Contributions

Commentary

A History of the Ecological Sciences, Part 29: Plant Disease Studies During the 1700s

Theophrastos discussed plant diseases in the first two textbooks on botany, *History of Plants* and *Causes of Plants,* in the late 300s BC, and many subsequent botanical authors did likewise. References, quotations, and discussions of plant diseases from Theophrastos until AD1665 are in Agrios (2005:8–16), Ainsworth (1981:12–20), and Orlob (1964, 1971, 1973). Robert Hooke, in *Micrographia* (1665:121 and facing 125; Egerton 2005*a*:94), described and illustrated a parasitic rose rust (*Phragmidium mucronatum*) and a saprophytic *Mucor*. Marcello Malpighi described and illustrated various fungi in his *Anatome plantarum* (two volumes, 1675–1679); for details, see Ainsworth (1981:18, 21) and Buller (1915:5–6). Most of these accounts are rather brief and mainly in the context of discussing the host species. During the 1700s, for the first time, insects were often postulated as causes of plant diseases—sometimes rightly, sometimes wrongly (Woolman and Humphrey 1924, Orlob 1964:221–224). Insect parasites will be discussed in a later part. Here the focus is on the presumed causes and remedies for what we now identify as fungal diseases.

Joseph Pitton de Tournefort (1656–1708), the leading botanist of France (de Virville 1954:35–39, Leroy 1976, Stafleu and Cowan 1976–88, VI:412–415, Greene 1983, II:938–964, Magnin-Gonze 2004:117–118), attempted to bring order to the miscellaneous information that had accumulated, in his "Observations sur les maladies des plantes" (1705). He classified plant diseases according to whether they had internal or external causes, but since he had no new insights, nothing was gained from this exercise.

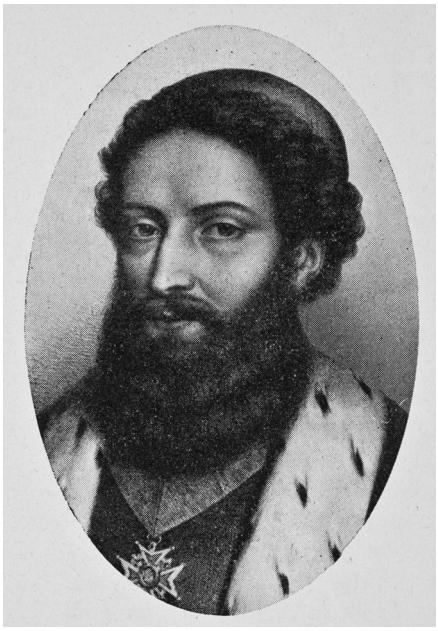

Fig. 1. Joseph Pitton de Tournefort. de Virville 1954:36.

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Fig. 2. Henri-Louis Duhamel de Monceau. de Virville 1954:97.

Fig. 3. Pier Antonio Micheli.

Two years later, however, he discussed and illustrated how to grow mushrooms for food, and these observations did have indirect relevance for understanding plant diseases, at a time when spontaneous generation was still hotly debated (Tournefort 1707, translated in Buller 1915:7, Ainsworth 1976:17)

> *According to appearance these white threads are none other than the developed seeds, or germs, of mushrooms, and all these germs were enclosed in the horse droppings in so small a volume, that one can only perceive them whatever care one takes, after they have grown out into little hairs.*

Tournefort did not isolate the fungal spores whose existence he postulated, but Jean Marchant (d.1734), at the Jardin du Roy, described and illustrated the spores of *Xylaria polymorpha* ("having some resemblance to [seeds] of vanilla, but infinitely smaller;" [Marchant 1711, translated in Ainsworth 1976:17]). Another French author, Noël Chomel, compiled a *Dictionnaire oeconomique* (1709, edition 2, 1718; English translation edited by Richard Bradley, 1725) that claimed that different crops have their own specific mildews (Ordish 1976:77).

The French botanist and chemist Henri-Louis Duhamel de Monceau (1700–1782) identified a fungal disease on the bulbs of saffron crocus (now named *Helicobasidium purpureum*) and illustrated its sclerotia on the bulbs (reproduced in Ainsworth 1981:20). His report was read to the Academie royale des Sciences in April 1728; it was "well-conceived, thorough, and conclusive, and led to his election as *adjoint chimiste* in the same year" (Eklund 1971:223). Duhamel discovered that this fungus spreads underground from one bulb to another. In his *Éléments d'agriculture* (two volumes, 1762; English edition, 1764), he also accepted insects as a cause of some plant diseases (Orlob 1964:224).

These promising French developments had parallels elsewhere. In Italy, the importation in 1711 of a bull from Hungary that turned out to be sick attracted medical attention when it reportedly infected other cattle near Venice in a plague not eliminated until 1714 (Egerton 2008*b*). This was in a country where Girolamo Fracastoro in the 1500s and Athanasius Kircher in the 1600s had already defended the contagion concept (Egerton 2004:27–28, 2005*b*:135), and several Italians revived the idea when the cattle plague struck (discussed in Part 30). One of these authors, Carlo Francesco Cogrossi (1682–1769), suggested a similarity between this cattle plague and insect and rust plagues that attack crops (Cogrossi 1714:28–31, 1953:28–31). His was the first clear argument for live contagion (Belloni 1961:12–14).

The Italian botanist Pier Antonio Micheli (1679–1737) was from the working class and had little formal education, but his passion for plants won him the support of the de' Medici family and a position in the botanical garden of his native Florence, from which he rose to the directorship (Rodolico 1974, Stafleu and Cowan 1976–1988:III, 466–488).

However, his interests went far beyond gardening. In 1718 he first grew fungi from spores (aside from the empirical techniques for growing domestic mushrooms described by Tournefort and others), but when he published his results (1729:136–139), he was met with skepticism among learned botanists. However, his experiments were described in minute detail (now in English: Buller 1915:18–23, Ainsworth 1976:84–88), and were repeatable. For example, he cut a melon in half and brushed "seeds" from *Mucor mucedo* onto the cut melon surface, then placed the half-melon in an enclosed place. In two weeks, mold had grown which resembled the mold from which he had taken spores. His *Nova plantarum genera* (1729) described some 1900 species, nearly 1400 of which were new, obtained during travels in central Europe. Since central Europe had been botanized for centuries, that seems surprising, but the new species included 900 fungi, and also lichens and mosses. Of his 108 copper plates, 73 were of fungi and lichens, including an illustration of a rust on juniper (fig. 4) His book marks the birth of mycology (Ainsworth 1976:49–53).

In England, naturalist Richard Bradley (1688?–1732) began publishing various ideas on contagion by 1720 (Egerton 2006:124–125). The idea he emphasized was that "All blights proceed from insects, and the black bunt powder is nothing but a mass of insect eggs"(Bradley 1725:325, Williamson 1955:45–50, Orlob 1964:221–222). Two contemporary physicians who also emphasized that diseases were caused by animate contagion were Englishman Benjamin Martin, *A New Theory of Consumptions* (1720) and Frenchman Jean-Baptiste Goiffon (b. 1658), *Relations et dissertation sur la peste du Gévaudan* (1722), though their focus was on human, not plant diseases (Williamson 1955:51–57, Singer 1991). Bradley's idea that insects cause plant diseases was, however, defended by a few other authors during the 1700s (Orlob 1964:221–224).

Stephen Hales, founder of plant physiology (Egerton 2008*a*), conducted the ninth experiment in his *Vegetable Staticks* (1727) on hop vines, about which he commented (1961:19)

> *...in a rainy moist state of air, without a due mixture of dry weather, too much moisture hovers about the hops, so as to hinder in a good measure the kindly perspiration of the leaves, whereby the stagnating sap corrupts, and breeds moldy fen, which often spoils vast quantities of flourishing hop-grounds.*

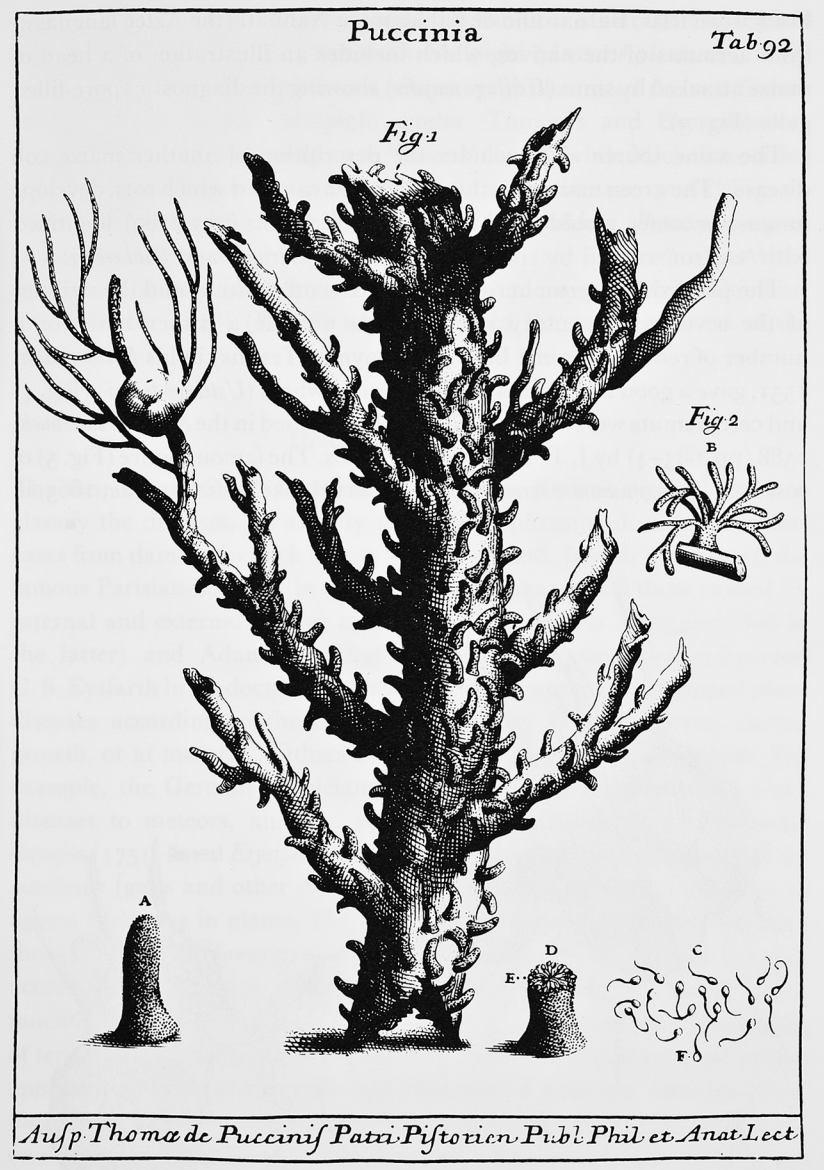

Fig. 4. A rust, *Gymnosporangium clavariiforme*, on juniper, showing teliospores (c). Micheli 1729: Plate 92.

One gets the impression from this passage that he thought hop mold (now named *Pseudoperonospora humuli*) was a physiological problem caused by unfavorable weather. Unfavorable weather was commonly considered a cause of plant disease in the 1700s (Orlob 1964:201). However, Hales' explanation of why it spreads so rapidly gives a different impression

> *Probably because the small seeds of this quick growing mold, which soon come to maturity, are blown over the whole ground: Which spreading of the seed may be the reason why some grounds are infected with fen for several years successively;* viz. *from the seeds of the last year's fen: Might it not then be advisable to burn the fenny hop-vines as soon as the hops are picked, in hopes thereby to destroy some of the seed of the mold?*

There was also speculation about contagion in plants in America. In Connecticut in 1726 the colonial legislature accepted the testimony of farmers that "the abounding of barberry bushes is thought to be very hurtful, it being by plentiful experience found that when they are in large quantities, they do occasion or at lease increase, the blast on all sorts of English grain." (quoted from Stevenson 1959:15). The legislature passed an ordinance against growing this European bush. The farmers believed this measure helped control the disease, and soon Rhode Island and Massachusetts passed similar statutes (Large 1940:123–124). In 1865 Anton de Bary showed that this conclusion was not merely folklore, but that it had a biological basis (Large 1940:131–135).

More persistently contentious was the question of spontaneous generation of life, which was commonly accepted since the time of Aristotle, and only creditably challenged since 1668 by Redi and his followers (Bulloch 1938:67–125). Redi had settled the question for visible insects, but not for microscopic life. Louis Joblot (1645–1723) was a professor of mathematics at the École Nationale des Beaux-Arts, Paris (Konarski 1895, van der Pas 1973). He wrote *Descriptions et usages de plusieurs nouveaux microscopes* (1718), in which he discussed (Chapter 15) controlled experiments he ran on hay infusions in water boiled for more than 15 minutes. He poured equal quantities of boiled infusion into two vessels, one enclosed and one left open. After several days, he found animals in the open vessel but none in the enclosed vessel. He concluded that "these animals [in the open vessel] had developed from eggs dispersed in the air" (translated in Bulloch 1938:71). Naturalists were not used to having mathematicians settle their disputes, and Englishman John Turberville Needham (1713–1781) revived the question with his own similar experiments (Bulloch 1938:72–75, Westbrook 1974, Roger 1997*a*:399–420). In 1747 he became the first Catholic priest elected a Fellow of the Royal Society of London, but he found better professional and scientific opportunities in Catholic France and Belgium. His experiments seemed to show that a heat-sterilized infusion kept enclosed at room temperature can have life arise in it (Needham 1748, partly reprinted in Brock 1961:11–12). He greatly expanded his brief article in English into a book in French (Needham 1750), and he briefly collaborated with Buffon, who believed that organic molecules exist free in nature, but that they can come together to form microorganisms (Bulloch 1938:71–72, Roger 1997*b*:146–147). Their conclusions were challenged by an Italian professor of natural history, Lazzaro Spallanzani (1729–1799), who was the most sophisticated experimentalist of the 1700s (Rostand 1951, Pietro 1979, Grmek 1991). A recent symposium (Montalenti and Rossi 1982) explored many dimensions of his achievements, including this controversy (Toellner 1981). Spallanzani repeated Needham's experiments under more rigorous conditions (Bulloch 1938:75–78, Belloni 1961:18–20, Dolman 1975).

Using more sterile procedures and prolonged heat, his infusions never developed spontaneous life (1765, English translation in Hall 1951:382–387, Brock 1961:13–16; Rook 1964:87–95). Needham was never convinced, and the controversy lingered until Louis Pasteur resolved the question in the 1860s and 1870s.

In Germany, Christian Sigismund Eysfarth wrote a doctoral dissertation (1723) on plant diseases, which he classified according to when they appeared in the life cycle—(1) at germination, (2) at vegetative growth, and (3) at fruiting—while emphasizing physiological causes (Whetzel 1918:26–27). His attempt provided little, if any, advances over Tournefort's failed endeavor of 1705. By 1750–1799, there were two approaches to the study of plant diseases: (1) the study of specific diseases to understand cause,

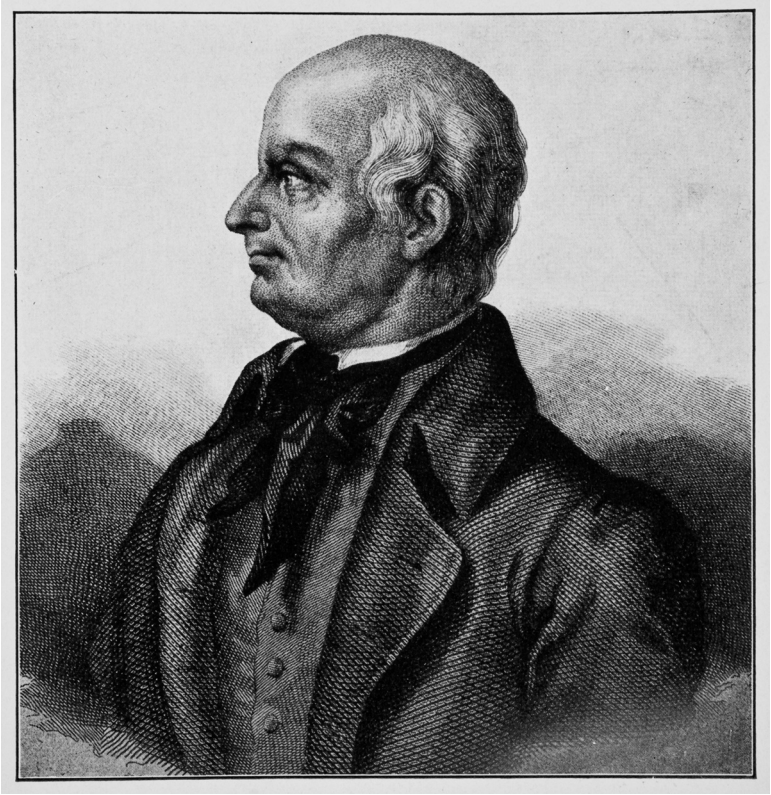

Fig. 5. Lazzaro Spallanzani. Locy 1908:83.

prevention, and cure, and (2) identification and classification of diseases. The first approach was more successful, since it is difficult to develop a useful classification until one understands what to classify. We start, therefore, with the study of specific diseases.

In 1750, the Académie Royale des Belles-Lettres, Sciences et Arts de Bordeaux offered a prize for the best dissertation on the causes and cure of blackening of wheat. An investigator lacking formal scientific training, Mathieu du Tillet (1726–1791), Director of the Mint in Troyes, France, responded. At the deadline in 1752, he could only offer the Academy preliminary results. He was invited to continue, and his *Dissertation sur la cause qui corrompt et noircit les grains de bled dans les épis* (1755) won the prize. His first chapter surveyed previous explanations, beginning with Theophrastos in antiquity; what emerged was a variety of arguments and opinions, but no consensus. His second chapter presented seven observed facts as a basis for demolishing the previous opinions. Part of the problem, he explained in Chapter 3, was that there were different diseases of wheat, which previously had not been carefully differentiated. Tillet discussed three minor and three major diseases. Duhamel had called "rust" a rust-colored powder that is found on some wheat, but Tillet decided this was not a disease, just dried sap that turns to dust (Tillet 1937:35–38). Duhamel's other minor diseases included blasted wheat, in which the head held small or no kernels, which he thought was caused by cold rains or lightning; and scalded and shriveled wheat, caused by great heat followed by excessive moisture or by insects. Tillet (1937:38–39) did not comment on blasted wheat or its cause, but he thought he had confirmed Duhamel's claim that scalded and shriveled wheat can be caused by excessive moisture followed by great heat; Tillet regretted

that Duhamel had not been specific about how insects cause scalded and shriveled wheat.

Tillet's three major diseases were aborted, smutted, and bunted wheats, and he was first to differentiate the three. Incidentally, he also discussed ergot in rye, which he concluded was caused by an insect sting, and despite his complaint about Duhamel not being specific about which insect caused scalded and shriveled wheat, he was guilty of the same neglect concerning rye ergot (Tillet 1937:48–54). His conclusion about the cause of rye ergot was possibly influenced by his early discoveries concerning wheat disease. In Chapter four he states (Tillet 1937:55–56) that he examined wheat plants with rolled leaves and found tiny black insects of the *Staphilinidae* inside the leaves. However, he never found when they entered the plant nor what harm they caused. He also found smaller red insects of the same shape which he thought were the same species at an earlier stage. He decided that the insects prevented fertilization of seeds and that this lack of fertilization caused smut (1937:60–61). This idea was consistent with Griffith Hughes, who concluded in *The Natural History of Barbados* (1750) that the smut of sugar cane was caused by little insects. On the other hand, the black powder of smut, viewed under a microscope, resembles the black powder of puffballs (*Lycoperdon*), which left Tillet uncertain (1937:66–67).

Tillet's casual observations and speculations thus far were no better than those of his predecessors. However, to resolve his uncertainty, he decided to take a wheat field 540 × 24 feet and divide it into five plots of 108 × 24 feet, and then subdivide each plot further until he had 120 subplots, which he could sew with wheat under different conditions. We have seen that Francesco Redi invented the controlled experiment, on a very small scale, in 1668 (Egerton 2005*b*:136–137), but no one had previously thought of a series of controlled experiments on such a grand scale (Large 1940:71–75, Ainsworth 1976:145–147, 1981:28–31, Ordish 1976:80–87). Tillet's *Dissertation* contains 10 pages of diagrams of all 120 subplots, showing how each differed from the others, for the growing seasons 1751–1752 and 1752–1753. These included plantings of clean seeds, seeds naturally contaminated, and seeds experimentally inoculated with bunt dust. Although his experiments seemed objective, he recognized that there were nevertheless four difficulties, such as the fact that the beds were adjacent to each other. Yet he felt that he had demonstrated (1937:127) that the cause of the bunt was the dust from diseased wheat (and not insects), and that his treatments of seed greatly reduced the effects of the contagion. In a supplement to his *Dissertation*, he also discussed his plantings in the 1753–1754 season, although without diagrams. He never determined what the black dust of bunt was. He could have used Micheli's methods of growing fungi to see if his black dust could be grown experimentally, but not being a botanist, he was unlikely to have known of Micheli's work. Tillet's experiments were repeated by four separate investigators, who confirmed his results (Goidànich 1952*b*:xxiii). Louis XV had him repeat his experiments at the Jardin du Roi, and his publication carried the royal authority. Tillet's use of large-scale controlled experiments first demonstrated that a plant disease was caused by an infectious agent, though he did not establish the agent as a parasitic fungus. In 1762 he and Duhamel collaborated on a book describing a moth that attacked stored grain.

Another example of response to a serious crop disease in a region came in 1766, when a wheat rust epidemic became widespread in Italy. This led two investigators to publish simultaneously their discoveries on rust in 1767 (though no prize was offered). The Florentine physician-naturalist Giovanni Targioni Tozzetti (1712–1783) was the son of a physician interested in botany who more or less apprenticed his son to Micheli in 1731, and in 1737, after Micheli's death, Targioni Tozzetti succeded

Fig. 6. Giovanni Targioni Tozzetti. Targioni Tozzetti 1952:frontispiece.

him as director of the Florence botanic garden (Goidànich 1952a, Rodolico 1976).

In 1734 Targioni Tozzetti obtained a doctorate in medicine at the University of Pisa, with a dissertation on medicinal plants. Although Targioni Tozzetti's treatise on diseases of wheat and oats is 139 pages long in a modern English translation, he added it as Part 5 to a treatise he had already begun—*Alimurgia, o sia Modo di render meno gravi le carestie proposto per sollievo de' poveri*—in order to publish it in 1767.

Tillet (1937:64–67) had used a microscope in the 1750s to determine that the black dust of wheat bunt resembled that of the puffball *Lycoperdon*, yet he lacked the expertise to pursue this line of research further. Targioni Tozzetti, on the other hand, had experience with microscopy, and when he had trouble seeing everything he wanted to see with one microscope, he had a whole range of alternatives available. He learned that his black stem rust (now named *Puccinia graminis*) was a "very tiny, parasitic Plant, which does not arise except between skin and skin, so to speak, of the Wheat, as do the Pellicles and Worms of the Mange of Animals" (1952:17). He studied and illustrated this species as it grew and changed and then did the same for a variety of other parasitic fungi (Fig. 7).

Although Targioni Tozzetti's treatise is a landmark—the first detailed monograph on fungal diseases of plants (Ainsworth 1976:149–151, 1981:27–28)—because of its publication as part of a larger, more general work, it received less attention than the more narrowly focused, simultaneously printed book of his countryman, Fontana.

Felice Fontana (1730–1805) had broad scientific interests but is most remembered for his contributions to animal physiology (Belloni 1972). He taught at the University of Pisa and established a science museum in Florence. His foray into phytopathology was occasioned by the rust plague that devastated the wheat crop of Northern Italy in 1766.

Being experienced in microscopy, he soon suspected that rust consists of "parasitic plants that were carried by the wind and lodged in a suitable and adapted place to feed at the expense of the grain" (Fontana 1932:17). He pointed out the similarity of some parts of the rust plant to parts of fungi described and illustrated in Micheli's *Nova plantarum genera*. He concluded that he had found two kinds of rust, red and black, and he discussed at length their structure, reproduction, and physiology. His book had a plate of illustrations, showing both the red and black rust. He established that his rusts were parasitic plants, but he lacked a technical vocabulary to describe precisely their structure. Ainsworth (1981:27) tells us that Fontana "described the macroscopic and microscopic features of both teliospores and urediniospores,"

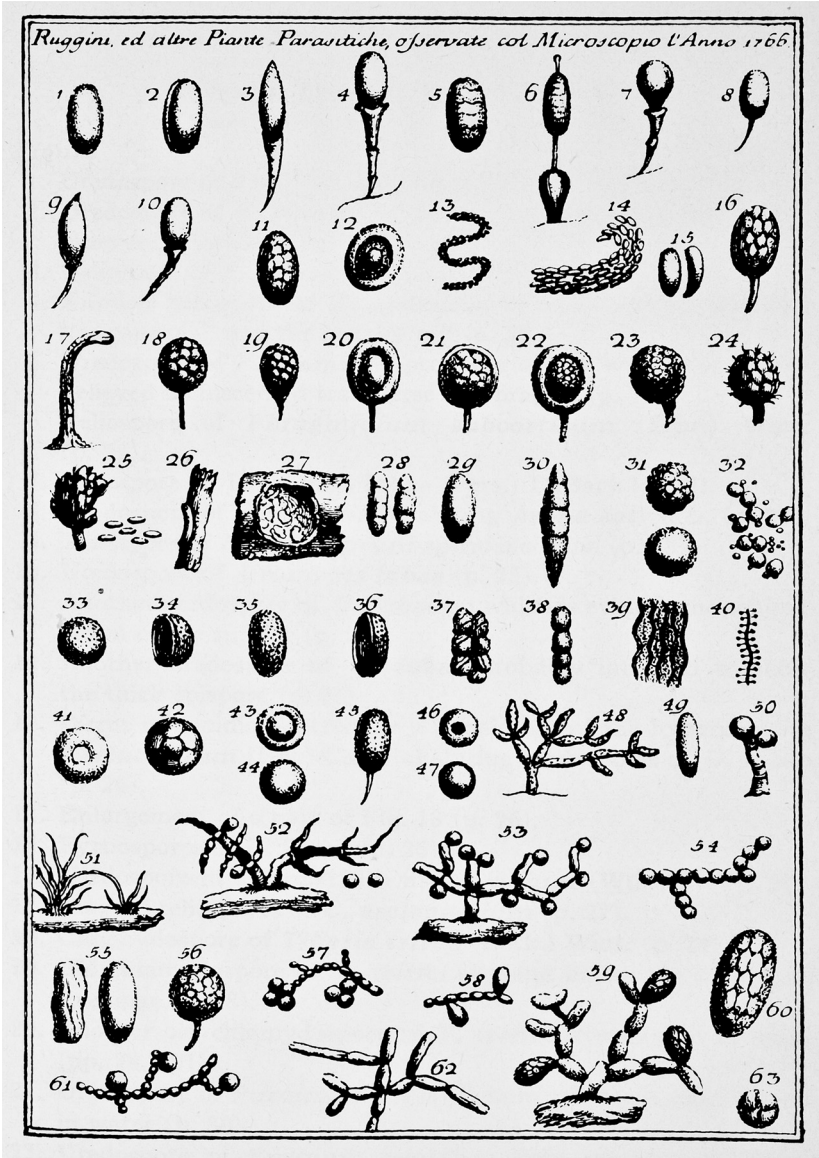

Fig. 7. Targioni Tozzetti's drawings of different stages of a variety of parasitic fungi. All 64 figures are identified by Gabriele Goidànich in Targioni Tozzetti 1952:137–139.

though he failed to name these two kinds of spores. His 1767 report was first translated into English in 1792 (Large 1940:123–124). Fontana and Targioni-Tozzetti were first to state that small parasitic plants cause plant diseases, and their conclusions were soon supported by Spallanzani (Spallanzani 1777, Denis 1993:101–102).

During the second half of the 1700s, a variety of plant disease classifications were published. Carl Linnaeus (discussed in Egerton 2007) provided five Latin names for diseases (1751, 2003:261): *Erysiphe* (mildew), *Rubigo* (rust), *Clavus* (nail or horn-like), *Ustilago* (smut), and *Nidus insectorum* (galls and other insect-caused deformations). His system at least provided a terminology that transcended

Fig. 8. Felice Fontana. Fontana 1932:frontispiece.

the various vernacular languages. In France the prominent iconoclastic naturalist Michel Adanson (1727–1806) studied plant diseases for his *Familles des plantes* (1763) and increased the list of diseases to 23 species (Lawrence 1964, Walker 1969:18, Nicolas 1970, Magnin-Gonze 2004:141–143). A German student, Johann Baptista Zallinger, wrote a doctoral dissertation on plant diseases in Latin (1773, German translation, 1779) in which he classified diseases into five classes: inflammatory, paralysis, discharges, bad constitution, and organ defects (Whetzel 1918:28–29, 1977). He thought that what we would identify as fungi were abnormal structures of plants rather than the cause of diseases. Another disease classification was by the leading entomologist of the second half of the century, Johann Christian Fabricius (1745–1808), who was Danish and had studied under Linnaeus (Tuxen 1967, Landin 1971). He taught for a while in Copenhagen, and he published his *Attempt at a Dissertation of the Diseases of Plants* in Danish (1774, English translation, 1926), which restricted his readership. However, in 1775 he moved to Kiel University, and there he published his numerous entomological publications in Latin or German. He was right in thinking a useful treatise on plant diseases was needed, but his six classes—rendering unproductive, wasting, decaying, discharging, rendering misshapen, and extraneous—would not have been much help, even if he had published in German. Although Fabricius did mention parasitic plants as a cause of disease (1926:33, 43, 59), he provided no details. He emphasized diseases caused by insects, environment, and physiological malfunctions. Joseph Jacob von Plenck of Vienna proposed a classification in *Physiologia et pathologia plantarum* (1794), which was later translated into German, French, and Italian. He accepted the contagious nature of some diseases (Parris 1968:20). His eight-part classification is quoted by Ainsworth (1981:21–22). Erasmus Darwin, in *Phytologia* (1800, Section 4), divided plant diseases into four groups: internal, external, insect, and vermin (Ainsworth 1981:23).

Agricultural disasters provided the stimulus to study plant diseases, though this was on a smaller scale than the concurrent study of animal and human diseases caused by parasites. There were substantial studies published during the 1700s indicating that a number of plant diseases are caused by parasitic fungi, but these studies did not lead to a clear understanding of the diseases. Weather, soils, and insects were also considered important factors. During the 1800s, further advances would be greatly assisted by improvements in microscopes. Even so, the germ theory of disease only became established after six decades of struggle during the 1800s.

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