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Historical corner

A 'misplaced chapter' in the history of photosynthesis research; the second publication (1796) on plant processes by Dr Jan Ingen-Housz, MD, discoverer of photosynthesis

A bicentenniel 'resurrection'

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Abstract

In 1779, the Dutch physician Jan Ingen-Housz (1730–1799) obtained a leave-of-absence from his post as Court Physician to Empress Maria Theresa of Austria in order to do research (in England) on plants during the summer months. He performed more than 500 experiments, and described the results in his exceptional book *Experiments Upon Vegetables* (1779). In addition to proving the requirement for light in photosynthesis, Ingen-Housz established that leaves were the primary sites of the photosynthetic process. Later, Ingen- Housz published research papers on various subjects but aside from his 1779 book, he published only one more communication on photosynthesis and plant physiology. This was entitled 'An Essay on the Food of Plants and the Renovation of Soils'. The essay was published in 1796 as an appendix to an obscure British government report, which is rare and virtually unknown. The present paper describes the 1796 essay, which is particularly interesting in that it shows how Ingen-Housz's concepts were modified by new interpretations of chemical phenomena described in Lavoisier's great and revolutionary book *Traité Élémentaire de Chimie* (1789). Ingen-Housz not only discovered photosynthesis, but plant respiration as well, and the 1796 essay is testimony to his remarkable insights.

The requirement for light in photosynthesis and a number of other important basic facts relating to plant physiology were established by the Dutch physician Jan Ingen-Housz (1730–1799) (Gest 1988). Ingen-Housz received the MD degree from the University of Lovain in 1753, and then continued basic studies (chemistry, physics, anatomy, etc.) for several years at the universities of Leiden, Paris and Edinburgh. In 1765 he moved to London and soon became known as an expert in the technique of inoculation against smallpox. The *Dictionary of Scientific Biography* (Van der Pas 1973) summarizes significant events from this phase of Ingen-Housz's career:

> In 1768 Ingen-Housz was sent by George III on the advice of a commission to the Austrian court to inoculate the royal family. After successfully inoculating the archdukes Ferdinand and Maximillian and the Archduchess Theresa, Ingen-Housz was showered with gifts and honors. Empress Maria Theresa appointed him court physician with a life-long annual income of 5000 gulden. While the empress was disappointed in her hopes that the shy, kind man would develop into an interesting courtier, Ingen-Housz's use of his financial independence – for research – proved of inestimable value. He travelled throughout the empire, inoculating relatives of the imperial family and practicing and teaching inoculation. In January 1771 he went to Paris and then to London, where he was admitted to the Royal Society on 21 March 1771.

In 1779, Ingen-Housz obtained a short leave from his post in Vienna, and returned to England for the summer months. At a country house near London, he performed more than 500 experiments on plants, and reported the results in his classic book (Ingen-Housz 1779): *Experiments Upon Vegetables, Discovering Their great Power of Purifying the Common Air in the Sun-shine, and of Injuring it in the Shade and at Night*. The book was hurriedly printed in London, allowing Ingen-Housz to take copies with him when he returned to Vienna. In addition to demonstrating that light was required for oxygen (known then as 'dephlogisticated' or 'vital' air) production, Ingen-Housz identified leaves as the sites of photosynthesis.

Ingen-Housz published a number of papers on various subjects (see Van der Pas 1973), but it appears that aside from his 1779 book, he published only one more communication on photosynthesis. The second publication appeared in the form of a 20-page paper, one of several appendices in an English government report that appeared in 1796 (Ingen-Housz 1796). In other words, eight years after Lavoisier began to demolish the phlogiston theory. Lavosier's great and revolutionary book 'Traité Élémentaire de Chimie' (Lavoisier 1789) was truly the beginning of modern chemistry. 'Dephlogisticated air' became *oxygen*, and the photosynthetic process could be viewed in a new context:

$$\text{carbonic acid} + \text{light} \longrightarrow \text{organic matter} + \text{oxygen}$$

How did Lavoisier's new chemistry influence Ingen-Housz's interpretations? This question started me on a search for Ingen-Housz's second publication, which I initially thought should not be difficult to obtain. In fact, it required considerable effort to obtain a genuine copy. In the following, I will refer to the 'misplaced' paper (Ingen-Housz 1796) as IH-2.

A detailed biography of Ingen-Housz was published in 1905 (in German) by Prof. Julius Wiesner, then Director of the Plant Physiology Institute of the University of Vienna (Wiesner 1905). Following are Wiesner's comments on his attempts to see I-H2 with his own eyes.

> This study is entitled 'An Essay on the Food of Plants and the Renovation of Soils'. The German translation which has been published (in 1798) as a free-standing/independent work is entitled 'Über die Ernährung der Pflanzen und die Fruchtbarkeit des Bodens'. In spite of the efforts of the Vienna University Library and of several of my friends, I could not find a copy of the English original on the continent. However, the German translation can be found in numerous libraries on the European continent and in England. Only after considerable effort was my esteemed friend, Dr O. Stapf of Kew (Gardens, London) able to locate in the library of the British Museum the collective volume which contains, among others, Ingen-Housz's original study. There is no doubt that most recent authors had available to them only the German translation even when they cite the English original.
>
> The German translation is considerably flawed and several sentences are reduced to nonsense as a result of omissions. For example, the German translation on p. 56 reads as follows: 'Ich war glücklich genug, die wahre Ursache zu entdecken, warum Pflanzen zu einer Zeit dieselbe (nämlich die umgebende Luft) noch schlechter machen, eine Ursache, welche von Priestley und Scheele nicht einmal geahndet wurde' ('I was fortunate enough to discover the true cause why plants at times cause the deterioration (of air quality), a cause which neither Priestley nor Scheele had imagined'). Sachs (*Geschichte der Botanik*, p. 534) reproduces this sentence verbatim. But the original has a much more significant meaning, explains the relationship of Ingen-Housz's work to that of Priestley and Scheele and reads as follows: 'I was fortunate enough to discover the true reason why plants *sometimes improve bad air* and sometimes make it worse'....The italicized words are missing in the German translation.
>
> The regulations of the British Museum prevented me from perusing the English original personally. Therefore, I asked Dr Stapf to copy for me those passages where the German translation seems to be inaccurate, particularly those containing the principal results of Ingen-Housz's investigations. Dr Stapf was particularly kind in copying these passages personally. Any subsequent German translations (i.e. in Wiesner's book) reflect my constant reference to the English original.

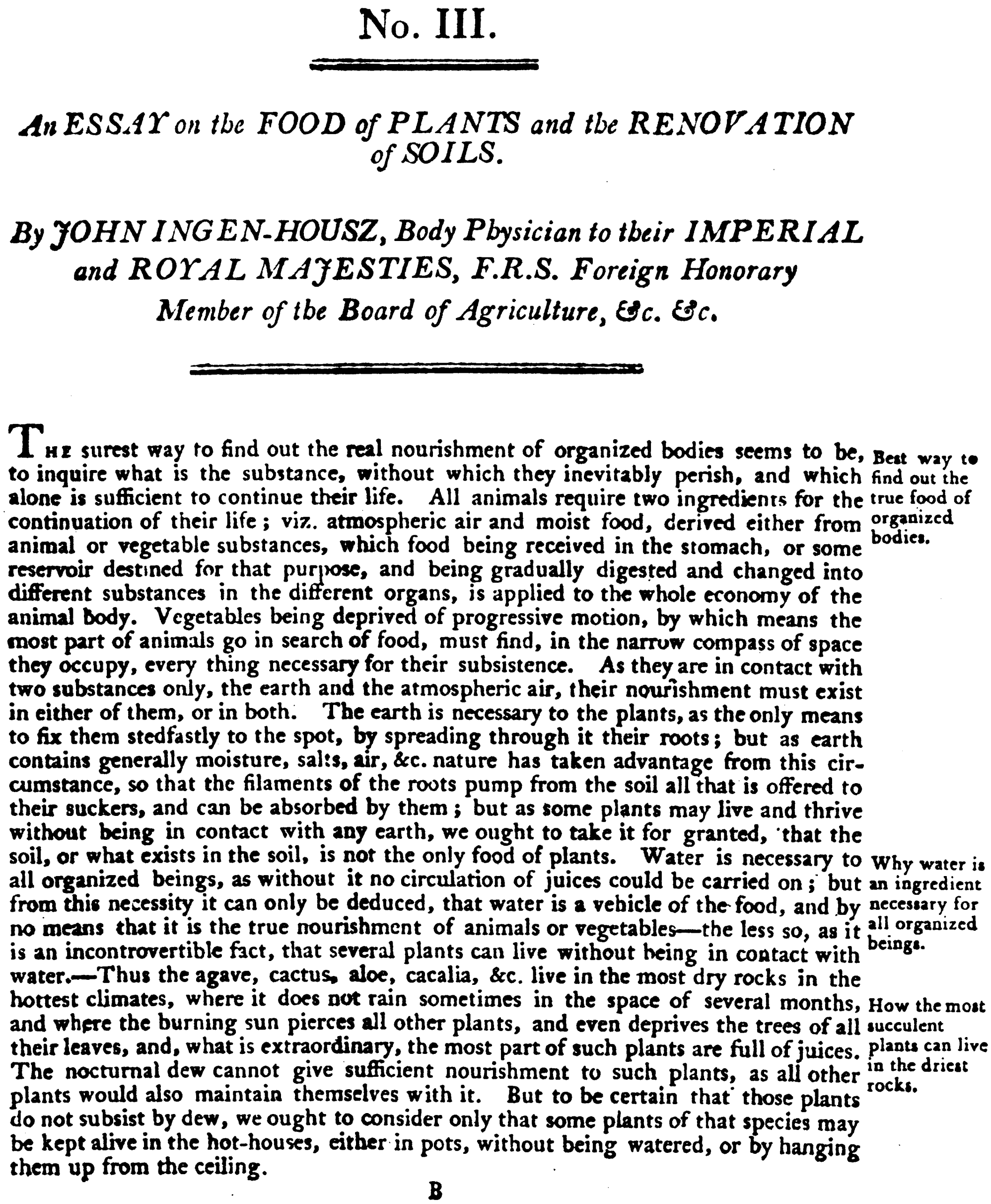
My attempts to find the original IH-2 in the United States were frustated in various ways. In 1949, Howard S. Reed republished Ingen-Housz's classic 1779 book in combined issues of *Chronica Botanica* (Reed 1949), with extensive commentaries. In a short preliminary chapter entitled 'Plant Physiological Investigations', Reed reviews the relevant background to Ingen-Housz's book and cites IH-2 with the

Figure 1. 'Starch picture' of Dr Jan Ingen-Housz on a geranium leaf (prepared by William Ruf and Howard Gest). The image of Ingen-Housz consists of photosynthetically-produced starch granules, which were 'developed' by staining with I_2-KI. An engraving of Ingen-Housz (in Reed 1949) was photographed, and the negative placed in a slide projector. Light passing through the negative was focused on a geranium leaf (depleted of starch by prior incubation in darkness) for about one hour. After extraction of pigments from the leaf with boiling 80% alcohol, the blanched leaf was flooded with I_2-KI solution to stain the starch granules. Within minutes, the details of the engraving dramatically appeared on the leaf. The inscription at the bottom refers to Dr Ingen-Housz's fame as a 'smallpox inoculator'. The 'starch picture' procedure was invented by Hans Molisch in 1914. Further details and an English translation of Molisch's paper 'On the production of photographs in foliage leaves' can be found in Gest 1991.

comment: 'This extremely rare paper was privately reprinted in 1933 by Dr J.C. Bay, Director of John Crerar Library.' It would seem that this 1933 'reprint' was Reed's source of comments on IH-2. The 'reprint' is available from the Library of Congress, but it has a major fault. Namely, all of the more than 40 of Ingen-Housz's marginal notes, comments, questions, etc. were omitted. Because of these deficiencies, I continued the search for a genuine copy of IH-2 and finally obtained one. Figure 2 is a reproduction of the first page; a photocopy of IH-2 can be obtained from the Bancroft Library, University of California, Berkeley, CA 94720-6000 at nominal cost.

The state of chemical and photosynthesis knowledge: 1779–1796

Ingen-Housz's contributions were made under the heavy pall of the Phlogiston Theory. Conant (1950) remarks that the theory can be traced back to the alchemists. It proposed that during the combustion of any substance, 'phlogiston' escaped and became com-



No. III.

An ESSAY on the FOOD of PLANTS and the RENOVATION of SOILS.

By JOHN INGEN-HOUSZ, Body Physician to their IMPERIAL and ROYAL MAJESTIES, F.R.S. Foreign Honorary Member of the Board of Agriculture, &c. &c.

Best way to find out the true food of organized bodies.

THE surest way to find out the real nourishment of organized bodies seems to be, to inquire what is the substance, without which they inevitably perish, and which alone is sufficient to continue their life. All animals require two ingredients for the continuation of their life; viz. atmospheric air and moist food, derived either from animal or vegetable substances, which food being received in the stomach, or some reservoir destined for that purpose, and being gradually digested and changed into different substances in the different organs, is applied to the whole economy of the animal body. Vegetables being deprived of progressive motion, by which means the most part of animals go in search of food, must find, in the narrow compass of space they occupy, every thing necessary for their subsistence. As they are in contact with two substances only, the earth and the atmospheric air, their nourishment must exist in either of them, or in both. The earth is necessary to the plants, as the only means to fix them stedfastly to the spot, by spreading through it their roots; but as earth contains generally moisture, salts, air, &c. nature has taken advantage from this circumstance, so that the filaments of the roots pump from the soil all that is offered to their suckers, and can be absorbed by them; but as some plants may live and thrive without being in contact with any earth, we ought to take it for granted, that the soil, or what exists in the soil, is not the only food of plants. Water is necessary to all organized beings, as without it no circulation of juices could be carried on; but from this necessity it can only be deduced, that water is a vehicle of the food, and by no means that it is the true nourishment of animals or vegetables—the less so, as it is an incontrovertible fact, that several plants can live without being in contact with water.—Thus the agave, cactus, aloe, cacalia, &c. live in the most dry rocks in the hottest climates, where it does not rain sometimes in the space of several months, and where the burning sun pierces all other plants, and even deprives the trees of all their leaves, and, what is extraordinary, the most part of such plants are full of juices. The nocturnal dew cannot give sufficient nourishment to such plants, as all other plants would also maintain themselves with it. But to be certain that those plants do not subsist by dew, we ought to consider only that some plants of that species may be kept alive in the hot-houses, either in pots, without being watered, or by hanging them up from the ceiling.

Why water is an ingredient necessary for all organized beings.

How the most succulent plants can live in the driest rocks.

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Figure 2. First page of Ingen-Housz 1796. Coutesy, The Bancroft Library, University of California, Berkeley, CA.

bined in some way with ‘air’. Thus, ‘dephlogisticated air’ meant ‘air’ which is free from phlogiston, i.e. does not contain the principle or element of inflammability. Priestley, who discovered production of dioxygen by plants called the gas ‘dephlogisticated air’. The Phlogiston Theory dominated interpretation of many chemical phenomena and photosynthesis research for a considerable period. When new facts seemed contradictory to the theory, ‘modified phlogiston theories’ were proposed and debated. Conant’s monograph (Conant 1950) ‘The Overthrow of the Phlogiston Theory’ summarizes the situation and its final resolution as follows:

> In retrospect, we can see that the adherents to the modified phlogiston theory were fighting a rearguard action. Before Lavoisier’s execution by the revolutionary tribunal in 1794, many chemists had come to accept his views. By the end of the century Priestley was almost alone in defending the

doctrine of phlogiston. The story of the last days of the phlogiston theory is of interest, however, in illustrating a recurring pattern in the history of science. It is often possible by adding a number of new special auxiliary postulates to a conceptual scheme to save the theory – at least temporarily. Sometimes, so modified, the conceptual scheme has a long life and is very fruitful; sometimes, as in the case of the phlogiston theory after 1785, so many new assumptions have to be added year by year that the structure collapses....The publication of Lavoisier's *Traité Élémentaire de Chimie*, with his exposition of the evidence in support of the new views and his new nomenclature, made the destruction of the phlogiston theory inevitable.

Partington's *A History of Chemistry* (Partington 1962) describes the traumatic reception of the new *antiphlogistic* theory, and notes that 'phlogistic fanatics' burnt Lavoisier in effigy in Berlin!

Thus, the history of photosynthesis research during Ingen-Housz's lifetime was befogged by the mythical phlogiston. Although there were a relatively limited number of investigators of photosynthesis at the time, there was much competition for credit of major discoveries. In the struggles for priority, Ingen-Housz was not particularly aggressive and there were frequent misattributions of his discoveries (some still persist). Priestley was one of the offenders in this connection – in his prolific writings he generally omitted reference to Ingen-Housz's previous findings (Gest 1988). Details of this aspect of Ingen-Housz's career can be found in a paper by Smit (1980), who notes: 'We have to wait until 1875 when Julius Sachs in his *Geschichte der Botanik* put the claims of Jan Ingen-Housz in their correct light.' In 1796, Ingen-Housz was still annoyed by Priestley in this connection. In IH-2 (pages 2,3), Ingen-Housz says:

> I was fortunate enough to discover the true reason, why plants did sometimes correct bad air, and sometimes made it worse, which reason was never so much as even suspected by Dr Priestley or by Scheele; and indeed if either of them had had the least suspicion of it, their known eagerness for fame would not have allowed them to keep the discovery from the public eye, and Dr Priestley would not have gone much further than Mr Scheele did; viz. to acknowledge openly, (even in his book printed 1779) that he had been mistaken, and that he was entirely ignorant of the reason why vegetables are so inconstant in their effects on the air in contact with them.

Ingen-Housz not only discovered photosynthesis, but plant respiration as well. Since CO_2 is a major product of plant respiration as well as the carbon source for autotrophic photosynthesis, many confusing observations were reported by early investigators who used different – and often not well-controlled – experimental conditions. I will not go into the many complexities of the controversies between ca. 1782 and 1796 regarding the question of how plants assimilate carbon. In his well known book on the history of botany, von Sachs (1890) refers to the German translation of IH-2 and comments:

> It appears therefore that Ingen-Housz not only discovered the assimilation of carbon and the true respiration of plants, but also kept the conditions and the meaning of the two phenomena distinct from one another. Accordingly he had a clear idea of the great distinction between the nutrition of germinating plants and of older green ones, the independence of the one, the dependence of the other, on light; and that he considered the carbon dioxide of the atmosphere to be the main if not the only source of the carbon in the plant, is shown by his remark on a foolish assertion of Hassenfratz that the carbon is taken from the earth by the roots; he (Ingen-Housz) replied that it was scarcely conceivable that a large tree should in that case find its food for hundreds of years in the same spot. There was a certain boldness in these utterances of Ingen-Housz, and a considerable confidence in his own convictions, for at that time the absolute amount of carbon dioxide in the air had not been ascertained, and the small quantity of it in proportion to the other constituents of air would certainly have deterred some persons from seeing in it the supply of the huge masses of carbon which plants accumulate in their structures.

Those interested in a blow-by-blow description of the early controversies regarding carbon asssimilation should consult the unsurpassed scholarly analysis by Nash (1952).

Ingen-Housz and the 'new chemistry'

Ingen-Housz was a careful and critical investigator and was somewhat cautious in using the 'new French chemistry' in explaining photosynthesis and other plant processes. On this point, Reed (1949) comments:

> We have, unfortunately, no definite statements concerning the influence of Lavoisier's work on Ingenhousz, but it seems justifiable to conclude that they were personally acquainted and that Ingenhousz was pretty familiar with the conclusions which Lavoisier had drawn from his careful analytical work. Lavoisier's epoch-making work, *Traité Élémentaire de la Chimie*, was not published until 1789, but his ideas had been communicated previously in notes to the Academy and in letters to prominent men. How well Ingenhousz comprehended all the discoveries of Lavoisier is not recorded. We can feel confident, however, that he realized that the nature of pure and vitiated air was concerned with the presence or absence of oxygen.

These comments are puzzling because they ignore IH-2, which Reed cites as an 'extremely rare paper'. Nash's excellent monograph (Nash 1952) details the evolution of Ingen-Housz's thinking between 1779 and 1796, and quotes extensively from the 1789 French edition of *Experiments Upon Vegetables* (Ingen-Housz 1789). It is important to note that this French edition was published the *same* year as Lavoisier's classic book. I recently had the pleasure of examining an original copy of Ingen-Housz 1789, in the Rare Book Room of the Library of Congress. This copy was given by Ingen-Housz to Thomas Jefferson, and is inscribed 'For Mr Jefferson, Ministre Plenipot. of the United States of America, from the Author.'

In the 1789 French edition, Ingen-Housz refers to the 'illustrious' and 'celebrated' Lavoisier, presents Lavoisier's new nomenclature (oxygene, carbonic acid, etc.) and his new theory of combustion, and reports Lavoisier's important contribution to elucidation of the composition of water (see McKie 1952 for an excellent account of Lavoisier's life and accomplishments). Nash (1952) summarizes Ingen-Housz's 1789 position as follows:

> By 1789 Ingen-Housz had come to look with more favor on Lavoisier's oxygen theory. He still did not accord it his unqualified acceptance; but he was at least willing to consider how the interaction of plants with the atmosphere might be construed in terms of the new system.

It is clear that in 1796 Ingen-Housz was comfortable in reinterpreting his work using the new chemical terms. Three quotes from IH-2 give examples:

> (page 3) The new light which chemistry has received in our age, affords us the means of understanding many phenomena, which we were either ignorant of, or which nobody understood anything of before. The new discoveries on the nature of water, air, salts, &c. open the door to an infinite number of and variety of new discoveries. The identity of the same principle of all acids called oxygen, which the French chemists have established, throws new light on the difference which exists in the various acids already known, and on the changes which these acids undergo.
>
> (page 14) As water itself is a composition of two airs, vital and inflammable, or oxygen and hydrogen, in which two substances, Mr Lavoisier found means to analyze water, and which analysis, as far as it regards the oxygen, I affirmed in my first volume on vegetables, to be performed by Vegetables, with the assistance of the sun even before Mr Lavoisier, as I think, published his Analysis.
>
> (pages 17/18) Besides this power of shifting carbonic acid from the air by attracting its oxygen and furnishing it with carbon, plants possess a most wonderful faculty of changing water itself into vital air, or oxygen; which I have maintained as early as 1779 (See my work on Vegetables).

Ingen-Housz's marginal comments at this point are: 'Plants possess more than one way of procuring oxygen, viz. by decomposing the air and the water itself.'

Nash (1952) gives a number of other quotations from IH-2, and there is no doubt that he was one of the few who has read an original copy of the 'misplaced' paper.

I was particularly struck by Ingen-Housz's recognition of gas (O_2, CO_2) exchange by soil 'itself' described on p.16 of IH-2.

> ...I found that the soil, even without the assistance of any plant, is incessantly employed in drawing this general and acidifying principle (i.e., oxygen) from the incumbent air, and in changing it into carbonic acid, by furnishing it with carbon, of which the ground is never deficient....

In this connection, he goes on to cite his experiments with 'good mouldy ground'. We can excuse Ingen-Housz for not realizing in 1796 that soil microorganisms were responsible for these particular observations. After all, in 1993, the 'ecological experiment' Biosphere 2 became a fiasco forcing an eight-person crew to abandon the sealed 3.15 acre terrarium because the overlooked microbial flora in the rich soil depleted O_2

in its atmosphere from 21 to 14% and simultaneously raised the CO_2 to levels that endangered the crew (Gest 1994).

Photosynthesis in a 1791 literary work

It is interesting that in IH-2, Ingen-Housz mentions an opinion of Dr Darwin, referring to him as a man of 'high reputation'. This Dr Darwin was Erasmus Darwin (1731–1802), the paternal grandfather of Charles. Erasmus was a successful physician, engineering inventor, and also made basic contributions to geology, meteorology, and upper atmospheric physics. In the sphere of biology, Darwin undertook the tremendous task of translating Linnaeus's most important works from Latin to English; in the course of this project, he added more than 100 new words to the English language. Another astonishing accomplishment was his long poem *The Botanic Garden* (1789, 1791). The latter consisted of 2000 couplets, backed by scientific notes running to some 100 000 words. He became the most famous poet of the 1790s, thought by many at the time to be the equal of Milton and Shakespeare. Richard Keynes (1995) has recently discussed Darwin's last poem 'Temple of Nature', published posthumously in 1803, and submits that 'Erasmus Darwin should be accorded an honored place in the hierarchy of the founding fathers of molecular evolution, among whom he must surely be the only poet.'

Darwin was a very prolific author, and an effective 'popularizer'. It is remarkable that in 1791, in Part I of *The Botanic Garden* (Canto IV), Darwin interpreted photosynthesis, in a footnote, as follows.

> *The enamour'd Oxygene*, l. 34. The common air of the atmosphere appears by the analysis of Dr Priestley and other philosophers to consist of about three parts of elastic fluid unfit for respiration or combustion, called azote (i.e., nitrogen) by the French school, and about one fourth of pure vital air fit for the support of animal life and of combustion, called oxygene. The principal source of the azote is probably from the decomposition of all vegetable and animal matters by putrefaction and combustion; the principal source of vital air or oxygene is perhaps from the decomposition of water by means of the sun's light. The difficulty of injecting vegetable vessels seems to shew that their perspirative pores are much less than those of animals, and that the water which constitutes their perspiration is so divided at the time of its exclusion, that by means of the sun's light it becomes decomposed, the inflammable air or hydrogene, which is one of its constituent parts, being retained to form the oil, resin, wax, honey, &c. of the vegetable economy; and the other part, which united with light or heat becomes vital air or oxygene gas, rises into the atmosphere and replenishes it with the food of life.

Darwin's many works clearly show that he was a very energetic person with wide interests, knowledge and skills, and that he had extraordinary imagination. His career and many exploits have been detailed in several books by Desmond King-Hele (1963, 1977, 1986, 1988).

A final note

At the end of our millenium, research on many aspects of photosynthesis continue unabated. During the past several decades, new techniques and discoveries have facilitated examination of biological photoenergy conversion at the molecular and sub-molecular levels. This became possible through the previous efforts of a long succession of highly gifted scientists working in diverse fields. As we concern ourselves with finer and finer details of photosynthetic processes, in both plants and bacteria, it is important to remember that our current research problems were gradually refined over a long period of time from the inspired ideas and experiments of early pioneers such as Ingen-Housz, Priestley, and Lavoisier, who wrested new and important facts from a very mysterious Nature. Ingen-Housz appreciated the great complexity of plant processes, and in the Preface to his 1779 classic (Ingen-Housz 1779) he says:

> I am far from thinking that I have discovered the whole of this salutory operation of the vegetable kingdom; but I cannot but flatter myself, that I have at least proceeded a step farther than others, and opened a new path for penetrating deeper into this mysterious labyrinth.

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