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Minute observations and theoretical framework of Darwin's studies on climbing plants

Observations précises et cadre théorique des recherches de Darwin sur les plantes grimpantes

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ABSTRACT

The role of movement in plants was unrecognised for a long time, due to the relative slowness of such movements by comparison with those of active animals such as insects and vertebrates, and to the difficulty with which they are distinguished from mere growth processes. Given this, the pioneer work of Darwin (*On the Movements and Habits of Climbing Plants 1865*) is a milestone in botany. It is always cited as the beginning of any rigorous analysis of plant movement. Such a successful approach results at once from Darwin's broad knowledge of natural history, his use of numerous direct observations and simple experiments, but also from his own talent, which compensated for technical gaps in several instances. His use of metaphorical descriptions was a response to the lack of a firm theoretical background. It facilitated a preliminary classification of plant movement and a comparison of observations. Perhaps his most fruitful metaphors were those drawn from economic concepts, such as division of labour. Darwin's legacy in plant physiology is impressive, as even the most recent biophysical interpretations of climbing plants (e.g. tendril perversion) take place inside the framework he constructed.

RÉSUMÉ

Le rôle des mouvements chez les végétaux a longtemps été méconnu, en raison de leur relative lenteur – si l'on compare avec des animaux très actifs comme les insectes ou les vertébrés – et aussi de la difficulté de les séparer des phénomènes de croissance. Dans un tel contexte, l'ouvrage fondateur de Darwin (*On the Movements and Habits of Climbing Plants 1865*) est une étape historique majeure de la botanique, constamment rappelée comme origine de toute analyse rigoureuse des mouvements végétaux. Une approche si féconde résulte d'abord de la vaste culture naturaliste de Darwin, de multiples observations directes et de la clarté des expériences, mais aussi de ses qualités personnelles, compensant les obstacles techniques à de nombreuses reprises. L'utilisation étendue de descriptions métaphoriques doit être considérée de même comme une réponse à l'absence de cadre théorique solide. Elle permet une classification préliminaire et une comparaison des résultats, à la lumière de concepts issus du domaine économique, particulièrement celui de division du travail. L'impulsion donnée à l'essor de la physiologie

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végétale est décisive, puisque même les interprétions biophysiques les plus récentes des mouvements des plantes grimpantes (par exemple la double torsion des vrilles) s'inscrivent logiquement dans le prolongement des hypothèses formulées par Darwin.

1. Introduction

The role of movement in plants was unrecognised for a long time, due to the relative slowness of such movements by comparison with those of active animals such as insects and vertebrates, and to the difficulty with which they are distinguished from mere growth processes. Sleep movement of leaves had been observed by Pliny the Elder and Linnaeus, and some peculiar plant motions had been reported since the seventieth century. However, no extensive studies of, or experiments on, their possible role were recorded before the works of Darwin, in particular his first paper to the *Journal of the Linnean Society of London*, in 1865 [1].

2. Recording devices and experimentation

As Beatrice Sweeney [2] reminds us, no method for making automatic recordings of plant movement was available in Darwin's time. To a great extent, this lack was compensated for, by the talent of Charles Darwin as an excellent observer, and by his own health problems. It is well known he was a semi-invalid and suffered many sleepless nights. So he had the opportunity to study plants of various kinds in his room continuously and over a long period of time, and thus to describe roughly the main motions of stems, leaves, and specialised organs such as tendrils.

He could thus record these movements thoroughly using a very simple graphical method (Fig. 1). In fact, Darwin used a kind of descriptive geometry, but with a conical projection from a fixed target (a black spot on a card), which amplified the motion. This mark was lined up by the naked eye with a minute bead of sealing wax, borne by the free tip of a thin glass fibre attached to the moving organ. The position of the bead was marked on a sheet of glass with a wax pencil, and the time was written beside it. Points were joined in chronological order. Darwin most often used a horizontal glass sheet above the plant, sometimes a hemispherical one (e.g. for the tendrils of *Dicentra thalictrifolia*, Fumariaceae). In some cases he used two paper triangles fixed to a thin glass fibre. Interestingly, he marked out meridian lines along the stem with ink, thus demonstrating torsion processes during movement.

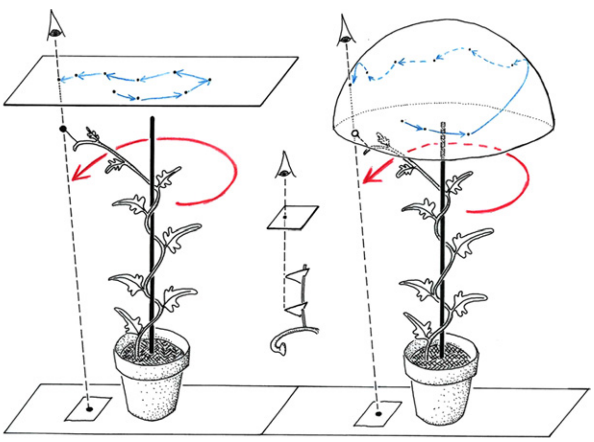

Fig. 1. Sketches of experimental devices used by Darwin for recording paths of mobile tips of climbing plants.

The resulting representation of movement demonstrates significant shortcomings: very often, Darwin considered only a polar view, yet he did not pinpoint the pole. Consequently, he gave a general description of motion patterns, rather than a precise description of movements. Darwin especially prioritised the circumnutation (a word he created) as an exploratory movement, *evocative* of plant "hunting" for support and light, and used it in parallel with several striking metaphors (e.g. likening parts of plants to fingers and birds' feet [tarse]).

Darwin was not able to take the parameter of time into account with as much detail as it was taken later. Automatic time recordings were perfected only at the end of Darwin's life (ca. 1875), and their availability coincided with a new interest in periodic phenomena [3]. Moreover, pinpointing the pole in diagrams of plant movements allowed later researchers to use polar coordinates, and thus to attempt a mathematical analysis of movement. This technique became especially common in the xxth century [4].

Darwin's experiments were *arranged observations* rather than *true experiments*, because they involved very simple stimuli such as shocks – sometimes repeated – with a pencil, the use of very light weights (ca. 1 mg cotton loops, threads), of poles of different diameters, and of more or less rough or fibrous supports. Darwin was obviously interested in touch, and in the texture of the touched substrate. So we should not be astonished that he spent so much time with prehensile organs, emphasizing some kind of tactile perception, while studying the possible resulting weak alterations of movements. He is always considered as a forerunner in several fields of plant physiology, including those that investigate sensory cells and periodic phenomena.

Although he examined a wide range of plants in his inquiry into the climbing habit, Darwin choose convenient varieties, such as potted plants, vines or small woody lianas, and excluded any combination with nutrition as in *e.g. Cassytha* or *Cuscuta*. In addition, he filed all his observations in four logical chapters, i.e. "Spirally twining Plants"; "Leaf-climbers"; "Tendril-bearers" and "Hook- and Root-climbers". Thus, he distinguished between climbers without or with peculiar prehensile organs, twining or upright stems. The methodology may be seen as Baconian, as Darwin tried to divide his queries about the processes into the simplest possible questions, leading thus to the simplest experiments. There is virtually no selective background at this stage. All of Darwin's interpretations were made within the classical frameworks of comparative anatomy and natural classification.

3. Theoretical principles

Darwin's evolutionary explanations of his observations on the habits of climbing plants rely on several theoretical principles, which for clarity of analysis can be formulated like this:

- vegetable species can gradually acquire habits, such as the diverse habits of climbing. In the concluding remarks, Darwin sums up his study, saying: "We have attempted to trace some of the stages in the genesis of climbing plants" [5][p. 199];
- vegetable species can also loose the habits which they have acquired. Darwin adds: "But, during the endless fluctuations of the conditions of life to which all organic beings have been exposed, it might be expected that some climbing plants would have lost the habit of climbing" [5] [pp. 199–200]. This principle explains why a plant's structure can be imperfectly suited to its habit. For instance in chapter III, Darwin remarked that one would expect that the *Smilax aspera* would climb "by the aid of its spines alone", as the brambles did. That is not the case. So we may suspect, as Darwin did, that the *Smilax aspera* possesses tendrils "solely from being descended from progenitors more highly organised in this respect" [5] [pp. 120–121];
- these kinds of changes are gradual ones. In the preface, Darwin expressed his conviction that his observations concerning the climbing plants "illustrate in a striking manner the principle of the gradual evolution of species" ([5] VI], not in [1]). Although Darwin did not explicitly make a parallel between the habits of climbing plants and the instincts of animals, we can notice that their changes are both gradual. This emphasis on gradual processes explains to some extent Darwin's concern with weak alterations, as in e.g. *Clematis vitalba* (Fig. 2). After clasping a support the structure of leaf petiole is slightly modified: there is an increase in diameter, an increase in secondary xylem; and especially, there is a sclerification of the parenchyma. So, as Darwin remarked, the primarily flexible petiole (due to collenchyma) becomes hardened by an underlying sclerenchyma;
- each organ has a function and a place in the structure. According to the definition given by Owen and accepted by all the naturalists, Darwin called the relation between organs having the same place in the structure *homology*, and he called the relation between organs having the same function *analogy*. According to these definitions, Darwin spoke about the "analogical nature" of a "tendril" [5][pp. 198–9]. This notion is understandable only if one recalls that "tendrils consist of *various* organs in a modified state, namely, leaves, flower-peduncles, branches, and perhaps stipules" [5] [pp. 195–197]. Tendrils themselves appear to be specialised structures linked to the *transfer* of twining ability to the tip of leaves, as demonstrated inside the Ranunculaceae family by *Clematis* (twining petioles, as we saw previously), and the closely related genus *Naravelia* (with terminal leaflets modified in tendrils);
- provided that the "advantage gained by climbing is to reach light and free air with as little expenditure of organic matter as possible", having specialised organs for climbing is more economical than the system of the

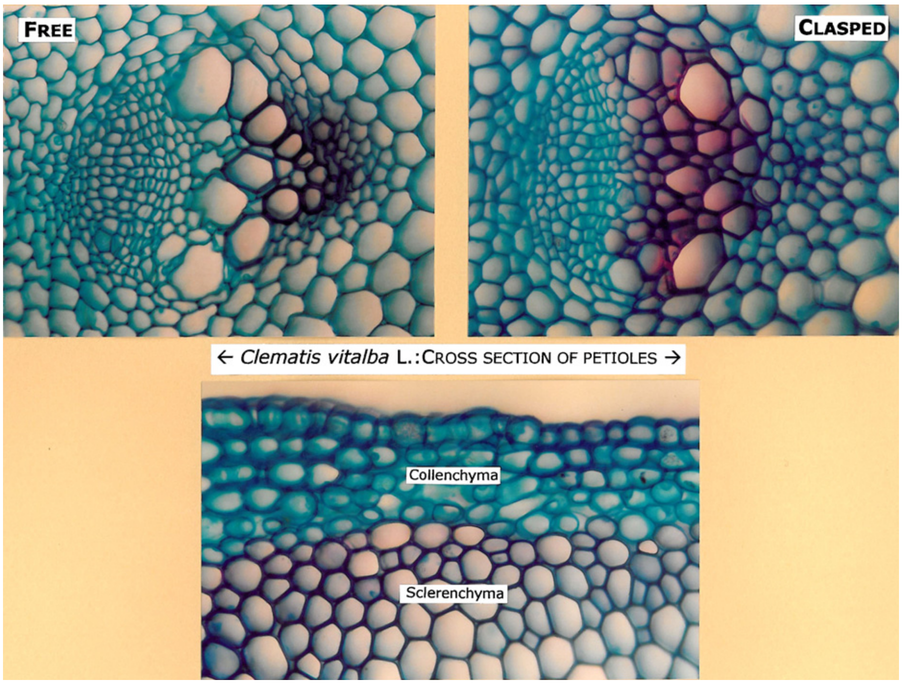

Fig. 2. Weak histological alterations in a petiole bundle of *Clematis vitalba* L., before and after clasping a stick. Below: outer part of petiole after clasping (hand transverse sections, stained by Astrablue and Ziehl's Fuchsine).

twining plants which need a strong stem, and so use more organic matter [5] [pp. 195–197]. This assumption can be related to the principle of division of labour, the development of which Camille Limoges thoroughly retraces through the works of Milne-Edwards, Darwin and Durkheim [6].

4. Biographical circumstances and subjective interpretation

Among the features that set *On the Movements and Habits of Climbing Plants* apart from contemporary scientific literature is the place occupied by its author. The presence of the author in the book influences its subjectivity in two ways.

Far from denying biographical circumstances, Darwin alluded several times to intimate facts of his life. For instance he portrayed himself "confined in a room by illness" [5] [p. 19]. He referred to an observation made by his sons visiting a hop-field for him [5] [p. 19]. He credited his son George for the illustrations, and especially his son William for having sketched for him "the earliest state of development of an hybrid of *Passiflora florifunda*" [5] [153]. Another aspect of subjectivity is evident in Darwin's use of metaphors for depicting the habits of climbing plants. The simplest case is the comparison with human movements.

For instance, Darwin describes *Bignonia littoralis* ascending a "vertical stick by twining spirally and by seizing it alternately with its opposite tendrils, like a sailor pulling himself up a rope hand over hand" [5] [91–92].

A more complicated case consists in imputing psychological motivation to plants.

Having placed a tall stick "as to arrest the lower and rigid internodes", he described the strange movement of the stem in the following terms: "This movement of the shoot has very odd appearance as if it were disgusted with its failure but was resolved to try again" [5] [21].

Darwin seemed to be a little uncomfortable concerning these metaphors, and especially with the word *disgust,* which he used frequently. Describing a *Bignonia capreolata* placed near a glass tube and a zinc plate which have been blackened, Darwin wrote: "they soon recoiled from these objects with what I can only call disgust" [5] [99].

These metaphors can be interpreted as rhetorical figures of speech or as heuristics. But they chiefly express Darwin's view of the unity of the living being.

Even the title of the book is significant from this point of view. The term "habit" applied to vegetables as well as animals, including man, occurs in *The Origin of Species* when Darwin compares the change in structure and the change in habits [7: 183]. It also occurs in *The Expression of emotion in man and animals,* particularly in the phrase "Principle of serviceable associated habits".

5. The legacy

As we have seen, Darwin obviously chose to study simplified processes, compensating for the relative inadequacy of the theoretical background with an extensive use of metaphors. In just a few cases only, he made further developments, as we saw with his observations of the anatomical alterations in twining petioles, or the preliminary – but nevertheless accurate – chemical analysis of the sticky cushions of *Bignonia* tendrils. All the results, organised according to his evolutionary interpretation, provided a sound basis, which immediately triggered a blossoming of new studies.

During the late nineteenth century and the twentieth century, the analysis of plant movements entailed the use of mathematical tools and more complex devices, eventually including cinematographic ones. This is well illustrated in France by the works of Commandon (see [8]). The resulting diagrams conformed to mere descriptive geometry, taking in account the stem basis (point ω), the support(s), the velocity and acceleration, and introduced new concepts such as e.g. the "efficient radius" (linked to curvature of stem). So, because of Darwin's work, a rigorous record of plant movements was made possible, and an experimental approach became easier (see [4] for a detailed historical account).

At the same time, thorough studies on perception in plants [9] were initiated. These led to the discovery of tactile cells, which also have some optical properties (e.g. in *Eccremocarpus scaber*, see [10]).

The tendril perversion, a process pinpointed by Linnaeus in his classical *Philosophia botanica*, and well-known by Darwin, was recently and rigorously studied by physicians [11]. The term tendril perversion expresses the intriguing feature of two opposite coiling directions in the same tendril, the two twisted regions being linked by a short segment, which is more or less straight. It appears that the phenomenon is very similar to that commonly exhibited by telephone chords, and results from the intrinsic curvature of these structures. As a result, a twistless spring is built. This is a very efficient structure for absorbing motion.

Some other aspects of plant movements were not tackled by Darwin for obvious technical reasons, but were implicit in his studies. They concern especially tropical woody lianas. We can here refer to the comparative anatomy of stems in tropical woody lianas (such needing extensive collections), and its ecophysiological interpretation [12,13].

The monitoring of growth and development of lianas in the field is also a recent development, due to foresters' renewed interest in climbing and epiphytic plants [14]. Following-up of each unit is necessary because of the complex branching and frequent deformation, and is feasible only by tagging plants, which is the same method Darwin used in his room (!). The study of climbing plants' specialised organs (hooks, spines, tendrils, etc.) remains an active field, and benefits from efficient tools for observing and analysing morphogenetic processes (well exemplified by the hooks of *Artabotrys*, homologous to inflorescences in [15]). Considering the limitations of biological investigation at his time, it is not astonishing that Darwin chose to focus on the most basic phenomena of plant movements [16].

6. Conclusions

In almost all works dealing with climbing plants, the Darwin study is recognised as a seminal work. This illustrates how his naturalistic works continue to be drawn upon in biology today.

However, his set of observations does not provide a basis for the theory of descent with modification. Rather, it is a kind of aftermath, which proves the heuristic fecundity of the theory in a new field of research.

François Jacob has read in Darwin's work a conception of evolution as tinkering, which is expressed in the book on orchids. *On the Movements and Habits of Climbing Plants* may thus be considered as "epistemic tinkering", involving potted plants in a bedroom, rough recording devices, few theoretical assumptions, and a bold use of anthropomorphic analogies.

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