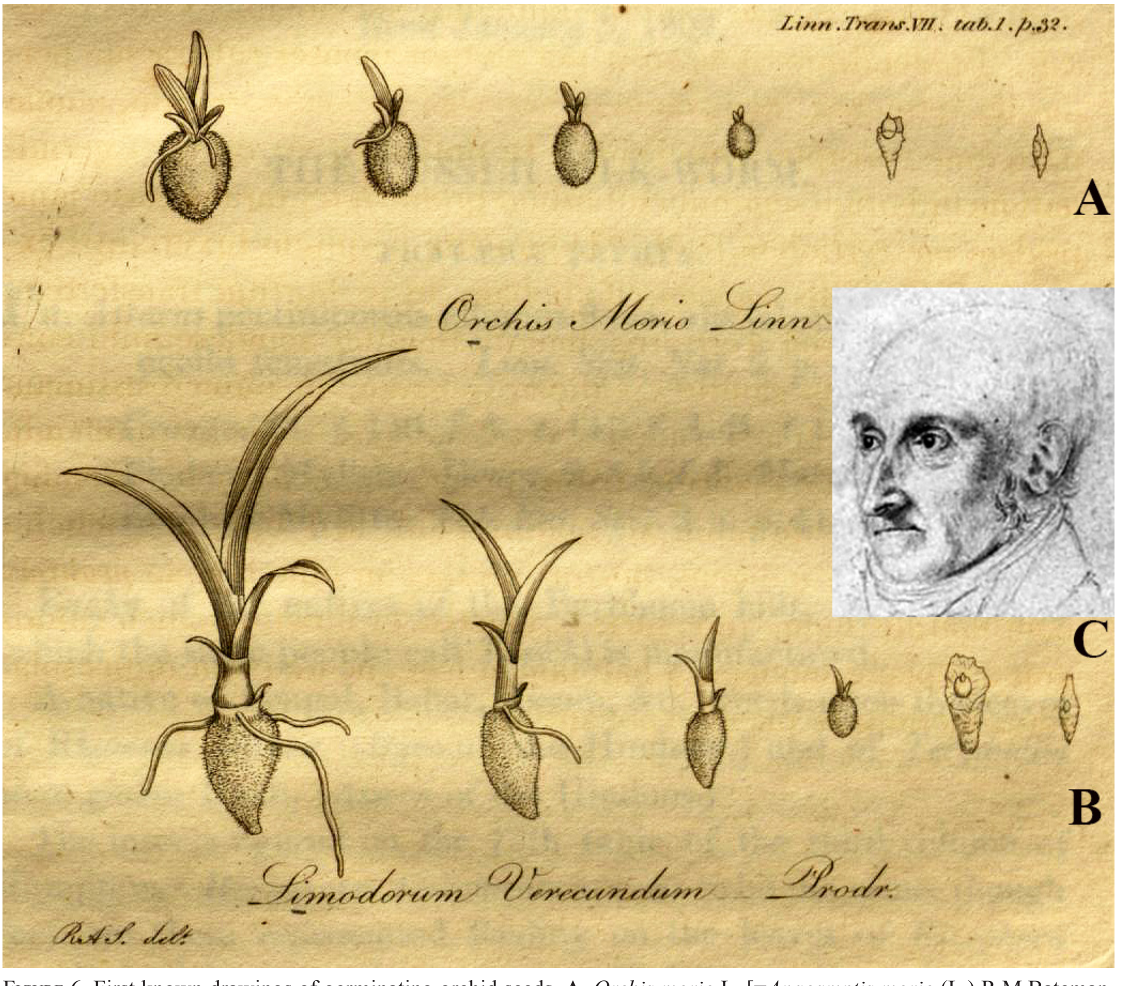

FIGURE 6. First known drawings of germinating orchid seeds. **A**. *Orchis morio* L. [=*Anacamptis morio* (L.) R.M.Bateman, Pridgeon & M.W.Chase]; **B**. *Limodorum verecundum* [=*Bletia purpurea* (Lam.) A.DC]. The original illustration did not contain size bars. The light brown cast and folds in the background are due to the aging of the original, which is 221 years old and not acid-free. This illustration was not post-produced to retain the feeling of the original. **C**. Richard Anthony Salisbury (1761–1829). Sources: A, B, Salisbury, 1804; C, Wikipedia.

substrates that contained the appropriate fungi. This fact remained a mystery for a long time.

As a result of these successful orchid seed germinations, the first horticultural orchid hybrid, *Calanthe* Dominyi, was produced in the United Kingdom in 1856 (for reviews, see Arditti, 1984; Yam *et al*., 2002). But, even 30 years after that, orchid growers seemed “far . . . from hitting upon a method by which even moderate amount of success” could be expected . . . (Veitch, 1886). Seeds were produced “in profusion . . . but little of it . . .” germinated. Few plants were produced even when thousands of seeds from hundreds of capsules were sown (Veitch, 1886; Veitch & Sons, 1878–1894). The first *Cattleya* hybrid flowered in 1859 (Table 1). It was followed by the first *Paphiopedilum* Pfitzer in 1869 (Table 1).

The seed germination methods used to produce these orchid hybrids in England did not spread quickly or widely, even within the British Empire. For instance, the first human-made orchid hybrid in Singapore (a British possession from 1819 to 1953, well-known for its orchids), *Spathoglottis* Primrose, was produced in 1932. This hybrid was created by Eric Holttum, the Di-

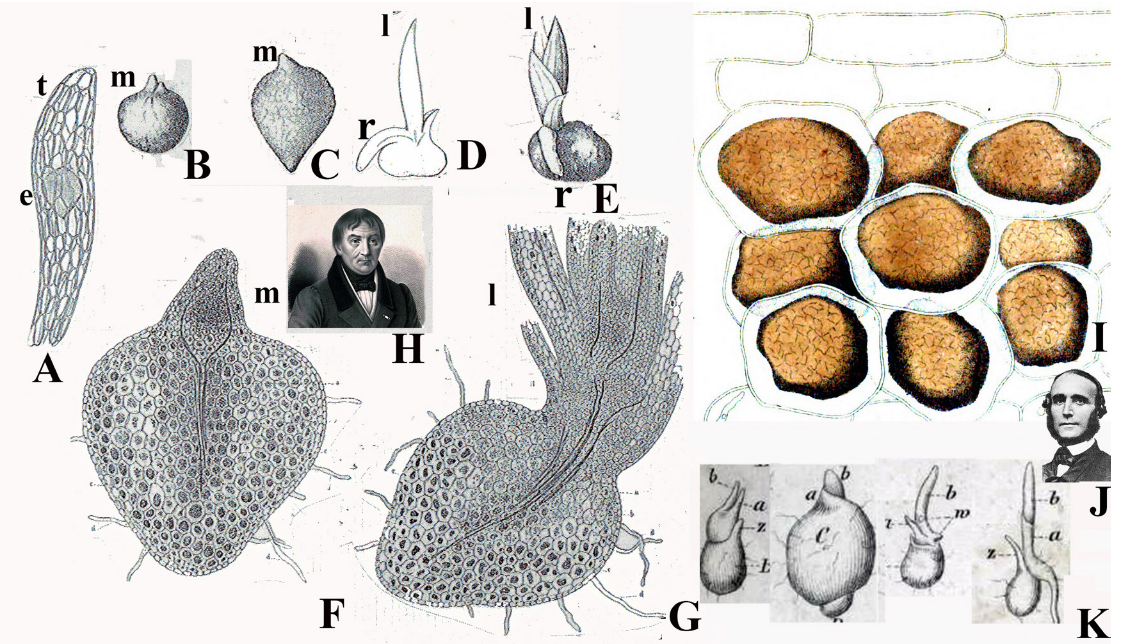

Figure 7. Early drawings of orchid seedlings which contain fungi. *Oeceoclades maculata* (Lindl.) Lindl. [= *Eulophia maculata* (Lindl.) Rchb.f.]. **A**. Seed. **B**. Young protocorm. **C**. Later protocorm. **D**. Young seedling with a single leaf and root. **E**. Older seedling with two leaves and a root. **F**. Cross-section of C. **G**. Leaf bearing seedling with fungus in cells. **H**. Heinrich Friedrich Link (1767–1851). **I**. Fungal masses in cells. **J**. Thilo Irmish (1816–1879). **K**. Seedlings of *Herminium monorchis* (L.) R.Br., which germinated symbiotically. Explanation of symbols: dark masses in cells (in F, G), fungus; e, embryo; l, leaf; m, meristem/shoot tip; r, root; t testa. Size/scalebars not available. All illustrations were post produced w1ith Photoshop. Sources: A–G, Link, 1840; H, Wikipedia; I, Reissek, 1847; J, provided by Margit Hartleb, Türinger Universitet und Landesbibliotek Universitätarchiv; K, Irmish, 1853. A–G, J, K were included in Yam *et al*., 2002.

rector of the Singapore Botanic Gardens at that time. He germinated the seeds asymbiotically by employing the technique developed by Professor Lewis Knudson at Cornell University (Knudson, 1921, 1922; for a review, see Arditti & Hew, 2007).

Mycorrhiza. Early illustrations of fungi in orchid seedlings (Fig. 7) were published by Heinrich Friedrich Link (1767–1851, Fig. 7) in Germany between 1824 and 1849. However, he neither recognized nor appreciated the role of fungi in orchid seed germination (for reviews, see Arditti ,1984; Link, 1840; Yam *et al*., 2002). The endophyte was first identified as a fungus in 1847 (Reissek, 1847; for a review, see Trappe & Berch, 1885; Table 1). Subsequent reports and illustrations (Fig. 7I, K) were published by Irmisch in 1853 and by Prillieux & Rivière in 1856. The significance of mycorrhizal fungi to plants was discovered in the 1880s. Albert Bernhard Frank (1839–1900), a German botanist, coined the term "mycorrhiza" in 1885 (for a translation, see Frank, 1985). This period also marked the beginning of mycorrhiza studies (Arditti, 1984; Harley, 1985; Trappe & Berch, 1985; Yam *et al.*, 2002). The discovery of the role of mycorrhiza in orchid seed germination by Noël Bernard (1874–1911, Fig. 11B) would not occur until later.

Neottia nidus avis. The chlorophyll-free orchid, *Neottia nidus avis* (Correvon, 1899; Drude, 1873), is widely distributed across Europe, the Caucasus, Siberia, and the Mediterranean region. It is often mistakenly referred to as a saprophytic orchid. Actually, it is parasitic on its fungal partner, which is saprophytic on forest litter or parasitic on green plants.

Honey-scented flowers are produced from May to June. The flowers are approximately 1.5 cm in size,

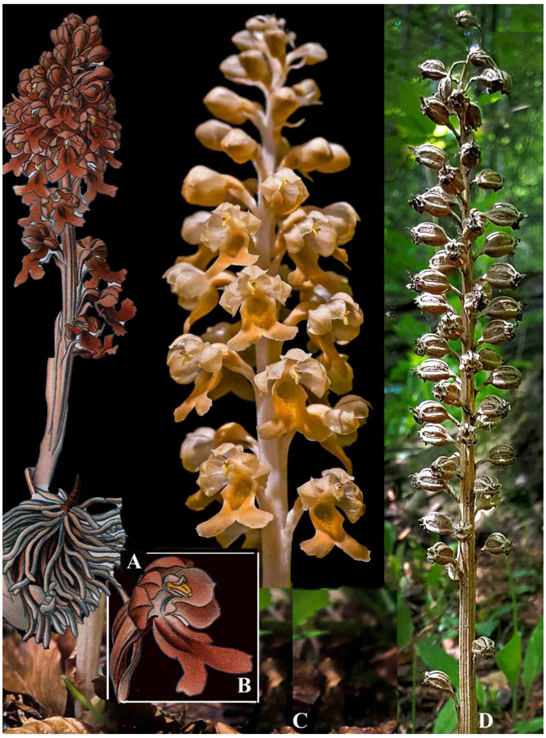

FIGURE 8. *Neottia nidus avis* (L.) Rich., the bird's nest orchid. **A**. Painting of inflorescence (30–50 cm tall, usually produced in France in May-June) and roots. **B**. Painting of flower (15 mm). A and B are of historical importance because they were published in the year Bernard made his discovery. The plants he saw probably looked like this Painting. **C**. Close-up of open flowers-bearing inflorescence. **D**. Fruits on inflorescence axis. Sources: A, B, plate XXX in Correvon, H. 1899. *Album de Orchideés de l'Europe Centrale et Septentrionale*. Libraire O. Doin, Paris, France; C, D, courtesy Dr. Nora De Angelli.

FIGURE 9. Rhizomes, roots and inflorescences of the bird's nest orchid. *Neottia nidus-avis*. **A, D**. External view of rhizome covered with roots. **B**. Appearance following removal of roots. **C**. Schematic drawing of cross section. Areas colonized by fungus are dotted. **E**. Inflorescences protruding above ground. **F**. Expanded inflorescence showing flower buds. Explanation of symbols (those in modern fonts were added: b_4, b_5, b_6, b_7, buds; e_1-e_5, scales; fb, flower bud; ii, inflorescence initial; in, inflorescence; rh, rhizome; ro, root; t_1-t_6, tubers. Size bars are not available. The light brown cast of the background of A–C is due to the aging of the original, which is 123 years old. Sources: A–C, Bernard, N. 1902. Études sur la tubérisation. *Revue Genérale de Botanique* 14: 58–71, plates 1–3; D-F, courtesy Dr. Nora De Angelli.

brown in color, and can range from 15 to 70 in number. They are borne on upright inflorescences 7 to 22 cm tall, which develop from the tips of rhizomes and rise above ground.

Rhizomes measure 5 to 6 cm long and 2 to 5 mm in diameter. They are covered with dense clusters of fleshy roots that are 1.5 to 4 cm long and 1 to 4 mm in diameter. The number of roots typically ranges from 50 to 90 but can vary from 20 to 120. (UkrBIN, 2024)

The flowers (Fig. 8A–8C) are capable of self-pollination but can also be pollinated by various insects, including flies, thrips, and ants. Most flowers (75%–97%) produce elliptical fruits which measure approximately 10–11 mm in length and 5–6 mm in width (Fig. 8D, 10A, 10C–D). They contain numerous seeds (Fig. 10B–10F) which measure 0.6–0.8 mm in length and 0.1 mm in diameter (Fig. 9B, 9E–F). When the seeds fall to the ground, they become colonized by a mycorrhizal fungus, either inside (Fig. 10C–D) or outside (Fig. 10B, 10E–F) the fruits. This colonization is sometimes referred to as an infection. Colonization is preferred as a term because the word infection carries pathological implications.

Noël Bernard. Noël Bernard (Fig. 11B) was born on March 13, 1874, to François Bernard, who was 46 years old, and his wife Marguerite Sabot, who was just 19. François passed away when Noël was 5 years old (or, according to his son Francis, 12 years old). As soon as he was able to, young Noël began working as a mathemat-

Figure 10. Fruits (capsules) and seeds of *Neottia nidus-avis*. **A**. Unopened fruit. **B**. Seeds. **C**. Open, seed-containing fruit with no hyphae. **D**. Seeds and hyphae in open fruit. This is what Bernard probably saw. The hyphae are on the fruit walls and mixed with the seeds. **E**. (1, 2). **F**. (1, 2, 4). Hyphae extend from seeds. Source: courtesy Dr. Nora De Angelli.

ics tutor (for reviews, see Arditti, 1984; Boullard, 1985; Sellosse *et al.*, 2011, 2017; Yam *et al.*, 2002). Fascinating, yet occasionally abrasive, Noël was an exceptional student at both the École Normale Supérieure and the École Polytechnique. Juliene Costantin (1857–1936) became his mentor when he changed his focus to biology. As Constantin's star pupil, Bernard earned his Licencié in Sciences Naturelles in November 1897. At the age of 25, he was drafted into military service and stationed at the Melum Barracks (Sellosse *et al.*, 2011) near Fontainebleau Forest, where he made his important discovery regarding orchid seed germination and mycorrhizal fungi on May 3 1899 (Bernard, 1899, in French; translated into English by Jacquet, 2007; a second English translation with annotations and additional details by Sellosse *et al.*, 2017; a biography, photographs, and an analysis of his research by Boulard, 1985; Table 1).

After completing his military service, Bernard worked at the École Normale Supérieure with Julien Costantin and Gaston Bonnier (1853–1922) until 1901, when he accepted a position at the University of Caen. On August 8, 1907, he married Marie Louise Martin (*ca.* 1878–1946). Their son, Francis, was born prematurely on April 30, 1908. Bernard managed to keep the tiny baby (weighing only 1.5 kg) alive with a mixture of malt and citrus juice. Francis became a well-known myrmecologist and marine biologist. He wrote memoirs about his father in 1990 (F. Bernard 1990a, 1990b).

In 1908, Bernard became a Professor of Botany at Poitiers, where he made numerous notable contributions to the study of orchids, potatoes, and botany in general in a relatively short period (Jacquet & Arditti, 2007; for translations, see Jacquet, 2007; Sellosse *et al.*, 2011; for a list of publications, see Arditti, 1990).

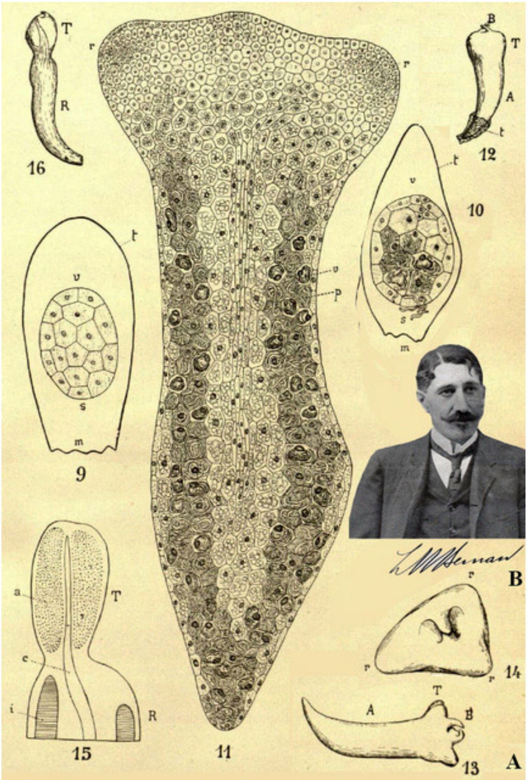

FIGURE 11. What Bernard saw and drew (somewhat rearranged with Photoshop to accommodate the photograph). **A**. Seed and seedlings of *Neottia nidus avis* (L.) Rich. **B**. Noël Bernard. Explanation of symbols: 9, seed (93× in original): m, area of attachment to the placenta; s, suspensor of the embryo. t, seed coat; v, vegetative point. 10 (98× in original), seed at start of germination: m, area of attachment to the placenta; s, suspensor of embryo. t, seed coat; v, vegetative point. 11(65× in original), longitudinal section through seedling during the first year of development, area colonized by fungi is below the epidermis; p, distinct hyphae; v, degenerated hyphae; in the center is the central cylinder surrounded by amylaceous parenchyma; r, initials of first roots. 12 (8× in original): A, embryonic axis; B, terminal bud (apical meristem); T, first tuber; t, remnant of seed coat. 13 (8× in original): advanced development of seedling; A, embryonic axis; B, terminal bud (apical meristem); T, first tuber; 14 (13× in original): advanced development of seedling, view from above: p, root initials of tuber. 15 (25× in original): longitudinal section of tuber: a, amylaceous parenchyma; c, central cylinder; R, root; T, t, area colonized by fungus. 16 (5× in original): external view of root detached from rhizome; R, root; T, terminal tuber detached from root cap. Sources: A (9-16), Bernard, N. 1902. Études sur la tubérisation. *Revue Genérale de Botanique* 14: 58–71, plates 1–3; B: Wikipedia.

Overall, Bernard published about forty texts and papers between 1899 and 1911 (Bernard, 1911; Sellosse *et al.*, 2011).

Bernard was diagnosed with tuberculosis in 1910. He died at 3:00 AM on January 26, 1911. His grave is in Saint Benoît, marked with the inscription: *Noël Bernard, Professeur A La Faculté de Sciences de l'Université de Poitiers–1874/1911* (Boullard, 1985).

Nobel Laureate (1926) Jean-Baptiste Perrin (1870–1942) added an epitaph: "*Bernard was probably the greatest hope of French botany and . . . his death [was] a bigger social loss than that of [Marie] Curie or [Henri] Poincare*" (Sellosse *et al.*, 2011).

Noël Bernard made one of the most important discoveries in orchid biology all on his own. His discovery (Bernard, 1899) led Lewis Knudson to formulate a method for asymbiotic orchid seed germination in 1921 (Knudson, 1921, 1922).

Bernard was denied a position he richly deserved at a major university in Paris because of his "spirit of independence and pitiless candor" (F. Bernard 1990a, 1990b); he was punished by the establishment (Boullard, 1885; Sellosse *et al.*, 2011). His detractors are now remembered mostly for their mistreatment of Bernard. History is merciless in meting out justice! Still, Noël Bernard himself, his notable scientific achievements, and his legacy went through "a long period of misunderstanding and oblivion" (Bernard, 1990a, 1990b; Jacquet & Arditti, 2007).

A major reason for the obscurity of Bernard's work is that his papers were not widely read because "the French language... lost its position as a preeminent international language" (Jacquet & Arditti, 2007). However, recent translations into English (Jacquet, 2007; Sellosse *et al.*, 2017) should make his papers more accessible to a broader audience. Several historical papers (Arditti, 1984, 1990; Bernard, 1990a, 1990b; Jacquet & Arditti, 2007; Sellosse *et al*., 2011; Yam *et al*., 2002) may also draw more attention to Bernard and his contributions.

Bernard's discovery. On Sunday, May 3, 1899, while walking in Fontainebleau, Bernard saw fruits (Fig. 10A) on a shoot of *Neottia nidus-avis* (Fig. 8D). These fruits contained seeds (Figs. 10B–10D), some of which were colonized by fungi (Fig. 10E1, E2, 10F2, F4). Bernard recognized that the relationship between the

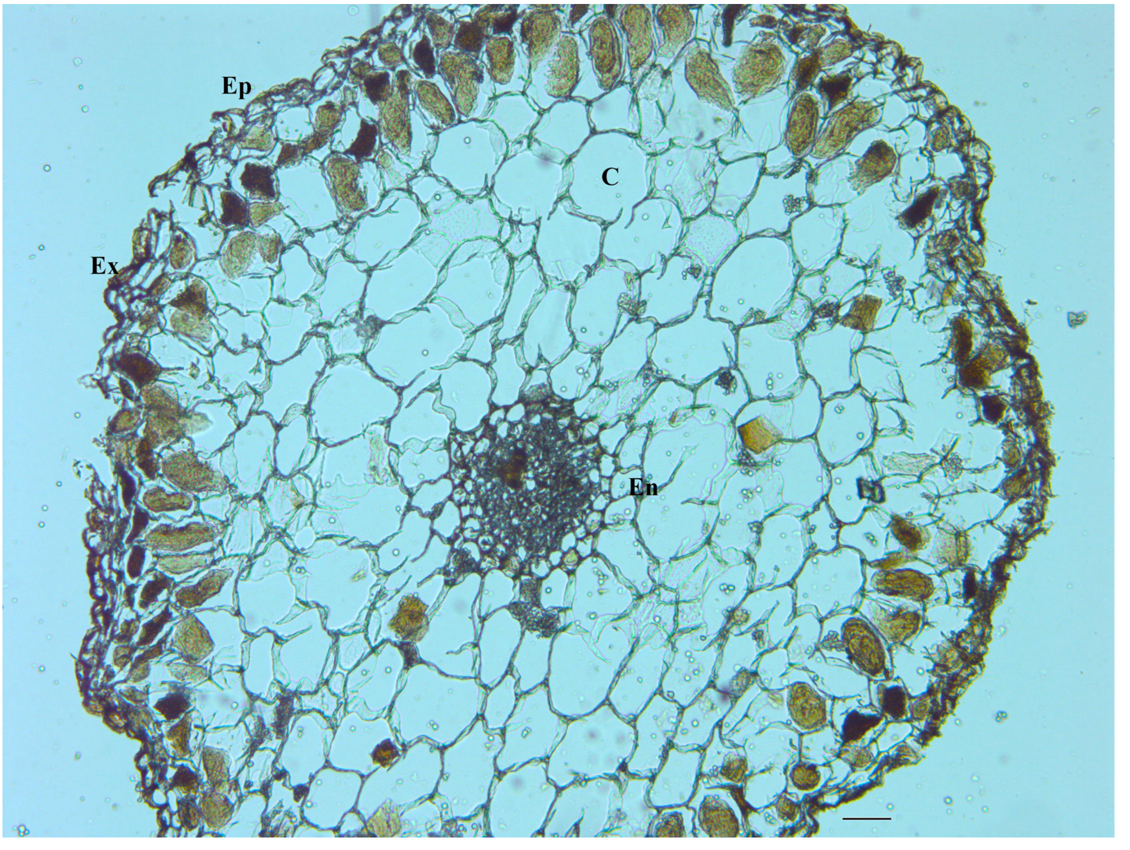

FIGURE 12. Modern cross-section of *Neottia nidus-avis*, root, which contains mycorrhizal fungi (dark masses in cells). Explanation of symbols: C, parenchyma of the cortex; dark masses in the cell, fungi; En, endodermis; Ep, epidermis; Ex, exodermis. Source: courtesy Anna Betekhtina from Betekhtina, A., D. E. Tukova, and D. V. Veselkin. 2023. Root structure syndromes of four families of monocots in the Middle Urals. *Plant Diversity,* 45, 722–731.

seeds, seedlings, and fungi was neither harmful nor understood at the time. He decided to write to his cousin, Jean Magrou:

"My studies from this afternoon have given me, . . . several hundreds of *Neottia* seeds in germination, and I have young plants (up to three millimeters in length) that no botanist's eye ever examined! Thus I have precious material for solving the question of orchid culture and for addressing two or three other questions" (Boullard, 1885 in Selosse *et al.*, 2017).

After Gaston Bonnier agreed to sponsor a presentation at the French Academy of Sciences, Bernard presented his findings at the academy meeting on May 15, 1899 (Bernard, 1899). During his presentation (Fig. 11), Bernard described his observations, which probably resembled those in Fig. 8D, 9D–F, 10, and 12 (Bernard, 1899). Translations of the entire paper are available (Jacquet, 2007; Sellosse *et al*., 2017). The latter contains excellent annotations and commentary.

"I had the opportunity to observe the germination of Neottia Nidus-Avis seeds in the following circumstances: An aerial shoot of this plant bearing its fruits filled with seeds had been accidentally buried in soil under a layer of dead leaves, likely last fall. In the spring, the seeds, still enclosed in the fruits, germinated in large numbers; this allowed me to observe the first germination stages, from seed to young seedlings 5 mm in length. These seedlings are shaped like a club, at the narrow end of which the tegument of the seed is torn apart; their surface is smooth and has no absorbing hairs. Sectioning reveals three kinds of cells: first, in the centre, cells with thin walls forming a starch-rich parenchyma; second, a few layers

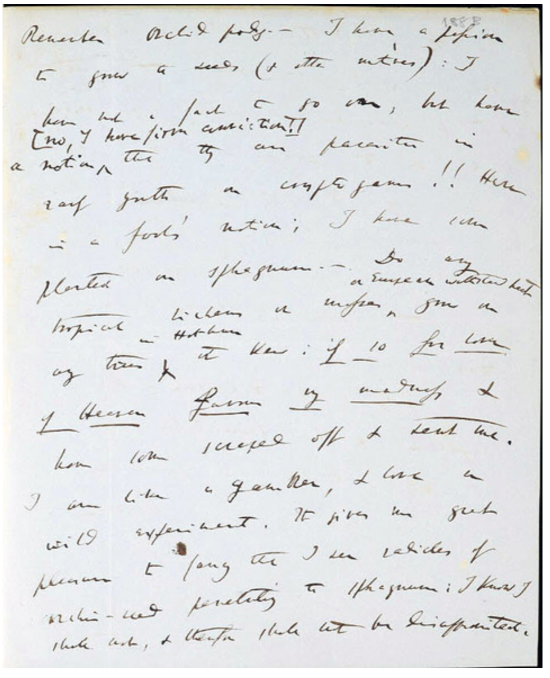
Remember Orchid pods.— I have a passion to grow the seeds (& other natives): I have had a fad to go on, but have [no, I have firm conviction!!] a notion that they are parasites in early growth on cryptogams!! Here is a fool's notion; I have some planted on sphagnum.— Do any tropical lichens or mosses or fungi encased within bark grow on any trees at Kew: if so for love of Heaven favour my madness & have some scraped off & sent me. I am like a gambler, & love a wild experiment. It gives me great pleasure to fancy that I see radicles of ... to sphagnum: I know I ... perceptibly ... shall not, & therefore shall not be disappointed.

FIGURE 13. Part of a letter from Charles R. Darwin to Joseph D. Hooker dated 26 March 1863. Sources: Darwin Correspondence Project, "Letter no. 4061," accessed on 31 July 2024, https://www.darwinproject.ac.uk/letter/?docId=letters/DCP-LETT-4061.xml. Also published in The Correspondence of Charles Darwin, vol. 11. Images of original letters from the Cambridge University Library collections are courtesy of Cambridge University Digital Library (cudl.lib.cam.ac.uk). The image was not post-processed with Photoshop to retain the original's feel.

of cells filled by a tight peloton of septate mycelial filaments [2]; and third, at the periphery, a layer of epidermal cells without starch and without mycelial filaments . . .

. . . I checked that mycelial filaments colonized all its parts: There were some in the fruit stalk, and the fruit cavity itself was filled with them. These fruits contain germinating seeds that are encased in these filaments and grouped in more or less voluminous clusters. **So, seed germination arose within a culture of free mycorrhizas** [emphasis added; a comment by the translators is that by mycorrhizas, "Bernard means the fungal partner itself; Sellosse *et al.*, 2017].

To repeat: The observations, reasoning, and discovery (Fig. 11) are Bernard's. He could not have seen Darwin's letter.

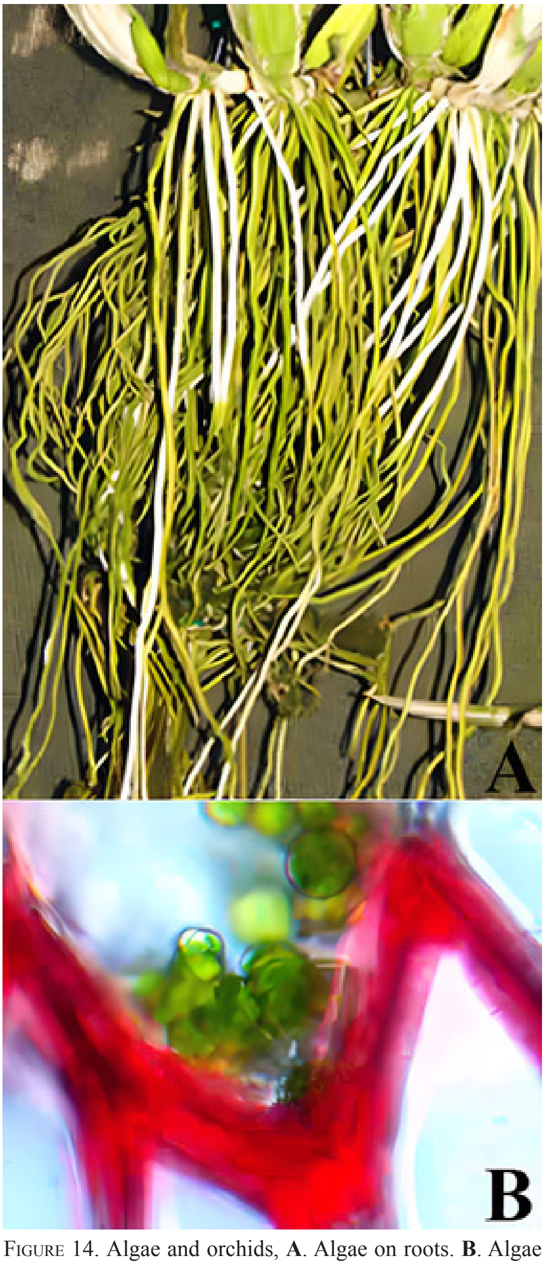

FIGURE 14. Algae and orchids, **A**. Algae on roots. **B**. Algae in roots. Source: Deepthi & Ray, 2020.

Darwin and his letter to Hooker. Charles Darwin's (Fig. 1A) interest in orchids is well documented, particularly in his book *On the Various Contrivances by which British and Foreign Orchids Are Fertilised by Insects* (Darwin, 1862, 1877a, b), as well as in his correspondence with several individuals (Darwin 1860a–c, 1861a–i, 1862a, b, 1863, 1880).

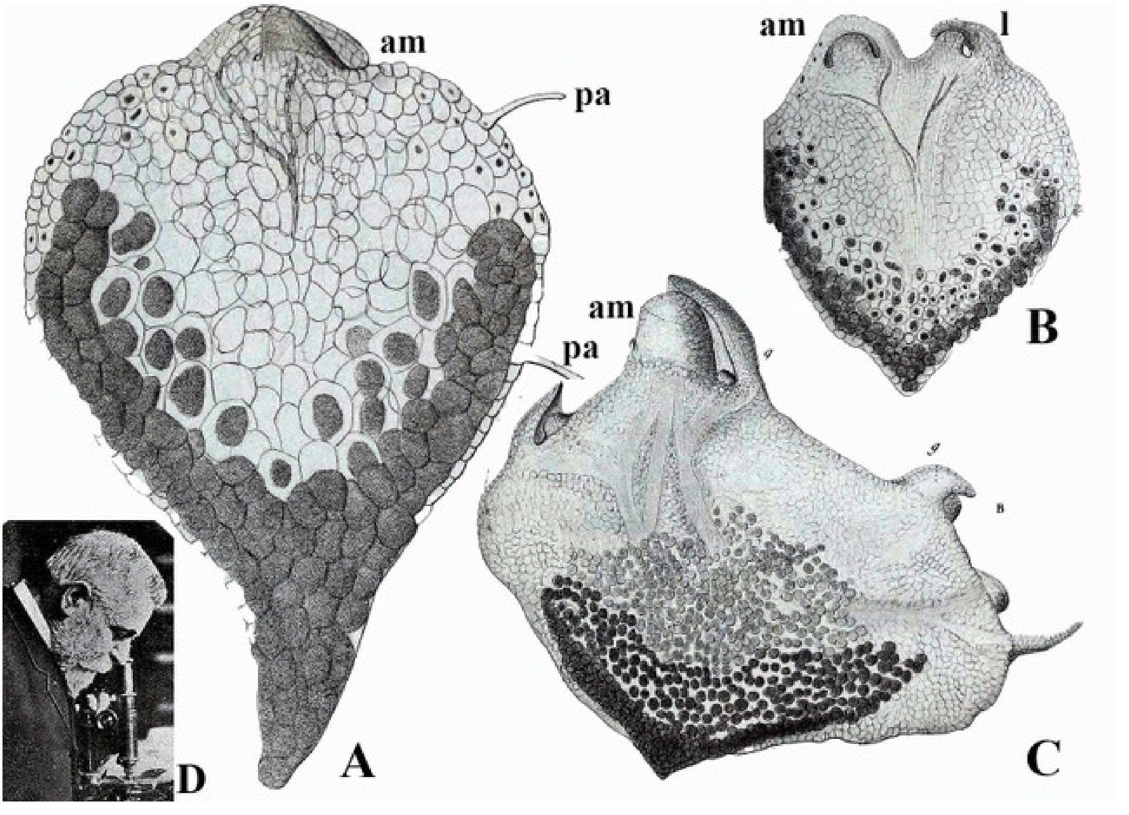

Figure 15. Fungus containing protocorms of *Oeceoclades maculata* (=*Eulophia maculata*) and E. E. Prillieux. **A**. Protocorm described as "larger embryo" in the original with papilae and an apical meristem. The cells containing dark masses were described as being "filled with a slightly granular yellowish material," which is presently known to be mycorrhizal fungi. **B–C**. More advanced developmental stages of proocorms. Dark masses are the "granular yellowish material" described above. **D**. Edouard Ernest Prillieux (1829–1915). Size bars are not available. The image was post-produced with Photoshop. Explanation of symbols: bold face capitals and lower case letters were added; small standard font letters are as in the original: am, B, apical meristem; g, l, leaf; pa, papilla. Sources: Prillieux & Rivière, 1856a, 1856b, also used in Yam *et al.,* 2002.

In the last paragraph of his letter to J.D. Hooker, dated March 26, 1863 (Fig. 1B; Fig. 13 shows the last page), he wrote:

"Remember Orchid pods.— I have a passion to grow the seeds (& other motives): I have not a fact to go on, but have a notion (no, I have firm conviction!) that they are parasites in early youth on cryptogams!! Here is a fool's notion; I have some planted on sphagnum. Do any tropical lichens or mosses or European withstand heat grow on any trees in Hothouse at Kew; *if so for love of Heaven favour my madness* & have some scraped off & sent me. I am like a gambler, & love a wild experiment. It gives me great pleasure to fancy that I see radicles of orchis-seed penetrating the sphagnum; I know I shall not, & therefore shall not be disappointed."

This paragraph raises questions.

Darwin appeared to expect that germinating orchid seeds would produce radicles, even though they do not. Illustrations available at the time confirm his misconception (Fig. 7; for a review with illustrations, see Yam *et al.*, 2002). He may have expected to see radicles because David Moore stated, "the protrusion of the young *radicle* (italics added) and cotyledon takes place" (Moore, 1849), even though most orchid seeds lack cotyledons. It is essential to acknowledge that during the time of Moore and Darwin, there was a limited understanding of orchid seeds and their germination processes. Their beliefs regarding cotyledons and radicles were incorrect only when viewed through the lens of current knowledge. In any case:

There is no mention of radicles or cotyledons in the two other reports regarding orchid seed germination published in the Gardeners' Chronicle (Cole, 1849; Gallier, 1849). None of the three reports (Cole, 1849; Gallier, 1849; Moore, 1849; Table 1) refer to a structure in seedlings, which Darwin (or anyone) could have equated to radicles. Darwin's statement, "I know I shall not," suggests that he hoped for radicles but understood that none would be produced, even if his seeds germinated.

It is possible that Darwin was unaware of, or chose to ignore, the three methods of orchid seed germination published in 1849 in the Gardeners' Chronicle. If he did ignore them, it is perplexing why he would do so, especially since Dr. John van Wyhe's comprehensive catalogue, "The Complete Library of Charles Darwin" (van Wyhe, 2002), indicates that Darwin had the complete 1849 volume of the Gardeners' Chronicle in his library. A review of a PDF downloaded from the link in van Wyhe's Catalog on the Darwin Online site (2002) confirms that the relevant pages are all present, intact, and readable: issue No. 35 (Saturday September 1, 1849, page 549); issue No. 37 (Saturday September 15, 1849, page 582); and issue No. 42 (Saturday October 20, 1849, page 661). Unfortunately, it remains unclear whether Darwin read them.

Epidendrum × *elongatum* Jacq., *Epidendrum crassifolium* Lindl. (=*Epidendrum ellipticum* Graham), *Cattleya forbesii* Lindl., and *Phaius albus* Lindl. (=*Thunia alba* (Lindl.) Rchb.f.) seeds were germinated by being gently shaken over the surfaces of orchid pots filled with loose growing material or, accidentally or intentionally, on bare wood (Moore, 1849). *Bletia tankervilleae* (Banks) Blume seeds germinated in "common soil" several years before 1849 (Cole 1849). *Epidendrum* × *elongatum* was also germinated on a block of wood covered with moss (Cole, 1849). Other orchid seeds germinated on the sides of wet pots (Cole, 1849). Attempts to germinate seeds on the tops of orchid pots, moss, and coconut shells were unsuccessful (Cole, 1849). Seeds of *Dendrobium nobile* Lindl. crossed with *Dendrobium chrysanthum* Wall. ex Lindl were germinated on wet cork pressed into sand (Gallier, 1849).

Starting around 1950–1953, seeds at the Veitch Royal Exotic Nurseries were sown upon blocks of wood, pieces of tree-fern stems, strips of cork, and moss that covered the surfaces of the pots with growing plants. They experimented in various situations that seemed promising, although successful germination was infrequent and limited (Veitch, 1885, 1887–1894).

Instead of using these methods, Darwin chose to plant his seeds in sphagnum, likely because it was a common potting substrate for orchids at the time (Williams, 1852, 1862). He did not provide specific details about the sphagnum. If the sphagnum was unused or had not come into contact with a substrate that supported orchids, it likely did not contain the fungi that could facilitate germination. According to Darwin's letter, the seeds did not germinate.

Questions that arise regarding Darwin's letter are how and why he developed the concept that led him to predict Bernard's discovery that orchid seeds (or seedlings) require fungi for germination and early growth. As he stated, they "are parasites in early youth on cryptogams". At the time, this concept was neither obvious nor the only possibility.

Algae can and do grow on the outside of the velamen of orchid roots, making them easily visible (Fig. 14A; Deepthi & Ray, 2020). They can also be found inside roots (Fig. 14B) but are less visible there. Since Darwin grew orchids in his greenhouse, he probably observed algae on the roots. At that time, there was no reason to assume that algae could not form a symbiotic relationship with orchids. Currently, it is known that blue-green algae are associated with orchids (Deepthi & Ray, 2020). For some reason, Darwin did not conclude that orchid seeds might depend on algae for germination or have a parasitic relationship with them.

Some orchid roots are associated with bacteria (Ansiya *et al.*, 2024; Kaur & Sharma, 2021). Since Darwin probably did not observe these bacteria, they did not factor into his considerations.

There are several possible reasons why Darwin might have been drawn to the idea of a symbiotic relationship (later termed mycorrhizal) between fungi and orchids, which seemed plausible to him.

- He had an interest in fungi, as evidenced by the collection he accumulated during his voyage on the H.M.S. Beagle (Berkeley, 1840).

- It is likely that he was aware of plant-fungus relationships at the time (Drude, 1873).

- His library contained several books on fungi (van Wyhe, 2002).

- He was particularly interested in molds (Darwin, 1838, 1840, 1844), although his primary focus was on those produced by earthworms. While this topic may not seem relevant today, it's worth noting that Darwin's perspective might have been different regarding whether earthworm molds contain fungi.

- Perhaps he read or at least saw illustrations in the works of Link, Prillieux, and Rivière (Link, 1840; Prillieux & Rivière, 1856a, b). However, most of Link's papers were not in his personal library. Darwin frequently utilized several libraries (https://darwin-online.org.uk/EditorialIntroductions/vanWyhe_The_Complete_Library_of_Charles_Darwin.html). Therefore, if he did read these papers, it may have been in the library of the Linnean Society of London (Linnean Society, 1866).

- His interest in the interaction between plants and pathogenic fungi is noted in a letter discussing a fungal disease he encountered in 1848 (Ristaino & Pfister, 2016). He observed how easily a pathological fungus could infect and spread within plants, like potatoes, which may have led him to assume that the same would apply to fungi that orchids might parasitize.

- He read a book (Irmisch, 1853), which mentions the presence of fungi in orchid roots. This exposure likely enabled him to draw accurate conclusions about the nature and role of fungi, or at least make an educated guess. This is plausible because Irmisch's book was in his library.

However, Darwin may have been unaware that *Epidendrum elongatum* could germinate on a "block of wood covered with moss" (Cole, 1849), a type of cryptogam. If he were aware of germination on moss, he may have underestimated its significance and considered fungi to be more likely candidates for parasitism by orchids.

Since Darwin used the term "cryptogams" in his letter, uncertainty remains about whether he specifically referred to fungi, despite the term commonly encompassing fungi during his time. It is possible to suggest that he might have meant bryophytes, such as mosses (particularly since he explicitly mentioned *sphagnum* in his experiments), pteridophytes (ferns and their relatives), or other non-vascular plants. However, bryophytes, ferns, and mosses can be excluded from consideration because, although they sometimes grow in or near containers where orchids are potted, orchid seedlings were never seen to be associated with them.

Because he was writing a letter to his friend Hooker, Darwin was likely less specific and less meticulous in defining his terms than he would have been in a formal paper or book. Given Darwin's interest in plant-fungal interactions (evidenced by his curiosity about the potato disease), it is possible that he at least considered fungi to be potential partners in the germination of orchids.

The claim that Darwin was prescient in predicting the orchid-fungal relationship might be debated terminologically (did he mean fungi by using "cryptogams"?). However, it is clear that his thoughts and considerations were in the right direction. He questioned whether orchids required an external biological partner for germination. The evidence for whether he was specifically thinking of fungi remains circumstantial. Still, the discussion highlights how forward-thinking Darwin was in making such connections, even if he did not arrive at the precise mechanism later discovered by Bernard.

Overall, it seems clear that Darwin's letter to Hooker was remarkably prescient in predicting what Bernard discovered: Orchid seeds depend on fungi for germination. Like Bernard, Darwin:

- Did not view the colonization of orchid seeds and seedlings by fungi as pathological.
- Recognized that orchids can be parasitic on fungi.
- Foresaw the lifelong relationship between orchid plants and their mycorrhizal fungi.

It is important to emphasize (and repeat more than once) that Darwin's insightful letter does not diminish Bernard's achievement in any way. Bernard deserves credit for his significant contribution to orchid science. He made his discovery independently of Darwin without ever having read Darwin's letter to Hooker.

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A NEW SPECIES OF *CHLORAEA* (CHLORAEINAE)

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Abstract. In Peru, *Chloraea* previously included five species. However, recent field explorations and herbarium specimen revisions have led to the discovery of a new species from northern Peru. Here, we describe and illustrate *Chloraea aequatorialis*, the species with the most northern distribution recorded for the genus, ranging from 5º50' to 7º56' S. The new species closely resembles *C. septentrionalis*, with which it grows partly in sympatry in the departments of Cajamarca and La Libertad, but it can be easily distinguished by its larger sepals and petals, a lip disc covered by thin, narrow, and long appendages, a longer lip claw, column, and anther, and a shorter stigma. We provide information on the habitat, distribution, and conservation status of the new species, along with an updated description of *C. septentrionalis* and a key to the Peruvian species of *Chloraea*.

Resumen. En Perú, *Chloraea* estaba conformado por cinco especies. Sin embargo, recientes exploraciones de campo y la revisión de ejemplares de herbario han permitido descubrir una nueva especie del norte del Perú. Aquí describimos e ilustramos a *Chloraea aequatorialis,* la especie con la distribución más al norte registrada para el género, entre los 5º50' y 7º56' S. La nueva especie es más similar a *C. septentrionalis*, con la que crece parcialmente en simpatría en los departamentos de Cajamarca y La Libertad, pero se diferencia fácilmente de esta por tener sépalos y pétalos más grandes, disco del labelo cubierto por apéndices largos, delgados y angostos, la uña del labelo, columna y antera más largas, y el estigma más corto. Proporcionamos información sobre el hábitat, distribución y estado de conservación de la nueva especie, una descripción actualizada de *C. septentrionalis* y una clave para las especies peruanas de *Chloraea*.

Keywords / Palabras clave: Andes peruanos, *Chloraea aequatorialis*, *Chloraea septentrionalis*, Orchidaceae, Peruvian Andes, taxonomía, taxonomy

Introduction. The South American genus *Chloraea* Lindl., with 52 species, is the largest of the subtribe Chloraeinae (Trujillo *et al*., 2023). It is distributed in disjunct areas from northern Peru and southeastern Brazil to southern Chile and Argentina, including the Falkland Islands (Cisternas *et al*., 2012; Correa, 1969). The genus consists of terrestrial herbs with several leaves in a basal rosette or spirally arranged along the stem. The roots are fleshy and fasciculate. The inflorescence is terminal, the peduncle is covered with several bracts similar to the leaves, and the raceme consists of few to many resupinate, white, greenish, yellow or orange flowers often with longitudinal or reticulate contrastingly colored nerves, or warts. The sepals and petals are free. The lip is clawed, entire, 3-lobed or pandurate, recurved, commonly provided with crests, warts, keels, or appendages, margins entire or pinnately divided, toothed or wavy. The column is elongate, arcuate, with narrow wings. The anther is terminal, erect or slightly incumbent, with a reflexed apex and bilocular. The stigma is ventral, concave, entire, ovate or oblong (Cisternas *et al*., 2012; Correa & Sánchez, 2003).

In Peru, *Chloraea* previously included five species: *C. densipapillosa* C. Schweinf., *C. multilineolata* C. Schweinf., *C. pavonii* Lindl., *C. reticulata* Schltr., and *C. septentrionalis* M.N. Correa. Except for *C. reticulata*, which also occurs in Bolivia and Argentina, they are endemic to the country (Roque & León, 2006). The species inhabit forest relicts, shrublands on rocky slopes of the dry inter-Andean valleys, and the Lomas formation in the desertic, coastal lowlands (Trujillo & Paredes-Burneo, 2020; Trujillo *et al.*, 2023).

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Chloraea septentrionalis, has the northernmost distribution recorded for the genus. This species occurs in the northwestern Peruvian Andean valleys, between 7º and 8º S, in the departments of Cajamarca and La Libertad. However, a recent botanical survey conducted by one of the authors (LO-H) in the department of Piura, led to the discovery of a new species of *Chloraea* at 5º 50'S (Fig. 1), making it the species with the most northern distribution recorded. The revision of the specimens of *Chloraea* from herbaria and photographic records on iNaturalist (2025) revealed that the new species is also distributed in the departments of Cajamarca and La Libertad.

In this study, we present a detailed morphological description, a line drawing and color photographs of the new species, along with information on its habitat, a map of its known distribution, and an assessment of its extinction risk are also provided. Additionally, we present an updated description of *C. septentrionalis* based on our field observations, alcohol-preserved material, and herbarium specimens, to supplement the information provided in its protologue. The distinguishing floral features of both species are contrasted in a comparative line drawing.

Materials and methods. Fieldwork was conducted in November 2017 and April 2024 in the district of Huarmaca, province of Huancabamba, Piura Department. Live plants were photographed, and notes on their habitat and phenology were recorded *in situ*. Three specimens were pressed and deposited at herbaria HUT, PRG, and USM. Line drawings, measurements, and descriptions were prepared from herbarium specimens, liquid-preserved flowers, and flowers from herbarium specimens softened by immersion in boiling water. The original descriptions and other relevant literature on the taxonomy of the genus *Chloraea* were consulted (e.g., Correa, 1969; Schweinfurth, 1941; Trujillo & Paredes-Burneo, 2020). Additionally, *Chloraea* specimens were physically reviewed at the herbaria CPUN, HAO, HUT, M, NY, and USM. High-resolution digital images of specimens housed at F, HUH, MO, P, and W were examined through the online platforms Field Museum's online Botanical Collections Database (F, 2025) Harvard University Herbaria (HUH, 2025), Missouri Botanical Garden (Tropicos.org, 2025), Muséum National d'Histoire Naturelle, Vascular Plants Database (P, 2025), and JACQ Consortium Virtual Herbarium (JACQ, 2025). Photographs were taken with a Canon® Rebel T3 digital camera equipped with a Canon EF-S 18-55 mm f/3.5-5.6 lens. Images were processed using Adobe Photoshop 24.0.1 (Adobe Inc., 2022). The conservation status was assessed following the categories and criteria of the International Union for Conservation of Nature Red List (IUCN, 2024), based on estimates of the Extent of Occurrence (EOO) and Area of Occupancy (AOO), both calculated using the online GeoCat Geospatial Conservation Assessment Tool (Bachman *et al*., 2011). The map was created with QGIS Desktop 3.40.5 (QGIS.org, 2024) and edited in Adobe Photoshop. Botanical terminology followed Beentje (2016) and Stearn (2004).

Taxonomic treatment

Chloraea aequatorialis D.Trujillo & Ocupa, ***sp. nov.*** (Fig. 1B, 2–3, 4A).

TYPE: PERU. Piura: Provincia de Huancabamba, distrito de Huarmaca, Cerro Porcuya, carretera hacia Tallacas, 2738 m, 08 June 2024, *L. Ocupa 348* (holotype: PRG-19952!; isotype: USM-357331!).

Diagnosis: *Chloraea aequatorialis* is most similar to *C. septentrionalis* M.N.Correa but differs in the longer sepals and petals (sepals 3.0–3.4 cm *vs*. 1.8–3.1 cm; petals 2.8–3.1 cm *vs*. 2.05–2.75 cm), the lip covered with warts, laterally flattened, long appendages at base, and thin, narrow, long appendages on the disc (*vs*. lip covered by fleshy long, non-laterally flattened appendages at base and disc), the claw of the lip 7–9 mm long (*vs*. claw 2 mm long), the column 2.3–2.6 cm long, strongly arcuate and apex with narrow wings (*vs*. column 1.60–2.05 cm long, slightly arcuate and wingless), the obtriangular stigma 5.0–5.5 mm long (*vs*. oblong stigma 6–8 mm long), and the anther 6–7 mm long (*vs*. 4.5–5.0 mm long).

Plant terrestrial about 32–52 cm high. *Roots* fasciculate, cylindrical and fleshy. *Stem* stout, leafy on its lower one half. *Leaves* spirally arranged along the stem, amplexicaul, blade ovate to elliptic, obtuse or acute, slightly carinate along the central vein, 5.0–9.5 × 2.2–4.2 cm, gradually decreasing in size and turning into bracts of the peduncle of the inflorescence from about the middle of the stem. *Raceme* erect, lax,

Figure 1. **A**. *Chloraea septentrionalis*. **B**. *Chloraea aequatorialis*. Photographs by D. Trujillo (A, from *D. Trujillo 210*) and S. Garrido (B, from *S. Garrido s.n*).

3–11-flowered, the flowers decreasing in size towards the apex, rachis 7.5–12.5 cm long. *Floral bracts* green, broadly elliptic to ovate, obtuse to acute, shorter to longer than the ovary, 2.5–4.0 × 1.3–3.0 cm (decreasing in size towards the apex of the raceme). *Flowers* resupinate, sepals and petals light greenish yellow with dark green, reticulate veins, lip light yellow near the base and bright yellow otherwise, with green, reticulate veins on the margins of the lateral lobes, column white to cream white with dark red spots at the base, anther yellow and greenish white. *Ovary* green, subclavate, slightly twisted and longitudinally sulcate, with a short pedicel, 2.4–3.0 cm long. *Dorsal sepal* elliptic, obtuse, with 5 main nerves, lateral nerves branched, 3.2–3.4 × 1.2–1.6 cm. *Lateral sepals* obliquely ovate-elliptic, obtuse to subacute, with 5–6 main nerves, lateral nerves branched, 3.0–3.3 × 1.2–1.6 cm. *Petals* broadly elliptic, obtuse to acute, with 7–9 main nerves, lateral nerves branched, 2.8–3.1 × 1.5–2.1 cm. *Lip* 3-lobed, recurved, clawed, 9 main longitudinal nerves, lateral nerves branched, claw 7–9 mm long, lip base densely covered by laterally flattened long appendages turning into warts near the claw; disc with numerous thin, narrow, long appendages along the main nerves of the lip which become shorter towards the apex, 2.0–2.4 × 1.6–2.0 cm; lateral lobes elliptic, incurved, entire, 1.15–1.25 × 0.5–0.6 cm; mid-lobe oblong to square, recurved, margin somewhat undulate, 0.95–1.0 × 0.9–1.2 cm. *Column* slender, strongly arcuate, nearly flat ventrally, base bearing a fovea and a small, rounded projection at each side, 2.3–2.6 cm long, apex with narrow wings 1 mm wide. *Stigma* obtriangular, basal part with prominent margins, 5.0–5.5 × 4–5 mm (about 1/5 column length). *Anther* terminal, partially incumbent, apex reflexed, 6–7 × 5 mm. *Fruit* not seen.

Paratypes: PERU. **Departamento de Cajamarca**, provincia de Contumazá, Chiñac (cerca a Guzmango), 2200 m, 28 Mar. 1985, *A. Sagástegui & S. Leiva 12539* (HUT-20194!). **Departamento de La Libertad**: provincia de Otuzco, entre Otuzco y Usquil, 3000 m, 26 Jun. 1962, *A. López, A. Sagástegui & A. Aldave s.n.* (HUT-3965!); Provincia de Otuzco, abajo San Miguel, 3100 m, 5 Jun. 1993, S. *Leiva & P. Leiva 526* (GH [HUH01940927, photo!], HAO-2838! [destroyed, photo record], HUT-21875!). **Departamento de Piura**: provincia de Huancabamba, carretera cuello de Porcuya – Tallacas, 2450 m, 8 Jun. 2017, *L. Ocupa 243* (HUT-65427!).

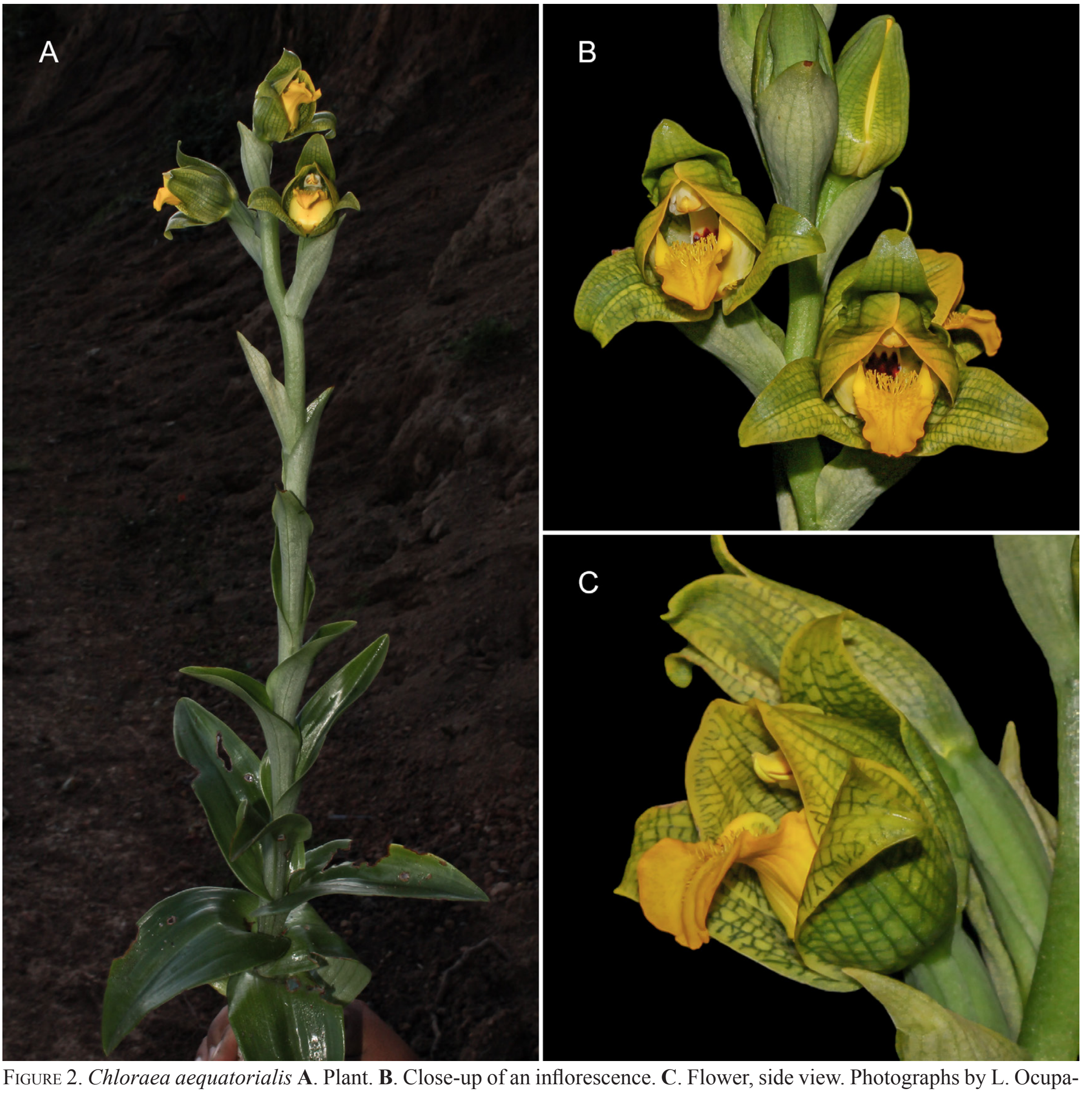

FIGURE 2. *Chloraea aequatorialis* **A**. Plant. **B**. Close-up of an inflorescence. **C**. Flower, side view. Photographs by L. Ocupa-Horna from *L. Ocupa 243* (A) and *L. Ocupa 348* (B, C).

OTHER RECORDS: PERU. **Departamento de Cajamarca**: provincia de San Pablo, 7°02'55.3"S 78°38'52.1"W, 4 Jun. 2024, *E. Gastolomendo s.n.* (Gastolomendo, 2024). Departamento de La Libertad, provincia de Pataz, 3027 m, 30 Mar. 2024. *S. Garrido s.n.* (photo record!).

ETYMOLOGY: From Latin *aequatorialis*, referring to the distribution of the new species, in the equatorial region.

DISTRIBUTION AND ECOLOGY: The species is endemic to the northwestern slopes of the Peruvian Andes, between 5º50' and 7º56'S, in the departments of Cajamarca, La Libertad and Piura (Fig. 5), at elevations of 2200–3100 m. Individuals were found growing in shrublands, among rocks on stony hillsides. In some locations in the Provinces of Contumaza and San Pablo (Cajamarca), and Otuzco (La Libertad), *C. equatorialis* lives sympatrically with *C. septentrionalis*. The population located near the Abra de Porcuya grows scattered on soils and slopes formed by sedimentary layers of clays, silts, sands and stony gravels, among dispersed shrubs of *Brachyotum* sp. (Melastomatace-

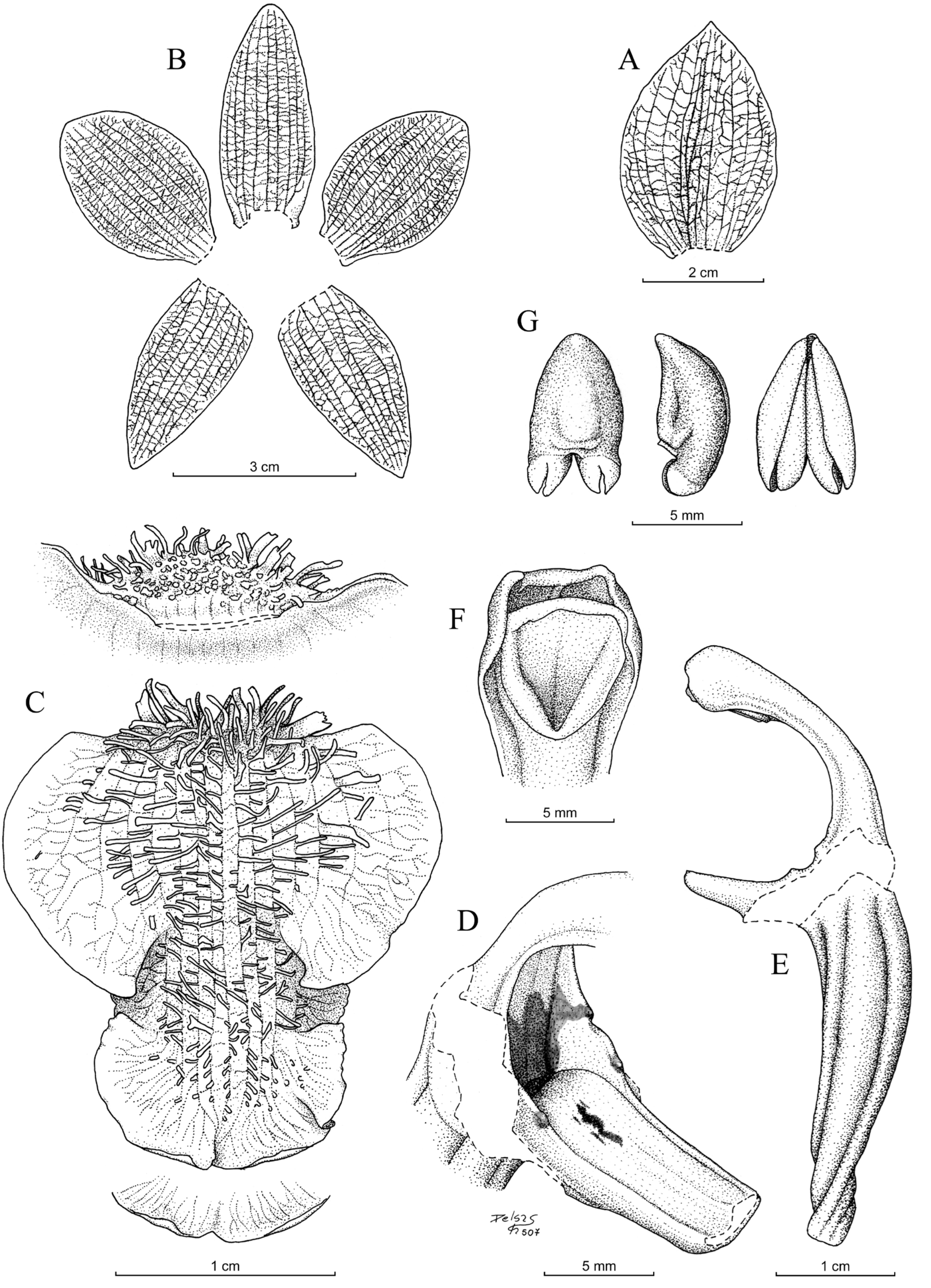

FIGURE 3. *Chloraea aequatorialis* **A**. Floral bract. **B**. Dissected perianth. **C**. Lip. **D**. Base of column and claw. **E** Column and ovary. **F**. Stigma. **G**. Anther, dorsal, side and ventral view. Drawing by D. Trujillo based on *L. Ocupa 348*.

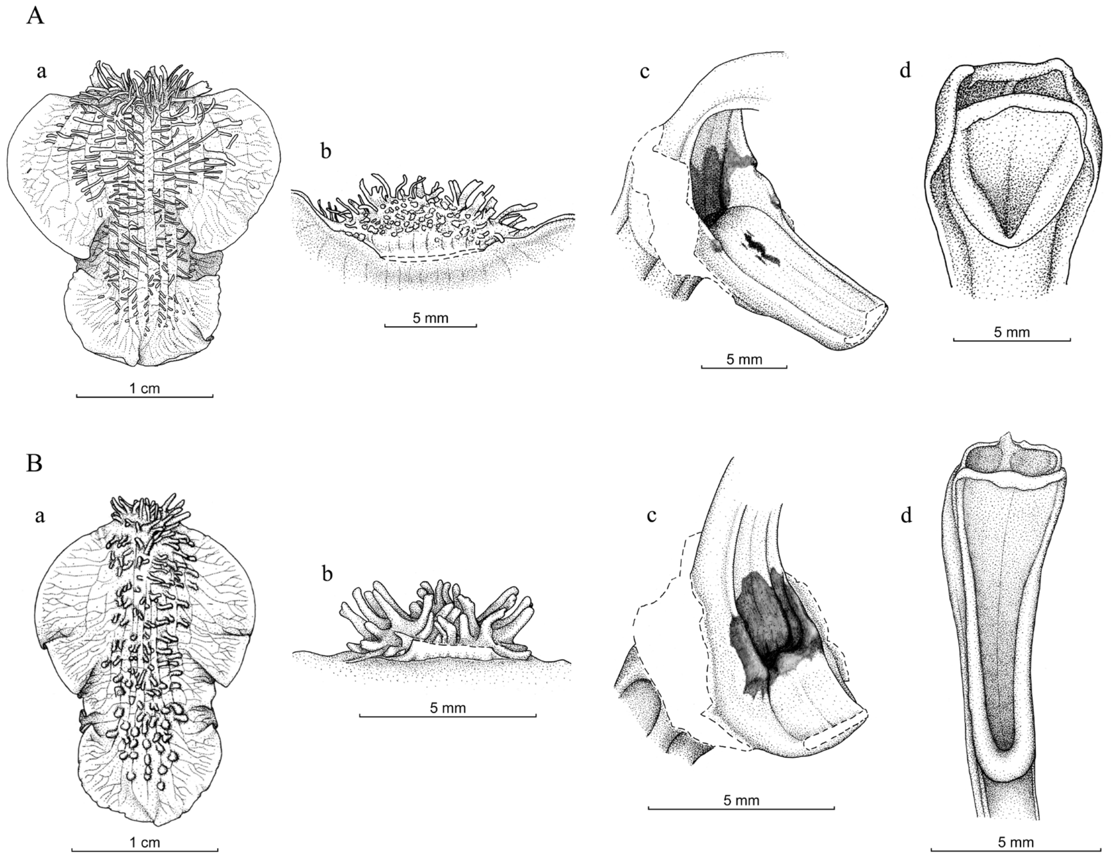

FIGURE 4. Morphological differences between *Chloraea aequatorialis* (A) and *Chloraea septentrionalis* (B). **a**. Lip. **b**. Base of the lip, back view. **c**. Base of column with the lip claw. **d**. Stigma. Drawing by D. Trujillo based on *L. Ocupa 348* (A) and *D. Trujillo 213* (B).

ae), *Clethra* sp. (Clethraceae), *Dodonaea viscosa* Jacq. (Sapindaceae), *Monnina* sp. (Polygalaceae), *Oreocallis grandiflora* (Lam.) R.Br. (Proteaceae), and other orchid species such as *Epidendrum rauhii* Hágsater, *Oncidium cajamarcae* Schltr. and *Sobralia aryaelizabethiana* Ocupa.

PHENOLOGY: Flowering occurs between March and June, at the beginning of the dry season.

CONSERVATION STATUS: *Chloraea aequatorialis* is endemic to the Peruvian Andes. It is known from six locations in the northwestern departments of Cajamarca, La Libertad, and Piura. Currently, the primary threats to *C. aequatorialis* are habitat loss and degradation caused by land conversion for agriculture, overgrazing, reforestation with exotic species of genera *Eucalyptus* L'Hér. (Myrtaceae) and *Pinus* L. (Pinaceae), and the traditional practice of burning of grasses on hillsides by farmers. For the population found in Cerro Porcuya (Piura), along the slopes of the road to Tallacas, maintenance work on the road that crosses this ecosystem, and ongoing landslides caused by erosion and heavy rains pose additional threats. Currently, no population of the new species has been recorded in a protected area that would adequately safeguard its habitat. Based on the six known locations, the estimated Extent of Occurrence is 14647.86 km^2, and the Area of Occupancy is 24 km^2. Therefore, *C. aequatorialis* is assessed as Vulnerable based on IUCN criteria B1 and B2 (VU, B1ab(i.iii) + B2ab(ii, iii)) (IUCN, 2024).

Discussion. The new species shows a similar distribution and overall morphology to *C. septentrionalis*

(Fig. 1). Their ranges partially overlap (Fig. 5), and both species have lax racemes of yellow flowers, with sepals and petals that have green reticulate veins and a 3-lobed lip. However, *C. aequatorialis* can be easily distinguished from *C. septentrionalis* by having larger sepals and petals, a lip covered with warts, laterally flattened, long appendages at base, and thin, narrow, and long appendages on the disc, a longer lip claw, column, and anther, and a shorter, differently shaped stigma (Fig. 3, 4).

Correa (1969) described *C. septentrionalis* based on the collection *A. López 651* (holotype: HUT-1515! (Fig. 6), isotypes: BAB000611 [photo!], LIL000242 [photo!], USM000595!), and cited *A. López et al. s.n.* (HUT-3965!) as additional material examined (Fig. 7). However, Correa overlooked some floral features of *A. López et al. s.n.* that conflict with *C. septentrionalis* but instead match *C. aequatorialis* (Fig. 7B). These include an obtriangular and a short stigma (about 1/5 column length), 7 mm long lip claw, and larger sepals and petals. Hence, here we assign *A. López et al. s.n.* to *C. aequatorialis*.

A close examination of herbarium specimens of *Chloraea* from northern Peru revealed that the specimens: *A. Sagástegui & S. Leiva 12539* (HUT-20194) and *S. Leiva & P. Leiva 526* (HAO-2838 (destroyed), HUT-28175), identified as *C. septentrionalis* by Trujillo & Paredes-Burneo (2020) and Trujillo *et al.* (2023), also belong to the new species described here.

The discovery of *Chloraea aequatorialis* emphasizes the limited understanding of certain orchid genera in Peru. To improve this, more extensive field explorations and a comprehensive review of herbarium materials are crucial to better identify and understand the diversity of this genus in the country.

Chloraea septentrionalis M.N.Correa, Darwiniana 15(3–4): 489. 1969.

TYPE: PERU. Departamento de La Libertad: Provincia de Otuzco, Shilte, hacienda Llaguén, [3100 m, 2 Junio 1951], *A. López 651* (holotype: HUT-1515! (Fig. 6); isotypes: BAB000611 [photo!], LIL000242 [photo!], USM000595!).

Plant terrestrial about 28–98 cm high. *Roots* fasciculate, cylindrical and fleshy. *Stem* stout, leafy. *Leaves* spirally arranged along the stem or com-

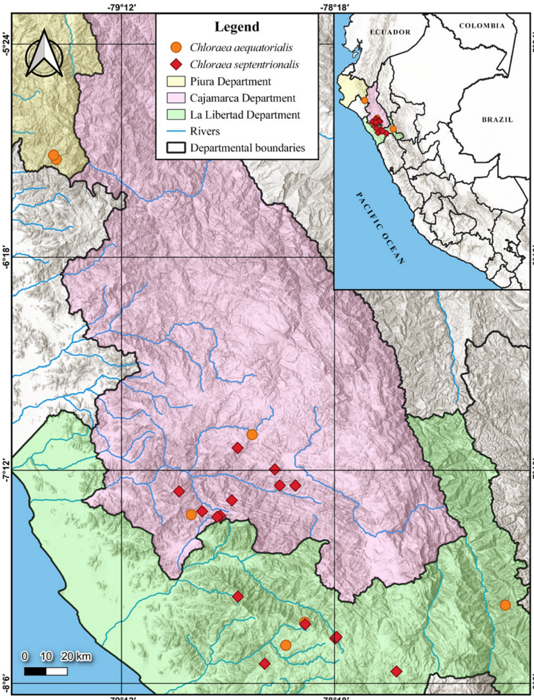

FIGURE 5. Distribution map of *Chloraea aequatorialis* and *C. septentrionalis* in Peru. Prepared by L. Ocupa-Horna.

pressed like a basal rosette, amplexicaul, blade ovate, ovate-lanceolate or oblong-lanceolate, acute to obtuse, 2.5–13.5 × 1.6–5.0 cm, gradually decreasing in size and becoming in bracts of the peduncle of the inflorescence. *Raceme* erect, lax, 3–20-flowered, flowers decreasing in size towards the apex, rachis 3–23 cm. *Floral bracts* green, broadly elliptic to ovate, acute to acuminate, 8–11 nerves, shorter to slightly longer than the ovary, 1.4–3.5 × 1.0–2.05 cm. *Flowers* resupinate, sepals and petals white near the base and yellow otherwise, with green reticulate veins, lip base and lateral lobes white with green reticulate veins, midlobe yellow, column white with red spots at the base, anther yellow and greenish white. *Ovary* green, subclavate, with a short pedicel, 1.6–3.8 × 0.20–0.45 cm. *Dorsal sepal* oblong to elliptic, obtuse to subacute, 5–7 main nerves, lateral nerves branched or not, 1.8–3.1 × 0.7–1.1 cm. *Lateral sepals* ovate-lanceolate to oblong-lanceolate, oblique, acute to sub-obtuse, 3–5 main nerves, lateral nerves branched, 2.4–2.8 × 0.7–1.2 cm. *Petals* elliptic to sub-rhombic, rounded to obtuse, 5–7 main nerves, lateral nerves branched, 2.05–2.75 × 0.95–1.60 cm.

FIGURE 6. Holotype of *Chloraea septentrionalis* (*A. López 651*). Reproduced with the kind permission of the Herbarium Truxillense, Universidad Nacional de Trujillo.

Figure 7. *Chloraea aequatorialis* (*A. López et al. s.n.*). **A**. Herbarium sheet. **B**. Close-up of the dissected flower. Reproduced with the kind permission of the Herbarium Truxillense, Universidad Nacional de Trujillo.

Lip 3-lobed, recurved, shortly clawed, 7–9 main longitudinal nerves, laterals nerves branched, claw 2 mm long; lip base densely covered by fleshy long appendages, disc with numerous fleshy long appendages along the main nerves of the lip getting shorter towards the apex turning into warts, 1.6–2.2 × 1.2–1.8 cm; lateral lobes elliptic, incurved, 1.0–1.3 × 0.4–0.6 cm; mid-lobe oblong to widely elliptic, recurved, margin somewhat undulate, 0.75–1.00 × 0.70–0.95 cm. *Column* slender, slightly arcuate, base bearing a shallow fovea and a small projection or transversal ridge, 1.60–2.05 cm long. *Stigma* oblong, basal part with prominent margin, 6–8 mm long (2/5 column length). *Anther* terminal, partially incumbent, 4.5–5.0 × 2.0–2.5 mm. *Fruit* ellipsoid, 2.5–3.5 × 0.6–1.1 cm.

Specimens examined: PERU. **Departamento de Cajamarca**: provincia de Cajamarca, distrito de Cajamarca, entre Cajamarca y Cumbe Mayo, km. 14, en el Arboretum cumbe Mayo de CICAFOR, ladera, suelo turboso, 3400 m, 18 Abr. 1981, *I. Sánchez, V. Torrel & E. Medina 2480* (CPUN-1008!); provincia de Cajamarca, distrito de Cajamarca, Tamiacocha, elevación al S. de Cerro Negro, a 5 km del Abra El Gavilán, jalca graminosa, 3569 m, 4 Jun. 2001, *I. Sánchez 10660* (CPUN-14772!); provincia de Cajamarca, distrito de San Juan, Yumagual, ladera que converge a la quebrada Yunagual, vegetación arbustiva y arbórea, 2600 m, 26 Jun. 1966, *I. Sánchez & A. Iparraguirre 251* (CPUN-1007!, HAO-1892! [destroyed, photo record]); provincia de Contumazá, entre La Travesía y el Bosque de Cachil, bosque de arbustos y arboles más o menos denso, 2700 m, 2 Jul. 1983, *I. Sánchez, J. Sánchez & A. León 3163* (CPUN-1009!); provincia de Contumazá, entrada al Bosque de Cachil, ladera, 2440 m, 28 Jul. 1993, *A. Sagástegui, S. Leiva & P. Lezama 14949* (F-2128307 [photo!], HAO-2438! [destroyed, photo record]); province of Contumazá, road Contumazá to Cascas, area above Bosque de Cachil, Lomo Limpio, 2800-3500 m, 19 Jun. 1998, *M. Weigend, T. Franke, J. Skrabal & M.*

Gonzales 1998/562 (CPUN-20224!, F-2209931 [photo!], M!, USM-174201!); province of Contumazá, road Contumazá to Guzmango, 5–10 km west of Contumazá, 2600 m, 20 Jun. 1998, *M. Weigend, T. Franke, J. Skrabal & M. Gonzales 1998/563* (CPUN-20248!, M!, USM-174199!); provincia de Contumazá, Amanchaloc, Guzmango-Contumazá, ladera abierta, 2600 m, 7 May 1965, *A. Sagástegui & M. Fukushima 5145* (AMES-113595 [HUH01941028, photo!]); provincia de Contumazá, Tantarica, ladera rocosa, 1 May 1982, *A. Sagástegui, E. Alvites, S. López & J. Mostacero 10394* (HUT-17019!, NY04027063!); provincia de Contumazá, arriba de Lledén, ladera rocosa, 2500–3000 m, 28 Jun. 1983, *A. Sagástegui, J. Mostacero & E. Alvitez 10829* (GH [HUH-1940920, photo!], HUT-17787!, MO-3122800 [photo!], SEL-26765 [photo!]); provincia de Contumazá, Cruz del Hueco, ladera, 2880 m, 6 Jun. 1994, *A. Sagástegui, S. Leiva & P. Lezama 15327* (F-2145077 [photo!], HAO-3270! [destroyed, photo record]). **Departamento de La Libertad**: provincia de Otuzco, Shilte, Hda. Llaguén, en ladera, 3100 m, 2 Jun. 1951, *A. López 1515* (AMES-88199 [HUH01940928], photo!); provinca de Otuzco, Cerro Ragache (Salpo), ladera rocosa, 3400 m, 23 May 1984, *A. Sagástegui, M. Diestra & S. Leiva 11612* (HUT-18877!, MO-3226558 [photo!]); province of Otuzco, road from Otuzco to Usquil, 3200 m, 30 May 2001, *T. Henning & C. Schneider 309* (HUT-41128!, NY04027050!, M!, USM-187355!); provincia de Otuzco, districto de Usquil, Canibamba Alto, en pequeños roquedales y en las márgenes del río Perejil, 3512 m, 26 May 2005, *D. Trujillo 213* (URP!, SEL); provincia de Santiago de Chuco, cerro Ingacorral, arriba de Cachicadan, jalca sobre rocas, 4100 m, 10 Jun. 2001, *A. Sagástegui, S. Leiva & M. Zapata 16671* (F-2240253 [photo!],, HAO-3104! [destroyed, photo record]); provincia de Santiago de Chuco, distrito de Quiruvilca, La Victoria, al costado de la carretera, cerca de una mina de carbón, 3392 m, 25 May 2005, *D. Trujillo 210* (USM-357398!).

Another record: **Departamento de Cajamarca**: provincia de San Pablo, 7°06’18.14”S 78°42’32.83”W, 27 Apr. 2024, *C. Diaz s.n.* (Diaz, 2024).

Key to the Peruvian species of *Chloraea*

1. Flowers yellow, without or with tenuous longitudinal green nerves on sepals and petals; lip disc covered by short warts or ridges 2
   2. Sepals about 2.7 cm or less long, petals about 2.1 cm or less long; lip disc covered by dense mass of yellow warts and ridges .... ***C. densipapillosa***
   2a. Sepals 2.8 cm or more long, petals 2.3 cm or more long; lip disc covered by yellow or green warts along the main nerves of the lip .... ***C. multilineolata***

1a. Flowers yellow, light yellow or creamy white, with reticulate green nerves on sepals and petals; lip disc covered by long warts, appendages, or laterally flattened keels 3
   3. Lip white or creamy white with dark green margin; column about 1.5 cm or less long .... ***C. reticulata***
   3a. Lip yellow with green nerves along the disc or in the margins of the lateral lobes; column 1.6 cm or more long 4
      4. Petals elliptic-ovate, asymmetric, with 4 main nerves; lip entire to obscurely 3-lobed .... ***C. pavonii***
      4a. Petals elliptic to sub-rhombic or broadly elliptic with 5 to 9 nerves; lip clearly 3-lobed 5
         5. Lip claw 2 mm long, disc with fleshy long appendages, stigma oblong, 6–8 mm long (about 2/5 column length) .... ***C. septentrionalis***
         5a. Lip claw 7.0–9.0 mm long, disc with thin, narrow, long appendages, stigma obtriangular, 5.0–5.5 mm long (about 1/5 column length) .... ***C. aequatorialis***

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A TALE OF TWO WOMEN: THE CARIBBEAN ORCHID PORTRAITS OF LOUISE AUGUSTE VON PANHUYS (1763–1844) AND NANCY ANNE KINGSBURY WOLLSTONECRAFT (1791–1828)

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Abstract. Louise von Panhuys (1763–1844) and Nancy Anne Kingsbury Wollstonecraft (1791–1828) stand out historically as the first female illustrators of neotropical orchids. Louise von Panhuys epitomized an era when high social status was equated with a refined education; as the writers of her time described, a classic "lady of leisure." In contrast, Nancy K. Wollstonecraft, was the daughter of a clergyman from New England, born into the broad American middle class, which shaped the early decades of the United States' independent life. Both shared a common passion for: the exuberant forests of the Caribbean European colonies: von Panhuys in the Dutch territory of Suriname and Wollstonecraft on the Spanish island of Cuba. The artistic result of these two women is astounding and took different directions: while von Panhuys painted to entertain herself and with a mostly descriptive purpose, Wollstonecraft combined her artistic talent and botanical knowledge into a three-volume manuscript, *Specimens of the Fruits and Plants of the Island of Cuba* (unfortunately never published), with accurate and detailed descriptions and beautiful illustrations. Biographies of these two extraordinary women are accompanied by complete sets of their orchid paintings, eight by Panhuys (along with several of her landscapes and scenes from Suriname) and nine by Wollstonecraft. A clarifying note: Wollstonecraft's name is indistinctly given as 'Nancy Anne', 'Anne', or 'Nancy'. The author has used the name as it appears in various bibliographical sources.

Keywords/Palabras clave: botanical illustration, Cuba, feminism, feminismo, ilustración botánica, orchids, orquídeas, Surinam, Suriname

Introduction. Contemporaries in the first decades of the 19th century, Louise von Panhuys (1763–1844) and Nancy Anne Kingsbury Wollstonecraft (1791–1828) exemplify women's century-long struggle for acceptance in the male-dominated world of art and science. However, their lives and careers could not have been more different, as they found themselves largely on opposite sides of the historically complex issue of rising feminism over the years.

Louise von Panhuys was a typical product of the cultural revolution brought upon the European upper classes by the Enlightenment, the European intellectual movement of the 18th century, where a high social status was generally accompanied by a refined education, but even more by the *Sturm und Drang* ('Storm and Impetus') a proto-Romanic movement in Germany that occurred between the late 1760's and the early 1780s, which sought to overthrow the Enlightenment cult of rationalism and preceded German Romanticism. Louise was –according to the writers of her time– a classic "lady of leisure."

Nancy K. Wollstonecraft, on the other side, was the daughter of a clergyman from New England, born as part of the broad American middle class that shaped the first decades of the United States' independent life. She was probably self-taught in botanical matters, making her manuscript on the flora of Cuba even more remarkable.

Both, however, shared a common passion for the wonders of nature, particularly botany, and they had a shared field of action: the exuberant forests of the European colonies in the Caribbean: von Panhuys in the Dutch territory of Suriname and Wollstonecraft in the Spanish island of Cuba. Both territories underwent important social and political changes during their time in the Caribbean. Suriname faced constant revolts of its large slave population until the abolition of slavery in the Dutch colony, including one in 1816 during which her husband was murdered (Fig. 1), while in Cuba, in June 1825, the island's countryside witnessed a large African-led

ORCID of the Author: CO
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FIGURE 1. Dance of the house slaves. By Louise van Panhuys. Courtesy of the Senkenberg Library in Frankfurt.

slave rebellion, a revolt that began a cycle of uprisings lasting until the mid-1840s, and that led to the abolition of slavery in 1869 (Fig. 2).

The artistic outcome of these two women's works is astounding and took different directions: while von Panhuys painted landscapes, social scenes, fruits and flowers solely to entertain herself with a purely descriptive purpose, Wollstonecraft merged her artistic talent with her botanical knowledge to create a three-volume manuscript, *Specimens of the Fruits and Plants of the Island of Cuba*, featuring accurate and detailed descriptions along with beautiful illustrations.

The scientific value of their work is quite distinct. The paintings by Panhuys omit the botanical names, presumably because she lacked the necessary scientific knowledge. However, it is interesting to note that von Panhuys left Suriname in 1816, and three orchids depicted in her botanical plates - *Rodriguezia secunda* Kunth (1816) [now regarded as *Rodriguezia lanceolata* Ruiz & Pav. (1798)], *Epidendrum emarginatum* G.Mey (1818) and *Camaridium ochroleucum* Lindl. (1824) [= *Maxillaria lutescens* Scheidw. (1839)] were described as new species only after her return to Germany. Nonetheless, the complete set of her paintings must be regarded as an invaluable testament of Suriname's land and people. Unfortunately, von Panhuys' paintings were never published.

On the other side, Wollstonecraft's figures "are carefully colored from the living specimens; and they appear to have been executed not with correctness merely, but elegance. The history which accompanies each is brief, but sententious and comprehensive, containing the leading facts and circumstances relative to their production" (Varela & Sacco, 1828). Wollstonecraft's occasional mention of Linnaeus in her descriptions indicates that she had some training in Botany and had access to botanical books while writing her manuscript. Not being a fully qualified botanist, she often made in-

Figure 2. Plantation life in Cuba. Unknown author.

correct determinations. Interestingly, in one case, she painted what she (wrongly) named *Epidendrum fragrans* Sw. [currently determined as *Encyclia plicata* (Lindl.) Schltr.] validly published only in 1847, 20 years after her death.

Louise von Panhuys (1763–1844) and Nancy Anne Kingsbury Wollstonecraft (1791–1828) were the first female illustrators of neotropical orchids, the only exceptions being Maria Sybilla Merian (1647–1717), with her watercolor of *Vanilla* and caterpillars, and Mary Delany (1700–1788), an English artist, who created the renowned '*Flora Delanica'*, also called *'Delany's paper garden'* which consists of nearly 1000 collages of cut flowers, including *Bletia purpurea*, likely the first neotropical orchid introduced at Kew. They were followed by Augusta Hanna Innes Withers (1792–1877) and Sarah Anne Drake (1803–1857), both English professional botanical illustrators who emerged after von Panhuys and Wollstonecraft soon becoming the undisputed queens among the female botanical illustrators of the Victorian era.

An important note is that von Panhuys' and Wollstonecraft's orchid paintings are here published for the first time since their creation in the 19th century. Burckhard (1991) and Cueto (2018) present poor reproductions of incomplete sets of paintings, which –with a few exceptions– are only reproduced in black and white.

Life in the plantations: Louise von Panhuys (1763–1844)

Louise Friederike Auguste von Panhuys (née von Barckhaus-Wiesenhütten) (Fig. 3), a botanical and landscape painter, was born in 1763 in Frankfurt am Main.

She came from a well-respected merchant family and received a comprehensive and attentive education. Her mother, an amateur painter herself and part of Frankfurt's upper circles, played a crucial role in her artistic apprenticeship, which was heavily influenced by the works of Maria Sybilla Merian and of the German explorer and naturalist Alexander von

Figure 3. Louise van Panhuys (1763–1844). Unknown artist. Courtesy of Johann Christian Senckenberg Library, University of Frankfurt.

Humboldt (1769–1859, Fig. 4). Furthermore, her family's close relationship with the German writer Johann Wolfgang von Goethe (1749–1842) (Fig. 5) was of utmost importance in Louise's general culture. Goethe was the most prominent member of the *Sturm und Drang* movement which proclaimed that Nature provided the utmost source of inspiration. This German literary movement of the late 18th century exalted nature, emotions, and human individualism while seeking to overthrow the Enlightenment's cult of rationalism, preceding German Romanticism. Louise´s landscapes are excellent examples of the ideals of *Sturm und Drang*, while her paintings of Suriname's people, especially the large population of slaves, evoke Rousseau's *bon sauvage* ('noble savage') published in 1755 as part of his *Second Discourse* [Discourse on the Origins of Inequality Among Men (1754)]. This concept idealises the uncivilized man, as one symbolizes the innate goodness of a person not exposed to the corrupting influences of civilization.

Even the residence of the Barckhaus-Wiesenhütten family was traditionally connected to the arts: von Panhuys' father had purchased the famous building named *Zu den Drei Königen* ('to the Three Kings') from his parents in-law, which was constructed by famous engraver and book-printer Matthäus Merian (1593–1650), the father of Maria Sybilla Merian.

Between 1802 and 1805, Louise traveled to England together with her brother Carl Ludwig. She established strong relations with English naturalists and botanical illustrators, and it is assumed that she learned under the guidance of the botanical painter James Sowerby (1757–1822) (Fig. 6). Sowerby, also a passionate botanist, began in 1790 with the publication of *English Botany, A Catalogue of Indigenous British Plants*, a work in which he was also responsible for the illustrations and engravings. The work, which was concluded in 1814, consisted of 36 volumes with a total of 2592 plates, engraved in copper sheets and hand coloured.

When Louise traveled to England, she was already 40 years old and still unmarried. This was a constant source of worry for her mother, especially since Louise's two older sisters, Charlotte and Helene, had married –according to the circumstances of their time– at a relatively old age.

In a letter to her friend, François de Théas von Thoranc (1719–1794), Louise's mother complained: "I still have three daughters, all in the age of marriage, but the pretenders are rare. I begin to fear that they are condemned to die as virgins and martyrs". (Burkhardt et *al.*, 1991).

Regarding her youngest daughter, she did not live to see her wish fulfilled. She passed away in 1804, shortly before Louise married the Dutch officer Willem Benjamin van Panhuys (1764–1816) (Fig. 7) in 1805. Together, they traveled to Suriname in 1811 (Fig. 8), where van Panhuys owned the coffee plantation *Nut en Schadelijk* (Fig. 9), located on the lower course of the Commewijne River. The following year they bought the sugar plantation *Alkmaar* on the opposite side of the stream (Fig. 10–11).

"When sailing into the Suriname River from the Atlantic Ocean in the 18th century one would see plantations along the river and defense works protecting the river mouth. There were sugar plantations

FIGURE 4. Alexander von Humboldt (1769–1859). Unknown author.

FIGURE 5. Johann Wolfgang von Goethe (1749–1832). By Josef Stieler.

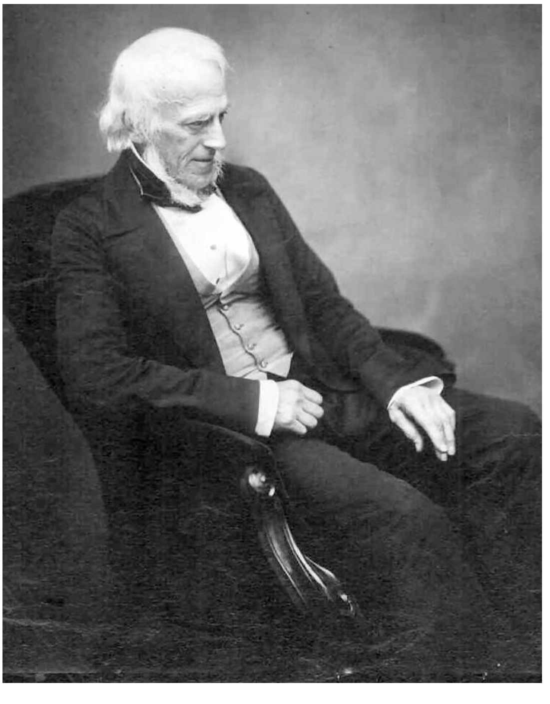

FIGURE 6. James Sowerby (1757–1822). Unknown Author.

FIGURE 7. Willem Benjamin van Panhuys (1764–1816). Unknown author.

Figure 8. Harbor of Paramaribo, with a ship similar to the one that brought Louise von Panhuys to Suriname, a so-called 'West Indiaman'. By Louise van Panhuys.

inland, but close to the coast one would find predominantly coffee plantations, lying on both sides of the river. After passing the first defenses and plantations, the very advantageous and strong fortress Zeelandia would come into view just north of Paramaribo. The city itself was a sight to behold with its white houses and fragrant trees lining the streets. Between 1650 and 1800 present-day Paramaribo was founded on the remnants of an indigenous village and developed into a bustling colonial city. The center of Paramaribo, as the indigenous village before it, is situated along the Suriname River on shell ridges several kilometers from the Atlantic coast, not far from where the Commewijne and Suriname River merge before they flow into the ocean [...]. The city's growth in size and function should not come as a surprise; the eighteenth century saw cities booming all along the American Atlantic coast, including the Caribbean. In Paramaribo's hinterland the number of enslaved Africans increased to almost 60,000 after the middle decades of the eighteenth century". (Fatah Black, 2013).

In the early decades of the 1800s, the number of plantations in Surinam, particularly sugar cane, wood, and coffee, grew to over 500. However, only their owners managed only about 60 or 80 of them (Burkhardt *et al.*, 1991).

Louise found herself living on her husband's plantations, which provided her with lots of opportunities and the necessary time to study the surrounding forests. She gradually began painting what would become her extraordinary legacy of 89 watercolors, capturing in vivid images the lives of the slaves, as well as the beauty of Suriname's flora. Her botanical paintings were meticulously and accurately drawn, and the illustrated genera can be easily determined. Among her works, we find several orchids, all painted with great attention to scientific detail and accuracy.

Figure 9. Plantation *Nut en Schadelijk* on the lower course of the Commewijne River. Watercolor by Louise van Panhuys.

FIGURE 10. Fishing in the Commewijne River, near plantation Alkmaar. By Louise van Panhuys.

The British had occupied the Dutch colonies during the Napoleonic wars (1799–1802 and 1804–1815) and returned Suriname and the Dutch Caribbean islands in 1815 on condition that the Dutch would comply with the abolition of the trans-Atlantic slave trade (which was abolished in the British territories in 1807).

After the British occupation, Willem van Panhuys was named first Governor-General by King William I, taking over from the British governor, Major-General Pinson Bonham. He immediately dismissed all the old directors and appointed new ones. He also limited the power of the powerful Court of Police and Criminal Justice. Van Panhuys was not able to do much more in his new position, because he passed away in July of the same year, murdered by revolting slaves. However, according to Möbius (1941) he was poisoned by his political rivals.

The first attempt to identify van Panhuys' orchids was by former director of the Frankfurt Botanic Garden, Martin August Johannes Möbius (1859–1946), with the assistance of August Adriaan Pulle from Utrecht. Pulle published in 1906 an Enumeration of the vascular plants known from Surinam.

The orchids illustrated by Louise van Panhuys, often misidentified by Möbius (Table 1), were: *Barkeria lindleyana* Bateman ex Lindl. (1842, Fig. 12), *Camaridium ochroleucum* Lindl. (1824, Fig. 13), *Epidendrum anceps* Jacq. (1788, Fig. 14), *Epidendrum ciliare* L. (1759, Fig. 15), *Epidendrum difforme* Jacq. (1760, Fig. 16), *Epidendrum nocturnum* Jacq. (1760, Fig. 17), *Oncidium ornithorhynchum* Kunth (1816, Fig. 18), and *Rodriguezia secunda* Kunth (1816, Fig. 19).

TABLE 1. The orchids of Louise van Panhuys.

Botanical name as given by Möbius	Correct or accepted name today
Barkeria lindleyana Bateman ex Lindl. (1842)	*Epidendrum* sp.
Camaridium ochroleucum Lindl. (1824)	*Camaridium ochroleucum* Lindl. (1824)
Epidendrum anceps Jacq. (1778)	*Epidendrum anceps* Jacq. (1778)
Epidendrum ciliare L. (1759)	*Epidendrum ciliare* L. (1759)
Epidendrum difforme Jacq. (1760)	*Epidendrum* sp.
Epidendrum fimbriatum Kunth (1816)	*Epidendrum fimbriatum* Kunth (1816)
Epidendrum nocturnum Jacq. (1760)	*Epidendrum nocturnum* Jacq. (1760)
Oncidium ornithorhynchum Kunth (1816)	*Ionopsis utricularioides* (Sw.) Lindl. (1821)
Rodriguezia secunda Kunth (1816)	*Rodriguezia lanceolata* Ruiz & Pav. (1798)

Figure 11. Plantation *Alkmaar.* Watercolor by Louise van Panhuys.

Louise van Panhuys returned to Germany after her husband's funeral in Paramaribo and moved once more into the family home in Frankfurt. In 1824, she gifted around 90 of her watercolors, created during her years in Suriname, to the Senckenberg Natural History Society and are held today at the Senckenberg Library of the Goethe University in Frankfurt.

Louise von Panhuys' work has been exhibited on different occasions, in 1898, 1991, 2007, 2009, and 2023.

FIGURE 12. *Barkeria lindleyana* Bateman ex Lindl. Watercolor by Louise van Panhuys.

FIGURE 13. *Camaridium ochroleucum* Lindl. Watercolor by Louise van Panhuys.

FIGURE 14. *Epidendrum anceps* Jacq. Watercolor by Louise van Panhuys.

FIGURE 15. *Epidendrum ciliare* L. Watercolor by Louise van Panhuys.

FIGURE 16. *Epidendrum difforme* Jacq. Watercolor by Louise van Panhuys.

FIGURE 17. *Epidendrum nocturnum* Jacq. Watercolor by Louise van Panhuys.

FIGURE 18. *Oncidium ornithorhynchum* Kunth. Watercolor by Louise van Panhuys.

FIGURE 19. *Rodriguezia secunda* Kunth. Watercolor by Louise van Panhuys.

The lost manuscript: Nancy Anne Kingsbury Wollstonecraft (1791–1828)

Lost for 190 years, a three-volume manuscript blooming with vivid color drawings of Cuban flora has resurfaced in upstate New York. Although there had been some references to its existence, it was only in 2018, that the Department of Rare and Manuscript Collections of the Library of the University of Cornell digitized the manuscript, making it accessible to the public and opening new research avenues concerning the history of female naturalists and illustrators (Garrido, 2022; 2023).

Cornell acquired the manuscript from one of her relatives, Benjamin Freeman Kingsbury (1872–1946). In 1923, a century after the drawings were made, Kingsbury, an alumnus and professor at Cornell, donated the volumes to the Cornell Libraries, which cataloged them in April 1923 as a manuscript. Because the title page misidentified the author's name, its significance was not recognised.

Nondescript marbled cardboard covers and a title page in cursive handwriting announce *Specimens of the Plants & Fruits of the Island of Cuba* by Mrs. A.K. Wollstonecraft. This simplicity belies the contents of the slim, well-worn volumes. Pages and pages showcase 121 illustrated plates showing plants in exquisite detail (Reid, 2019).

Wollstonecraft, aside from her obvious talent for botanical descriptions and illustrations, became one of the most distinguished voices of feminism in the United States in the early 1800s. The first paragraph of her essay *The Natural Rights of Woman* (Wollstonecraft, 1825) is strongly influenced by her religious education; a passionate account of God's creation of the world and the equal standings of men and women, read as follows: "Nearly six thousand years have passed since the Great Creator of the universe, crowned his labors by giving being to the most noble and intelligent of his creatures –immortal man. Male and females, created them; but declared them of one bone –one flesh– one *mind*. To *them* he directed his divine commands –and gave them rule over all that he had made. Their wisdom –their intelligence– their sovereignty was equal. God blessed them *both* and gave them united dominion over the earth and the sea; and bade them to continue as he had created them, in love and harmony. He looked upon all that he had made; and beholding it was good, he rested from his labors….

But it seems that man soon became wiser than his Maker, and discovered that the Almighty was mistaken, or had made a mistake, and that all the *mind*, or at least the greatest part of it, had been bestowed upon *himself* and that *woman* had received only a poor pittance, the mere leavings, and scrapings that could be gathered after his own wise brain was furnished."

Wollstonecraft soon returned to the reality of her time and continued (Wollstonecraft, 1825), "She [the woman] was not permitted to enjoy a single ray of the light of science, nor to feel the genial influence of its invigorating beams; but was immersed within the prison gates of ignorance and superstition, and every avenue to escape guarded with Turkish vigilance, Pagan superstition, and Popish bigotry. And this system of female exclusion prevailed in all countries, up to so late a period, that the immortal Milton, himself the intellectual sun that enlightened the whole literary hemisphere, refused to let his own daughters be taught to write" (Wollstonecraft, 1825).

Anne had married Charles Wollstonecraft, whose sister Mary (1759–1797) had achieved fame in England as an advocate for the women's rights. It is undeniable that her well-known work *The Vindication on the Rights of Woman* (1792) exerted an important influence on her sister-in-law. However, "part of the attraction for many of those who encountered this essay [Anne's *The Natural Rights of Woman*] was surely the curiosity factor of reading a treatment of the rights of woman by 'another Wollstonecraft'. Certainly, that was the case for me. It does not take one more than a few paragraphs, however, to realize that Kingsbury speaks with her own assured and forthright voice, presenting a distinctive and penetrating analysis that is fully deserving of sustained scholarly attention in its own right". (Coffee, 2021).

After marrying Charles Wollstonecraft, a major in the United States Army, the couple lived in New Orleans until Charles died in 1817. During this time, Anne was engaged in various charitable works in New Orleans, particularly with the *Poydras Female Asylum,* a shelter for orphans that offered education for women with limited resources. Then, following her husband's death, she left for Cuba, never to return.

FIGURE 20. Map of the island of Cuba by José María de la Torre. Library of Congress. Internet, public domain.

The reasons for Anne's emigration to Cuba (Fig. 20) have been the subject of much speculation. Her husband Charles had a daughter from his first marriage, by the name of Jane Nelson Wollstonecraft (1806–1882). Before his death from yellow fever, he left his daughter in the custody of Anne. Claire Tomalin, in the biography *The life and death of Mary Wollstonecraft*, speculates that Anne, after losing the legal battle about the custody of the child fled to Cuba with Jane Nelson, where all traces of her future life were lost (Tomalin, 2012). Other sources suggest that Anne traveled to Cuba for health reasons, and still others that she fled because of her husband's unpaid debts.

The first news we have about Anne Wollstonecraft after her move to Cuba are her article about *The Natural Rights of Woman* (Wollstonecraft, 1825) and the two *Letters from Cuba* she wrote for the *Boston Monthly Magazine* in 1826 (Wollstonecraft, 1826b; Knapp, 1826). The *Two letters from Cuba* describe in detail the geography, climate, and plants native to the island, but are otherwise of no further interest for this work.

It would not be until 1828 when Cuban exiles and human rights advocates Father Félix Varela and José Antonio Saco published a note in their periodical *El Mensajero Semanal* mentioning an American woman in Cuba drawing Cuban plants. "A lady has occupied herself for several years in delineating and describing the more select vegetables growing on this interesting island. Three quarto volumes of descriptions and drawings have been sent to New York, by Nathaniel H. Carter, Esq., corresponding secretary of our Horticultural Society, from Havana. The figures are carefully colored from the living specimens; and they appear to have been executed not with correctness merely, but elegance. The history which accompanies each is brief, but sententious and comprehensive, containing the leading facts and circumstances relative to their production. The author of this beautiful and instructive performance is Mrs. Walstoncraft [sic]; and it may be safely said that it is fully equal to the plates that embellish the celebrated book on the insects of Surinam, and the plants they fed upon, by Sybella Merian!" (Fig. 21).

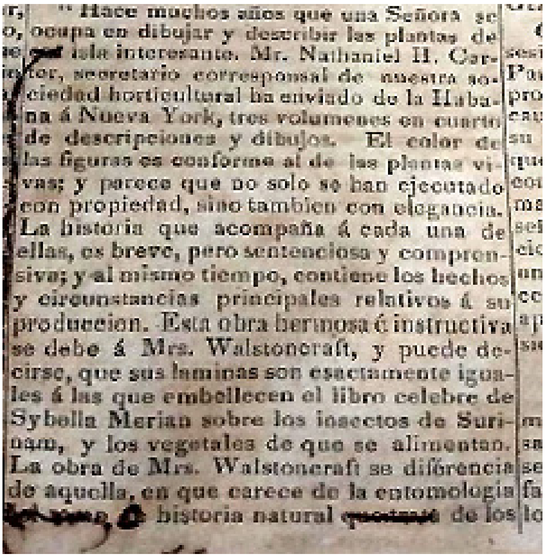
"Hace muchos años que una Señora se ocupa en dibujar y describir las plantas de esta isla interesante. Mr. Nathaniel H. Carter, secretario corresponsal de nuestra sociedad horticultural ha enviado de la Habana á Nueva York, tres volumenes en cuarto de descripciones y dibujos. El color de las figuras es conforme al de las plantas vivas; y parece que no solo se han ejecutado con propiedad, sino tambien con elegancia. La historia que acompaña á cada una de ellas, es breve, pero sentenciosa y comprensiva; y al mismo tiempo, contiene los hechos y circunstancias principales relativos á su produccion. Esta obra hermosa é instructiva se debe á Mrs. Walstonecraft, y puede decirse, que sus laminas son esactamente iguales á las que embellecen el libro celebre de Sybella Merian sobre los insectos de Surinam, y los vegetales de que se alimentan. La obra de Mrs. Walstonecraft se diferencia de aquella, en que carece de la entomologia ... historia natural ... de los

FIGURE 21. Article by Varela and Saco (fragment) from *El Mensajero Semanal*. August 26, 1828.

News traveled slowly in those times, and Varela and Saco were not aware that Anne Wollstonecraft had passed away three months earlier.

As to Anne's surname, she is generally referred to as 'Mrs. Wollstonecraft', but on at least one occasion as on 'Mrs. Walstonecraft'. It will remain an unsolved riddle, especially, since in her own handwriting, she names herself 'Wollstonecroft' (Fig. 22). To make things even more complicated, some authors have written about her as "Anne" Wollstonecraft, others as "Nancy" Wollstonecraft and still others as "Nancy Anne" Wollstonecraft!

Anne Kingsbury Wollstonecraft established herself in the city of Matanzas (Fig. 23), one of Cuba's most important ports of commerce, located on the north shore of the island, surrounding the Bay of Matanzas. The bay cuts deep into the island, and three rivers flow in the bay inside city limits: Rio Yumuri, San Juan, and Canimar. Matanzas lies about 100 kilometers east of Havanna.

Matanzas is also known as the 'Athens of Cuba', for its cultural and literary development. Anna arrived in the city only a few years after the introduction to Matanzas of the printing press, which marked the beginning of the so-called 'Matanzas Golden Age'. At that time, the city had a population at that time of approximately 15,000 inhabitants.

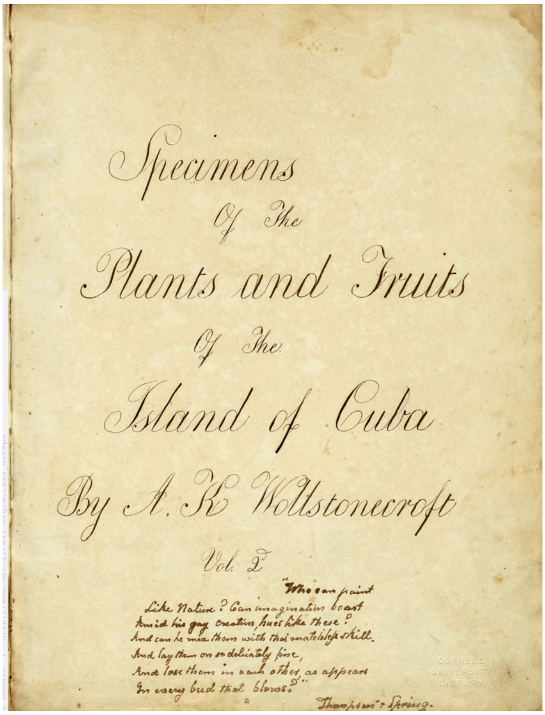

FIGURE 22. Title page of Wollstonecraft's manuscript where she spells her name as 'Wollstonecroft' (1826a).

In her famous manuscript, Wollstonecraft illustrated a total of 145 Cuban fruits and plants, among which we have identified nine species of orchids, all accompanied by handwritten descriptions. Among the drawings are trees, flowers and fruits, such as the palm, pineapple or papaya, and our favorites: the orchids. The complexity and the number of illustrations makes it one of the first documents of its kind known about the region's botany. The detailed notes made by the author on the common names and native uses of the species add a completely new and very useful dimension to ethnobotanical knowledge.

The illustrations are accompanied by approximately 220 pages of descriptions written in English, the author's native language, which shows her great ability to connect various historical facts with the local uses of natural resources and her personal observations, which also encompass details about her lifestyle and her perspectives on various topics related to the environment and its context. The use of Latin nomenclature and the drawings of the various dissections of plants suggest that A. K. Wollstonecraft possessed at

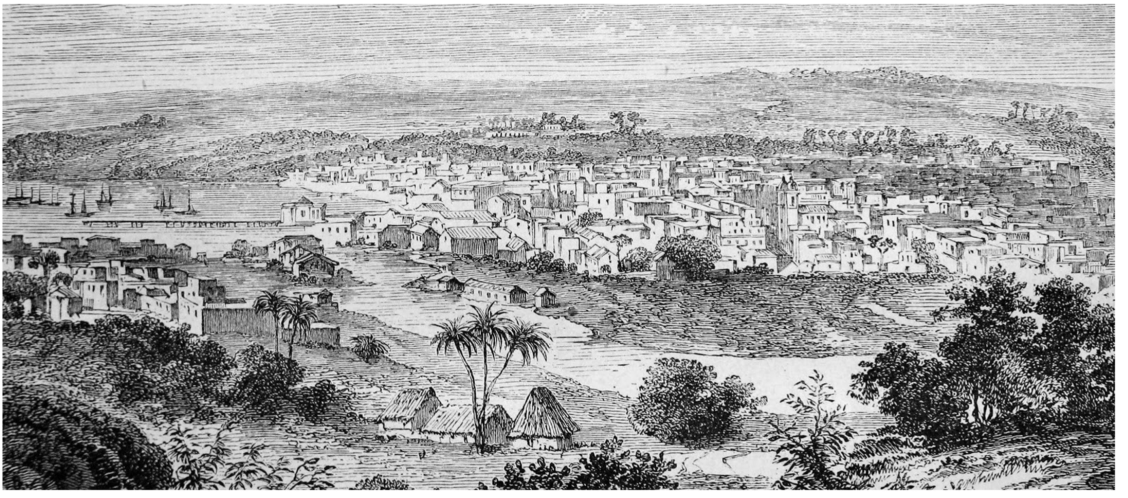

FIGURE 23. The city of Matanzas *ca*. 1820. Unknown author.

least a basic understanding of Linnaean science and taxonomy. In many plates the different enlarged parts are also shown sectioned, indicating that the author us think that the author may have had dissection materials and optical instruments, such as the magnifying glass or microscope. In a comment to her plate 66 [*Aeschynomene grandiflora* (L.) L. (1763)] we read:

"The tree which bears the flower and the legume represented in plate 66 grows in this island to twenty feet high. It may be that I have mistaken the genus, and species to which botanists have assigned it. But without either books to inform or scientific friends to correct, it would be astonishing if I did not make any mistakes in the nomenclatur[e] and in the artificial arrangement of plants which have been presented to me and their characters unfolded by Nature only without the slightest aid from scientific persons. I have not yet had so much as a single conversation with a botanist, much less a lesson […] I describe the plants, as I have found, or thought I found them. No aid from others have aided me. It must be therefore that my descriptions shall prove faulty, yet I can affirm it is unavoidable, not willful faults that I shall deface these pages". (Wollstonecraft, 1826a)

Whether self-taught or not, A. K. Wollstonecraft was a cultured, well-educated and precise individual. Her work was a result of direct observation and sketching, later completed with data contrast and color reproduction through watercolors. Certainly, if it had been published, her work could have become an unprecedented reference on Cuban flora.

TABLE 2. The orchids of Nancy Kingsbury Wollstonecraft.

Botanical name as given by Wollstonecraft	Correct or accepted name today
Cranichis sp.	*Cyrtopodium punctatum* (L.) Lindl. (1833).
Epidendron [Epidendrum] sp.	*Encyclia* cf. *altissima* Schltr. (1914)
Epidendron [Epidendrum] angustifolium Sw.	*Broughtonia* cf. *sanguinea* (Sw.) R.Br. (1813)
Epidendron [Epidendrum] cochleatum L. (1763)	*Prosthechea cochleata* (L.) W.E.Higgins (1998)
Epidendron [Epidendrum] fragrans Lindl.	*Encyclia plicata* Britton & Millsp. (1920)
Epidendron [Epidendrum] imbricatum Lindl. (1831)	*Prosthechea boothiana* (Lindl.) W.E.Higgins (1998)
Epidendron [Epidendrum] undulatum Sw. (1788)	*Trichocentrum undulatum* (Sw.) Ackerman & M.W.Chase (2001)
Epidendron [Epidendrum] vanilla L. (1853)	*Vanilla* cf. *phaeantha* Rchb.f. (1865)
Satyrium plantagineum L.	*Govenia utriculata* Lindl. (1839)

The following are the nine orchid species illustrated by Wollstonecraft (Table 2): *Cranichis* sp. (Fig. 24), *Epidendron* [*Epidendrum*] sp. (Fig. 25), *Epidendron angustifolium* Sw. (1788, Fig. 26), *Epidendron cochleatum* L. (1753, Fig. 27), *Epidendron fragrans* Lindl. (1847, Fig. 28), *Epidendron imbricatum* Lindl. (1831, Fig. 29), *Epidendron undulatum* Sw. (1788, Fig. 30, 33), *Epidendron vanilla* L. (1753, Fig. 31), *Satyrium plantagineum* L. (1759, Fig. 32).

FIGURE 24. Plate 80 of Wollstonecraft's manuscript, *Cranichis* sp.

FIGURE 25. Plate 83 of Wollstonecraft's manuscript, *Epidendron* sp.


FIGURE 26. Plate 119 of Wollstonecraft's manuscript, *Epidendron angustifolium*.

FIGURE 27. Plate 76 of Wollstonecraft's manuscript, *Epidendron cochleatum*.

FIGURE 28. Plate 86 of Wollstonecraft's manuscript, *Epidendron fragrans*.

FIGURE 29. Plate 85 of Wollstonecraft's manuscript, *Epidendron imbricatum*.

FIGURE 30. Plate 82 of Wollstonecraft's manuscript, *Epidendron undulatum*.

FIGURE 31. Plate 75 of Wollstonecraft's manuscript, *Epidendron vanilla*.

FIGURE 32. Plate 88 of Wollstonecraft's manuscript, *Satyrium plantagineum*.

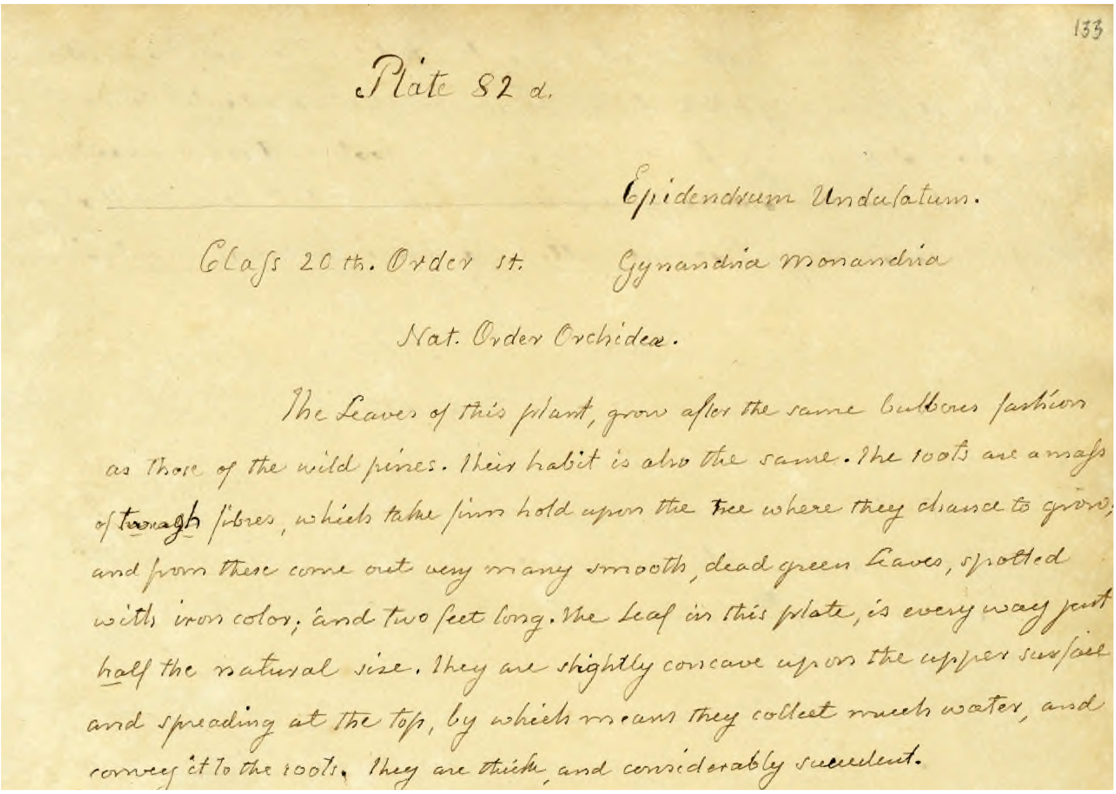
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Plate 82 d.

Epidendrum Undulatum.

Class 20th. Order 1st. Gynandria Monandria

Nat. Order Orchidea.

The Leaves of this plant, grow after the same bulbous fashion as those of the wild pines. Their habit is also the same. The roots are a mass of tough fibres, which take firm hold upon the tree where they chance to grow; and from these come out very many smooth, dead green Leaves, spotted with iron color; and two feet long. The Leaf in this plate, is every way just half the natural size. They are slightly concave upon the upper surface and spreading at the top, by which means they collect much water, and convey it to the roots. They are thick, and considerably succulent.

FIGURE 33. Description of *Epidendrum undulatum* in Wollstonecraft's manuscript.

According to Knapp (1834), the illustrations showed not only plants, but also birds, fish and other animals. However, in the volume *Specimens and the plants and fruits* we only find the illustrated botany collection, which leads us to affirm that A. K. Wollstonecraft work's could be even broader than we think and that it is likely that new documents may exist that are not included in this article.

Anne Kinsgsbury Wollstonecraft produced an extraordinary manuscript, combining science, art, and travel journals (Knapp, 1834).

AUTHOR CONTRIBUTION. CO: Conceptualization, Investigation, Writing - Original Draft, Writing – Review & Editing, Visualization.

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FIRST NATURALIZATION OF THE ORCHID *CYMBIDIUM ALOIFOLIUM*, A POPULATION FOUND IN SOUTHERN FLORIDA

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Abstract. The first naturalization of the orchid *Cymbidium aloifolium* in the world is reported in a residential neighborhood in southern Florida near Miami. A survey for naturalized plants of this epiphytic orchid, which is native to South and Southeast Asia, found 101 plants growing on 38 different trees belonging to 13 different species. Of these 101 plants, 53 were mature, capable of reproduction, 37 were juveniles, and 11 were seedlings. Seven plants bore a total of 86 fruit. The tree hosts with the most plants were the palms *Phoenix roebelenii* and *Thrinax radiata*, and a mahogany (*Swietenia macrophylla*). A small remnant of the Pine Rockland within this residential area had three native tree species with four plants of this orchid, indicating the potential of the orchid to invade this unique, rare plant community. *Cymbidium aloifolium*'s occurrence at higher latitudes and elevations in its native Asia than where it has naturalized in Florida suggests that it should be able to live farther north in Florida.

Keywords / Palabras clave: biological invasion, epífita, epiphyte, establecimiento de frutos, forófitos, fruit set, invasión biológica, phorophytes, Pine Rocklands, suburban residential area, zona residencial suburbana

Introduction. Orchids naturalize much less than other flowering plants or ferns, probably due to the absence of specialist pollinators and appropriate mycorrhizae required by most orchids (Daehler, 1998). For instance, most orchid species have a single pollinator (Ackerman *et al*., 2023), and for orchid seeds to germinate they require particular mycorrhizal fungi to penetrate their seed (Liu *et al*., 2010). Florida's flora has 12 naturalized orchids (Wunderlin *et al*., 2025), but only three of these species have spread widely in the state, with most of the others, such as *Phaius tankervilleae* (Banks) Blume (Robinson *et al*., 2011), being limited to one or two counties. Ten of the 12 orchid species are terrestrials while the other two are epiphytes. The greater naturalization of terrestrial orchids may be due to the large array of mycorrhizae in the soil and mulch environments in which they grow. Of the widely occurring naturalized orchids in Florida, *Zeuxine strateumatica* (L.) Schltr. thought to have been introduced to the United States from China in grass seed, was first found in Florida in 1936 (Ames, 1938). *Oeceoclades maculata* (Lindl.) Lindl. is an African orchid which spread slowly northward after it appeared in Brazil, reaching Florida by 1974 (Wetterer & Wetterer, 2022). *Eulophia graminea* Lindl. first found in South Miami in 2007 (Pemberton *et al*., 2008), has spread widely in the state (Pemberton, 2013), and is currently documented to occur in Duval County in northern Florida almost to the Georgia border (Wunderlin *et al*., 2025).

In this communication, we report the naturalization of *Cymbidium aloifolium* (L.) Sw., an epiphytic-lithophytic Asian orchid, in southern Florida. This marks the first known naturalization of this orchid species in the world and only second naturalization among the 89 species of *Cymbidium* Sw. (POWO, 2025). The first, *Cymbidium dayanum* Rchb.f. is naturalized in Hawaii (Ackerman, 2012). Like most naturalized orchids, these *Cymbidium* species are escapees from horticulture. *Cymbidium aloifolium* has a wide distribution in South and Southeast Asia, occurring in semideciduous seasonal forests and savanna-like woodlands (Pfahl, 2025). The distribution of the orchid, summarized from the literature (POWO, 2025) is in the eastern Himalayas in Nepal and Bhutan, South Asia in India, Bangladesh, Sri Lanka and the Andaman Islands, in Southeast Asian countries of Myanmar, Thailand, Laos,

ORCID of the Author: RWP, JLD
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Cambodia, Vietnam, Malaysia, Sumatra and Java, and in the southern Chinese provinces of Guangdong, Guangxi, Guizhou and Yunnan. This orchid is medically important in its native South Asia where various parts of the plant are used to treat many different ailments (Kumar *et al*., 2022). The plant is cultivated in its native region and elsewhere due to its abundant, long-lived, attractive flowers, which are born on long, pendulous stalks (Kumar *et al*., 2022).

After discovering what appeared to be plants of a *Cymbidium* orchid growing in trees in a residential area of Pinecrest, a city just south of Miami, Florida, in Miami-Dade County, we sought to identify the orchid and to learn of its occurrence and possible origins.

Materials and methods. *Identification of the plant.*— To confirm the identity of *C. aloifolium*, which was first identified by its characteristic vegetative and floral morphology, molecular techniques and DNA barcoding were employed at Fairchild Tropical Botanic Gardens. Total genomic DNA from six plants was extracted from silica-dried leaf tissue using DNeasy Mini Plant Kit (QIAGEN, Venlo Limburg, The Netherlands). Following DNA isolation, two sets of primers were used to amplify specific genetic regions through polymerase chain reaction (PCR): the nuclear ribosomal internal transcribed spacer (ITS) region using four ITS1 and ITS2 primers, and the plastid region using trnL-F using trnL- R primers. These regions are commonly used for DNA barcoding due to their variability among species. The ITS region is particularly useful in identifying orchids, including members of the genus *Cymbidium*, and allows for resolution at the species level (Sharma *et al*., 2012). The plastid trnL-F region offers a complementary, maternally inherited marker that provides additional evidence for *Cymbidium* species identity (Zhang *et al*., 2021). Although more conserved than ITS, it helps corroborate findings and provides insight into hybridization events or maternal lineage. Using both nuclear and plastid markers enhances the reliability of identification and reduces the risk of error due to incomplete lineage sorting or hybrid ancestry. After PCR amplification, the products were visualized via gel electrophoresis to confirm successful amplification. Amplicons were then purified using ExoSAP-IT reagent (Affymetrix, Santa Clara, California, USA). Samples were sent for Sanger Sequencing at Eurofins Genomics. The resulting sequences were aligned using Geneious (Biomatters, Auckland, New Zealand) and compared against reference sequences from GenBank through nucleotide BLAST. Sequence similarity greater than 97% confirms the identity of the samples. Sequences obtained from this project will be deposited in GenBank.

Surveys for naturalized plants.— Surveys were made in the suburban residential area of Pinecrest, Florida in Miami-Dade County, where naturalized orchids plants were first observed in 2017. Searches for naturalized plants of this orchid were also made in the gardens of Fairchild Tropical Botanic Garden and the Montgomery Foundation in Coral Gables, Florida, a city adjacent to Pinecrest, were made in January 2025. The surveys in the residential area of Pinecrest were primarily of trees along the right of way between the street and the sidewalk and in the front yards of residences with the permission of the owners. When plants were found on a phorophyte, the number of plants, their size-age class (seedling, juvenile, and mature –medium and large reproductives), the presence and number of fruit, and the plants' position on the trees including their height above the ground were recorded. Seedlings were those that sprouted from seed during the current year and usually bore a single leaf fan of growth. Juvenile plants were small plants with multiple leaf fan growths. Mature plants were categorized as medium in size if they were no more than 30 cm across at their centers, between leaf base and leaf tips, and large if they were more than 30 cm across at their centers. The host tree species was recorded as was the size of the host tree, indicated by its diameter at breast height (DBH). Casual walking searches for plants of the orchid were made in the trees of the botanical gardens.

Horticultural presence.— Horticultural literature and historical sales catalogues were searched to attempt to learn when the orchid entered horticulture. Current marketing information about the orchid was sought including its presence at regional orchid shows and online sales. Social media was searched for information related to its cultivation.

Figure 1. *Cymbidium aloifolium*. **A**. Flowering plant with multiple pendulous inflorescences. **B**. Inflorescence detail.

Results and Discussion. *Identity of the orchid.*— Species identity was confirmed using a combination of morphological and molecular characteristics. Morphologically, the plants were identified as hot to warm-growing epiphytes with very small pseudobulbs enclosed by leaf bases. The leaves are coriaceous, suberect, linear-ligulate, and obscurely bilobed at the apex. Flowers are borne on long, basal, pendent, racemose inflorescences (Fig. 1A) that appear during the spring and early summer. Diagnostic floral features consistent with *C. aloifolium* include the distinctive strap-like petals and a prominently veined labellum (Fig. 1B).

While vegetative traits alone were insufficient for definitive identification —particularly in non-flowering or juvenile individuals— molecular analysis via DNA barcoding provided robust support. The internal transcribed spacer (ITS) region and the chloroplast *trnL-F* intergenic spacer that were amplified and sequenced, revealed high sequence similarity (>99%) with reference sequences of *C. aloifolium* (GenBank accession numbers: PQ809756.1, PQ815665.1). All six individual samples showed consistent matches, confirming their identity as *C. aloifolium*.

Survey findings.— The results of the surveys in Pinecrest and the botanical gardens are shown in Table 1. A total of 101 *C. aloifolium* plants were found on 38 different individual phorophytes in an area of *ca*. 13 km^2. An additional large plant was found on the tiled roof at a building at the Montgomery Foundation. Fifty-three of these plants were judged to be mature, with 24 being large and 29 as medium. Large plants were often 50 to 75 cm across, frequently wrapping around their host tree trunks and large branches. Thirty-seven plants were characterized as juveniles, and 11 were seedlings, thought to have germinated during the past rainy season during the summer of 2024. Nine of these mature plants bore a total of 86 fruit. Two of these plants, however, bore most of the fruit. A single large plant growing on a pygmy date palm (*Phoenix roebelenii* O'brien) bore 34 fruits, while four large plants growing on a mahogany (*Swietenia macrophylla* King) bore 43 fruits. The remaining 9 fruits included 4 produced by a single plant growing on a palm, probably *Copernicia hospita* Mart., and 5 fruits on another plant growing on a Southern live oak (*Quercus virginiana* Mill.).

Table 1. *Cymbidium aloifolium* naturalized plants in Pinecrest and Coral Gables, Florida. Family, scientific name and common name are provided for the phorophytes (hosts); native species in bold. DBH=diameter at breast height; x̄=mean; sd=stand. deviation.

	No. Hosts	No. Plants	No. [1]Mature plants	No. Fruiting plants	No. Fruit	No. [1]Juvenile	No. [1]Seedlings	Host DBH (m)	Plant height (m)
Arecaceae									
1. *Copernicia* cf. *hospita* None	1	1	1 large	3	4			0.93	0.75
2. *Phoenix roebelenii* Pygmy date palm	8	24	4 large 6 medium	1	34	13	1	0.26–0.41 x̄=0.32 sd=0.05	0.90–2.12 x̄=1.73 sd=0.47
3. ***Sabal palmetto*** Palmetto palm	2	5	5 medium					1.07	2.12–3.45 x̄=3.32 sd=1.19
4. ***Serenoa repens*** Saw palmetto	2	2					2	0.57	0.3–0.6 x̄=0.45 sd=0.21
5. ***Thrinax radiata*** Florida thatch palm	5	27	3 large 6 medium			11	7	0.29–0.43 x̄=0.38 sd=0.05	1.6–3.6 x̄=2.83 sd=0.97
Burseraceae									
6. ***Bursera simaruba*** Gumbo limbo	1	1				1		0.87	2.4
Combretaceae									
7. ***Conocarpus erectus*** Buttonwood	1	4	1 large 1 medium			2		1.48	3.0–4.2 x̄=3.48 sd=0.56
Fabaceae									
8. *Bauhinia* cf. *purpurea* orchid tree	1	10	3 large			5	2	1.73	1.96–4.24 x̄=3.28 sd=0.76
Fagaceae									
9. ***Quercus virginiana*** Southern live oak	6	8	2 large 4 medium	1	5	2		1.78–3.03 x̄= 2.47 sd=0.57	1.2–3.6 x̄=2.2 sd=3.19
Lauraceae									
10. *Persea americana* Avocado	1	1	1 large					1.03	1.36
Meliaceae									
11. ***Swietenia macrophylla*** Mahogany	8	16	7 large 7 medium	4	43	2		1.06–2.92 x̄=2.26 sd=0.75	2.42–5.45 x̄= 4.36 sd=1.19
Moraceae									
12. *Ficus* cf. *benjamina* Benjamin fig	1	1	1 large					1.5	2.7
Pinaceae									
13. ***Pinus ellioti*** Slash pine	1	2				1	1	1.19	2.4
Unknown (N/A)									
14. Building roof (Montogomery Foundation)		1	1 large						3
Total	38	103	53 (29 medium, 24 large)	9	86	37	11		

[1]Mature plants, those capable of fruiting, are divided in medium and large: medium plants are those with five growth shoots and a width estimated to be less than 30 cm at their centers, between the leaf bases and leaf tips; large plants are wider than 30 cm across, commonly reaching 50 cm or more. Juvenile plants are small plants with multiple leaf fan growths. Seedlings are those that sprouted and grew during the last 2024 growing season.

FIGURE 2. **A**. Large plant of *Cymbidium aloifolium* on a Southern live oak (*Quercus virginiana*) tree trunk. **B**. Large plants in the canopy of a mahogany (*Swietenia macrophylla*) tree. **C**. Juvenile plants growing on a pygmy date palm (*Phoenix roebelenii*).

Thirteen different phorophyte species hosted the naturalized *Cymbidium* plants (Table 1). Seven of these are native and six non-native introduced species. Five of the 13 species are palms belonging to five different genera, but only two of these palms hosted half (51/103) of the orchid plants. These were the Florida thatch palm trees (*Thrinax radiata* Lodd. ex Schult. & Schult.f.) that bore 27 plants of the orchid, and eight non-native pygmy date palm trees that bore 24 plants. Other host trees with numerous orchid plants were mahogany with 8 trees hosting 16 plants and Southern live oak with six trees hosting 8 plants. Most of the host species have rough bark, with textures that may help catch and hold the airborne orchid seed and provide microhabitats for mutualistic mycorrhizae that foster seed germination. Three host species, *Bursera simaruba* (L.) Sarg., *Ficus benjamina* L. and *Bauhinia* L., have smooth bark but the orchid plants found on them grew at cut ends of branches and or on partially decayed areas, which may have been the habitats of mutualistic mycorrhizae. Some saprophytic and plant parasitic fungi can serve as orchid seed germination mutualists (Sathiyadash *et al*., 2020).

Data on the size of host trees, diameters at breast height, and heights above the ground where the *C. aloifolium* plants were found, did not reveal any patterns among host species, except that all the hosts were large and mature. Within host species, however, the sites where the orchids occurred were more consistent. Most of the plants growing on the oaks were lower on the trunks *ca*. 2.5 m above the ground and often at the junction of the trunk and a major branch (Fig. 2A). Most of the large plants in the mahogany trees were high (*ca*. 3–4 m) in the canopy (Fig. 2B). Both the pygmy date and the thatch palms are small and most of the numerous orchids they hosted grew beneath the fronds below 2 to 3 m above the ground. The moist fibrous of old frond bases of the pygmy date palms supported many seedlings and juvenile plants (Fig. 2C).

We identified hosts as native or introduced but all these species were cultivated in the front yards or in the right of ways in this old residential neighborhood. An interesting exception was a remnant native Pine Rockland plant community occupying a 50 × 75 m or 0.375 ha lot within this neighborhood. In this lot, six *C. aloifolium* plants were found on four hosts of three native species; a slash pine (*Pinus elliottii* Engelm.), a palmetto palm [*Sabal palmetto* (Walter) Lodd. ex Schult. & Schult.f.] and two saw palmettos [*Serenoa repens* (W.Bartram) Small], the latter are more shrubs than trees. Among these naturalized orchids were two mature plants, a single juvenile and three seedlings. The presence of the orchid in this Pine Rockland remnant demonstrates the ability of this orchid to invade this plant community and the suitability of this community for the orchid. The Pine Rockland is a unique and highly endangered community in South Florida (U.S. Fish and Wildlife Service, 1999). It is notable that another invasive orchid, the yellow cowhorn orchid (*Cyrtopodium flavum* Link & Otto ex Rchb.) from Brazil, has a large population on another Pine Rockland remnant (Pemberton & Liu, 2011). The yellow cowhorn is lithophilic, while *Cymbidium aloifolium* is known to be both epiphytic and lithophilic. The naturalized *C. aloifolium* plants that we have encountered thus far, including those in the Pinecrest neighborhood Pine Rockland remnant, have been epiphytic except for one plant growing on a building at the Mongomery garden. The orchid's ability to be lithophytic may increase its invasion potential of this important community type.

In addition to the plants found during our survey in Pinecrest, a single large reproductive plant was found in Fairchild Botanic Garden in Coral Cables. The naturalized *C. aloifolium* plant was growing on a planted palm, *Copernicia* species, probably *C. hospita*, adjacent to a mangrove creek next to Matheson Hammock State Park. The plant was at 0.75 m above ground and bore three infructescences with 1, 1, and 2 fruits. At the Montogomery garden a single large plant without apparent fruit was found growing on the edge of the tiled roof of the building that houses the herbarium of Fairchild Tropical Garden. It is interesting to note that this building is located about 100 m from mahogany trees bearing numerous large fruiting *C. aloifolium* growing along Old Cutler Road in Pinecrest. Voucher specimens of naturalized *C. aloifolium* have been placed in the herbaria of Fairchild Tropical Botanic Garden, the University of Florida and the University of South Florida.

Horticultural presence.— There are three main groups of cultivated *Cymbidium* species. The longest cultivated are the terrestrial species, such as *C. ensifolium* (L.) Sw. and its hybrids, which have been highly favored fragrant orchids cultivated for thousands of years in China (Hew & Wong, 2023). Then there are the large flowered cooler growing *Cymbidium* species such as *C. insigne* Rolfe from the Himalayas, Indochina and South China and their hybrids (Pridgeon, 1992). Lastly are the so called small-flowered *Cymbidium* species that are tropical epiphytes with pendulous flowers, which is the group to which *C. aloifolium* belongs (Pridgeon, 1992; Staples & Herbst, 2005).

The first evidence of the cultivation of *C. aloifolium* in the United States that we located was its listing in the 1876 book, *New and Choice Orchids* (William Rollisson & Sons, 1876). Not long after that, in 1889, it appeared in the sales catalogue of The United States Nursery in Short Hills, New Jersey. In 1890, it was offered in John Saul nursery catalogue of orchids, Washington DC (Saul, 1890). The Reasoner Brother's Royal Palm Nurseries near Ft. Meyers, Florida, which operated from 1887 to 1930, was one of the most important early horticultural nurseries in Florida (Pemberton & Liu, 2009). This nursery sold many orchids but no *Cymbidium* species or their hybrids. The orchid did not occur in any of the other examined 15 US orchid nursery sales catalogues published from 1911 to 1960, available on The Internet Archive (2025). *Cymbidium aloifolium* was not included in the book *100 Orchids for Florida* (Kramer, 2006) or in *Orchids to Know and Grow* (Sheehan & Black, 2007).

We have not noticed *C. aloifolium* being sold in recent years at the large orchid shows in southern Florida (Ft Lauderdale Orchid Society Show, Tamiami International Orchid Festival in Miami, the Fairchild Orchid Festival or the Redland International Orchid Show. A search for online sales of *C. aloifolium* plants on Google, (accessed 24 April 2025), found 25 companies offering the orchid. A limited search of social media, YouTube, (accessed 19 January 2025) found 20 posts related to this orchid, mostly dealing with its cultivation. This information suggests that *C. aloifolium* has had and still has more limited popularity as a horticultural subject than many orchids. The many online companies selling plants and the social media posts related to its cultivation, however, indicate an interest in this orchid. The cultivation of *C. aloifolium* in tropical and subtropical regions may present more opportunities for it to escape and naturalize.

Reproductive biology.— In India, *C. aloifolium* is pollinated by the most common Asian honeybee, *Apis cerana* Fabricius, 1793 (Adit *et al*., 2022; Buragohain *et al*., 2016). The flowers (Fig. 1) lack nectar and appear to be pollinated through deception. Due to the similarity in the morphology and size of the Indian honeybee and the ubiquitous common honeybee (*A. mellifera* L. 1758) in Florida, we suspect that the common honeybee is probably the pollinator of the orchid in Florida, but this remains to be verified.

Finding 101 naturalized plants on 38 different phorophytes belonging to 13 species in nine different families during the surveys indicates that suitable mycorrhizae were present at many different specific sites where the seed of this orchid germinated and grew. We suspect *C. aloifolium* is a mycorrhizal generalist, capable of germinating on broad spectrum of mycorrhizae as has been recently found with other naturalized orchids in Florida (Downing *et al*., 2020), but this also needs to be determined. *Cymbidium aloifolium* has thus overcome two significant barriers to orchid naturalization, the acquisition of suitable mycorrhizae for seed germination and capable pollinators of its flowers.

Description of the plant.— The following description of *C. aloifolium* is based on the one given in the Native orchids of China in Color (Chen *et al*., 1999). *Plants* epiphytic or lithophytic. *Pseudobulbs* ovoid, slightly flattened, 3–6 cm long, 2.5–4.0 cm thick, usually enclosed in persistent leaf bases. *Leaves* 4–5, strap shaped, thickly coriaceous, ridged, 40–90 cm long, 1.5–4 cm wide, unequally round-bilobed at the apex. *Inflorescence* (Fig. 1A), lateral, pendulous, 20–60 cm long, raceme with 15–35 flowers, bracts small. *Flowers* (Fig. 1B) 3–4 cm across, slightly scented, sepals and petals pale yellow with a broad maroon-brown central stripe and some dark streaks; lip white or cream colored with maroon-veined side lobes and mid lobes. *Sepals* oblong to narrowly elliptic, 1.5–2.0 cm long, 4–6 cm wide. *Petals* narrowly elliptic, slightly shorter than the sepals. *Lip* subovate, 1.3–2.0 cm long, 3 lobed; callus 2-lamellate, lamellae often broken in the middle. *Column* 1.0–1.2 cm long.

Cymbidium aloifolium is distinguished from other epiphytic *Cymbidium* species cultivated in Florida by its small, hidden pseudobulbs, stiff, bilobed leaves, and especially its long, pendant inflorescence bearing many striped flowers with a veined labellum. In contrast, many other epiphytic species have more visible pseudobulbs, arched or erect inflorescences, and different floral shapes and markings. This species is often confused with *C. dayanum* but *C. aloifolium* is distinguished by its smaller pseudobulbs, strap-like petals, veined labellum, and pendant inflorescence, whereas *C. dayanum* has more prominent pseudobulbs, narrower, striped flowers, and a more arching inflorescence. Flower structure and markings are the most reliable way to tell them apart, especially when vegetative features are ambiguous. The flowers of *C. dayanum* differ from *C. aloifolium* in having a rounded lip edge and an hourglass shape in the center of the lip.

Potential to spread and persist.— The native distribution of *C. aloifolium* reaches Sikkim in northern India (POWO, 2025). The southern border of Sikkim is 27 degrees north and the lowest elevation in the province is *ca*. 300 m above sea level (Government of Sikkim, 2021). The areas where this orchid grows in Sikkim should be much cooler than the area where the orchid has naturalized in Florida, which is at 26 degrees north and at near sea level. This suggests that *C. aloifolium* may be able to live well north of its present location in Miami-Dade County, particularly along both the eastern and western southern coasts which rarely get frost. The plant's leathery leaves, which help it survive the dry season in monsoonal South and Southeast Asia, should preadapt the plant to survive the long dry season in Florida. Being a tropical species, the orchid has the potential to spread south and/or to escape from cultivation into the American tropics in tropical America. In 2024, a research-grade iNaturalist observation of *Cymbidium aloifolium* from French Guiana in South America was posted (Léotard, 2024).

Only two epiphytic orchids have naturalized in Florida prior to the naturalization of *C. aloifolium* described here, but the persistence of these species is questionable. *Laelia rubescens* Lindl. is listed in the Florida Plant Atlas (Wunderlin *et al*., 2025) as occurring in Miami Dade County. It was found growing on Southern live oak trees in Matheson Hammock in Miami- Dade County by Roger Hammer (pers. com.), but recent searches by the present authors have failed to locate plants of this orchid. A research grade iNaturalist post in 2019 shows what appears to be an orchid in Big Cypress National Wildlife Preserve in Collier County.

Encyclia rufa (Lindl.) Britton & Millsp. is a Bahamian orchid reported from Brevard County on the east coast of Florida by the Florida Plant Atlas (Wunderland *et al*., 2025). We have been unable to find herbarium specimens of these orchids. Naturalized terrestrial orchids are probably better able to survive the variable weather of the subtropical Florida because their subterranean parts of these orchids may survive periodic freezes. Some of the massive, naturalized plants of *C. aloifolium,* that we have encountered, may be self-insulating against the rare freezes that occur in South Florida. If so, *C. aloifolium* may be the exceptional naturalized epiphytic orchid to persist and perhaps spread in the southern part of Florida, but time will tell.

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- Check the English carefully for correct language use before submission. Use either British or American English spelling consistently.
- Ensure the manuscript follows the latest International Code of Nomenclature for algae, fungi, and plants.
- If the paper includes newly described taxa, they must be illustrated, preferably by ink line drawings or color composite plates. Grey-scale drawings are difficult to reproduce accurately and may be challenging to understand; therefore, they are generally not accepted for publication.
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Title, Running title, Addresses, Abstract [+ optional Abstract in second language] & Keywords

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include brief but complete references to the paper's results. Diagnostic characters for newly described taxa should be briefly stated. An optional abstract in a second language should follow in a separate paragraph in the same format.
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- Cite authors of all names at the rank of genus and below when first used in the text, without repeating citations after the first name's use. Refer to the International Plant Names Index (IPNI) for correct abbreviations (https://www.ipni.org).
- Italicize all scientific names at the generic level or below.
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- Begin each new page for figures and tables, continuing the page number sequence.
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Outer floral bract. E. Inner floral bract. F. Petal. G. Column, profile view (left) and 3/4 dorsal view (right). H. Pollinarium. (Drawn from the holotype). Illustration by Who Nobody. Figure 2. *Luisia inedita*. A. Habit. B. Fruit (Somebody 567, CR). Illustration by Who Nobody. Note that labels on the figure ("A") should be in upper case and match that on the legend. Italicize the collector's name and number.

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LANKESTERIANA, the International Journal on Orchidology, has been dedicated to publishing articles focused mainly (today exclusively) on orchid science, spanning a wide variety of topics, including anatomy, ecology, evolution, history, physiology, phylogenetics, and systematics. Founded in 2001, LANKESTERIANA is hosted by the University of Costa Rica. The first issue published on the 15th of May, 2001, with the support of Jorge Warner, former Director of Lankester Botanical Garden, and Franco Pupulin, its inaugural Editor in Chief, was funded by Brian Holley from Cleveland Botanical Garden. The journal's early years were marked by enthusiasm and rapid growth despite initial challenges in distinguishing itself from other botanical journals. However, it quickly gained recognition within the scientific community, largely due to contributions from prominent figures in orchid science, including James Ackerman, Germán Carnevali, Phillip Cribb, Stig Dälstrom, Mark Chase, Calaway H. Dodson, Robert L. Dressler, Eric Hágsater, Günter Gerlach, Alec Pridgeon, Gerardo Salazar, and Norris H. Williams.

Initially not exclusively focused on orchids, LANKESTERIANA shifted its scope to solely cover orchid-related research in 2007, filling a gap in orchidology left by the discontinuation of other recognized journals in the field, such as Lindleyana, Orquídea, Orquideología, and Selbyana. With the continuous support of the Vice-Rectorate for Research at the University of Costa Rica and the incorporation of Diego Bogarín, Adam P. Karremans, and Melissa Díaz as Associate and Managing Editors and Noelia Belfort-Oconitrillo as Technical Editor, the journal maintained a steady flow of high-quality publications. Today, LANKESTERIANA is the only scientific journal dedicated exclusively to publishing original research articles on orchid science, along with correspondence, comments, corrigendum, opinions, obituaries, special issue contributions, conference proceedings, checklists, and reviews.

The journal continues to assert its influence within the field of orchidology, evidenced by its high citation in orchid-related literature worldwide and its inclusion in well-recognized indexes such as Scimago and Scopus. LANKESTERIANA is a peer-reviewed, electronic, open-access journal that still distributes printed copies to over 50 institutions worldwide.

Aims and scope: LANKESTERIANA, the International Journal on Orchidology, is an international scientific journal published by the Lankester Botanical Garden Research Center – University of Costa Rica. The journal is globally recognized for its specialization and contributions to the knowledge of the orchid family. In addition to research articles, LANKESTERIANA is dedicated to facilitating scholarly communication and exchange by publishing a comprehensive array of content, including book reviews, checklists, comments, conference proceedings, correspondence, corrigendum, obituaries, opinions, reviews, and special issue contributions.

LANKESTERIANA maintains rigorous academic standards as a peer-reviewed journal, ensuring that only the highest quality research articles are published. Through this rigorous review process, the journal upholds its reputation for excellence and reliability, providing readers with access to credible and authoritative scientific information on orchids.

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