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Our sisters the plants? notes from phylogenetics and botany on plant kinship blindness

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ABSTRACT

Before the upheaval brought about by phylogenetic classification, classical taxonomy separated living beings into two distinct kingdoms, animals and plants. Rooted in ‘naturalist’ cosmology, Western science has built its theoretical apparatus on this dichotomy mostly based on ancient Aristotelian ideas. Nowadays, despite the adoption of the Darwinian paradigm that unifies living organisms as a kinship, the concept of the “scale of beings” continues to structure our analysis and understanding of living species. Our aim is to combine developments in phylogeny, recent advances in biology, and renewed interest in plant agency to craft an interdisciplinary stance on the living realm. The lines at the origin of plant or animal have a common evolutionary history dating back to about 3.9 Ga, separating only 1.6 Ga ago. From a phylogenetic perspective of living species history, plants and animals belong to sister groups. With recent data related to the field of Plant Neurobiology, our aim is to discuss some socio-cultural obstacles, mainly in Western naturalist epistemology, that have prevented the integration of living organisms as relatives, while suggesting a few avenues inspired by practices principally from other ontologies that could help overcome these obstacles and build bridges between different ways of connecting to life.

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Introduction

Our sisters the plants. At first glance, thinking about life in terms of fraternity or sorority seems more indebted to animist ontology than modern scientific rationality. And yet, for more than a century and a half, biology has been unified under the Darwinian paradigm that inscribes all living beings in a unique historical process.¹ Extant species originate from ancestral species via a mechanism of descent with modification, so much so that, going back through the emergence of original species, all current species show a degree of kinship to a greater or lesser extent (Figure 1, left). However, the consideration of living beings as relatives does not readily obtain in modern scientific contexts, given science’s adherence to an Aristotelian vision^{2,3} and a genesiac understanding that places humans at the top of the pyramid of living beings (Figure 1, right). These visions certainly participate in the origin of the concept of “plant blindness”, a philosophical vision of the plant as a form inferior to the animal, and thus the human tendency to ignore the importance of plant life outside of its utility as a resource. However, some authors favor the hypothesis that the inattention to plants could be more due to human cognitive specificities than to cultural biases.⁴

As biologists, cognitive scientists and geographers working in a multidisciplinary context it seemed necessary to us to put these questions to work collectively. Students and teachers had the

greatest difficulty in extracting themselves from dichotomizing between animals and plants, which made it very difficult to think about relationships and links among living organisms. We felt it was necessary to initiate a discussion on homologies, in the biological sense, i.e. similarities inherited from a common ancestor, between human and non-human animals, and plants, and this in the light of recent scientific work by comparing work from the life sciences with that from the humanities.

In this preliminary article, we aim to point out why scientists still have trouble viewing plants and animals¹ as related, when it has been shown, particularly by scientific studies and numerous studies conducted on science, that most scientists are not the naturalists² that some would like to see, and that there is a big gap between the discourse on science and scientific actions in laboratories for example^{5, 6–8}. Of course, it is not necessary to share kinship to feel proximity or attachment, but we question here the blindness to animal genetic kinship with plants because of an ideological positioning that categorizes the latter as “other”. Other issues are also on the agenda. What does genetic and biological research show about the homologies between plants and animals? How can we go beyond the borders built between these “kingdoms” in modern science to better think and help find appropriate forms of cohabitation between humans and non-humans in times of major ecological crises⁹?

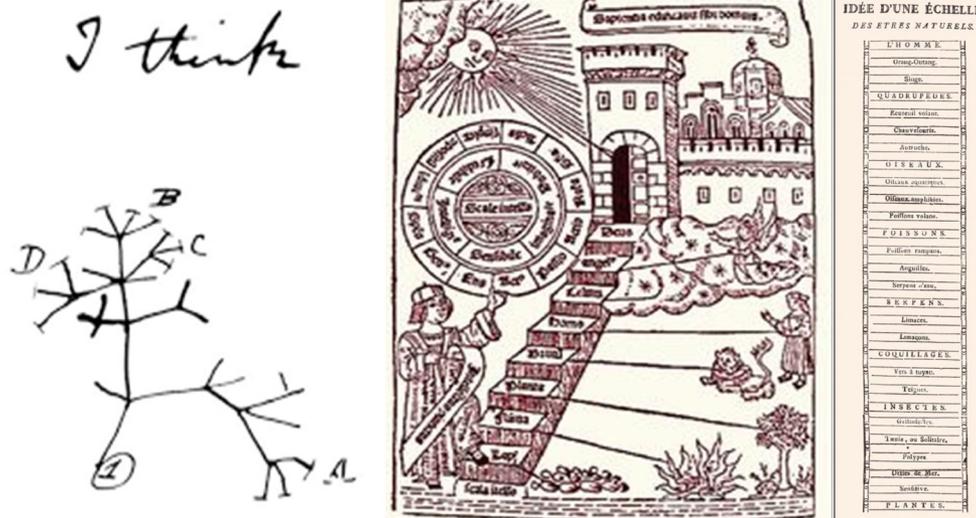


Figure 1. On the left, Darwin's tree of life (1837) schematizing the phylogenetic view of the evolution of the living. On the right, the scales of Lull (1305) and Bonnet (1745) representing the hierarchy (stairs) of the beings, *scala naturae*, inspired by Aristotle (343 BC).

First, we will look at works in the life sciences showing the homologies between animals and plants through genetics and biology. Then, we will outline the socio-cultural obstacles to such a rapprochement and will try to understand how scientific debates on plant agency,¹⁰ echoing the emergence of public debate on plant intelligence, allow us to think differently about our relationship with life that could open up other research vistas for a better understanding and openness to what connects humans and plants.

Homologies between plants and animals

Phylogenetic classification makes plants and animals sisters

The Earth formed within the solar system about 4.56 billion years ago (giga-annum, Ga), thus, the history of the earth spans ca. 1/3 of the history of the universe, which dates back to ca. 13.8 Ga ago. The conditions for the development of prebiotic processes, including the presence of liquid water, were not met until about -4.4 Ga. Cellular life, i.e. self-replicating units separated from the external environment by a biological membrane, would have appeared at around -3.9 Ga in an oxygen-free environment. Presence of 3.77–4.28 Ga-old putative fossilized microorganisms supports the view that life on earth can be dated back to ca. -4.0 Ga.¹¹ The oldest evidence of biological activity, in this case anoxygenic photosynthesis, is revealed by the enrichment of carbon isotope 12 in graphites from the Isua Formation (Greenland) at -3.85 Ga.¹² This photosynthesis was probably due to bacteria, single-celled prokaryotic organisms whose existence is attested as early as -3.46 Ga, the age of the oldest rocks of biogenic origin such as the stromatolites of the North Pole Formation (Australia). Eukaryotic cells, or eukaryotes, are thought to have appeared around -2.7 Ga (as evidenced by the presence of steranes³ in Australian shales, 13). Eukaryotes are thought to be the result

of the fusion of bacteria and archaea^{14,15} in a world where the increasing activity of cyanobacteria (this time using oxygen-based photosynthesis) saturated environment with a poison that was lethal to most species at that time: oxygen. Around 2.4 Ga, this oxygen became prevalent in the atmosphere, marking a turning point in the history of life, called the great oxidation. The lineage of eukaryotes with internal organelles capable of detoxifying oxygen, the mitochondria, was able to survive this ecological crisis. These mitochondria are the result of an endosymbiotic process, corresponding to the incorporation of α -proteobacteria by a primitive eukaryotic cell about 2 billion years ago.¹⁶ This lineage, ancestor of all current eukaryotes, diversifies into several groups around -1.6 Ga, including, among others, the lineages at the origin of plants or that at the origin of animals.^{17,18} The evolutionary history of the cellular lineage of living cells goes back to about -3.9 Ga, or even to -4.4 Ga if we consider the protobiontic forms,⁴ thus plants and animals shared nearly two thirds of a common evolution before separating (Figure 2). At the scale of the history of life, and from a phylogenetic point of view, plants and animals are therefore sister groups. The main difference between animals and plants is that the latter have benefited from an additional endosymbiosis developed through internalization of cyanobacteria as the origin of the plastid.¹⁶ The very first acquisition of the plastid gave them their photosynthetic capacity, and thus their autotrophy. It is probably the main driving force behind their evolutionary success. It should be noted, in this case, that it is the plants that present an additional evolutionary innovation, just like the brown algae resulting from secondary endosymbiosis, while all the other eukaryotes (including humans) have preserved their ancestral cellular organization.

What have we, animals and plants, inherited in common from this evolutionary kinship? As living organisms, we share the basic cellular machinery: we code and store genetic information in the form of DNA and transport it as messenger RNA to the ribosomes where we decode it identically in order to

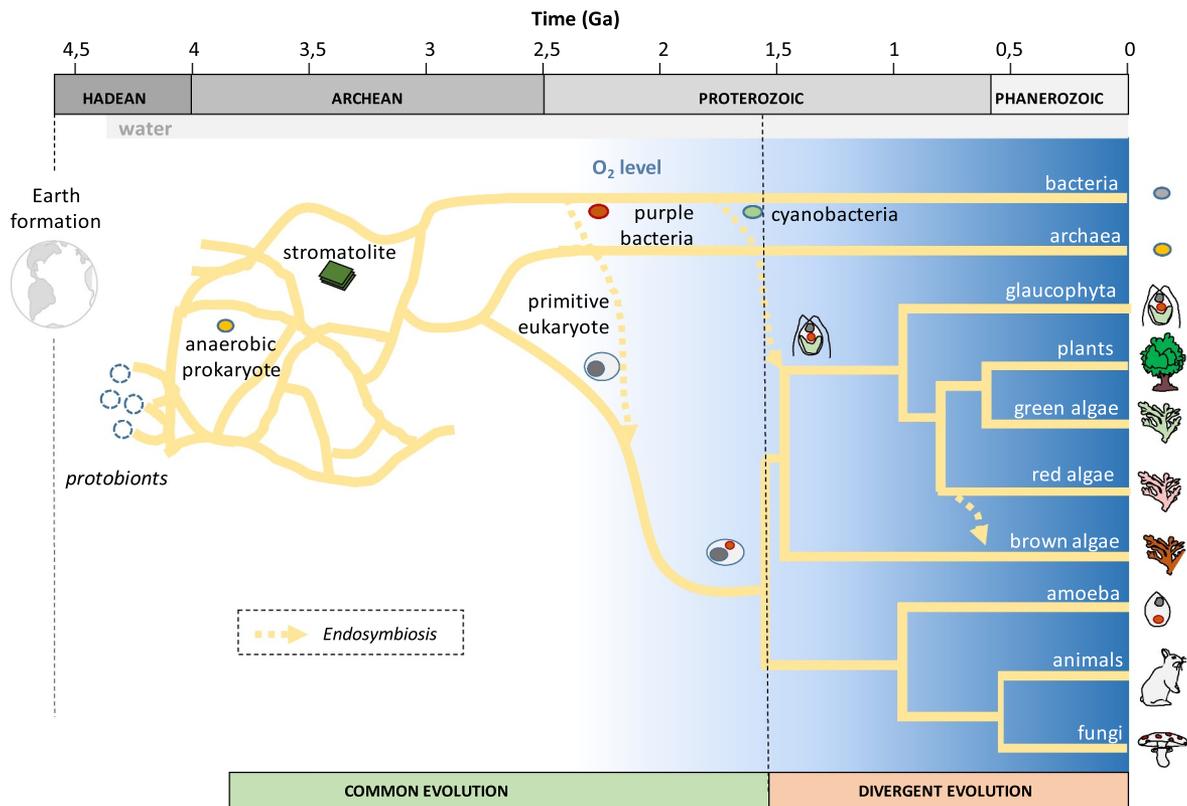


Figure 2. Diagram of the evolution of living organisms since the formation of the earth. From -4.4 Ga the stabilization of the presence of water on Earth makes possible the development of prebiotic self-replicating processes that would have led to the formation of protobiontic cell forms even before -4 Ga. Changes in the isotopic proportions of carbon (-3.85 Ga) and the formation of stromatolites (-3.45 Ga) attest to the photosynthetic activity of primitive prokaryotic cells. These primitive forms, like today's prokaryotic cells, probably exchanged their genetic inheritance directly between individuals in addition to being passed on by progeny from generation to generation. During the Archean, two major prokaryotic lines emerged from this network: bacteria and archaea, which, by fusion, led to the appearance of a third line: the eukaryotes. The development of oxygenic photosynthetic activity led to the accumulation of oxygen consequently radically modifying the earth's atmosphere at the Archean – Proterozoic hinge. Between -2.5 and -2.2 Ga, the endosymbiosis of an alpha-purple bacterium as the origin of the mitochondria might have allowed the survival of a primitive group of eukaryotes as the origin of all current eukaryotes. Finally, toward 1.5 Ga, the additional endosymbiosis of a cyanobacteria, as the origin of the plastid, by a group of eukaryotes gave rise to the line of "green plants" which thus acquired the capacity to carry out photosynthesis. It should be noted that other lines of algae appeared later following additional endosymbiotic events between eukaryotes.

synthesize proteins. Similarly, we share many signaling and basic metabolic regulatory molecules. In addition, as eukaryotes, our cells contain a nucleus that confines chromosomes and share in their cytoplasm a cytoskeleton, endoplasmic reticulum, Golgi apparatus, lysosomes, peroxisomes and mitochondria. Thanks to the latter, animal and plant cells produce energy from sugars and respire in the same way. In addition, plants can synthesize sugars through photosynthesis.

A nervous system in plants?

The above elements might suggest that plants are living beings endowed with all biological bricks, to allow some form of agency. Such an assumption is anything but new. Luigi Galvani at the end of the 18th century, like Alexander von Humboldt, carried out pioneering work that led to the conclusion that the bioelectric nature of animals and plants was similar (Baluška, 2009a,b). At the end of the 19th and beginning of the 20th century, the existence of action potentials was demonstrated in various plants (mainly in *Dionaea* and *Mimosa pudica*, plants with rapid movements) suggesting that the excitability of certain plant cells could be a mean of intercellular communication in these organisms.¹⁹ Soon after, Jagadis Chandra Bose^{20,21}

highlighted the importance and pervasiveness of electrical signaling between plant cells to coordinate their responses to the environment.²² Bose's general conclusion was that plants have a "nervous system", a form of intelligence, and are capable of remembering and learning,²³ as had already been proposed by Charles²⁴, and his son Francis²⁵. Since then, evidence has demonstrated that electrical signaling over long distances is an effective means of cell-to-cell communication in response to many biotic and abiotic sources of stimulation in plants, as well as in eukaryotes as a whole^{26–29; 30}. Despite these repeated demonstrations, the concept of the "plant nervous system" was neglected by most of the scientific community until the beginning of our century.^{31–35}

Convergences or common heritage?

Recently, strong similarities between plants and animals have been discovered for mechanisms long considered the exclusive prerogative of animals, such as innate immunity for example. These similarities are classically explained through the idea of evolutionary convergence, i.e. the independent appearance in two lines of equivalent adaptive solutions in response to the same problem [36,b]. An alternative hypothesis exists: that of

the conservation of ancestral processes developed prior to the separation of lineages. For example, the innate immunity of animals and plants thus features common principles.^{37,38} While multicellular eukaryotic organisms use sophisticated immune systems at several levels to prevent microbial infections, the first barrier is the activation of innate immunity that displays strong similarity between animals and plants. The recognition of microbes (viruses, bacteria, fungi, oomycetes) is based on molecular patterns recognized as non-self-perceived by structurally similar receptors [eg. Toll-like receptor 39] that activate similar signaling pathways. These data lead to a holistic view of innate immunity as a general characteristic of eukaryotes derived from their common ancestor. In addition, the mechanism for oxidative burst (represented by generation of reactive oxygen species) required for the immune mechanism found in animals and plants share numerous similarities⁴⁰ that indicates a potential homology.

Similarly, given the need for systemic communication in multicellular organisms, neurobiological-type processes that require electrical signaling based on the activation of ion channels may originate from deep homology.^{26,41} Interestingly, the plant GLR glutamate receptors emerge to predate the metazoan NMDA glutamate receptors (Figure 1 in 42, 43). This new hypothesis challenges the long-held view that these similarities were due to evolutionary convergences. And yet, strong similarities between plants and animals regarding this electrical signaling and its role in plants have recently been (re)discovered. Indeed, the recording of action potential (the electrical messages that are transmitted along neurons in animals) has been known in both plants and animals for a very long time.^{19,21} This field of research has benefited from a strong resurgence of interest over the last 15 years, some authors now propose a broadened definition of nervous system to better understand the evolution of plants and animals.⁴⁴

Numerous data obtained by molecular, electrophysiological or imaging techniques have largely confirmed the existence of these processes in plants.^{45,46} It has also recently been shown that the fungi *Pleurotus djamor* generate action potential-like spikes that might manifest propagation of growing mycelium and communication processes in the mycelium network⁴⁷ that could be involved in fungal behavior.^{48,49} The bacterium *Escherichia coli* can also perceive changes in its environment through changes in membrane voltage inducing depolarization and calcium influx, resembling action potentials recorded in animals.^{50,51} These action potentials can be detected during the growth phase of biofilm-forming bacteria, whereas they are absent when the biofilm stops growing or in a strain that does not form a biofilm.⁵² The genes encoding the majority of ion channel families that enable membrane potential regulation are very similar in plants, animals and even bacteria. Certain ion channels are indeed archetypal channels found in animals as well as in plants, fungi, bacteria or archaea.^{53–56}

Similarly, homologues of all molecules serving as neurotransmitters in animals (acetylcholine, dopamine, norepinephrine, adrenaline, serotonin, histamine, melatonin, GABA or glutamate) exist in plants even though their roles may be different and their functions are not yet fully elucidated. At least, members of catecholamine precursors, chiefly

phenylethylamine, are known to stimulate the oxidative and calcium signaling mechanisms in plant cells [57,b]. František Baluška's team has shown that polar transport of auxin (a tryptophan derivative, as is serotonin) at the apex of the root is accomplished by exocytosis and active vesicle recycling, as in animal chemical synapses [58; 58]. The cells in which "plant synapses" have been described appear to share similarities with neurons, most notably, the capacity to spontaneously generate action potentials.⁵⁹ These researchers have also shown that glutamate coupled to plant homologues of glutamate receptors controls the flow of endocytic vesicles in these cells of the root apex as well as transient calcium variations during the induction of action potentials. Recently, it has been shown that the model plant *Arabidopsis thaliana* can detect exogenous signals, such as herbivore attack, and use glutamate to transmit information throughout the plant. This is achieved through glutamate receptors that convert this signal into an increase in intracellular calcium that spreads to distant organs.⁶⁰ This allows rapid activation of defense responses in undamaged parts of the plant. This function is equivalent to that observed in the vertebrate nervous system of animals for which glutamate is the most abundant excitatory neurotransmitter used by nerve cells to send long-range signals to other cells. Interestingly in this respect, the plant GLR glutamate receptors appear to predate the metazoan NMDA glutamate receptors (Figure 1 in 42, 43).

These data, together with numerous molecular homologies, reveal strong functional similarities with "neurobiological" processes even in the absence of neurons [but see 61]. Here again, evidence points to a holistic view of neurobiological processes as a general characteristic of eukaryotes, or even of the whole of life. All these elements show that plants are biologically close to animals and yet the scientific community often struggles to recognize this reality. Why is this?

Plant/animal: A brief explanation of some origins of the division

A first frontier that goes through the separation between nature and humans

In the Western world, distance between human and non-human has been imposed, materialized in an acceptance of the word nature that has evolved throughout history. A first factor to explain the distance can be found in etymology. This distance is revealed first of all in the term 'nature', which comes from the Latin *natura*, itself derived from *nascor*, meaning "to come into the world, to be born, to take one's origin". Nature is therefore what comes to life, which happens by itself. By defining this concept of nature, some humans have excluded themselves from it by attributing to it its own dynamics, its own temporality, its mobility, its structural mechanisms of growth and reproduction. For the ancient Greek the concept of *phusis* (nature) prolongs this distancing since it designates "that which contains within itself its principle of existence and change".⁶² Introducing a new separation between matter on the one hand, whatever it may be, and thought on the other, specific to the human being, the modern separation of the

human being and nature, of subject and object, was established (*Ibid.*). We can think that this separation of the human, an animal, from nature is part of the separation between plant and animal.

In the 17th century, René Descartes conceptualized all objects, whether artificial or natural, according to a mechanical logic. The philosopher thus contributed to forging in Europe the rational scientific approach that Newtonian physics epitomized.⁶³ In the 19th century, the Physiocratic school assimilated plants only to resources that biophysical elements provide to human societies from a strong hygienist perspective.⁶⁴ Nature then becomes a living environment. It provides the raw material for humans to feed and house themselves. The notion of ecosystem service is undoubtedly one of the latest avatars of this utilitarian relationship to nature.^{65–67} The vision of nature as a resource and resourcing is also expressed in the notion of landscape as seen by the tourism society, which appeared at the end of the 19th century in North America and Europe, combined with hygienic or artistic concerns. François Terrasson has also shown that this split was reflected in a fear of nature, which is constitutive of the way Western societies perceive nature.⁶⁸ This nature is not controllable. It escapes human laws and institutes the myth: nature/culture. For him, this separatism contains a repressed part of what is natural in human beings and in fact removes any idea of kinship between human and non-human life. This westernized view has been largely strengthened after the age of enlightenment coinciding with the industrial revolution in Europe, the period recently referred to as Great Divergence in the Anthropocene. Then, for example, non-westernized visions endemic to Asian countries have been wiped out as anthropogenic and industrial waves reached Asia with a century of delay.⁶⁹

A second frontier that involves distinguishing between plants and humans

Modern classical views are based on fundamental differences between plants and animals as set forth in ancient biblical texts and by Aristotle. In Genesis, vegetation⁵ is created on the third day and is presented in a utilitarian form: “Herbs bearing seed and fruit trees yielding fruit on the earth according to their kind, containing their seed, and it was so.” (Jerusalem Bible, Gen 1:11). It arrives as the first living organism on Earth. In the chronology that becomes hierarchical it incarnates the elementary living. This utilitarian vision is renewed in the New Testament. According to Aristotle, plants have a vegetative soul, or *threptikon*, which gives them the capacity for nourishment and reproduction, the ancient Greek idea of “soul”, *psukhe*. *Psukhe* is a set of active capacities of an organism, not an invisible entity connected to the divine. For Aristotle, the capacities of plants are common to all living beings, with humans having additional capacities, sensation and rational thought, added to the vegetative soul. The vegetative soul present in plants always exists in other organisms considered more evolved indicating a clear continuity between the different classes of organisms.⁷⁰ Although Aristotle embraced the hypothesis of the existence of a soul, he considered it to be inferior to that of man and animals to such an extent that he

described plants as “deficient animals”. This vision remained largely unchanged until the 20th century, due to the renewed support for this theory by some philosophers,⁷¹ some religious people (Vatican Council II⁶; Paul VI⁷) and the productivism which has governed the social, economic and political life of our modern societies since the 19th century.⁷²

Recent discoveries in “plant neurobiology” and “plant intelligence”: reopening the debate and forcing a change in conceptual frameworks

Plants, even if they do not have dedicated organs, possess, just like us, senses that allow them to adapt to their environment.

Contemporary biology still very often adopts an Aristotelian paradigm of the world according to which plants differ profoundly from animals because of their insensitivity and lack of ability to interact with their environment. At the same time, the current craze around the idea of plant intelligence mainly among the general public is leading to the reemergence of an old idea. Over the past 15 years or so, there has been a heated debate on the unsuspected capacities of plants, with some authors taking up the hypothesis of their intelligence.^{22,26,73–77} In 2005, Stefano Mancuso and František Baluška, building on the work of intellectual forebears such as Wilhelm Pfeffer, Charles Darwin, Jagadis Chandra Bose or Julius von Sachs,^{78,79} and following the discovery in plants of a large number of characteristics found in the neuronal system of animals, proposed the concept of ‘plant neurobiology’.³⁴ This initiative very quickly led to a strong controversy. Scientists from no less than thirty-three institutions working in plant research claimed that plant neurobiology was based only on superficial analogies and dubious extrapolations that added nothing to the understanding of plant biology.³¹ It is notable that the title of the response to the paper by Brenner and colleagues, “Plant neurobiology: no brain, no gain?”, once again referred to an idealistic vision of the classification of living things, perceiving plants as passive organisms and forgetting in passing that neurons exist in brainless animals such as starfish, sea urchins, bivalves and jellyfish. This controversy is reminiscent of what happened to JC Bose’s conclusion that plants have a “nervous system”, he became a scientific pariah whose work was erased from the Western history of plant biology for almost a century.⁸⁰ One of the objectives of the Society of Plant Neurobiology was to change the paradigm of the Aristotelian view of plants and thus our way of understanding research around questions related to the capacity they possess to react to environmental stimuli in ecological and agricultural contexts. In 2009, this society chose to change its name to The Society of Plant Signaling and Behavior [<https://plantbehavior.org/>] to limit the ostracizing reactions of a number of colleagues and avoid danger for the scientific career of scientists attending our conference, illustrating the always living conservatism of the scientific community. Things are just getting worse, with 81, clearly asking in print that research on plant neurobiology should not be funded or published.

In recent years, numerous studies have supported the hypothesis that plants are sensitive to many stimuli. As sessile organisms that must adapt quickly and efficiently to changes in their environment, they would not have evolutionary gain by

depriving themselves of information available in that environment. Thus plants, even if they do not have dedicated organs, possess senses equivalent to those of humans. They use light information for many purposes including root reorientation (82), they are able to perceive sound frequencies,^{83,84} they are sensitive to touch and gravity^{85,86} and with regard to odors, they not only perceive them but also communicate with each other and with other organisms through volatile compounds.⁸⁷ Plants have also been shown to be capable of memorization and possibly learning by association [88–90, see 91–93, for the latest exchanges in this dispute]. Plants could also communicate through mycorrhiza building hyphal networks connecting different plants.⁹⁴ The plant *Boquila trifoliolata* is able to mimic the neighboring plant leaves.⁹⁵ The capabilities of adaptation to their environment, communication, imitation or cooperation are used, among others, by ethologists to define animal intelligence.⁹⁶ In more general terms, the key issues underlying these capacities for perceiving information are: (i) the integration over time and space of these complex signals, their prioritization and the adoption of elaborate behaviors,⁹⁷ which should be addressed by a “phytoneurological” system according to 98, and (ii) the emergence of intentionality⁷⁵ or the ability to make choices involving consciousness.⁹⁹ A specific consciousness of plants in their environment would therefore be necessary to solve the problems inherent to life, adaptation and survival [26, 28; 100, 101], as it was also proposed for animals, or even for all living organisms.^{49,102,103} Charles Minot proposed as early as 1902 that “consciousness is a device for regulating the actions of organisms to accomplish goals that are useful to organisms and are therefore teleological”.¹⁰⁴ In any case, the use of the term consciousness for plants has not failed to elicit a lively response from some colleagues,^{81,105} even if the main question remains a problem of definition as discussed for a very long time (cf. *psukhe*, Aristotle’s vegetative soul).

In science, an optimal strategy, even if it also has its limits, is to start the analysis with simple systems and only then to continue with systems that are more complex. Unfortunately, life sciences dealing with cognition and learning started with a complex system (the human brain) and only later included less complex systems. This situation certainly causes fundamental problems and misunderstandings in current attempts to explore the cognitive behavior of plants, but also fungi, bacteria, protozoa etc. Beyond intelligence and consciousness, for which many definitions exist, fundamental biological phenomena such as learning, memory, cognition, sensitivity and others have for many years been reserved only for humans. Any attempt to extend these basic and fundamental biological concepts to other organisms is therefore still often dismissed as an example of anthropomorphism,²⁶ even though it is recognized that “it is not possible to do science without using language full of metaphors” and it is true that “the price of metaphor is eternal vigilance” [cited in 106]. The use of these terms by biologists studying plant behavior is probably due to the fact that there is no better term for what these scientists have discovered, namely that these organisms use information exchanges with the environment and other cells in the organism to guide and control their behavior. This position is perfectly harmless if used as a metaphor, but if cognitive descriptions are true, then it is not

harmless.^{74,107,108} Concepts related to plant neurobiology should lead us to fruitfully reconsider the evolutionary origin of “neurosystems”⁴⁴ and view recent specializations of the animal nervous system as emerging from ancient and fundamental processes of communication and cell survival. This consideration of deep homologies could also allow and encourage us to reconsider the bonds of kinship.

Opening up to other ontologies to fully recognize plants as our sisters?

It is now clear that there is no longer any objective justification for claiming today that humans form a community of organisms entirely separated from the other biotic components of the environment. This must have consequences for the way we think and work. Indeed, we hypothesize that in order to fully understand and work on these deep homologies, on plant agency, it is time to extract ourselves consciously from a dualistic nature-culture vision and from the subject/object dichotomy. In other words, extract yourself from an overly naturalistic conception¹⁰⁹ that imbues our common sense, our conception of science, and thus structures our epistemology as well as our perception of other modes of perceiving nature.¹¹⁰ Even if, as many science studies have shown, the nature-culture dualism is “a mask for a practice that contradicts it” [...] this “does not eliminate its guiding function in the organization of science” [109, p. 130].⁸

In any case, and even if these ontologies defined by Descola can sometimes hybridize, it is a question of trying to get out of a perspective that is too naturalistic to reconsider more fully what plants can be. Some already seem to be doing this; biologists such as Monica 90, or Robin 111, or anthropologists such as Eduardo 112, Florence Brunois 113) or Anna 114. Others call, among other things, for a reconsideration of animism that would encourage, for example, “humans to see the world as a diverse community of living people with whom we find different species of respect” (115, pp. 138–139) and to make room for other ways of knowing and telling about the living world.¹¹⁶ Thus, Florence Brunois shows how the Kasua of Papua New Guinea recognize that plants have “agency and sensitivity and willingly admit to talking to them in an inter-specific and audible communication” [58, p. 10].

These approaches do not aim to establish a neo-animism that would intend to define a spirituality of nature as evoked by Gérald 117. On the other hand, like the debates around the intelligence and consciousness of plants and other non-humans, they probably mark the end of the naturalist cycle in Western societies (Descola in Rhamani, 118). As we have shown with recent data from phylogeny and “plant neurobiology”, it is thus important to take a holistic view of biological processes as a general characteristic of eukaryotes, or even of all living things, and to understand and accept what we have in common and thus reconsider kinship. It is a matter of using the knowledge related to these different approaches to open up and explore how other ontologies understand and perceive interdependent relationships between living beings^{43,119} and their relatives in order to think about the way living beings deal with each other.¹²⁰ These approaches will allow better understanding of how our

perception of otherness delays the full recognition of the living as relatives. These approaches are also to be compared with the one proposed by Donna Haraway,^{121,122} who, based on her own experience, proposes a vision of kinship extended by examining our deep links with other non-human “creatures” (plants, microbes, animals). She writes: “I believe that the broadening and recomposition of kinship is enabled by the fact that all Earthlings are close relatives in the deepest sense, and it is high time to practice better genus-by-genus care (because a species is never alone). Kinship is a kind of word that engages a notion of assemblage. All creatures and other bugs share a common “flesh” literally, semiotically, and genealogically.” [123, pp. 79–80]. Kinship is a reciprocal relationship.

Conclusion

Echoing Haraway, we therefore believe that “making kinship” with the world more than human is a path, indeed an urgent ethical responsibility to think and promote a sustainable future for the planet, for humans and other than humans. A new understanding of our common evolutionary history that leads us to think of the living as a kinship is very useful for this, as is its resonant with other ontologies. Above all, as Sophie Gosselin has rightly pointed out after many others, it is a matter of finding new models and inspirations from other knowledge, practices and realities to expand our epistemological frameworks and acknowledge that plants “cannot be isolated . . .”.¹²⁴ The issue is not anecdotal. It is indeed a question of reconsidering plants and their position in our changing world, while opening up to other forms of knowledge in which these plants have a very different place from that which we accord them in the modern world.⁴³ This knowledge could help us to finally accept relatives and thus the total inclusion of humans in the living world. The trajectories of recent scientific discoveries brought into friction with other ontologies, with other practices, will be more than useful to fundamentally shake up an Aristotelian vision of living things that is still predominant.³⁶ It will allow us to rethink and renew the links between animals (including humans) and plants, by seeking and thinking about what we have and live in common, in a world that calls for new forms of care and cohabitation between all living beings.^{125–133, 137}

Notes

1. In the article, we take an openly biological definition by considering man as an animal, more precisely as a great ape since the genomes of humans, chimpanzees, gorillas and orangutans are so close.
2. In the article, we take Philippe Descola’s definition “it is the combination between the distinctive character of a human mind (..) and on the other hand the recognition that human beings, in spite of this moral singularity, have a physical constitution that does not make them fundamentally different from other organized beings” [translate from 134, p. 23].
3. Specific marker for biological membranes of eukaryotic cells.¹³
4. Protobionts: microdroplets isolating their internal contents from the external environment, precursors of living cells.¹³⁵

5. The term vegetation is not used in ancient biblical texts. Vegetation is named and associated with the color green. It is therefore the color of the vegetation that gives its singularity. We find this analogy in the expression “green space”.
6. In the Second Vatican Council in the Pastoral Constitution *Gaudium et Spes*, (1965), it is written: “Man, created in the image of God, has indeed received the mission to subdue the earth and all that it contains, to rule the cosmos in holiness and justice and, recognizing God as the Creator of all things, to refer his being as well as the universe to him: so that, all being subject to man, the very name of God may be glorified by the whole earth”.
7. In 1967, Paul VI in his encyclical letter *Populorum Progressio* (the Development of Peoples) wrote: “Fill up the earth and subdue it” (Gen. 1:29): the Bible, from its very first page, teaches us that the whole of creation is for man to apply his intelligent effort to make the most of it and, through his work, to complete it, so to speak, in his service. If the earth is made to provide every man with the means of his subsistence and the instruments of his progress, then every man has the right to find in it what he needs”.
8. It should be noted that while the ontologies presented by Descola have been very useful in classifying human societies in terms of how they view and relate to nonhumans, they are obviously open to criticism, as is any attempt at categorization that necessarily simplifies the complexity of the relationships described.^{136,135}

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References

1. Lecointre G. Guide critique de l’évolution. Paris, France: Belin; 2009.
2. Casane D, Laurenti P. Penser la biologie dans un cadre phylogénétique: l’exemple de l’évolution des vertébrés. *Médecine Science*, Paris. 2011;28(12):1121–1127. doi:10.1051/medsci/20122812024.
3. Dayrat B. The roots of phylogeny: how did Haeckel build his trees? *Systematic Biology*. 2003;52(4):515–527. doi:10.1080/10635150309310.
4. Wandersee JH, Schussler EE. Toward a theory of plant blindness. *Bulletin of the Botanical Society of America*. 2001;47:2–9.
5. Brives C. Que font les scientifiques quand ils ne sont pas naturalistes? Le cas des levuristes. *L’Homme*. 2017;222:35–56.

6. Houdart S. La Cour des miracles. Ethnologie d'un laboratoire japonais. Paris, France: Cnrs Éd; 2007.
7. Latour B. La Science en action. Introduction à la sociologie des sciences. In: Trad. de l'anglais par Michel Biezunski. Paris, France: La Découverte (La Découverte- poche. Sciences humaines et sociales); 2005 [1987].
8. Latour B, Woolgar S. La Vie de laboratoire. La production des faits scientifiques. Trad. de l'anglais par Michel Biezunski. Paris, France: La Découverte (Sciences et société); 1988 [1979].
9. Lawrence N, Calvo P. Learning to see 'green' in an ecological crisis. In: Weir L, ed. Springer: Philosophy as Practice in the Ecological Emergency; 2021.
10. Ryan JC. Passive flora? Reconsidering nature's agency through human-plant studies (HPS). *Societies*. 2012;2(3):101–102. doi:10.3390/soc2030101.
11. Dodd M, Papineau D, Grenne T, Slack JF, Rittner P, O'Neil F, Little J, Little CTS; C.T.S. Evidence for early life in Earth's oldest hydrothermal vent precipitates. *Nature*. 2017;543(7643):60–64. doi:10.1038/nature21377.
12. Tashiro T, Ishida A, Hori M, Igisu M, Koike M, Méjean P, Takahata N, Sano Y, Komiya T. Early trace of life from 3.95 Ga sedimentary rocks in Labrador, Canada. *Nature*. 2017;549(7673):516–518. doi:10.1038/nature24019.
13. Brocks JJ, Logan GA, Buick R, Summons RE. Archean molecular fossils and the early rise of eukaryotes. *Science*. 1999;285(5430):1033–1036. doi:10.1126/science.285.5430.1033.
14. Baluška F, Lyons S. Archaeal origins of eukaryotic cell and nucleus. *BioSystems*. 2021;203:104375. doi:10.1016/j.biosystems.2021.104375.
15. Martin W, Müller M. The hydrogen hypothesis for the first eukaryote. *Nature*. 1998;392(6671):37–41. doi:10.1038/32096.
16. Margulis (Sagan) L. On the origin of mitosing cells. *Journal of Theoretical Biology*. 1967;14(3):225–274. doi:10.1016/0022-5193(67)90079-3.
17. Butterfield NJ. Early evolution of the eukaryota. *Palaeontology*. 2015;58(1):5–17. doi:10.1111/pala.12139.
18. Porter SM. Insights into eukaryogenesis from the fossil record. *Interface Focus*. 2020;10(4):20190105. doi:10.1098/rsfs.2019.0105.
19. Burdon-Sanderson JI. Note on the electrical phenomena which accompany irritation of the leaf of *Dionaea muscipula*. *Proceedings of the Royal Society, London*. 1873;21:495–496.
20. Bose JC. Electric response in ordinary plants under mechanical stimulus. *Journal of the Linnean Society of London, Botany*. 1902;35(245):275–304. doi:10.1111/j.1095-8339.1902.tb00596.x.
21. Bose JC. The nervous mechanism of plants. London, England: Longmans, Green and Co., Ltd; 1926.
22. Calvo P, Sahi VP, Trewavas A. Are plants sentient? *Plant Cell and Environment*. 2017;40(11):2858–2869. doi:10.1111/pce.13065.
23. Shepherd VA. From semi-conductors to the rhythms of sensitive plants: the research of J.C. Bose. *Cellular and Molecular Biology*. 2005;51:607–619.
24. Darwin C. The power of movement in plants. London, England: John Murray; 1880.
25. Darwin F. Do plants really possess the power of thinking? *The New York Times*. 1909;February:28.
26. Baluška F, Mancuso S. Plant cognition and behavior: from environmental awareness to synaptic circuits navigating root apices. In: Baluška F editor. *Memory and learning in plants*, signaling and communication in plants. Springer International Publishing; 2019. p. 51–77.
27. Baluška F, Mancuso S, Van Volkenburgh E, Barbara G, Pickard - queen of plant electrophysiology. *Plant Signaling and Behavior*. 2021 3;16(6):1911400. doi:10.1080/15592324.2021.1911400.
28. Calvo P, Baluška F, Trewavas A. Integrated information as a possible basis for plant consciousness. *Biochemical and Biophysical Research Communications*. 2020;564:158–165. doi:10.1016/j.bbrc.2020.10.022.
29. Pickard BG. Action potentials in higher plants. *Botanical Reviews*. 1973;39(2):172–201. doi:10.1007/BF02859299.
30. Wildon DC, Thain JF, Minchin PEH, Gubb IR, Reilly AJ, Skipper YD, Doherty HM, O'Donnell PJ, Bowles DJ. Electrical signalling and systemic proteinase inhibitor Induction in the wounded plant. *Nature*. 1992;360(6399):62–65. doi:10.1038/360062a0.
31. Alpi A, Amrhein N, Bertl A, Blatt MR, Blumwald E, Cervone F, Dainty J, De Michelis MI, Epstein E, Galston AW, et al. Plant neurobiology: no brain, no gain? *Trends in Plant Science*. 2007;12(4):135–136. doi:10.1016/j.tplants.2007.03.002.
32. Baluška F, Mancuso S, Volkmann D, Barlow PW. Root apices as plant command centres: the unique 'brain-like' status of the root apex transition zone. *Biologia*. 2004;59:9–17.
33. Baluška F, Hlavacka A, Mancuso S, Volkmann D, Barlow PW. Neurobiological view of plants and their body plan. In: Life P, Baluška F, Volkmann D, Barlow PW editors. *Communication in plants: Neuronal aspects of*. Springer Verlag; 2006. p. 19–35.
34. Brenner ED, Stahlberg R, Mancuso S, Vivanco J, Baluška F, Van Volkenburgh E. Plant neurobiology: an integrated view of plant signaling. *Trends in Plant Science*. 2006;11:413–419.
35. Stahlberg R. Historical overview on plant neurobiology. *Plant Signaling & Behavior*. 2006;1(1):6–8. doi:10.4161/psb.1.1.2278.
36. Baluška F, Mancuso S. Deep evolutionary origins of neurobiology: turning the essence of 'neural' upside-down. *Communicative and Integrative Biology*. 2009a;2(1):60–65. doi:10.4161/cib.2.1.7620.
37. Coll NS, Epple P, Dangl JL. Programmed cell death in the plant immune system. *Cell Death and Differentiation*. 2011;18(8):1247–1256. doi:10.1038/cdd.2011.37.
38. Gust AA, Pruitt R, Nürnberger T. Sensing danger: key to activating plant immunity. *Trends in Plant Science*. 2017;22,9(9):779–791. doi:10.1016/j.tplants.2017.07.005.
39. Gómez-Gómez L, Boller T. Flagellin perception: a paradigm for innate immunity. *Trends Plant Sci*. 2002;7(6):251–256. doi:10.1016/S1360-1385(02)02261-6.
40. Yoshioka H, Bouteau F, Kawano T. Discovery of oxidative burst in the field of plant immunity: looking back at the early pioneering works and towards the future development. *Plant Signaling & Behavior*. 2008;3(3):153–155. doi:10.4161/psb.3.3.5537.
41. Bouteau F, Laurenti P. La neurobiologie végétale, une idée folle? Pour la science, Hors-série. 2018;101:36–41.
42. Stroebel D, Paoletti P. Architecture and function of NMDA receptors: an evolutionary perspective. *Journal of Physiology*. 2021;599(10):2615–2638. doi:10.1113/JP279028.
43. Baluška F, Mancuso S. Plants, climate and humans - plant intelligence changes everything. *EMBO Rep*. 2020;21(3):e50109. doi:10.15252/embr.202050109.
44. Miguel-Tomé S, Llinás RR. Broadening the definition of a nervous system to better understand the evolution of plants and animals. *Plant Signaling & Behavior*. 2021;16(10):e1927562. doi:10.1080/15592324.2021.1927562.
45. Choi WG, Hilleary R, Swanson SJ, Kim SH, Gilroy S. Rapid, long-distance electrical and calcium signaling in plants. *Annual Review of Plant Biology*. 2016;67(1):287–307. doi:10.1146/annurev-arplant-043015-112130.
46. Huber AE, Bauerle TL. Long-distance plant signaling pathways in response to multiple stressors: the gap in knowledge. *Journal of Experimental Botany*. 2016;67(7):2063–2079. doi:10.1093/jxb/erw099.
47. Dehshibi MM, Adamatzky A. Electrical activity of fungi: spikes detection and complexity analysis. *Biosystems*. 2021;203:e104373. doi:10.1016/j.biosystems.2021.104373.
48. Akelett K, Body L. Fungal behavior: a new frontier in behavioral ecology. *Trends in Ecology & Evolution*. 2021. doi:10.1016/j.tree.2021.05.006.
49. Money NP. Hyphal and mycelial consciousness: the concept of the fungal mind. *Fungal Biology*. 2021;125(4):257e259. doi:10.1016/j.funbio.2021.02.001.
50. Bruni GN, Weekley RA, Dodd BJT, Kralj JM. Voltage-gated calcium flux mediates *escherichia coli* mechanosensation. *Proceedings of the National Academy of Sciences USA*. 2017;114(35):9445–9450. doi:10.1073/pnas.1703084114.

51. Masi E, Ciszak M, Santopolo L, Frascella A, Giovannetti L, Marchi E, Viti C, Mancuso S. Electrical spiking in bacterial biofilms. *Journal of the Royal Society Interface*. 2015;12(102):20141036. doi:10.1098/rsif.2014.1036.
52. Humphries J, Xiong L, Liu J, Prindle A, Yuan F, Arjes HA, Tsimring L, Süel GM. Species-independent attraction to biofilms through electrical signaling. *Cell*. 2017;168(1–2):200–209. doi:10.1016/j.cell.2016.12.014.
53. Estévez R, Jentsch TJ. CLC chloride channels: correlating structure with function. *Current Opinion in Structural Biology*. 2002;12(4):531–539. doi:10.1016/S0959-440X(02)00358-5.
54. Ludewig U. Ion transport versus gas conduction: function of AMT/Rh-type proteins. *Transfusion and Clinical Biology*. 2006;13(1–2):111–116. doi:10.1016/j.tracbi.2006.02.012.
55. Nieves-Cordones M, Gaillard I. Involvement of the S4-S5 linker and the C-linker domain regions to voltage-gating in plant Shaker channels: comparison with animal HCN and Kv channels. *Plant Signalling and Behavior*. 2014;9:e972892.
56. Sula A, Wallace BA. Interpreting the functional role of a novel interaction motif in prokaryotic sodium channels. *Journal of General Physiology*. 2017;149(6):613–622. doi:10.1085/jgp.201611740.
57. Kawano T, Pinontoan R, Uozumi N, Morimitsu Y, Miyake C, Asada K, Muto S. Phenylethylamine-induced generation of reactive oxygen species and ascorbate free radicals in tobacco suspension culture: mechanism for oxidative burst mediating Ca²⁺ influx. *Plant and Cell Physiology*. 2000a;41:1259–1266.
58. Baluška F, Schlicht M, Volkmann D, Mancuso S. Vesicular secretion of auxin: evidences and implications. *Plant Signaling & Behavior*. 2008;3(4):254–256. doi:10.4161/psb.3.4.5183.
59. Masi E, Ciszak M, Stefano G, Renna L, Azzarello E, Pandolfi C, Mugnai S, Baluška F, Arecchi FT, Mancuso S. Spatiotemporal dynamics of the electrical network activity in the root apex. *Proceedings of the National Academy of Sciences USA*. 2009;106(10):4048–4053. doi:10.1073/pnas.0804640106.
60. Toyota M, Spencer D, Sawai-Toyota S, Jiaqi W, Zhang T, Koo AJ, Howe GA, Gilroy S. Glutamate triggers long-distance, calcium-based plant defense signaling. *Science*. 2018;361(6407):1112–1115. doi:10.1126/science.aat7744.
61. Baluška F. Recent surprising similarities between plant cells and neurons. *Plant Signaling & Behavior*. 2010;5(2):87–89. doi:10.4161/psb.5.2.11237.
62. Larrère C, Larrère R. Penser et agir avec la nature. Une enquête philosophique. In: Découverte L, editor. *Sciences humaines*; 2015.
63. Larrère C, Larrère R. *La crise environnementale*. Paris, France: INRA; 1997. dir.
64. Spiegel HW. *The growth of economic thought*, revised and expanded edition. Vol. 189, Duke University Press; 1983. p. 195–196.
65. Arnauld, de, Sartre X, Castro M, Dufour S, Oszwald J. *Political ecology des services écosystémiques*, Bruxelles. Peter Lang. 2014.
66. Maris V. *Nature à vendre. Les limites des services écosystémiques*. Quae; 2014.
67. Méral P. Le concept de service écosystémique en économie: origine et tendances récentes. *Natures Sciences Sociétés*. 2012;20(1):3–15. doi:10.1051/nss/2012002.
68. Terrasson F. *La peur de la Nature*. Paris, France: Sang de la terre; 1991.
69. Nakao K, Kawano T. History of Kitakyushu along with the great divergence in Anthropocene: an implication for possible periodization. *Bulletin du Centre Franco-Japonais d'Histoire des Sciences*. 2019;13:37–49.
70. Linson A, Calvo P. Zoocentrism in the weeds? Cultivating plant models for cognitive yield. *Biology & Philosophy*. 2020;35(5):49. doi:10.1007/s10539-020-09766-y.
71. Ferry L. *Le nouvel ordre écologique. L'arbre, l'animal et l'homme*. Paris: Grasset & Fasquelle; 1992.
72. Gorz A. *Capitalism, Socialism, Ecology*. London, UK: Verso; 1994.
73. Baluška F, Mancuso S. Individuality, self and sociality of vascular plants. *Philosophical Transactions of the Royal Society B Biological Science*. 2021;376(1821):20190760. doi:10.1098/rstb.2019.0760.
74. Calvo P, Trewavas A. Physiology and the (neuro) biology of plant behavior: a farewell to arms. *Trends in Plant Science*. 2020;25(3):214–216. doi:10.1016/j.tplants.2019.12.016.
75. Marder M. Plant intentionality and the phenomenological framework of plant intelligence. *Plant Signalling and Behavior*. 2012;7(11):1365–1372. doi:10.4161/psb.21954.
76. Trewavas A. Aspects of plant intelligence. *Annals of Botany*. 2003;92(1):1–20. doi:10.1093/aob/mcg101.
77. van Loon LC. The intelligent behavior of plants. *Trends in Plant Science*. 2016;21(4):286–294. doi:10.1016/j.tplants.2015.11.009.
78. Kutcher U, Baluška F. Julius Sachs (1832–1897) and the Unity of Life. *Plant Signaling & Behavior*. 2015;10(9):e1079679. doi:10.1080/15592324.2015.1079679.
79. Kutcher U, Niklas KJ. Julius Sachs (1868): the father of plant physiology. *American Journal of Botany*. 2018;105(4):656–666. doi:10.1002/ajb2.1078.
80. Minorsky PV. American racism and the lost legacy of Sir Jagadis Chandra Bose, the father of plant neurobiology. *Plant Signalling & Behavior* 16 . 2020;e1818030n.
81. Mallatt J, Blatt MR, Draguhn A, Robinson DG, Taiz L. Debunking a myth: plant consciousness. *Protoplasma*. 2021;258(3):459–476. doi:10.1007/s00709-026-01579-w.
82. Mo M, Yokawa K, Wan Y, Baluška F. How and why do root apices sense light under the soil surface? *Frontiers in Plant Sciences*. 2015;6:1–8.
83. Gagliano M, Grimonprez M, Depczynski M, Renton M. Tuned in: plant roots use sound to locate water. *Oecologia*. 2017;184(1):151–160. doi:10.1007/s00442-017-3862-z.
84. Rodrigo-Moreno A, Bazihizina N, Azzarello E, Masi E, Tran D, Bouteau F, Baluška F, Mancuso S. Root phonotropism: early signalling events following sound perception in Arabidopsis roots. *Plant Science*. 2017;264:9–15. doi:10.1016/j.plantsci.2017.08.001.
85. Chaffey N, Volkmann D, Baluška F. The botanical multiverse of Peter Barlow. *Communication and Integrative Biology*. 2019;12(1):14–30. doi:10.1080/19420889.2019.1575788.
86. Demidchik V, Shabala S, Isayenkov S, Cuin TA, Pottosin I. Calcium transport across plant membranes: mechanisms and functions. *New Phytologist*. 2018;220(1):49–69. doi:10.1111/nph.15266.
87. Beck JJ, Alborn HT, Block AK, Christensen SA, Hunter CT, Rering CC, Seidl-Adams I, Stuhl CJ, Torto B, Tumlinson JH. Interactions among plants, insects, and microbes: elucidation of inter-organismal chemical communications in agricultural ecology. *Journal of Agriculture and Food Chemistry*. 2018;66(26):6663–6674. doi:10.1021/acs.jafc.8b01763.
88. Gagliano M, Renton M, Depczynski M, Mancuso S. Experience teaches plants to learn faster and forget slower in environments where it matters. *Oecologia*. 2014;175(1):63–72. doi:10.1007/s00442-013-2873-7.
89. Gagliano M, Vyazovskiy VV, Borbély AA, Grimonprez M, Depczynski M. Learning by association in plants. *Scientific Reports*. 2016;2:38427.
90. Gagliano M. *Thus Spoke the Plant*. Berkeley: North Atlantic Books; 2018.
91. Gagliano M, Vyazovskiy VV, Borbély AA, Depczynski M, Radford B. Comment on 'Lack of evidence for associative learning in pea plants'. *eLife*. 2020;9:e61141. doi:10.7554/eLife.61141.
92. Markel K. Lack of evidence for associative learning in pea plants. *ELife*. 2020a;9:e57614. doi:10.7554/eLife.57614.
93. Markel K. Response to comment on "Lack of evidence for associative learning in pea plants.". *ELife*. 2020b;9:e61689. doi:10.7554/eLife.61689.
94. Vahabi K, Reichelt M, Scholz S, Furch ACU, Matsuo M, Johnson JM, Sherameti I, Gershenzon J, Oelmüller R. *Alternaria brassicae* induces systemic jasmonate responses in

- arabidopsis which travel to neighboring plants via a *piriform-sopora indica* hyphal network and activate abscisic acid responses. *Frontiers in Plant Science*. 2018;9:1–18. doi:10.3389/fpls.2018.00626.
95. Gianoli E, Carrasco-Urra F. Leaf mimicry in a climbing plant protects against herbivory. *Current Biology*. 2014;24(9):984–989. doi:10.1016/j.cub.2014.03.010.
 96. Lefebvre L. Continuités et ruptures dans le monde animal. *Esprit*. 2010;365(6):133–141. doi:10.3917/espri.1006.0133.
 97. Novoplansky A. 2019. What plant roots know? *Seminars in Cell & Developmental Biology*, 92:126–133., .
 98. Calvo P, Friston K. Predicting green: really radical (plant) predictive processing. *Journal of the Royal Society Interface*. 2017;14(131):20170096. doi:10.1098/rsif.2017.0096.
 99. Bergson H, 1911. La conscience et la vie. Conférence donnée à l'Université de Birmingham (Birmingham, UK).
 100. Mediano PAM, Trewavas A, Calvo P. Information and integration in plants: Towards a quantitative search for plant Sentience. *Journal of Consciousness Studies*. 2021;28:80–105.
 101. Trewavas A, Baluška F, Mancuso S, Calvo P. Consciousness facilitates plant behavior. *Trends in Plant Science*. 2020;25(3):216–217. doi:10.1016/j.tplants.2019.12.015.
 102. Baluška F, Reber A. Sentience and consciousness in single cells: how the first minds emerged in unicellular species. *Bioessays*. 2019;41(3):e1800229. doi:10.1002/bies.201800229.
 103. Trewavas A, Baluška F. The ubiquity of consciousness, cognition and intelligence in life. *EMBO Reports*. 2011;12(12):1221–1225. doi:10.1038/embor.2011.218.
 104. Minot CS. The problem of consciousness in its biological aspects. *Science*. 1902;16(392):1–12. doi:10.1126/science.16.392.1.
 105. Taiz L, Alkon D, Draguhn A, Murphy A, Blatt M, Hawes C, Thiel G, Robinson DG. Plants neither possess nor require consciousness. *Trends in Plant Science*. 2019;24:677–687.
 106. Ameisen JC. On the origin, evolution, and nature of programmed cell death: a timeline of four billion years. *Cell Death and Differentiation*. 2002;9(4):367–393. doi:10.1038/sj.cdd.4400950.
 107. Segundo-Ortin M, Calvo P. Are plants cognitive? A reply to Adams. *Studies in History and Philosophy of Science*. 2019;73:64–71. doi:10.1016/j.shpsa.2018.12.001.
 108. Segundo-Ortin M, Calvo P. Consciousness and cognition in plants. *WIREs Cognitive Science* 2021; forthcoming. doi:10.1002/wcs.1578.
 109. Descola P. Par-delà Nature et Culture. Paris, France: Gallimard; 2005.
 110. Descola P. La composition des Mondes. Entretiens avec Pierre Charbonnier. Paris, France: Flammarion; 2014.
 111. Kimmerer WR. Braiding sweetgrass. indigenous wisdom, scientific knowledge, and the teaching of plants. Minneapolis, Minnesota, États-Unis: Milkweed Editions; 2013.
 112. Kohn E. How forests think. toward an anthropology beyond the human. Berkeley: University of California Press; 2013.
 113. Bruno-Pasina F., 2018. “Savoir-vivre avec les plantes : un vide ontologique”, *Cahiers philosophiques*, 153, 9–24.
 114. Tsing A. Le champignon de la fin du monde. Paris, France: La découverte; 2017. 7–19.
 115. Lestel D. À quoi sert l'homme ? Paris, France: Fayard; 2015.
 116. Myers N. *How to grow livable worlds*: ten not-so-easy steps. In: Smith O, editor. *The World to Come*. Gainesville (Florida): Harn Museum of Art. 2018.
 117. Bronner G. Ce néoanimisme qui vient. *Pour la Science*. 2017;481:16.
 118. Rahmani S. 2016. Les plantes ces grandes communicantes. *Le Monde*, 2 mars 2016.
 119. Gilbert SF, Sapp J, Tauber AI. A symbiotic view of life: we have never been individuals. *The Quarterly Review of Biology*. 2012;87(4):325–341. doi:10.1086/668166.
 120. Stengers I. Preface in Lowenhaupt Tsing A., *Le champignon de la fin du monde*. Paris, France: La découverte; 2017. 7–19.
 121. Haraway D. The companion species manifesto. Chicago University, Prickly Paradigm Press; 2003.
 122. Haraway D. Staying with the Trouble. Making Kin in the Chthulucene. Duke University Press; 2016a.
 123. Haraway D. Anthropocène, capiitalocène, plantiatonocène, chtulucène. Faire des parents. *Multitudes*. 2016b;65(4):75–81. doi:10.3917/mult.065.0075.
 124. Gosselin S. Redonner corps à l'esprit des plantes. *Terrestres*. 2019;4. <https://www.terrestres.org/2019/03/05/redonner-corps-a-lesprit-des-plantes/> .
 125. Baluška F, Mancuso S. Plants and animals: convergent evolution in action? In: Baluška F editor. *Plant-Environment Interactions: from sensory plant biology to active plant behavior*. Germany: Springer Verlag; 2009b. p. 285–301.
 126. Baluška F, Mancuso S. Actin cytoskeleton and action potentials: forgotten connections. In: Sahi VP, Baluška F, editors. *The Cytoskeleton*. Springer Nature Switzerland AG; 2019. p. 63–83. *Plant Cell Monographs* 24.
 127. Baluška F, Yokawa K. Anaesthetics and plants: from sensory systems to cognition-based adaptive behaviour. *Protoplasma*. 2021;258(2):449–454. doi:10.1007/s00709-020-01594-x.
 128. Bruno F. Savoir-vivre avec les plantes: un vide ontologique. *Cahiers philosophiques*. 2018;153(2):9–24. doi:10.3917/caph1.153.0009.
 129. Calvo P, Gagliano M, Souza G, Trewavas A. Plants are intelligent, here's how. *Annals of Botany*. 2020;125(1):11–28. doi:10.1093/aob/mcz155.
 130. Descola P. Les cosmologies des indiens d'amazonie. *La Recherche*. 1996;292:62–67.
 131. Gagliano M, Abramson CI, Depczynski M. Plants learn and remember: lets get used to it. *Oecologia*. 2018;186(1):29–31. doi:10.1007/s00442-017-4029-7.
 132. Kawano T, Pinontoan R, Uozumi N, Miyake C, Asada K, Kolattukudy PE, Muto S. Aromatic monoamine-induced immediate oxidative burst leading to an increase in cytosolic Ca²⁺ concentration in tobacco suspension culture. *Plant and Cell Physiology*. 2000b;41(11):1251–1258. doi:10.1093/pcp/pcd052.
 133. Rahmani S. Les plantes ces grandes communicantes. *Le Monde*. 2016;2:2016.
 134. Descola P. Entretien avec Philippe Descola. *Cahiers philosophiques*. 2011;127(4):23–40. doi:10.3917/caph.127.0023.
 135. Oparin AI. L'origine de la vie sur la Terre. Paris, France: Masson; 1965.
 136. Friedberg C. Par-delà le visible. *Natures Sciences Sociétés*. 2007;15(2):167–176. doi:10.1051/nss:2007044.
 137. Ingold T. A naturalist abroad in the museum of ontology: philippe Descola's beyond nature and culture. *Anthropological Forum*. 2016;26(3):1–20. doi:10.1080/00664677.2015.1136591.