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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

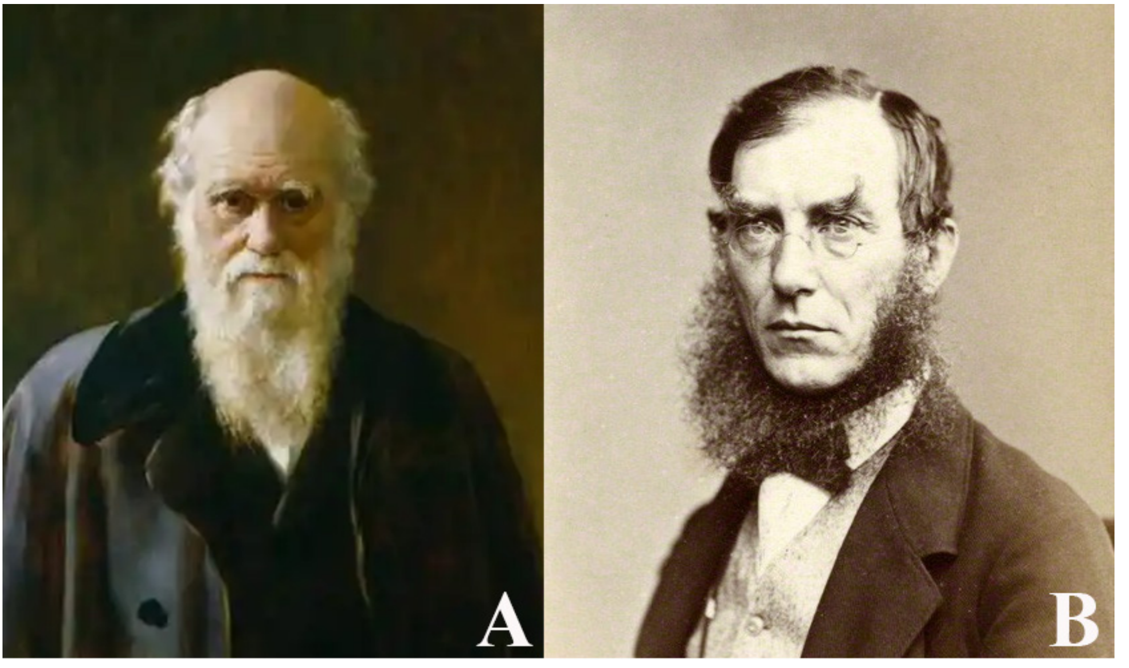

Figure 1. **A**. Charles Robert Darwin (1809–1982). **B**. Joseph Dalton Hooker (1817–1911). Sources: A, B, Wikipedia.

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.

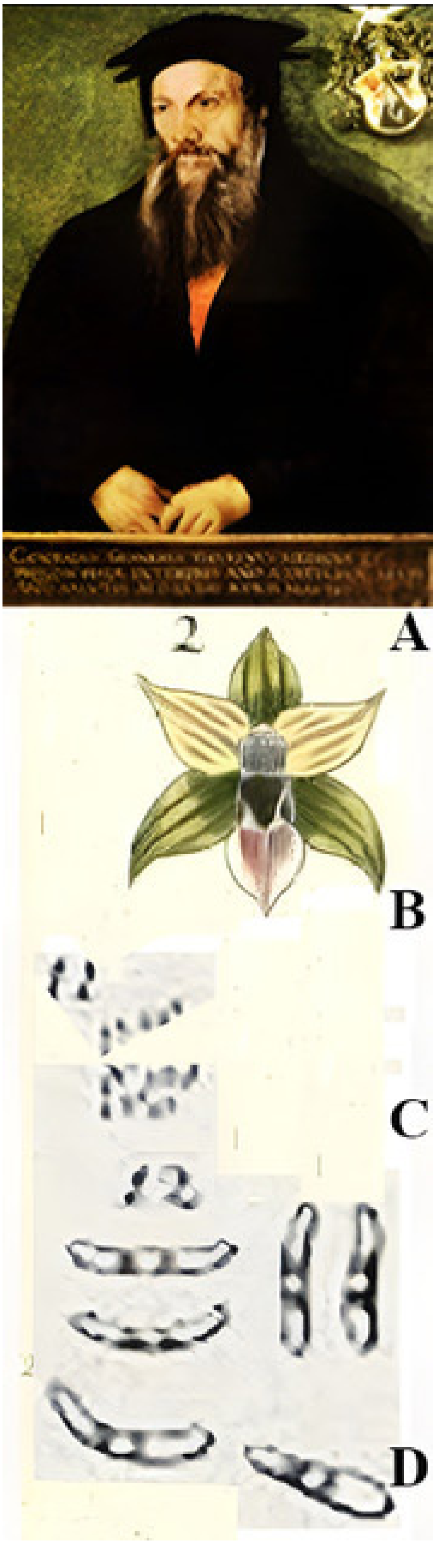

FIGURE 3. RIGHT. Conrad Gesner and the first known drawings of orchid seeds. **A**. Conrad Gesner (1516–1565). **B**. *Epipactis helleborine* (L.) Crantz, flower. **C**. Seeds drawn as dots. **D**. Seed showing embryos in their centers. Handwritten numerals 2, 11 and 12 are in the original Painting, 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).

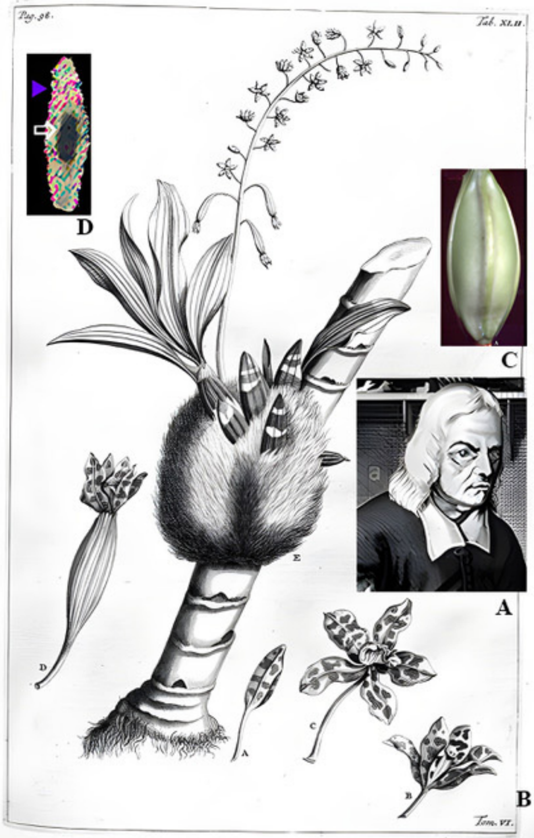

FIGURE 4. Georgius Everhardus Rumphius and his drawings of *Grammatophyllum scriptum* (L.) Blume. **A**. *Georgius Everhardus Rumphius* (1627–1702). **B**. *Grammatophyllum scriptum*, small capitals A–E in small non-bold face capital letters are as in the original. A. Unopened bud. B. Flower in the process 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.

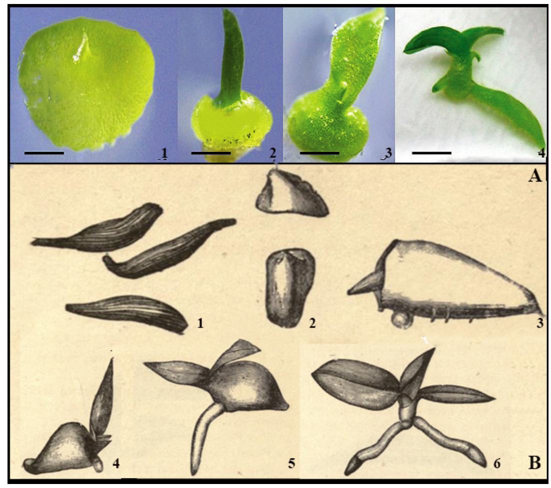

FIGURE 5. Seed germination and seedling development. **A**. Development of a Brazilian orchid from protocorm to plant. 1. Early protocorm. 2. First leaves. 3. Expansion of the first leaf and appearance of the second leaf. 4. Seedling with leaves and roots. Bars: 1–3, 1 mm; 4, 1 cm. **B**. Symbiotic seed 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

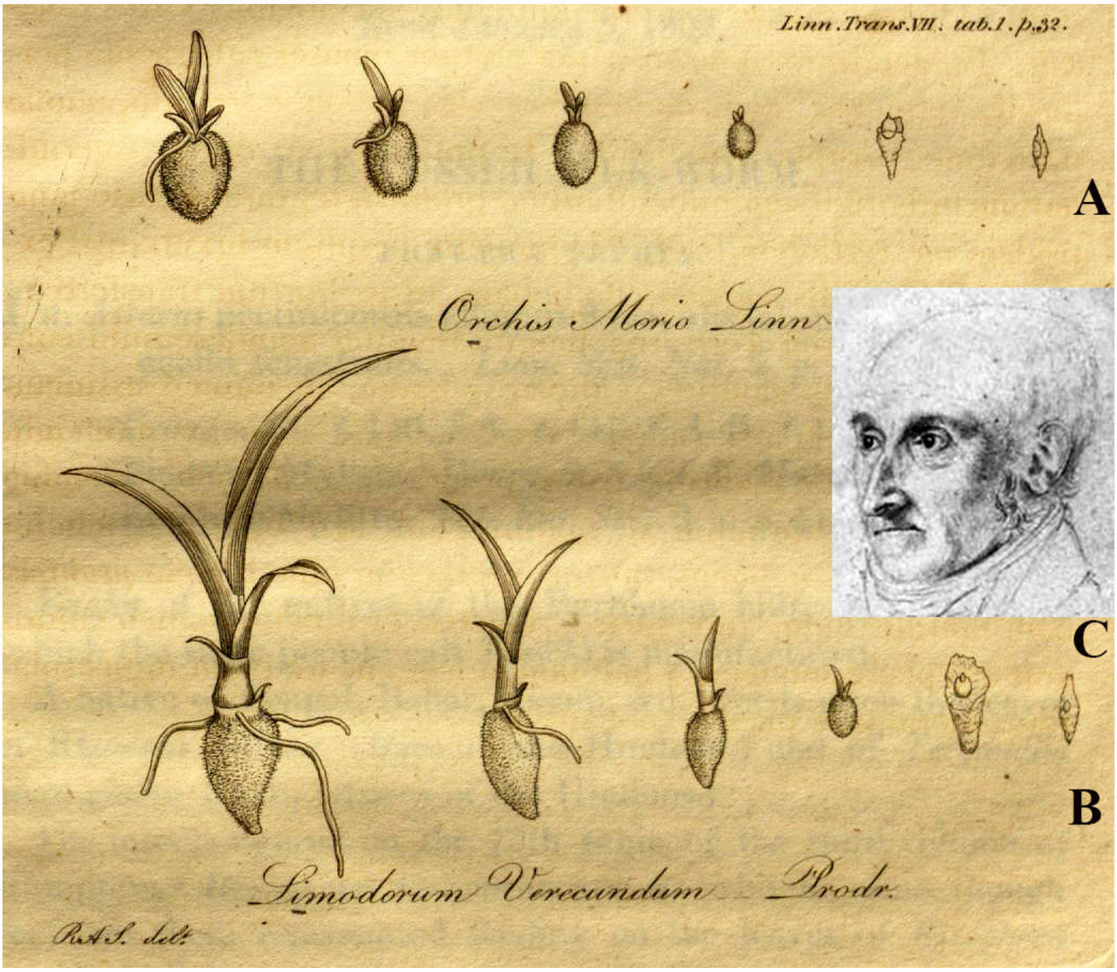

FIGURE 6. First known drawings of germinating orchid seeds. **A**. *Orchis morio* L. [=*Anacamptis morio* (L.) R.M.Bateman, Pridgeon & M.W.Chase]; **B**. *Limodorum verecundum* [=*Bletia purpurea* (Lam.) A.DC]. The original illustration did not contain size bars. The light brown cast and folds in the 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-

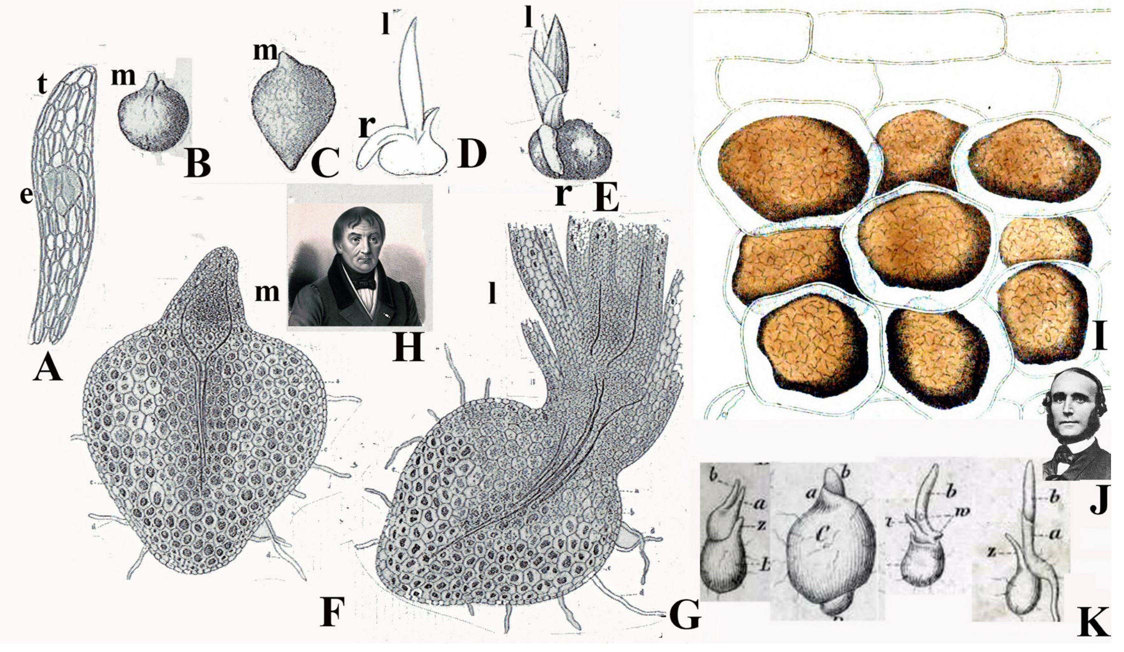

Figure 7. Early drawings of orchid seedlings which contain fungi. *Oeceoclades maculata* (Lindl.) Lindl. [= *Eulophia maculata* (Lindl.) Rchb.f.]. **A**. Seed. **B**. Young protocorm. **C**. Later protocorm. **D**. Young seedling with a single leaf and root. **E**. Older seedling with two leaves and 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 with 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,

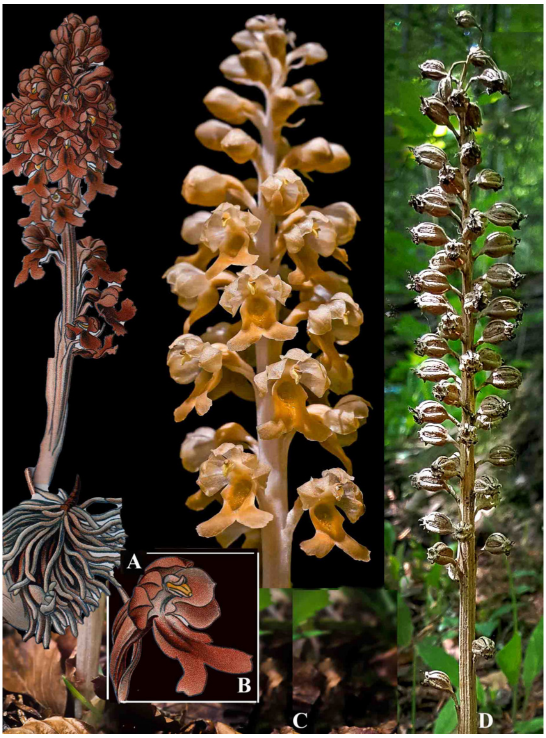

FIGURE 8. *Neottia nidus avis* (L.) Rich., the bird's nest orchid. **A**. Painting of inflorescence (30–50 cm tall, usually produced in France in May-June) and roots. **B**. Painting of flower (15 mm). A and B are of historical importance because they were published in the year Bernard made his discovery. 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.

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

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.

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).

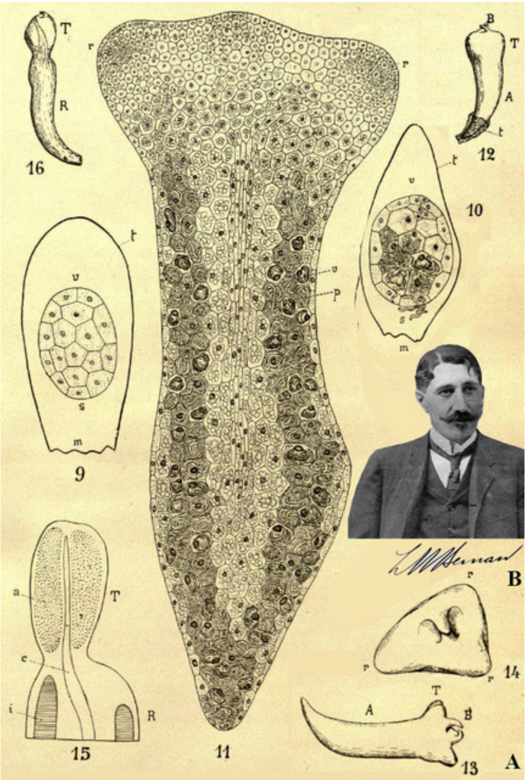

FIGURE 11. What Bernard saw and drew (somewhat rearranged with Photoshop to accommodate the photograph). **A**. Seed and seedlings of *Neottia nidus avis* (L.) Rich. **B**. Noël Bernard. Explanation of symbols: 9, seed (93× in original): m, area of attachment to the placenta; s, suspensor of the embryo. 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

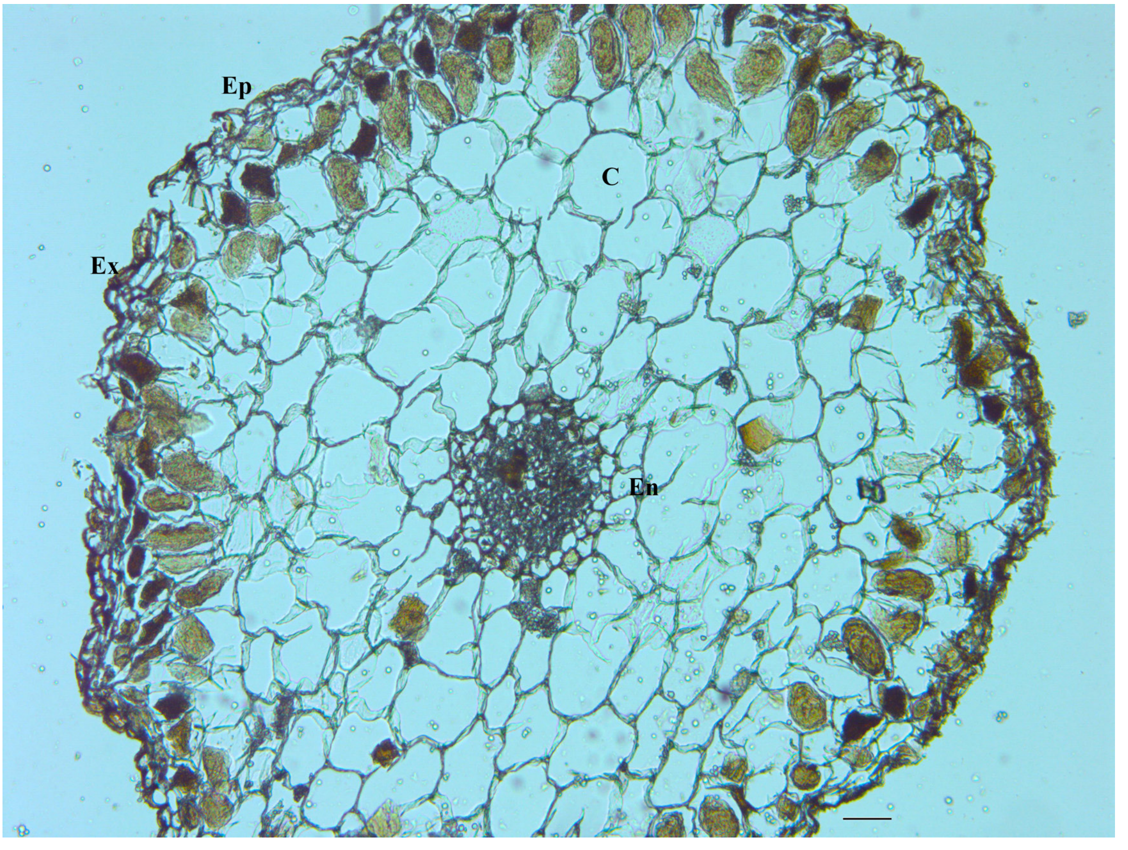

Figure 12. Modern cross-section of *Neottia nidus-avis*, root, which contains mycorrhizal fungi (dark masses in cells). Explanation of symbols: C, parenchyma of the cortex; dark masses in the cell, fungi; En, endodermis; Ep, epidermis; Ex, exodermis. Source: courtesy Anna Betekhtina from Betekhtina, 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

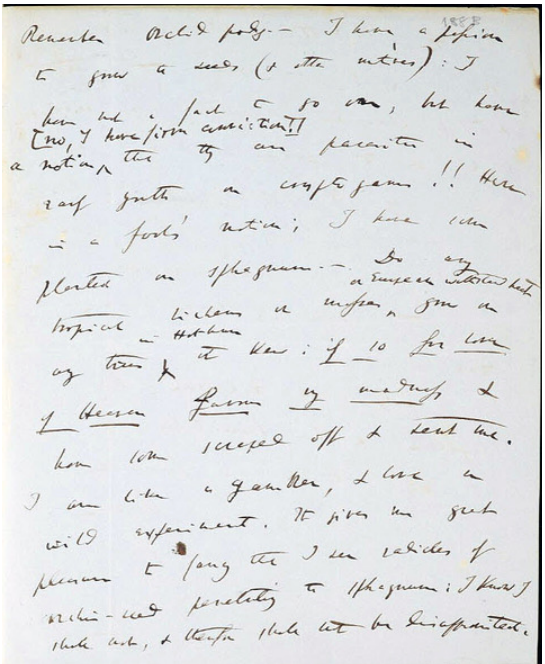

FIGURE 13. Part of a letter from Charles R. Darwin to Joseph D. Hooker dated 26 March 1863. Sources: Darwin Correspondence Project, "Letter no. 4061," accessed on 31 July 2024, https://www.darwinproject.ac.uk/letter/?docId=letters/DCP-LETT-4061.xml. Also published in The Correspondence of Charles Darwin, 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.

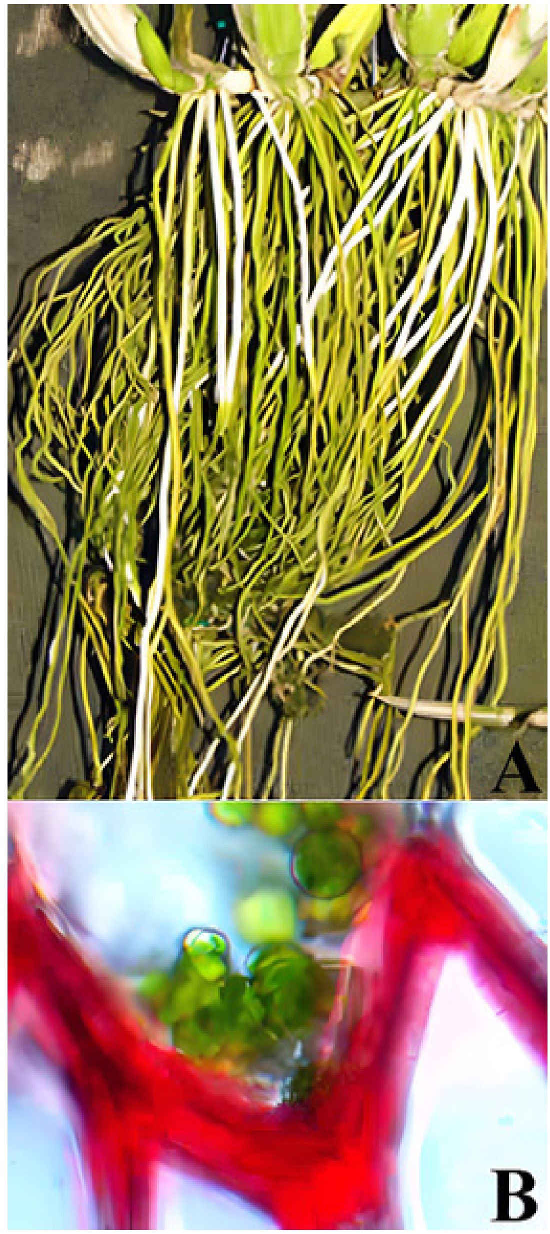

FIGURE 14. Algae and orchids, **A**. Algae on roots. **B**. Algae in roots. Source: Deepthi & Ray, 2020.

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).

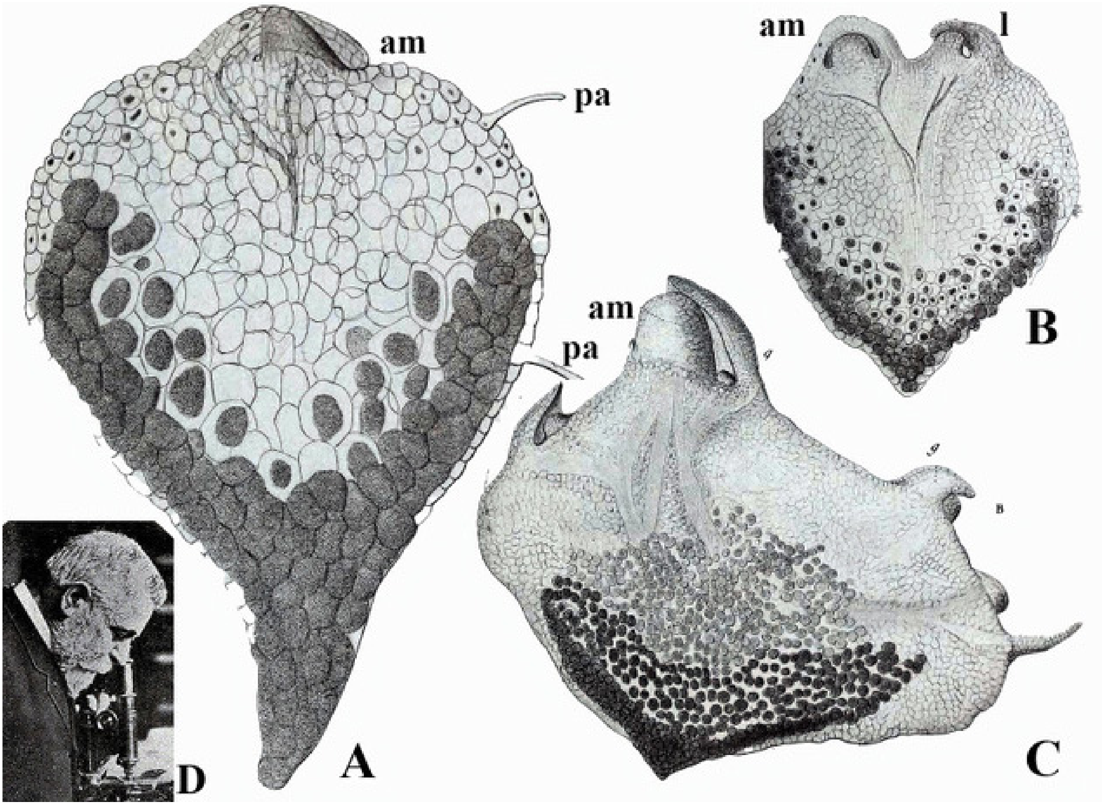

Figure 15. Fungus containing protocorms of *Oeceoclades maculata* (=*Eulophia maculata*) and E. E. Prillieux. **A**. Protocorm described as "larger embryo" in the original with papilae and an apical meristem. The cells containing dark masses were described as being "filled with a slightly granular yellowish 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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