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Federico Delpino and the foundation of plant biology

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In 1867, Federico Delpino, with his seminal work "*Pensieri sulla biologia vegetale*" (Thoughts on plant biology) established plant biology by defining it not in the broad general sense, namely as the science of living beings, but as a branch of natural science dedicated to the study of plant life in relation to the environment. Today, the figure and achievements of this outstanding plant scientist is almost unknown. In the following pages, I will concisely describe the main realizations of Federico Delpino and outline the significance of his work for modern plant science.

Introduction

From the first description of the collaborative behavior between ants and plants in hundreds of different species, to the seminal works on the *various contrivances* by which many plants are fertilized with the aid of insects, the *cursus honorum* of Federico Delpino embraces all the crucial advances in the understanding of plants. He was internationally respected, and scientists as Axell S, Hildebrand F, Müller F and Darwin C appreciated his works.[1] Certainly, Charles Darwin was one of the Delpino's major admirers. Despite that they had a number of scientific disagreements, their epistolary relationship was constantly erupting into episodes of sincere friendship: "*Pray oblige me by sending me your photograph and I enclose one of my own in case you would like to possess it*".[2]

Despite the indisputable worth of this plant scientist, the fact that he wrote exclusively in Italian prevented many plant scientists becoming familiar with his outstanding works. Already Darwin complained of the impossibility of reading directly Delpino's work, having to rely on his wife for translation: "*Unfortunately, very few of our scientific men read Italian, and, as you know, this is my case; but I will ask my wife to translate some portions, as I am sure the whole would interest me greatly*". Since Darwin's time the situation has not improved, and Delpino's name and role in the history of botany is today practically unknown. In this paper, I will concisely describe the main realizations of Federico Delpino and outline the significance of his work for modern plant science.

Biographical Sketch

Federico Delpino (**Fig. 1**) was born December 27, 1833 in Chiavari (**Fig. 2**), the first of the five children born to the lawyer Enrico Delpino, and of his learned wife Carlotta. A few days after his birth, Federico was baptized by the hands of the future Saint Antonio Maria Gianelli, at that time priest of the parish of St. John the Baptist in Chiavari. The little Federico was so delicate in constitution that, for his fortification, his mother compelled him to spend long hours in their garden. This is what Delpino writes in remembering those childhood days: "*The character of the naturalist is, at were, born with him, or is acquired in the first years of life… My mother, a woman of choice spirits, worried by the frailty of my constitution, kept me all the time, from four to seven years, in the open air of a small garden adjoining the house. What could a child do who was left to himself for so many hours in complete solitude? I spent all my time studying the habits of ants, bees and wasps. I discovered the curious nesting habit of a large black bee* (Xylocopa violacea)".[3]

Delpino studied mathematics and natural sciences at the University of Genoa. Following the death of his father and the resulting worsening of the economic possibilities of the family, in 1850 he dropped out of university and at the age of 19 years he became an official at the Customs House of Chiavari. In 1867 Delpino moved to Florence, then capital of the kingdom of Italy, to work as assistant of Filippo Parlatore within the local Botanical Institute. In 1871 he was hired as professor of natural history in the Royal Institute of Vallombrosa, where he remained until 1875 the year when he won the competition for the chair of botany at the University of Genoa. In 1884 he moved to the University of Bologna where he remained for 10 years. He arrived, finally, at the University of Naples where he headed the local botanical garden, and where he died on May 14, 1905.

From Biology to Plant biology

In 1802, two botanists, Lamarck J-B and Treviranus LC, introduced, independently, the concept of biology. As was emphasized

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Figure 1. Federico Delpino.

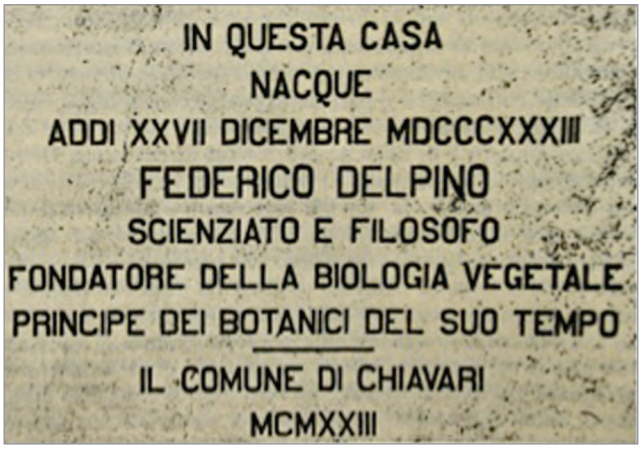

Figure 2. Commemorative plaque on the birthplace of Federico Delpino. The inscription reads: "In this house was born December 27, 1833 Federico Delpino, scientist and philosopher, founder of plant biology. Prince of botanists of his time."

by the philosopher Michel Foucault, before that date, biology as science didn't exist for the reason that the notion of life itself was unknown in the eighteenth century: "*all that existed were living beings, which were viewed through a grid of knowledge constituted by natural history*".[4] Despite some little difference in the definition of this new field of science, both Lamarck and Treviranus seemed to realize the necessity to revise the traditional division of natural objects into three different kingdoms, as was characteristic of contemporary natural history, in favour of a more fundamental division between living and non-living. The concept of biology was created to fill the demand of a different way to study living organisms, concentrating on what differentiated them from inorganic matter. The notions of *sensitivity* or *irritability* were taken from medical physiology and applied to every living creature. On this, certainly, Lamark's revolutionary idea of the linear scale of being had a big importance.

The concept of biology, which, in its original formulation, had a very broad spectrum of meanings, was, with time, more and more identified with the idea of physiology. Perhaps this was because biology proposed the study of functional processes as opposed to that of morphology and systematic, which at that time was characteristic of the natural history approach; or perhaps because, on entering the nineteenth century, there was a demand for specialization of knowledge. For one reason or another, the fact is that the concept of *unitarity life* was soon expurgated from biology.

In 1867, Federico Delpino, with his seminal work "*Pensieri sulla biologia vegetale…*" (Thoughts on plant biology…) established plant biology by defining it not in the broad general sense, namely as the science of living beings, but as a branch of natural science dedicated to the study of plant life in relation to the environment.[5]

With this new discipline, Delpino introduced into the scene of natural sciences a specific area of study focused on the mechanisms utilized by plants to interact with the environment. Delpino initiated the study of the interaction of the plant with its environment, regarding this as being a normal function of plant. At the same time, De Candolle, just to cite the opinion of a great botanist of that period, defined these interactions as "curious accidents". In addition, Delpino provided plant biology with a technical language, which was found necessary to describe the new phenomena investigated. Many expressions that are today in the common use of botanists, originated in that period. Terms, as *dichogamy*, a*nemophily* and *entomophily*, just to cite some, were coined by Delpino in 1867 and entered soon in the common botanical use, being adopted by botanists such as Severin Axell[6] and Asa Gray.[7]

Delpino's original idea was to borrow from zoology the definition of *instincts* intended as meaning the behaviors developed by animals to survive, individually and as a species, in a changing environment; and *ethology*, to define the study of them. For Delpino, the same terminology had to be used to describe the many complex activities of plant such as: defence, reproduction, seed dispersal, social life; but he was also well aware of the difficulties associated with the use of the term *instinct* in relation to the plants. In fact, the term implies both sensitivity and responsiveness that were denied to plants, mainly because of the apparent lack of movements; "*But let's raise the veil of apparent immobility and insensitivity of plants, and below it you will see.... a number of curious phenomena, which compete for the number, variety, talent and effectiveness with those presented by the animal kingdom*".[5]

A convinced supporter of the theory of evolution, Federico Delpino recognized in plant biology the key to demonstrate the Darwinian theory on the variability of the species. "*The main incentive*—he wrote in 1881—*to the variation of organisms is their progressive adaptability to changing external circumstances…. Now, the study of adaptations, or the account of the complex relationships which exist between one organism and another, or between one organism and external agencies, is the exclusive responsibility of biology*".[8] On the basis solely of morphological studies, he claimed, the Darwinian theory could never be proved. In fact, even the physiological (internal) features, which are related to general functions common to all plants, remain stationary for a large number of generations, because of isolation from direct contact with the environment. On the contrary, the attributes that are exposed to a variable environment need to change accordingly, generating modifications that become elements of specific taxonomic groups. Thus, plant biology provides the most appropriate way to assess the transformation and evolution of species. In 1899 he wrote: "*Without the assistance of biology, what is morphology if not an ungrateful, arid and unproductive contemplation of shapes and metamorphosis, from which escapes every significance? What is morphology, if not the measure of our ignorance? Appropriately supported by biology, however, they mutually form together a set of high scientific interest*".[9]

Many botanists of the second half on the eighteenth century adopted the new idea of plant biology and Delpino soon became one of the leading plant scientists in Europe. Friederich Ludwig in 1887 defined Delpino as "*the most important living phytobiologist*", and in 1895 he began his *Lehrbuch der Biologie der Pflanzen* with the following words: "*the foundation of plant biology is due to Federico Delpino*";[10] Paul Knuth, by recognising the great merits of Delpino's work, introduced the second volume of his "*Handubch der Blütenbiologie*" (1898–1904) with a big table (**Fig. 3**) depicting Charles Darwin in the middle surrounded by four great botanists: Federico Delpino, Severin Axell, Fritz Müller and Friedrich Hildebrand;[11] Dodel-Port (1883) wrote that "*after Darwin, Delpino is the most important living botanist*";[12] Ernst Loew (1895) dedicated to him many chapters of his *Einfuhrung in die Blutenbiologie auf Historischer Grundlage*;[13] and the list could be much longer, confirming the high opinion in which Delpino was held by his contemporaries.

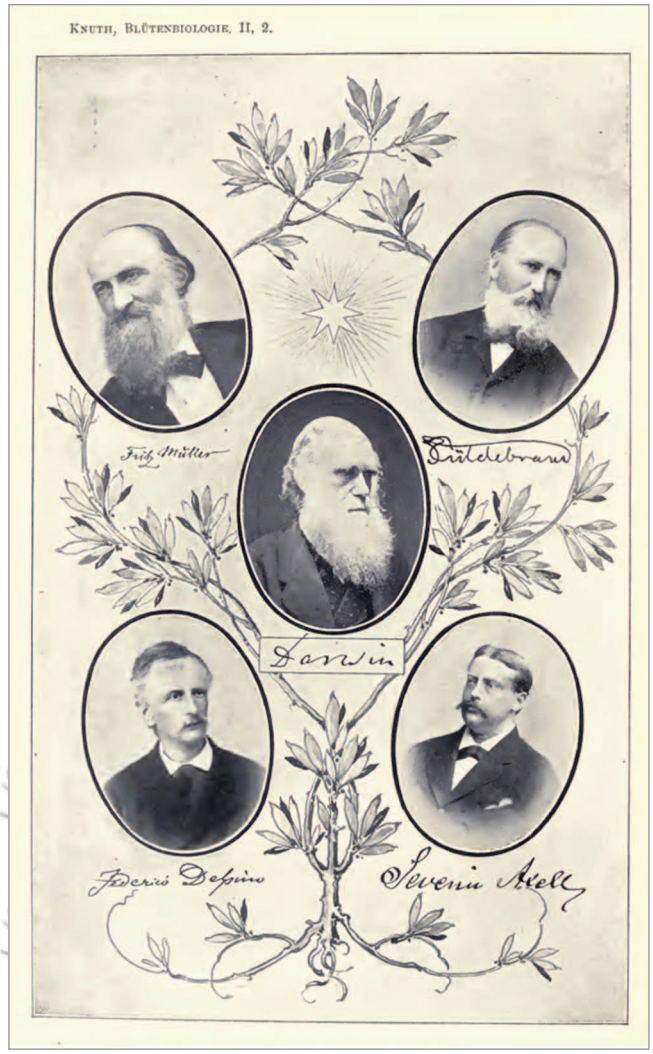

Figure 3. Charles Darwin in the middle surrounded by Federico Delpino, Severin Axell, Fritz Müller and Friedrich Hildebrand from the Handubch der Blütenbiologie (1898–1904) by Paul Knuth.

Myrmecophily

In accord with his idea of plant biology, Federico Delpino was always fascinated by the many strategies used by plants in the attempt to defend themselves against animal predation. In response to the many organisms that use plants as food, from microorganisms to mammalian herbivores, plants have evolved a variety of direct or indirect defenses to prevent, discourage or kill their predators.[14] Examples of direct defensive tools such as thorns or toxins have a direct impact on animals and represent a remarkable adaptation to the necessity. More complex and difficult to investigate are form of indirect defences achieved thanks to different strategies of protection. To these indirect defence systems, Delpino devoted a methodical study identifying for the first time in plants the phenomenon of the so-called myrmecophily. Literally "ant-love", myrmecophily is the term used to describe a positive interspecies association between ants and other species. Delpino was inspired by a previous research on the coexistence between Cidadelline and ants. Ants, very combative species, offer protection to Cicadelline, receiving in change the possibility to suck from the abdomen a nourishing and sweet juice.[15] Two years later he applied the same scheme to plants, describing a new form of cooperation between ants and plants.[16] Already in this first study, almost entirely carried out in Tuscany and Liguria, he discovered and described about 80 myrmecophilic plant species belonging to 13 families and 20 genera.

The opportunity to deal with myrmecophilic plants came to Delpino from a disagreement which arose between him and Darwin on the interpretation of extrafloral nectar. This was believed by Darwin, as he wrote in the Origin (1859), to represent just an excretion with no value for the plant: "*Certain plants excrete sweet juice, apparently for the sake of eliminating something*

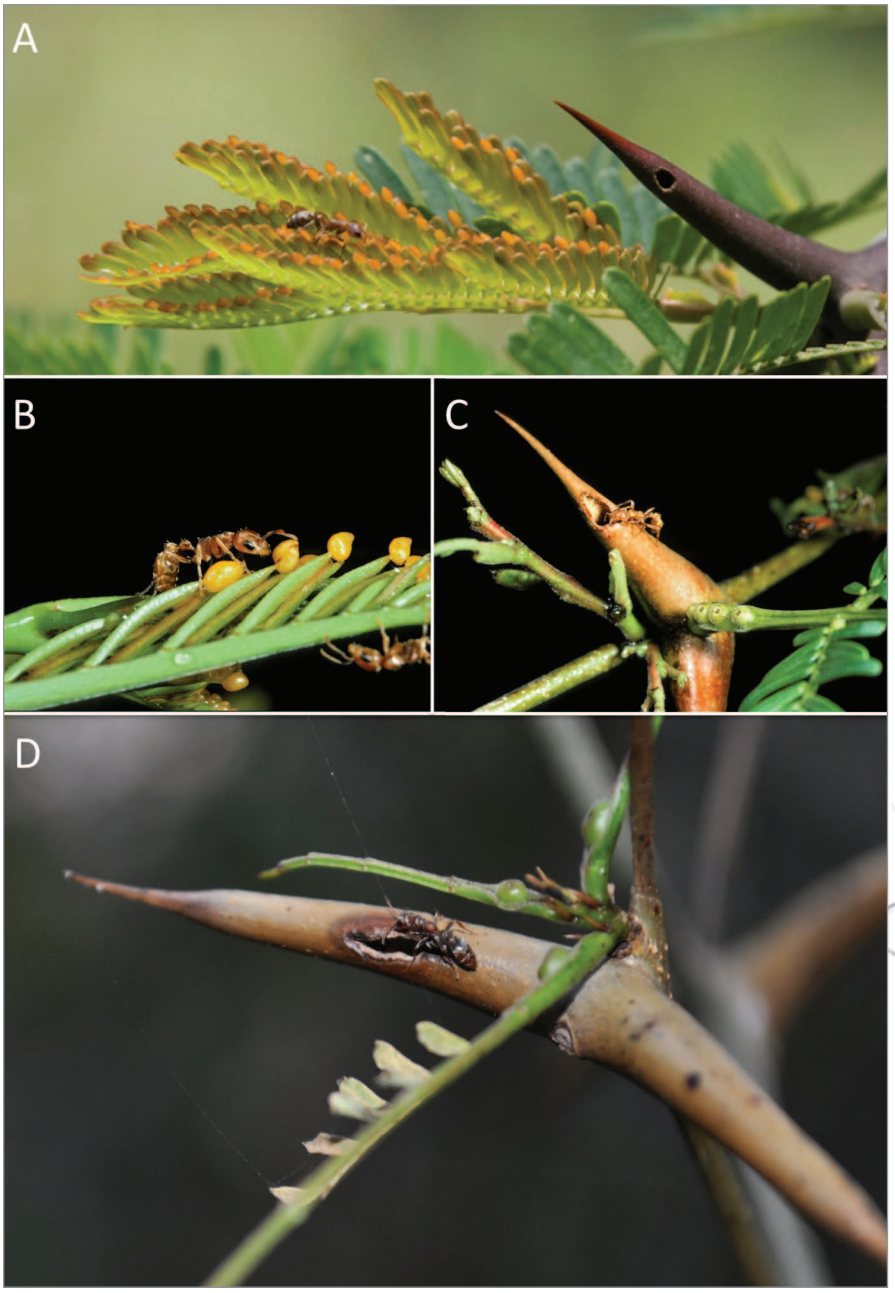

Figure 4. Myrmecophily in plants. Federico Delpino was the first to describe a positive interspecies association between ants and plants. (A, C and D) bullhorn acacia; the ants live in the hollowed-out thorns for which the tree is named. (B) Pseudomyrmex ant collecting protein-rich Beltian bodies from a bullhorn acacia, Costa Rica. Photo (B and C) Credit to Dan L. Perlman/ EcoLibrary 2008.

injurious from the sap: this is effected, for instance, by glands at the base of the stipules in some Leguminosae, and at the backs of the leaves of the common laurel. This juice, though small in quantity, is greedily sought by insects; but their visits do not in any way benefit the plant. Now, let us suppose that the juice or nectar was excreted from the inside of the flowers of a certain number of plants of any species. Insects in seeking the nectar would get dusted with pollen, and would often transport it from one flower to another. The flowers of two distinct individuals of the same species would thus get crossed; and the act of crossing, as can be fully proved, gives rise to vigorous seedlings, which consequently would have the best chance of flourishing and surviving. The plants which produced flowers with the largest glands or nectaries, excreting most nectar, would oftenest be visited by insects, and would oftenest be crossed; and so in the long-run would gain the upper hand and form a local variety".[17] Darwin believed that the extrafloral nectaries were excretory organs designated by the plant to expel substances somewhat superfluous; the same organs were used, later in evolution, due to subsequent adjustments, in floral organs to attract bees or other insects for cross-pollination. Delpino immediately recognized the weakness of this hypothesis: how can a substance that contains such an important quantity of sugars be described as an excrement? If the plant tolerates this sugar loss through extrafloral nectaries, this means that they exert a function similar to that of floral nectaries, which is to attract insects beneficial for the plant life.

To prove his theory, Delpino analyzed the benefits brought by the ants to the defence and conservation of plants and produced a detailed statistic of the myrmecophilic species.

Delpino described his results in an important monograph published in 1886, which lists nearly 3,000 species (distributed in about 300 genera and in 50 families), scattered especially in the warmer parts of the Earth, which are provided with extrafloral nectaries.[18] In addition to the plants that attract ants with a supply of food, he added also 130 species, distributed in 19 genera and 11 families, which attract ants by providing a nest or a shelter (**Fig. 4**).

Plant Intelligence— On the Instinct and the Reason

Delpino had a lucid idea of what intelligence is. He believed, in fact, that a correct description of intelligence was the first step to identify intelligent living organisms. For Delpino intelligence is not a confined phenomenon, but rather a continuous gradation of the same principle: "*Instinct and reason are but two forms or two different shades of a single principle, the intelligence. Pure intelligence is not recognizable by itself, in order to recognise intelligence, it must be translated into action*". To define an action as intelligent three stages must concur: "*the starting point (first term), the trajectory (middle term) and the objective (last term)… Is the case of the arrow that starts from the eye of the bow, travels through space and hits*

the mark".[5] These three phases are present both in the instinctive actions and in those of reason, because the difference between instinct and reason is not a difference of *quality or category*, but simply a difference in *quantity*. The key factor that distinguishes the instinctive actions, from those arising as a result of reasoning, is only the consciousness or awareness. Consequently, every living creature can be: (1) totally unaware about the first, middle and last term, (2) gradually aware about the first and last term, but completely unaware of the middle term, and (3) gradually aware across all three terms.

The life of plants, as well as the embryonic life in animals is characterized by only minimal awareness, but this lack of awareness doesn't mean that plants are in any way unintelligent. On the contrary, "*On this incongruity have stumbled many botanists who, in the books they wrote, were unable to describe the external activities of plants and thus neglected them. It is easy to explain these inconsistencies if we think that they had to be the reasonable consequence of some deep-rooted and widespread opinions, which nevertheless seems to me absolutely wrong. In animals obvious and easily recognizable seem to be the acts and the manifestations of their sensitivity and intelligence, and that thanks to their sure indication of movement in time and space. While the plants... mostly relentlessly fixed to the floor, do not give, except in very rare cases, evidence of sensitivity. And since the sensitivity is considered the only real prodrome and certain sign of intelligence, here it is that intelligence is generally denied to plants. This conclusion seems to me a serious mistake, born of a superficial appreciation of the facts*." The solutions implemented by plants, in fact "*are successful in achieving the same results of animal locomotion and with the same perfection. In this I do not see any difference in the degrees of intelligence exhibited by animals and plants*".[5]

Conclusion

By reading today Delpino's powerful works, the main feeling of a plant scientist is that he cannot escape a strong surprise for the "modernity" of the ideas exposed, and for Delpino's vision of plants as purposeful and intelligent organisms. In general, a truly original prospective permeates Delpino's approach to science. It is always perceptible in his many works. Even when he records simple events in an almost diaristic style, as in the following story describing for the first time the technique of dissemination of seeds used by Tilia and many other species, and with which I will conclude this small tribute to Federico Delpino. He narrates that during a walk on a windy day, along the Arno River in Florence, something flying next to him which at a first glance he thought was a butterfly, attracted his attention. Actually, it was something else: "*I realised, not without surprise, to have caught a fruit of linden... I was struck by the simplicity and perfection of that small flying device, which for the well-calculated proportions of its elements, I am persuaded would have amazed a mathematician. The fruit that is the weightiest part of the device, serves as a counterweight, and maintains the apparatus in a position such that the peduncle is kept upright and the bract is slanted in the direction of its length. Thus, the result of this device is quite similar to that of a kite. With the difference.... that the small linen's fruit proceed forward with a rotary motion, whose revolutions are more or less frequent depending on the greater or lesser violence of the wind. This modification, although it may seem at first sight fortuitous and inconclusive, is rather ingenious and essential. Indeed, in the kite the length of the wire behind the wing, the gravity of the weight that holds out the thread, as well as the long appendix that serves as a rudder, make it possible that even a violent wind does not disturb the balance of the equipment and fails to overturn it. Now Nature, wonderfully simple and efficient in its variety, imparts to the apparatus the translational motion on a rotating axis…, thereby resolving with the minimum cost of material the problem of ensuring a stable equilibrium, even in the face of a fierce wind, whose strength is precisely to be diminished or eliminated by the increased frequency of rotation. Otherwise plants would have had to spend large amounts of matter by producing a caudal appendage, a very long peduncle, and a heavy fruit*".[5]

With this extraordinary note, which combines a fascinating style and a detailed technical description of the flying device of the linden's fruit, Delpino uses what we call today "a bio-inspired approach", namely the capacity to suggest technical solutions by observing the nature, demonstrating, once more, that he was indeed a plant scientist ahead of his time.

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