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An annotated translation of Noël Bernard's 1899 article 'On the germination of *Neottia nidus-avis*'

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Abstract We translate Noël Bernard's discovery of orchid symbiotic germination discovered on *Neottia nidus-avis*, as published in the May 1899 issue of the *Comptes rendus hebdomadaires des séances de l'Académie des sciences*. In his note, Bernard (1874–1911) establishes the need for a fungus, which is also forming mycorrhizae in adults, for seeds germination. We provide illustrations reproduced from his later works, and summaries of the French text he cited. In our annotations, we show how early this discovery was done in Bernard's career, and insist on the scientific framework at the end of the nineteenth century, where orchid germination was mysterious and the need for vicinity of parents was not fully understood. We comment the text of Bernard on the basis of the most recent knowledge on *Neottia nidus-avis* and on orchid mycorrhizal fungi. Introducing his following papers, we finally discuss the emergence of the concept of peloton digestion, and how Bernard's work quickly paved the way to a general understanding of mycoheterotrophic germination in orchids and beyond.

Keywords Dust seeds · Germination · Mycoheterotrophy · Orchids · Pelotons · Protocorm

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Introduction

Noël Bernard (1874–1911) discovered the symbiotic germination of orchids serendipitously on the wild Eurasiatic species *Neottia nidus-avis* (the bird's-nest orchid; Fig. 1). He made this remarkable discovery at the very beginning of his scientific career (Boullard 1985; Yam and Arditti 2009; Selosse et al. 2011). We translate here his short 1899 note to the French Académie des Sciences (Bernard 1899), which was his very first article, reporting his findings. Beyond the anecdotes surrounding this discovery, we feel that this translation sheds valuable light on the history of science and on the research perspectives identified by Bernard. This was also a major step in the study of mycoheterotrophy, a process whereby plants obtain carbon from mycorrhizal fungi. Yet Bernard's work is sometimes overlooked, even in otherwise excellently documented historical surveys (e.g. Bidartondo 2005). Jacquet (2007) offered a good comprehensive translation of Bernard's works, but without contextualizing the papers, especially from the mycorrhizal side. Our aim here is to offer to a large mycorrhizal readership a new translation of Bernard's first article, using annotations to place the article in its historical scientific background and reproducing pictures derived from his later papers. We believe that such comments are required to understand the novelty and meaning of Bernard's finding. We also offer comments on the 1899 findings, based on current knowledge, in a final section.

Scientific context

At the time Bernard's note was published, orchid seed germination remained mysterious. Germination of orchid seeds turned into a nightmare for many orchid growers: In the eighteenth century, this difficult task even casted doubt on the ability of orchid seeds in general to germinate, an opinion that

was finally rejected by Salisbury (1804). During the nineteenth century, it was recognized, but not explained, that seed germination was only obtained in the vicinity of adult plants (Neumann 1844). Although we now know that this is explained by the presence of mycorrhizal fungi (see McCormick and Jacquemyn 2014 for a review of fungal factors shaping orchids distribution), the reasons remained unclear at that time. French growers even believed that the presence of adult plants made the substrate safer and cleaner (see Bernard 1900 and references therein).

Darwin (1862) himself described the paradox: Although orchids produce very numerous small seeds, most species remain quite rare. Counting 6200 seeds in a capsule of *Orchis* (= *Dactylorhiza*) *maculata* and assuming a shoot produces >30 capsules per year, Darwin (1862) estimated that a plant can produce 186,300 seeds, so that ‘*an acre would be thickly clothed by the progeny of a single plant. At the same rate of increase, the grandchildren would cover a space slightly exceeding the Island of Anglesea; and the great grandchildren of a single plant would nearly clothe with one uniform green carpet the entire surface of the land throughout the globe*’ (Darwin 1862).

In other words, in the second half of the nineteenth century, limited orchid seed germination remained a matter of speculation. Nowadays, we know that fungal partners are required

to enhance germination by bringing nutrients to the heterotrophic seedlings, called protocorms (reviewed in Rasmussen 1995; Dearnaley et al. 2016). Such nutrition assisted by a fungus is called mycoheterotrophy (Merckx 2013), and it accounts for the limited reserves in the tiny seeds. Mycoheterotrophy persists at adulthood in some non-photosynthetic, achlorophyllous orchids, such as *Neottia nidus-avis*, the species investigated by Bernard (Fig. 1). Fungal partners later form mycorrhizal association in roots, when they emerge (Fig. 2a), and this is why these fungi, from the very beginning, were often called ‘mycorrhizal’, even though a protocorm is not a root (Dearnaley et al. 2016). In protocorms and roots, fungi colonize some host cells by forming hyphal coils called pelotons, whose colonization is dynamic: After some time, fungal hyphae undergo a poorly understood lysis, leaving conspicuous brownish-yellowish material (sometimes called ‘clumps’) in host cells, which can then undergo recolonization by new, living hyphae (Rasmussen 1995). Funnily, this brownish-yellowish material was also first discovered on *Neottia nidus-avis* roots (Schleiden 1845–1846), but its link to fungi was not generally understood until the end of the nineteenth century (see below). Symbiotic fungi mostly belong to ‘rhizoctonias’ (a word coined by Bernard himself): ‘Rhizoctonias’ turned out, toward the end of the twentieth century, to be a polyphyletic grouping of Basidiomycetes

Fig. 1 *Neottia nidus-avis* (the bird’s-nest orchid), a forest achlorophyllous, mycoheterotrophic orchid. **a** Whole plant at the flowering stage (photo M.-A.S.). **b** An excavated root system, bar 4 cm (photo M.-A.S.). **c** An erect, dried infructescence from the previous year (photo Stephane Vitzthum)



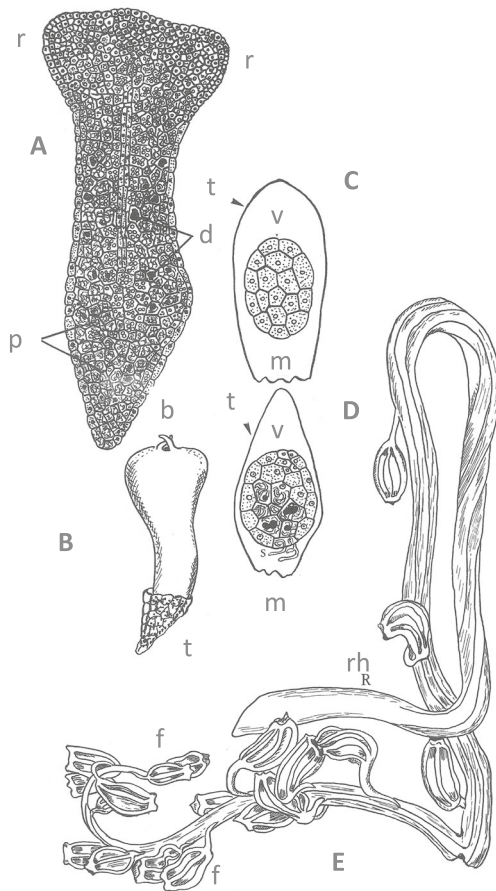


Fig. 2 Germinations of *Neottia nidus-avis* in the earliest published drawings by Bernard (1902; facsimile from Bernard 1985, with permission). **a** Seedlings (protocorm) with initiation of the meristem of the first two roots (*r*), and colonized zone with pelotons (*p*) and degenerated pelotons (*d*). **b** Older plantlet with apical bud (*b*) and cracked seed envelope (= testa, *t*) at its base. **c**, **d**, Seeds, respectively, at the ungerminated and early germination stage, with fungal penetration, with testa (*t*) and a region of attachment to the maternal placenta (*m*; side of the embryo suspensor) and vegetative pole (*v*). **e** Subterranean infructescence and shoot base whose semi-open fruits (*f*) contained germinated seeds with dried rhizome (*rh*)

encompassing representatives from the Cantharellales and the Serendipitaceae (Sebacinales; Deamaley et al. 2013; Weiß et al. 2016). The name ‘rhizoctonias’ now remains in use with the latter polyphyletic coverage in orchid mycorrhizal research, although in modern taxonomy *Rhizoctonia* represents a small monophyletic group in the Cantharellales (Oberwinkler et al. 2013) that does not, to our knowledge, contain orchid symbionts. Yet different fungi have been found in orchids that remain mycoheterotrophic at adulthood, such as *Neottia nidus-avis*. Instead of ‘rhizoctonias’, mycoheterotrophic orchids harbour various fungal partners (reviewed in Deamaley et al. 2013), which, in temperate forests at least, include fungi usually forming ectomycorrhizas on tree roots. While most ‘rhizoctonias’ are cultivable, most fungi in mycoheterotrophic orchids hitherto have not been cultivable (van der Heijden et al. 2015).

In 1899, the contribution of fungi to orchid germination was not suspected, although many researchers had described the presence of fungi in roots of some mycoheterotrophic orchids like *Neottia nidus-avis* (Irmish 1853; Prillieux 1856; Drude 1873; Wahrlich 1886). Due to their unexpected achlorophyllous habit, mycoheterotrophic orchids, and also mycoheterotrophic Ericaceae such as *Hypopitys monotropa*, prompted observations that led to the discovery of fungal colonization of their roots, well before the concept of mycorrhiza was formally established by Frank (1885, 2005). There were lively debates about the *raison d’être* and relevance of this fungal colonization (Bidartondo 2005): despite early suggestions that the fungus had no relevance, its role in connecting *Hypopitys monotropa* to surrounding trees was suspected at the end of the nineteenth century (Rylands 1842; Kamienski 1881, 1882; MacDougal 1899; MacDougal and Lloyd 1900), but we are not aware that the same was proposed for mycoheterotrophic orchids. Moreover, it is unclear how these works were an inspiration to Bernard that does not cite them.

To summarize, what limits the germination of orchid seeds was not known, although their mycorrhiza had been seen (albeit without this name before 1885). The origin of the brownish-yellowish material in some orchid root cells was unclear. The idea of symbiotic germination did not exist, while nutrient transfer from a fungus to a mycoheterotrophic plant was scarcely admitted for *Hypopitys monotropa* and not proposed in other contexts.

Context within Bernard’s professional career

At time of his discovery, Bernard had been working for a few months, since the end of 1898, on a thesis on orchids in the laboratory of Jean Costantin, at the Botany Department of the Ecole Normale Supérieure, in Paris. In 1899, he started one-year military service at Melun, near Paris. On Sunday, May 3, 1899, at the age of 25, while walking in the nearby Fontainebleau forest during a break, he discovered an infructescence (i.e. a group of fruits on a shoot; Figs. 1c and 2e) of the mycoheterotrophic orchid *Neottia nidus-avis* from the previous year, bent and buried under the litter layer. Fruits harbouring germinating seeds and fungi inspired him to propose a mechanism for orchid seed germination.

Bernard immediately understood the importance of his finding, as was clear in two (nearly identical) letters he wrote in the evening of that day to his cousin Jean Magrou (a biologist too) and his uncle Joseph Bernard (Boullard 1985). To the latter, he wrote: ‘Indeed, my studies from this afternoon have given me, by an unexpected chance, several hundreds of *Neottia* seeds in germination, and I have young plants (up to three millimetres in length) that no botanist’s eye ever examined! I thus have precious material for solving the question of orchids culture and for addressing two or three other questions, so that my thesis, which was slightly drifting in another

direction, will, I hope, go fast, in its primary direction again. This Sunday afternoon will thus have been usefully employed.’ (Boullard 1985). Indeed, the reader may observe that the start of Bernard’s thesis was probably difficult, because in the note below he reports his previous failed attempts to germinate orchid seeds in abiotic conditions.

Things thereafter went fast, and the report of his finding was produced very quickly. Gaston Bonnier, a botany teacher at the Ecole Normale Supérieure, and a powerful and renowned academician, agreed to support a note by Bernard; an introduction strictly required at the Académie des Sciences at that time. Bernard’s colonel, after some insistence, gave him leave to present the note orally at the Académie, in the session of May 15, 1899, i.e. less than 2 weeks after the field discovery. The note was then published in the May 1899 issue of the *Comptes rendus hebdomadaires des séances de l’Académie des sciences*, the weekly reports of the meetings of the Académie (Bernard 1899). His letter of May 3 to his family clearly shows that he understood the consequences for orchid culture, and this fast process supports the view of a ‘stroke of brilliance’, as qualified by Jacquet (2007).

We translate below the 1899 note from the *Comptes rendus*, which are fully available in French from *Gallica* at <http://gallica.bnf.fr/ark:/12148/cb343481087/date>. Footnotes numbered in round brackets () are by Bernard himself; our comments on the text are numbered in square brackets []. Since no picture accompanied the note, we provide a selection of pictures from a later paper (Fig. 2; Bernard 1902) to enable readers to imagine what Bernard saw in 1899.

Full translation of Bernard’s (1899) note.

BOTANY—On the germination of *Neottia Nidus-Avis*.¹ Note by Mr. Noël Bernard, presented by Mr. Gaston Bonnier.

I had the opportunity to observe the germination of *Neottia Nidus-Avis* [1] 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 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.

These three cell types can be found with the same features in the roots and rhizomes of adult plants; especially, the cells of the second type, with mycelial filaments called *mycorrhizas* [3], have often been described. The presence of these mycorrhizas in the cells from the earliest stages of germination on, even though seeds are wholly devoid of such structures [4], is explained by the following observations:

One can find, at this time of the year in the Fontainebleau forest, stems of *Neottia* upright in the soil and bearing the fruits formed the previous summer. These stems are desiccated and hollow as a result of the destruction of the central parenchyma. The ca. 30 stems I investigated always displayed, at their base, in the part under the soil and in moisture, a tight web of mycelial filaments filling the inner cavity. These filaments are ramified, septate and brown in colour; one can normally observe clamp connections between successive cells [5]. At the base of the stem, these mycelial filaments are in contact with old cells with easily recognizable mycorrhizas; inside the cells, filaments have a thinner membrane [6] and one can sometimes, but not always, observe clamp connections [5].

In old stems, therefore, a lot of filaments of free mycorrhizas only extend within the buried and moist part of the stems; the aerial part above the soil is completely dry and devoid of them [4].

Now, the fully buried stem I described above was kept in wetness throughout its length. 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 [3].

Authors who have tried to germinate *Neottia* seeds in conditions of humidity, aeration and temperature, which normally allow germination, did not observe any modifications of these seeds.² I myself failed to obtain any result in experiments of this kind, repeated several times. I am thus led to conclude that mycorrhizas are essential for the plant at the time of germination.

Mr. Prillieux³ mentioned the propagation of *Neottia Nidus-Avis* by persistence through winter of their underground parts (roots containing mycorrhizas) [7]. To my knowledge, propagation by seeds has not been observed up to now. But however, the species preserves itself, one can see that *Neottia* individuals live in symbiosis with fungi at all stages of their development. From the descriptions by Messrs. Prillieux and Rivière for *Angraecum maculatum*⁴ and by Mr. Fabre for

¹ work done at the Laboratoire de Biologie végétale in Fontainebleau

² GERMAIN DE SAINT-PIERRE, La collection d’Orchidées des latitudes tempérées cultivées au château d’Eu (Bulletin de la Société botanique de France, t. XXIII, Session extraordinaire).

³ ED. PRILLIEUX, De la structure anatomique et du mode de végétation du *Neottia Nidus-Avis* (Ann. Sc. nat. Bot., 4e série, t. V, 1856).

⁴ E. PRILLIEUX & A. RIVIÈRE, Observations sur la germination et le développement d’une Orchidée (*Angraecum maculatum*) (Ann. Sc. nat. Bot., t. V, p. 119; 1856).

*Ophrys apifera*⁵ [8], a similar symbiosis also seems to operate at germination.

Symbiosis would thus be more complete for these species, and without doubt for many orchids, than for plants with mycorrhizas whose seeds can germinate and become established in sterilized soil.

Comments

Comments on the translation

First, we would like to comment on seven sections of the above text, [1]–[7], based on today's knowledge (as described above).

- [1]. At the time of writing, some Latin species names had captions; this would now be *Neottia nidus-avis*.
- [2]. Throughout, we would now call 'mycelial filaments' more simply hyphae.
- [3]. Bernard here follows an old way of using the word mycorrhiza in French, enlarging the use of Frank (1885, 2005): by the mycorrhiza, Bernard means the fungal partner itself.
- [4]. Bernard (1902) later mentions that he also observed seeds from infructescences that stayed erect (their presence is mentioned in the 1899 note), and that there was no fungus around the seeds in these cases (see following block).
- [5]. Such clamp connections ('*anastomoses en boucle*' in original text, literally 'anastomoses in loop') characterize the septa of some, but not all, Basidiomycetes with dikaryotic hyphae. Even in clamped species, they are not always present at each septum. All fungi described by Bernard are Asco- or Basidiomycetes, due to their septate hyphae, and those with clamp connections are thus Basidiomycetes. But the fungus observed in old stems and soil was not a 'rhizoctonia', nor even a Sebacinaceae, which is now known to be mycorrhizal on *Neottia nidus-avis* (McKendrick et al. 2002; Selosse et al. 2002a, 2002b), since all these groups do not display clamp connections (see general comments below).
- [6]. A modern wording for 'membrane' here would rather be cell wall.
- [7]. This section refers to the fact that in old *Neottia* roots separated from the rhizome, the root meristem transforms into an apical one. This changes a root into a rhizome and achieves underground asexual reproduction. It had already been described by Prillieux (1856), and Champagnat (1971) further studied this

phenomenon; see Selosse (2003) for illustrations. Prillieux (1856) also opened the debate about monocarpic development, questioning whether *Neottia* rhizomes survived or not after flowering (indeed, they may survive by forming axillary buds; Selosse 2003). Prillieux, of course, did not use the word mycorrhizas (coined by Frank, 1885), but clearly mentions that '*the presence of a fungus in the tissues of the root of Neottia nidus-avis looks... constant*'. Insisting that mycorrhizal fungi may be overwintering within the roots is, in our view, a way of describing the symbiosis specific to Bernard.

- [8]. The references to Fabre and Prillieux & Rivière are inverted in the original text, and we correct this here. These two works deserve a short mention regarding their content. They are only cited here to support the notion that orchids can germinate, since some readers at that time may still have had doubts about their ability to do so; they do not contain any mention of fungal presence at all. These citations also support the idea that as the general shape of seedlings is the same in these other species, there may be a similar fungal presence. Fabre (1856) describes *Ophrys apifera* and some germinations he found, but without microscopic investigations. He only notices absorbing hairs, but no fungus, even when describing roots and tubers. Prillieux and Rivière (1856) report a serendipitous germination of *Angraecum maculatum* in the Botanical Garden of the Medical Faculty in Paris, but do not report any fungus either. However, they report that '*the mass of the embryo is made of translucent cells whose appearance has no particularity; but at its base, a layer of cells filled with opaque, yellowish material that is stained brown by iodine is conspicuous; it has in all a funnel-like shape*'. We can now interpret this zone as that of the cells formerly colonized by the fungus, where old, lysed pelotons form the yellowish material. This zone may have been inconspicuous in the very young seedlings investigated by Bernard (although some decayed pelotons can be seen in Fig. 2a, c from Bernard's 1902 publication), and he did not mention it before his next 1901 publication.

General comments

The length and informal style of this note without illustration may look odd to modern readers, but one should keep in mind that it relates to an extinct way of communicating in science. Such notes are transcriptions of simple descriptions with main conclusions, which were presented in public meetings of the academy, with no way of illustrating the data, before a longer paper was produced (see below). It was a way of announcing

⁵ J.-H. FABRE, De la germination des Ophrydées et de la nature de leurs tubercules (Ann. Sc. nat. Bot., t. V, p. 163; 1856)

novelties quickly, making a statement of ownership on the new ideas, in an equivalent of modern-days posters in congress. Yet, Bernard's 1899 much-cited short note paved the way to a full, modern understanding of orchid germination. He suspected (i) the need for a fungus to invade the seed before germination (although no clear role was proposed for the fungus), (ii) the identity between fungus in mycorrhizas and that in germinating seedlings (although he observed, among others, basidiomycetes unrelated to the process), and (iii) the existence of such dependence in most if not all orchids. This finding, 14 years after the introduction of the concept of mycorrhiza (Frank 1885), exemplifies the fast growth of microbiology and symbiosis research toward the very end of the nineteenth century.

This is also, to our knowledge, the first use of the word 'peloton', a French word meaning 'coiled filament(s)', which is now widely used as a synonym for hyphal coil in English (e.g. Rasmussen 1995; Smith and Read 2008). However, Bernard's 1899 description of fungi involved in the process can now be interpreted as (partly at least) a misunderstanding: He describes basidiomycetes with clamp connections, whereas such features are absent from the mycorrhizal fungi of *Neottia nidus-avis* (see above; Selosse et al. 2002a; Weiß et al. 2016). Thus, Bernard likely observed basidiomycetes unrelated to the germination, probably simple saprotrophs proliferating in dead fruits and stems. One year later, Bernard (1900) reported isolation of *Fusarium*, which is now considered as a contaminant or a non-mycorrhizal endophyte. Cultivation of the fungal partner of *Neottia nidus-avis* has still not been achieved, despite many attempts (see review of further attempts to isolate *Neottia* fungi in Burgeff 1909, 1932, Rasmussen 1995 and Selosse et al. 2002b). But the finding of an ascomycete like *Fusarium* is at odds with the observation of at least some clamp connections in the 1899 paper. Bernard does not discuss this discrepancy further, but this tacitly suggests that he abandoned this part of his conclusions. Fungal partners were finally identified thanks to molecular tools in roots (McKendrick et al. 2002; Selosse et al. 2002a, 2002b) and seedlings (McKendrick et al. 2002), and turned out to belong to ectomycorrhizal Sebacinaceae (these Sebacinaceae do not belong to rhizoctonias) and to lack clamp connections (Weiß et al. 2016). Thus, even if the proximity of plant roots likely gave access to the required fungus, this was not seen by Bernard in 1899. Later, Bernard isolated fungi from green orchids (Boullard 1985; Jacquet 2007) and demonstrated symbiotic germination in vitro on more tractable rhizoctonias.

After this first 1899 note, Bernard produced a second, longer article in 1900, and defended his thesis in 1901. The 1900 paper '*On several difficult germinations*' (Bernard 1900; translated in Jacquet 2007 and here for some sections) details and enlarges his views. It was published in the *Revue générale de Botanique* edited by Gaston Bonnier, who had already introduced Bernard's note at the Académie. Again without any picture, Bernard further describes germinations in

Neottia and also *Laelia* seedlings, confirming the occurrence of fungi in seedlings smaller than 0.5 mm in length. Let us introduce just two ways that Bernard enlarged his views in this second paper, which further clarifies the 1899 note in terms of (i) digested pelotons and (ii) other plants requiring fungi to germinate.

First, the 1900 paper clarifies the nature of the brown digested pelotons. From his 1902 (see Fig. 2d) drawings, Bernard may have seen these brown structures in *Neottia* protocorms, but he does not report this in 1899 and only comments on them in 1900, as follows. '*In the oldest seedlings, one can see, close to cells with distinguishable pelotons, cells probably infested for longer where filaments are less and less distinguishable, and where the whole peloton ends up in a brown mass close to the nucleus. These old infected cells attract the attention at first glance; one cannot miss them, whereas one cannot be sure of recognizing recently infested cells, except after cuttings and with suitable staining*'. He then acknowledges that, for this reason, other authors describe these cells with brownish-yellowish material (we already mentioned Prillieux and Rivière 1856). He acknowledges as well that Prillieux (1856) drew a parallel between brown cortical cells in *Neottia nidus-avis* roots and those in the seedlings of other orchids. Prillieux (1856) discussed this brownish-yellowish material and rejected that it was an indication '*of the cessation of life of the cell*', finally considering that it was a material '*used in the plant's nutrition*' with no clear link to the fungus (funnily, we still do not know whether peloton digestion actually contributes to exchange between the plant and the fungus; see updates and controversies in Selosse 2014). In identifying brownish-yellowish material as decaying hyphae, Bernard supports a hypothesis already raised earlier by German authors (Schleiden 1845–1846; Reissek 1847; Wahrlich 1886), but he does not cite them. The reasons for this omission remain unclear to us: Did Bernard not read German? Was he not aware of these papers? At the end of the nineteenth century, reciprocal omissions were usual on both sides of the French-German border, due to the acute rivalry of that time. Yet Bernard, who had anarchist tendencies (Boullard 1985; Selosse et al. 2011), was unlikely to be so nationalistic: rather we believe that he had limited ability or opportunity to read German. Indeed, the German orchidologist Burgeff, who was exchanging a dense and friendly correspondence with Bernard, spoke French fluently and used it with Bernard (Boullard, pers. com. with Burgeff in 1954).

Second, the 1900 paper further emphasizes that symbiotic germination is a general trait in orchids, since brown decaying pelotons (or even living hyphae) are always observed. He uses the argument that cases have been claimed in four independent tribes that are '*as different as possible in such a homogeneous family*'. In a second step, Bernard extends symbiotic germination to other species that are difficult to germinate away from adults, namely the spore-producing Lycopodiaceae and

Ophioglossaceae. Bernard further underlines that even in such soil, the germination of spores remains unsure ('capricious'), exactly as for orchids. Moreover, the roots of these plants also display endophytic fungi. Although his arguments remain indirect (and not derived from the observation of germination, as for orchids), Bernard drew here a broad picture of mycoheterotrophic germination, bridging plants dispersed by seeds and by spores in a common mycoheterotrophic germination, which is now better described (Boullard 1979; Leake et al. 2008; Merckx 2013).

On a final note, Bernard's proposed interpretation of the role of fungi in orchid germination looks somewhat outdated, and at least not in frame with the modern, twenty-first century interpretation. Acknowledging that this role is unknown, Bernard suggested at the end of his 1900 paper that '*what seems... the most probable is that [the fungi] act mainly by secretion of diastases, which digest the reserves of the plant they inhabit, thereby favouring growth and germination.*' In his further work, he insisted on the role of fungi in inducing 'tuberization', i.e. plant tissue growth in many plants (Selosse et al. 2011). We now know that reserves are scarce or lacking in orchid seeds, and that the fungus primarily acts by providing carbon and mineral nutrients (N, P; Merckx 2013). But at that time, there was still a long way to go in understanding the exact contribution of fungi to orchid nutrition.

Conclusion

Within 2 years, Bernard made steps into an understanding of mycoheterotrophic germination, as acknowledged by Burgeff (1909) and others (see Boullard 1985); he actively paved the way to horticultural applications (Boullard 1985; Selosse et al. 2011) and, even later, to in vitro cultivation (Yam and Arditti 2009). These field observations also initiated understanding of the reproductive dynamics of orchid populations in situ (McCormick and Jacquemyn 2014). This discovery also underlines how some achlorophyllous plants were instrumental in the awareness of more general properties of plant-fungal interactions. His too short career (12 years only) still allowed Bernard to leave a trace worth remembering. To end with a quote from Louis Pasteur, whom Bernard admired (Selosse et al. 2011), '*le hasard ne favorise que les esprits préparés*' (chance favours the prepared mind only). It is noteworthy that the findings of Bernard allowed him to reach a relevant conclusion within a few hours, probably because he was prepared to look close enough to see a fungus, which all other investigators had previously missed in germination, and to make links with other observations (those made on mycorrhizal roots). There is for sure a timeless lesson here on how to be careful with our field observations.

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