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Linnaeus, smut disease and living contagion

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ABSTRACT: This paper examines the rise and fall of Carl Linnaeus's ideas on living contagion, focusing on his work with plant smut diseases. Early in his career, Linnaeus named a plant altered by anther-smut disease as a separate species, but then, probably realizing it was a diseased specimen, demoted it to a variety. He later drew direct parallels between minute insects attacking plants and infectious diseases in humans, but did not yet draw an analogy to smut diseases. After Otto von Münchhausen had sent Linnaeus the first instalment of his book *Der Hausvater* (1764), Linnaeus realized smuts were contagious. He carried out his own investigations that appeared to confirm Münchhausen's conclusion that smut spores germinated to produce living and mobile animalcules. This cemented Linnaeus's view that animalcules caused contagion in human diseases, a view which he expressed forcefully, urging further studies. However, his results were questioned and discounted by others, especially John Ellis. An analysis of correspondence between Linnaeus and other microscopists shows that it is likely Linnaeus did actually see "animalcules" emerging from cereal grains. He was unaware that smut-like symptoms in wheat could also be caused by seed-gall nematodes in the genus *Anguina*. Linnaeus himself came to doubt the connection between fungi and contagion, and did not pursue these studies further. The presumption that Linnaeus was fanciful in his observations of animalcules may partly explain why his views had only a tangential impact on the germ-theory of disease, and why his insights remain unappreciated to this day.

KEYWORDS: germ theory – Otto von Münchhausen – *Silene latifolia* – *Microbotryum* – *Ustilago* – *Anguina*.

INTRODUCTION

Carl Linnaeus (1707–1778) is recognized as the father of plant and animal systematics, and his general system of classification survives into the present, certainly modified in detail, but remarkably resilient in the face of dramatic advances based on DNA sequence data. During Linnaeus's time, there was intense debate about whether diseases were caused by humoural imbalances in the body, environmental conditions, astrologic phenomena or by living organisms (DeLacy 1999). Theories of bodily imbalances of the humours still held sway, as did the idea that disease was caused by morbific particles in the atmosphere (Keele 1974). In the early 1700s, several authors, for example Marten (1720) and Fuller (1730), had posited that living contagion ("contagium vivum") might be responsible for diseases such as smallpox or measles, but these were "an embattled minority" (DeLacy 1999).

In this paper we analyze the development of Linnaeus's ideas about the causes of diseases, emphasizing the role played by his understanding of plant and animal diseases in his conviction that contagion was caused by parasitic organisms. We focus in particular on Linnaeus's involvement with the diseases of cereals and other plants, as these played a recurring role in his thinking about contagion, and serve to define distinct periods in his life with regard to his understanding of infectious disease. Early in his career, Linnaeus gave a unique species name to a plant showing profoundly altered floral morphology as the result of anther-smut disease. We examine when and why he eventually realized this plant did not represent a distinct species, and we trace the further role of smut diseases in his eventual conviction that many diseases, including human ones, were caused by living organisms.

LINNAEUS AND ANTHER SMUT

In 1735, at the age of 27 and recently engaged to his future wife, Linnaeus set out for Holland, where the University of Harderwijk was renowned for the speed with which it awarded medical degrees.[1] There, all that was needed for a degree was a pre-written thesis in Latin and, of course, a fee. His thesis, *Hypothesis nova de febrium intermittentium causa* (A new theory on the cause of intermittent fevers[2]) (Linnaeus 1735a, 1790) was on malaria, a disease common in Europe at the time (Huden 2011), and it concluded that turbidity in the water was its likely cause.

While in Holland, he was offered a position on the estate of George Clifford III (1685–1760), a wealthy banker and an avid collector. Linnaeus's acceptance of the position was driven by his enthusiasm for the plants in the garden, as well as those preserved in the estate's large herbarium collection.[3] The catalogue that Linnaeus made of these plants, *Hortus Cliffortianus* (Linnaeus 1737), is now a milestone in the history of plant systematics because it is here that plants were first formally classified based on the number of male and female parts of the flower (Stearn 1957).

It was in *Hortus Cliffortianus* that Linnaeus described as a distinct species a plant with sexual organs affected by anther-smut disease. The characteristics of this *Cucubalus floribus hermaphroditis* were: "Flowers hermaphrodite, calyx large, globose and angular. Marriage bed bright snowy white, while in the venereal act all the sheets are seen spotted with an ash-coloured blackish powder. Calyx can be said to resemble a pig's scrotum being hairy" (Linnaeus 1737).[4] This colourful language was not atypical of Linnaeus's use of analogies between the sexual organs of animals and those of plants (Schiebinger 1993).

The ash-coloured powder and the hermaphrodite condition, plus the description of the calyx, all indicate that Linnaeus was looking at a specimen of *Silene latifolia* (White Campion) diseased with anther-smut (Figures 1).[5] When the females are infected by the anther-smut fungus, *Microbotryum violaceum* (formerly classified with the cereal smuts in the genus *Ustilago*), the parasite induces the female flowers to produce anthers containing fungal spores, so the flowers appear to be hermaphroditic (Becker 1870; Alexander *et al*. 1996). It was such a diseased hermaphrodite that Linnaeus considered to be a distinct species. White Campion normally has separate male and female plants, with the sex determined by X and Y chromosomes in a way similar to humans; healthy hermaphrodite plants are very rare mutants (Meagher 1988).

Although we could not find a diseased plant in the Clifford Herbarium (now housed at the Natural History Museum, London),[6] a plant with diseased anthers is in Linnaeus's herbarium at the Linnean Society, London (Figure 2). Linnaeus was not the first or the last to think that diseased flowers of White Campion represented a new species. Plot (1705: 149) had described a hermaphroditic plant with dark anthers, but cautiously added: "We are not so bold as to make them distinct Species, not knowing as yet whence they should be propagated." Lydia Becker (1827–1890), best known for her contributions to the women's suffrage movement, wrote

Figure 1 (left). Healthy (left) and diseased (right) flowers of *Silene latifolia* (White Campion). Note the hermaphroditic morphology of the diseased flower (Linnaeus's *Cucubalus floribus hermaphroditis*) with dark smutted anthers and a reduced and sterile, but still visible, ovary.

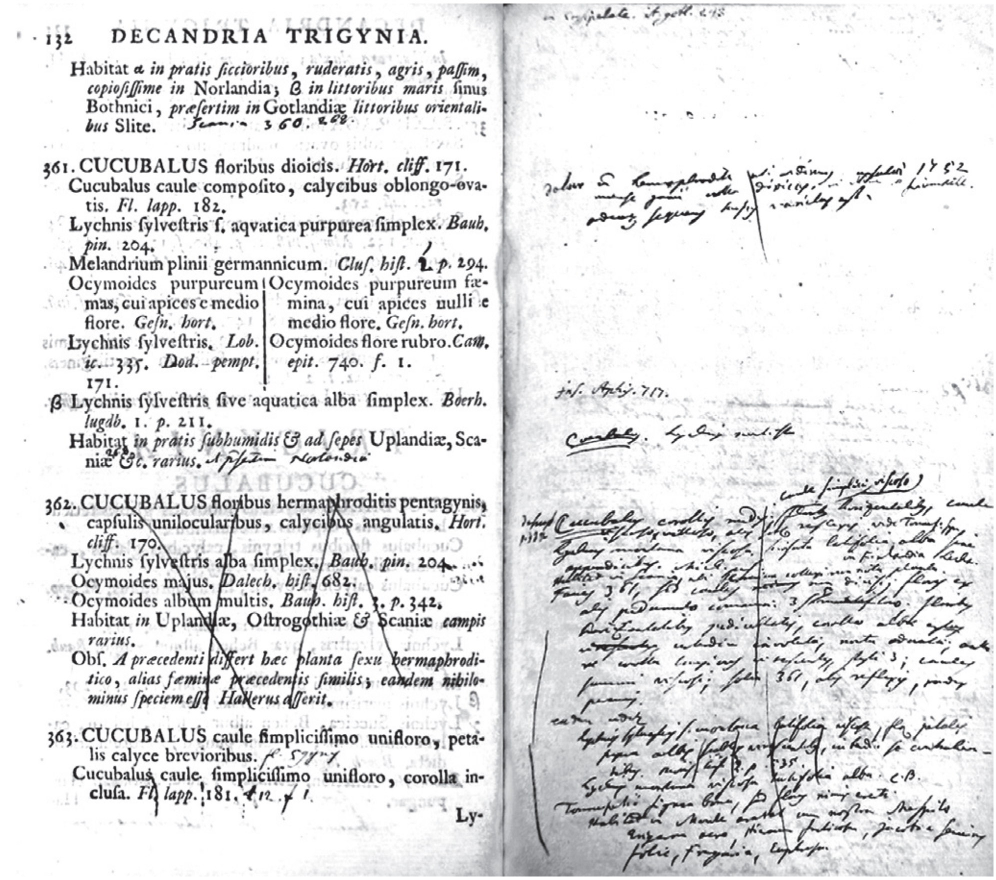
Figure 2 (right). Close-up of a diseased flower of *Silene latifolia* (*Lychnis alba*)[5] from the Linnaean herbarium (specimen 602.8, which Linnaeus annotated "Hermaphroditis dioica 6B"). The dark diseased anthers are visible, and the reduced ovary can be seen through the calyx wall. (© Reproduced by courtesy of the Linnean Society of London.)

to Charles Darwin (1809–1882) in 1853, believing she had found a hermaphrodite form of *Silene dioica* (Red Campion), but Darwin eventually realized it was a plant infected with anther-smut (Gianquitto 2013).

It is important to note that Linnaeus's decision to designate *Cucubalus floribus hermaphroditis* as a distinct species could not have been a casual one. He argued many times that nomenclatural chaos would result if every variety of a species were given a different name. In a letter to Albrecht Haller (1708–1777) in 1737,[7] he had noted (Smith 1821: 277): "If every minute difference, every trifling variation is to establish a new species, why should I delay to exhibit ten thousand such species? … I have always preferred taking two distinct species for one, … so long as I was doubtful of a clear and obvious mark of difference." Linnaeus was also aware that diseases could change a plant's appearance, declaring: "It is usually superfluous to include diseased plants … in the names of varieties" (Linnaeus 1751; Freer 2003: 261).

To understand why and when Linnaeus realized that *Cucubalus floribus hermaphroditis* might be diseased, we traced the fate of this name in Linnaeus's own and other's writings. Seven years later in *Flora Svecica*, Linnaeus (1745: 132) retained *Cucubalus floribus hermaphroditis*, but added: "Differs from the preceding one in that the plants are hermaphroditic in sex ... nevertheless Haller asserts that it is the same species" (see Figure 3). This is a reference to Haller (1742), where *Cucubalis floribus hermaphroditis* was listed as a variety. Linnaeus had a stormy relationship with Albrecht von Haller, the Swiss botanist and physician, and they often disagreed on points of classification (Hjelt 1880). Linnaeus's addition in *Flora Svecica* confirms that he was unwilling, in spite of Haller, to demote it to a variety, and that he remained confident that his *Cucubalus floribus hermaphroditis* was a distinct species. His classification was also accepted by other botanists.[8]

With new specimens coming into his hands daily, Linnaeus made extensive notes on his own texts (Savage 1948), using copies with interleaved blank pages to allow space for notes (Charmantier and Müller-Wille 2012). His interleaved copy of *Flora Svecica*[9]



132 DECANDRIA TRIGYNIA.

Habitat α *in pratis ficcioribus, ruderatis, agris, passim, copiosissime in* Norlandia; β *in littoribus maris* sinus Bothnici, *præsertim in* Gotlandiæ *littoribus orientalibus* Slite.

361. CUCUBALUS floribus dioicis. *Hort. cliff.* 171.
Cucubalus caule composito, calycibus oblongo-ovatis. *Fl. lapp.* 182.
Lychnis sylvestris f. aqvatica purpurea simplex. *Bauh. pin.* 204.
Melandrium plinii germannicum. *Clus. hist.* 1. *p.* 294.

Ocymoides purpureum mas, cui apices e medio flore. *Gesn. hort.*	Ocymoides purpureum fæmina, cui apices nulli e medio flore. *Gesn. hort.*
Lychnis sylvestris. *Lob. ic.* 335. *Dod. pempt.* 171.	Ocymoides flore rubro. *Cam. epit.* 740. *f.* 1.

β Lychnis sylvestris sive aquatica alba simplex. *Boerh. lugdb.* 1. *p.* 211.
Habitat *in pratis subhumidis & ad sepes* Uplandiæ, Scaniæ *&c. rarius.*

362. CUCUBALUS floribus hermaphroditis pentagynis, capsulis unilocularibus, calycibus angulatis. *Hort. cliff.* 170.
Lychnis sylvestris alba simplex. *Bauh. pin.* 204.
Ocymoides majus. *Dalech. hist.* 682.
Ocymoides album multis. *Bauh. hist.* 3. *p.* 342.
Habitat *in* Uplandiæ, Ostrogothiæ & Scaniæ *campis rarius.*
Obs. *A præcedenti differt hæc planta sexu hermaphroditico, alias fæminæ præcedentis similis; eandem nihilominus speciem esse Hallerus asserit.*

363. CUCUBALUS caule simplicissimo unifloro, petalis calyce brevioribus.
Cucubalus caule simplicissimo unifloro, corolla inclusa. *Fl. lapp.* 181.

Ly-

Figure 3. Linnaeus's interleaved copy of *Flora Svecica*. *Cucubalis floribus hermaphroditis* is boldly crossed out and annotations added on the right-hand interleaved page (© Linnean Society of London).

provided us with a time and place of Linnaeus's realization that he had made an error. In this copy, the printed entry for *Cucubalus floribus hermaphroditis* has been boldly crossed out (Figure 3), and in the upper half of the opposite page Linnaeus noted: "in Uppsala 1752 near Jumkihl" (Jumkil, a town about 15 kilometres northwest of Uppsala).[10] Correspondingly, in the subsequent second edition of the *Flora Svecica* (Linnaeus 1755: 156), *Cucubalus floribus hermaphroditis* was demoted to a variety of *Lychnis floribus dioicis* with the remark: "The dioecious form is common and the hermaphrodite rare … In 1752, I examined and proved their existence beyond doubt near Jumkihl, accompanied by more than a hundred young botanists."[11]

While it is clear that in 1752 Linnaeus re-classified *Cucubalis floribus hermaphroditis* as a variety, it is not immediately obvious how he came to this conclusion. Did he simply think it was a hermaphrodite variant growing among individuals with separate sexes, or did he realize it was diseased with a "blackish powder"? Was Linnaeus familiar with smut diseases, and, if so, was he aware that they might be contagious? Smut diseases of cereals were well known before the Linnaean era (Egerton 2008). Gerard (1597) pictured "burnt or smootie corne",[12] and Bauhin *et al*. (1650) devoted a page to *Ustilago*, copying Gerard's illustrations.

Contagion in smut had also been noted by Worlidge (1669): "The sowing of Wheat that is mixed with Smut, doth generally produce a Smutty Crop."[13] Smuts were also well known to Linnaeus, as just a year before his discovery of the diseased hermaphrodites, he included them in his list of plant diseases in *Philosophia botanica*: "*Ustilago*, when the fruits produce black powder instead of seeds" (Linnaeus 1751; Freer 2003: 261). Among these he listed the smuts of barley and oats.

Near this time, in 1751, Linnaeus had also been alerted to smut diseases by Otto von Münchhausen (1716–1774), a German agriculturalist and landowner (Seedorf 1906), who wrote to him that over 200 experiments on *Ustilago frumento* had shown him that the smut consisted of the eggs of "insects" (small organisms) that emerge when the "seeds" (spores) become wet.[14] Münchhausen continued to write to Linnaeus about smut diseases, reasserting that "all experiments confirm that Ustilago is caused by insects", and he repeated this in several subsequent letters.[15] It is puzzling that in seven extant letters from Linnaeus to Münchhausen during this period, some of which were direct replies, none commented on Münchhausen's observations. This is in strong contrast to their correspondence 15 years later (as discussed below), when Linnaeus responded enthusiastically and glowingly to Münchhausen's results after receiving his book *Der Hausvater*.

The first person to call attention to Linnaeus's mis-classification of the diseased plant was the French naturalist Jean Baptiste Aymen (1729–1784) in a paper on smut diseases in cereals (Aymen 1760). There he added, in a footnote on *Lychnis* (as *Cucubalis floribus hermaphroditis* had been renamed by Linnaeus (1753)) that: "Mr. Linnaeus in his Hort. Cliff. 170 had reported an observation on this plant in which he had seen females all covered with the fecundating dust. I positively believe that this great botanist had seen flowers attacked by smut."[16] Aymen could not have passed this information to Linnaeus before 1752, because based on the salutations it is clear that their correspondence did not start till 1753.[17]

It is difficult to think that Linnaeus would not have realized that the *Cucubalus floribus hermaphroditis* he had discovered in 1752 had smutted flowers; the black powder would have been all too obvious. However, his correspondence at that time suggests he was not particularly interested in smut diseases, was unaware that they were contagious, and simply treated them as a nuisance in his classifications. This is consistent with his lack of interest in Münchhausen's observations at that time. It is also plausible that Linnaeus was actually embarrassed by his mis-classification and did not want to draw attention to the fact that he had named a diseased plant as a new species. This notion is supported by evidence that Münchhausen's letters during this period (1751–1754) did actually make some impression on Linnaeus. Years later, the correspondence was recalled in Roos's (1767) dissertation, *Mundum invisibilem*:[18] "This highly distinguished Man [Münchhausen] wrote to Our Lord President [Linnaeus] a decade before, that he had found that *Ustilago Hordei* consisted of living animalcules."[19] By many accounts (Lindroth 1983, 1996), Linnaeus was a rather vain and arrogant person: "even with advancing age, [his] need for praise, as well as self-confidence, was intense" (Broberg 2012: 14). Not to admit the error with *Cucubalis floribus hermaphroditis* would have been well within the bounds of his personality.

His note in the second edition of *Flora Svecica* (Linnaeus 1755: 157) that he had seen the hermaphrodite in the presence of a hundred other botanists is also noteworthy, because such detailed and explicit evidence for his taxonomic decisions is rare in his systematic work. Indeed, it suggests that the event was very memorable for him. But if so, why then demote the hermaphrodite to a variety rather than hail it as a rare species that he had truly discovered? It is indeed likely that he did not want to acknowledge his failure to recognize a diseased plant.

His interaction with Aymen is also revealing in this regard. In 1753, Aymen wrote to Linnaeus asking if he knew anything about the smut of wheat. Unfortunately, Linnaeus's reply has not been traced.[20] However, in 1755 in their last extant letter, Aymen gave information about the control of smut: "With Ustilago, ergot of rye, and carbuncled wheat, it is best to prepare the seeds in lime solution."[21] If Linnaeus had mentioned his observations from Jumkil, Aymen would surely have attributed the realization about *Cucubalis floribus hermaphroditis* to Linnaeus directly rather than pointing it out as an error by "this great botanist" (Aymen 1760).

What is more certain is that for the rest of Linnaeus's career, there is a complete absence of any mention of smut on *Cucubalis floribus hermaphroditis* (or on *Lychnis dioica*, which was the binomial that Linnaeus (1753) assigned to it). Even in the twelfth edition of *Systema naturae* (Linnaeus 1766–1767), when smut diseases were classified for the first time, there is no reference to diseased *Lychnis*.

LINNAEUS AND CONTAGION

Linnaeus, as a physician, must have been aware of contagion, but his conviction that contagion might be caused by living organisms grew as much out of his studies with plants and animals as from his experiences as a doctor. In 1748, a dissertation on tapeworms (*Cestoda*) by one of his students drew parallels between human parasites and other harmful animalcules and insects (Dubois 1748); the dissertations of Linnaeus's students were usually elaborations of Linneaus's own ideas, or even transcriptions of his lectures or dictations that reflected his opinions (Stearn 1957). A little later, in a paper on damage to cereals caused by insect pests, Linnaeus (1750: 188–189) himself posited these parallels explicitly:

> If we only thought about it, we would find that in nature it is the smallest things that have the greatest effects. … Perhaps invisible worms have carried the cattle-plague among all the cattle of Europe; perhaps smallpox, measles, dysentery, French disease, even plague itself are caused by the smallest worms.

His growing interest in contagion was also reflected in further dissertations by his students. Three dissertations in 1752, the same year Linnaeus reclassified the diseased *Cucubalis floribus hermaphroditis*, specifically addressed insects damaging plants. *Hospita insectorum flora* (Forsskål 1752) listed aphids, caterpillars, scale insects, mites and weevils; *Miracula insectorum* (Avelin 1752) described insects causing galls; and *Noxa insectorum* (Baeckner 1752) considered insects that were detrimental to agriculture. The parallels with human diseases were ever-present. Baeckner listed fleas, lice, mites, bed-bugs, horse-flies and mosquitoes, adding (Brand 1781: 379):

> I entertain no very great doubt, but rather propose it as a probable conjecture, that the Dysentery, the Venereal Distemper, the Small Pox, Spotted Fever, Plague and all those distempers which are called contagious, produce Exanthemata, and make such havoc in the human species are derived from different species of Acari [which then were included in insects].

The most direct elaboration of Linnaeus's ideas on disease appeared only a few years later in a dissertation on *Exanthemata viva* (Living rashes) (Nyander 1757; DeLacy and Cain 1995). This argued that there was a continuum between diseases caused by parasites that can be seen and those that are too small to be seen. It also rejected spontaneous generation (specifically, that processes such as putrefaction produce organic life and disease) on the grounds that when a particular species reproduces, it always gives rise to individuals of the same species. Mites, insects and worms were posited as causes of a wide range of ailments, including the horrifying disease elephantiasis and scabies (both correct inferences). Correspondingly, minute animalcules were speculated to cause whooping cough, smallpox, measles, plague, syphilis and dysentery. Another thesis, *Genera morborum* (Schröder 1759), was a classification of diseases, with the Exanthematici (the rash-causing fevers) being the first class. Within this, the first order Contagiosi consisted of six "species", including pestis (plague), variola (smallpox), rubeola (measles), petechia (spotted rashes) and syphilis. When Linnaeus (1763) republished it as a book under his own name (Egdahl 1907), he added that these *Exanthemata* resulted from "living moving and reproducing things".

SMUT DISEASES COME TO LIFE AGAIN

Smut diseases suddenly reappeared in Linnaeus's letters in 1766, when he responded with unbridled enthusiasm to Münchhausen's (1764, 1765, 1766a, 1766b) studies on smut diseases that had been published in a series of volumes under the title *Der Hausvater*: "Every day I read it and re-read it without being able to stop, up to two or three times."[22] Linnaeus also described his own investigations**:**

> I have put the black dust of Ustilago in naturally tepid water, where the dust driving out living animalcules brought me the greatest joy, and my eyes cannot be sufficiently satisfied by this delightful spectacle. I will briefly give a dissertation[23] about this amazing finding of yours and I will invite as many people I can, to pursue this argument further; and there is no doubt that the cause of contagious diseases becomes clearer through this.

So great was his excitement that in the course of a month Linnaeus wrote at least five letters publicizing his and Münchhausen's observations.[24] In one to the Royal Swedish Academy in October 1766, he exclaimed: "Who would have believed it, unless he had seen it?"[25]

It is especially striking that the accounts in *Der Hausvater* of smut and fungal spores germinating into animalcules add relatively little beyond what Münchhausen had already written in his 1751 letter to Linnaeus.[14] Clearly, Linnaeus was now excited by what had barely caught his attention 15 years previously (or that may have even raised a subject he wanted to avoid).

Two factors might have contributed to Linnaeus's renewed enthusiasm. First was his increased interest in the causal agents of disease. On receiving *Der Hausvater*, Linnaeus realized there was a parallel between smut diseases of cereals and infectious disease in humans. Indeed, Münchhausen was explicit about these parallels, writing: "scabies in man clearly is caused by a small insect; and one can compare this to the diseases in cereals" (Münchhausen 1766a: preface: 24). Second, Linnaeus had long been intrigued by the possibility that there might be organisms at the boundary between plants and animals. The discovery of regeneration in *Hydra* by Abraham Trembley (1710–1784) in the 1740s, and the controversies surrounding the nature of corals and bryozoans had led him into a long correspondence with John Ellis (1710–1776), the authority of the day on these animals (Groner and Cornelius 1996). Linnaeus never quite overcame his first excitement that these small marine organisms might be clues to the nature of plant versus animal life, and persisted in this view by placing them in the class Zoophyta even after Ellis convincingly argued they were true animals, producing stalks just as molluscs build shells (Osorio 2007). For Linnaeus therefore, Münchhausen's results revived the possibility that he might have been correct after all, and that the searched-for continuum between the plant and animal kingdoms might be the fungi. It was therefore Münchhausen's book, rather than re-finding *Cucubalis floribus hermaphroditis*, that probably was the "eureka moment" for Linnaeus. In none of his writings before his 1766 letter to Münchhausen was there mention of parallels between smut diseases and human diseases.[26]

Much of Linnaeus's excitement was encapsulated in a 1767 thesis, *Mundum invisibilem* (The invisible world: see Antonovics and Kritzinger 2016), by his student Johan Carl Roos (1745–1828). The first part of the thesis highlighted many discoveries made by use of the microscope, such as the nature of corals and sponges, and the intricate sculpturing of a leaf surface. There was discussion about the lack of a clear separation of the animal and vegetable kingdoms, and Linnaeus was praised for solving the problem by creating the class Zoophyta. The second part of the thesis was "about more obscure things", and immediately praised the discoveries by Münchhausen of smut fungi producing animalcules. After describing Münchhausen's observations, Roos boldly added: "Truly this is contagion in the plant kingdom." From there, the extrapolation to human diseases was direct: "This argument will also lead doctors to the cause of exanthematic and contagious fevers. … He who has considered that only one small part of ustilago flour is multiplied through all the ears of that same Wheat or Barley plant will find a considerable analogy" (Antonovics and Kritzinger 2016: 376).

DOUBTS EMERGE

Doubts about Linnaeus's observations soon came from John Ellis, one of the leading microscopists of the day, who had corresponded with Linnaeus for nearly 20 years. Ellis wrote to Linnaeus in December 1766, saying that Peter Collinson (1694–1768), an avid botanist who also financed the importation of seeds from the Americas, had just showed him a letter he had received from Linnaeus about fungi producing animals "swimming about like fish".[27] Ellis then asked for more information, adding perhaps by way of flattery, "if you have examined the seeds of them yourself, and found them to be little animals, I should believe it." Linnaeus replied on 1 January 1767 (Smith 1821: 194–195):

> With regard to Fungi, you may pick up, in most barns or stacks of corn, spikes of wheat or barley, full of black powder, which we call Ustilago, or smut. Shake out some of this powder, and put it into tepid water, about the warmth of a pond in summer, for three or four days. This water, though pellucid, when examined in a concave glass under your own microscope, will be found to contain thousands of little worms. These ought first to be observed to prevent ocular deception. In mold, Mucor, you will find the same, but not so easily as in the larger Fungi. In the course of from 8 to 14 days, the water has been kept up to the same temperature, you may observe how these minute worm-like bodies become fixed, one after the other, and acquire roots. I have just printed a dissertation on the Invisible World, which shall be sent to you by the first opportunity. These chaotic worms are nearly akin to the last species of animals which I have placed in my Systema under the genus Chaos.

Ellis replied later that summer that he had not yet been able to experiment with smut fungi, but spores of field mushrooms, *Agaricus*, "have no animal life of their own, and are only moved about by the *animalcula infusoria*" (Smith 1821: 213).[28] Linnaeus begged Ellis to "lend me your lynx-like eyes [to see] whether these bodies do not change to plants of Mucor", adding: "Having once discovered the little worms in the Ustilago, by the help of the microscope, I can now see them with my naked eyes, though less distinctly: and I showed them a fortnight ago to some of my pupils" (Smith 1821: 215).[29] On 30 October 1767, after Ellis again asked Linnaeus for smut samples, Linnaeus replied: "I have been seeking for branded spikes of corn with all diligence, but in vain, the wheat being all thrashed out long ago. If I live, I will send you some next summer" (Smith 1821: 220).[30] Their discussion of smut fungi ended later that year,[31] and subsequently Ellis never replicated Linnaeus's experiments. However, Linnaeus was sufficiently chastened by Ellis's doubts that in the later *Amoenitates* version of Roos's dissertation (Roos 1769), he added a further point for discussion, namely: "Are Animalcula infusoria disseminated out of the Seeds of Mould?" (Antonovics and Kritzinger 2016: 382). Ellis went further, openly publishing a letter he had first written in 1771, describing his strong efforts over several years "to prevent the growth of an absurd, unnatural doctrine" that had captured "even the celebrated Linnaeus" (Ellis 1773: 316). There is evidence that Linnaeus himself initially had doubts about Münchhausen's claims, because he received the first edition of *Der Hausvater* fully a year before he expressed his enthusiasm for it in October 1766.[32] The most likely explanation for the delay is that Linnaeus had read *Der Hausvater* and decided to carry out his own investigations before replying.

It is ironic, given the potential implications for the germ theory of disease, that Linnaeus and Münchhausen may actually have been at least partly correct when they observed animalcules emerging from smutted grains. Wheat can have several superficially similar diseases that result in blackening of the grains, and one of them, wheat seed-gall, is caused by the roundworm or nematode *Anguina tritici* (Bauer 1823). Its symptoms and life-cycle closely resemble those of the fungi that cause smut: the grains are blackened, and when they are crushed and wetted, juvenile eel-worms emerge from a dormant, desiccated state and infect young healthy plants; they are just visible to the naked eye "moving and racing about like fish" (Roos 1769).

These nematodes were first observed by John Turberville Needham (1713–1781), and his descriptions (Needham 1743) and drawings (Needham 1745) (Figure 4) leave little doubt that he was observing seed-gall nematodes, a fact also recognized by professional nematologists (Hemming 1945). There was incredulity about Needham's discoveries among the intellectuals of the day (Roe 1983, 1985). Voltaire (1694–1778) labelled Needham an "eelmonger": "You had made a small reputation for yourself among atheists by having created eels from flour, and from that you have concluded that if flour produces eels, all animals starting with man could be born … from a lump of earth" (Mesler and Cleaves 2015: 66). Voltaire also satirized Needham in a play, where the "gallant president" of the Berlin Academy of Sciences served the ladies "a superb dish composed of a plate of eels … formed immediately from grains of germinated wheat" (Roe 1983: 181). Even Münchhausen had been disbelieving when writing to Linnaeus in 1751 about *Ustilago*: he posited that Needham's eels came from rotting material ("ex corruptione").[33]

That Linnaeus actually saw seed-gall nematodes is not merely speculative, but is supported by tracing his correspondence. On 13 May 1762, Daniel Solander (1733–1782), a former student of Linnaeus then living in London, wrote to him about how he and Ellis had amused themselves with microscopic observations of blackened wheat grains which, when wetted, exhibited the properties of animals.[34] The wheat grains had come to Solander from Henry Baker (1698–1774), a microscopist who had decided to check Needham's findings, having obtained samples from Needham himself. Baker (1753: 252–253) wrote: "In … August 1743, a small Parcel of *blighted Wheat* was sent by Mr. *Needham* to *Martin Folkes*, Esq; President of the Royal Society, … which Parcel the President was pleased to give me, desiring I would examine it carefully." To Baker's surprise, he confirmed Needham's results, and also produced drawings of "eels" emerging from "blighted" wheat (Baker 1753: plate 10). Solander then sent

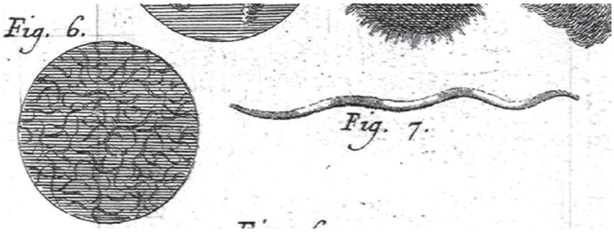


Figure 4. Needham's illustration (1750: plate V) of the wheat nematode. His caption read (translated from French): "In figure 6 one sees a drop of water full of small eels which are found in wheat spoilt by smut ("nielle"). Figure 7 is one of the eels from this spoilt wheat, seen with the lens that has the greatest magnification." No scale was given, but the nematodes of *Anguina tritici* at this stage are just under 1mm long.

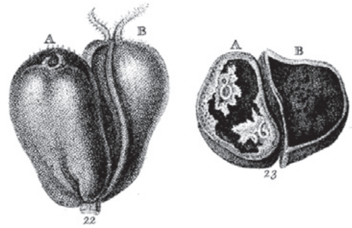


Figure 5. Drawing of a wheat grain (Bauer 1823) infected with both nematodes and *Tilletia*. The nematode that is visible in the section 23A is a mature adult; the young nematodes are in the white area and the black areas are filled with *Tilletia* spores (magnification ×10).

Linnaeus some of Baker's (Needham's) samples. These presumably would have survived, because the nematodes inside a dried seed-gall can remain viable for many years. Whether Baker's blighted wheat reached Linnaeus is not known, but it is probable that it did, and that Linnaeus actually looked at the same samples of blighted wheat that Needham had originally studied. This is also consistent with Linnaeus's repeated description of "worms" visible "with his naked eye", and with him not having another source of material to send to Ellis. Moreover, the same ear of wheat or even single grains can be infected with both smut and eel-worm (Figure 5), so Linnaeus may well have seen both.[35] A recent re-creation of Linnaeus's observations, using Linnaeus's own microscope (Nyman and Nilsson 2009), assumed he had been looking at barley smut (*Ustilago hordeum*), not at wheat gall nematodes. Of course, they came to the conclusion that all he had seen were contaminating infusoria. So it was a lack of knowledge of systematics of the micro-organisms causing smut and smut-like diseases, a systematics that Linnaeus was himself trying to initiate, that in large measure contributed to doubts about his observations.[36]

PERSPECTIVE

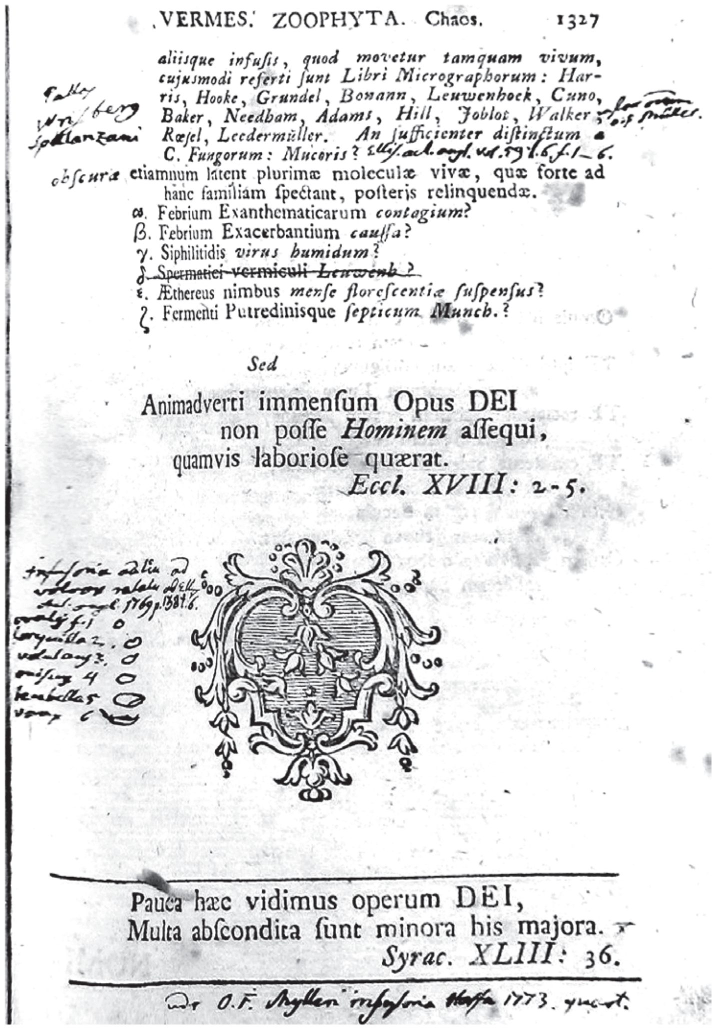
The first edition of Linnaeus's *Systema naturae* (1735b) was a synopsis of a mere eleven pages. By 1767, the twelfth edition had expanded to 1,327 pages (Linnaeus 1766–1777). On the two final pages of this edition (Linnaeus 1777: 1326–1327), for the first time in the history of biology, disease-causing micro-organisms were given binomial names (Ratcliff 2009). They were placed in the kingdom Animalia, class Vermes, order Zoophyta and in the genus *Chaos*.[37] This genus included both the smut fungi, *C. ustilago*, and organisms causing human disease, *C. obscurae*. The latter included the living rashes ("Febrium Exanthematicarum *contagium* ?"), the exacerbated fevers ("Febrium Exacerbantium *caussa* ?"), syphilis ("Siphilitidis *virus humidum* ?"), and particles suspended in the air (we could say germs) as well as fermentations (Figure 6).[38] They were identified by Greek letters, as was usual with Linnaeus for varieties, and each was followed by a question mark. The smuts were described as destroying the grains of barley, wheat, various grasses, and other plants such as species of *Scorzonera* (salsify) and *Tragopogon* (goatsbeard). Anther-smut on *Silene* (or *Lychnis* as it was then known) was not included, and no reference was made to Aymen.

From Linnaeus's annotated version of the twelfth edition[39] it is evident that he planned a thirteenth edition; however it was never published (see below). In the annotated twelfth edition, disease causing organisms remain, and Linnaeus has added "infusoria", with drawings of their different morphologies copied from Ellis (1769), plus a reference to Müller's (1773) work on this subject. However, Linnaeus did not continue any work on micro-organisms. During this period, he was heavily engaged in what he saw as his next major work, *Clavis medicinae duplex* (Linnaeus 1766). In it Linnaeus tried to set out a classification of the major diseases co-ordinated with a classification of the plants that could cure those diseases (Hansen 2012). It was focused on dietetics, and therefore familiar territory for him compared to the uncertain world of microscopy and animalcules. Although no subsequent edition of *Clavis medicinae* was published, Linnaeus continued to make extensive notes in preparation for a revised edition. Correspondingly, of the 37 dissertations produced by his students after *Mundum invisibilem*, by far the majority were about medicinal plants and dietetics, and none ever returned to the invisible world.[40]

In contrast to his botanical students, who often became passionate scholarly disciples (Hansen 2007–2011), the students with dissertations on contagious disease did not pursue the subject, and we know little about them (Olsen 1997). Johan Nyander, author of *Exanthemata viva*, published no other text (DeLacy 1999). Johan Roos's *Mundum invisibilem* was for an intermediate degree. His subsequent medical dissertation was on lumbago (Roos 1775) under Jonas Sidrén (1723–1799), who was himself a student of Linnaeus (Sidrén 1750). Sidrén became a professor of anatomy and medicine in Uppsala and supervised a large number of theses on medical subjects, including one on cholera (Salberg 1768), but we do not know of an analysis of his contributions to medicine. Johan Schröder, author of *Genera morborum*, became a health officer in Göteborg (Fries 1907: 84, footnote 2). There clearly was no long-lasting legacy.

Among Linnaeus's contemporaries, most reactions to the assertion of "contagium vivum" were cautionary. Richard Pulteney (1730–1801), a physician and admirer of Linnaeus, in English summaries of the dissertations, described *Exanthemata viva* (Nyander 1757) as "ingenious", and "well worthy of attention of all those wishing to become acquainted with the doctrine that it favours" (Pulteney 1781: 298). He was more dismissive of *Mundum invisibilem* (Roos 1767). After pointing out that the thesis proffered suggestions on the control of smut in crops, he concluded: "The author descants on exanthematic animalcula … candidly confessing however, the difficulties that occur, and concluding with a string of doubts, proposed by way of queries, relating to this abstruse point" (Pulteney 1781: 368).

Although, as noted above, a planned thirteenth edition of *Systema naturae* was never produced by Linnaeus,[41] an enlarged so-named thirteenth edition was published after his death by Johann Friedrich Gmelin (1748–1804), with Linnaeus still as the stated author (Gmelin 1788). Here, and in subsequent Gmelin editions produced up until 1793 (Hopkinson 1907), the last two pages of the twelfth edition that had included the genus *Chaos* were removed. We can only speculate that Gmelin thought these sections reflected badly on Linnaeus or that they were wrong. The last two pages of the twelfth edition of *Systema naturae* were, in many respects, inconsistent with his principles of classification, and this would have done Linnaeus no favours. For example, under *Chaos obscurae*, human sperm were given a separate name – "Spermatici vermiculi" – attributed to Leeuwenhoek, and even though some like Lazzaro Spallanzani (1729–1799) thought they were parasites of testes, by that time Linnaeus was convinced that sperm were responsible for activating the egg (Farley 1982). Other aspects must have seemed incongruent even in Linnaeus's time. The spores of various mushrooms and



.VERMES. ZOOPHYTA. Chaos. 1327

aliisque infusis, quod movetur tamquam vivum, cujusmodi referti sunt Libri Micrographorum: Harris, Hooke, Grundel, Bonann, Leuwenhoek, Cuno, Baker, Needham, Adams, Hill, Joblot, Walker, Rœsel, Ledermüller. An sufficienter distinctum a C. Fungorum: Mucoris?

obscura etiamnum latent plurimæ moleculæ vivæ, quæ forte ad hanc familiam spectant, posteris relinquendæ.

α. Febrium Exanthematicarum *contagium?*
β. Febrium Exacerbantium *caussa?*
γ. Siphilitidis *virus humidum?*
δ. ~~Spermatici vermiculi *Leuwenh.*~~?
ε. Æthereus nimbus *mense florescentiæ suspensus?*
ζ. Fermenti Putredinisque *septicum Munch.?*

Sed

Animadverti immensum Opus DEI
non posse *Hominem* assequi,
quamvis laboriose quærat.
Eccl. XVIII: 2-5.

Pauca hæc vidimus operum DEI,
Multa abscondita sunt minora his majora.
Syrac. XLIII: 36.

Figure 6. Linnaeus's annotations on the last page of his own copy of the twelfth edition of *Systema naturae* (1777) (© Linnean Society of London).

moulds are listed under *C. Fungorum*, even though these same taxa appear under Fungi elsewhere in *Systema naturae*. Ratcliff (2009) has pointed out other ways in which *Chaos* departed from Linnaean norms: the genus was not defined by characters but by negatives (absence of limbs and sense organs), the binomial names did not designate single species but several species, and there was no attempt to synonymize Linnaeus's names with those used by previous authors. Clearly, Linnaeus's thoughts were also somewhat chaotic, which he probably realized. For example, in his annotated version in preparation for the thirteenth edition, "Spermatici vermiculi" was crossed out (Figure 6); he must have known that human sperm should not be classified as a separate species.

Assessing the long-term impact of Linnaeus's ideas on living contagion would require a more thorough study than is possible here, and the evidence we do have is conflicting.

DeLacy and Cain (1995) have argued that Linnaeus's ideas may indeed have hastened the acceptance of contagionism. They mention that John Pringle (1707–1782), Physician-General to the British Army, included extracts from *Exanthemata viva* in his *Diseases of the army* (Pringle 1764: 265). Pringle had a broad range of friends and influences, and this book "marked an important moment in the history of British disease theory" (DeLacy and Cain 1995: 172). Further tangible evidence, not mentioned by DeLacy and Cain, comes from the writings of Henry Holland (1788–1873), Darwin's personal doctor and eventually physician to Queen Victoria (Holland 1872). In his *Medical notes and reflections* (Holland 1839), the final chapter, "On the hypothesis of insect life as a cause of disease", refers directly to *Exanthemata viva* and *Mundum invisibilem*. His arguments for micro-organisms causing disease are uncannily, even suspiciously, Linnaean, reiterating the main themes of the dissertations mentioned above, adding only that small organisms are known to produce toxins harmful to man, and that their susceptibility to the environment may explain the variability in disease expression. Holland's *Medical notes and reflections* went into at least three further editions.[42]

However, other studies putting forward ideas of contagionism in human diseases fail to mention Linnaeus (such as for puerperal fever: Gordon 1795; Dunn 1998). Therefore, while there is a need for more thorough studies of how Linnaeus's ideas about living contagion were, or were not, pursued by doctors and naturalists, his influence appears to have been little more than a ripple; there is no evidence of a large, immediate and consequential shift towards studying micro-organisms as the cause of disease. The degree to which this was a consequence of Ellis's (1773) stern admonitions that discredited Linnaeus's observations also needs further analysis, especially in the light of the new perspective presented here, namely that these observations, in and of themselves, were likely to have been correct.

In our own experience, Linnaeus's involvement in the germ theory comes as a complete surprise to most research biologists, even though this is by no means new to the specialized Linnaean historian. Nevertheless, even in the historical literature, it is probably fair to say that there has been a general neglect of Linnaeus's ideas on "contagium vivum". DeLacy and Cain (1995: 160) made the same point with the telling understatement that Linnaeus's investigations and ideas on contagion "are not entirely unknown to historians". Much earlier, in what is probably the most comprehensive, if not always the most critical, summary of Linnaeus's impact on medicine, Hjelt (1909) also acknowledged that these contributions had received only scant attention. Many biographies of Linnaeus (Stoever 1784; Blunt 1971; Koerner 1996) make absolutely no mention of his ideas about "contagium vivum", even when the biography deals directly with his work as a physician (Hagberg 1953; Landell 2008). Exceptions include Broberg (1975) and Goerke (1973). Correspondingly, accounts of the history of plant disease largely omit Linnaeus's contributions (Large 1940; Zadoks and Koster 1976; Ainsworth 1981). Egerton's (2008) article on plant diseases during the 1700s mentioned diseases listed in Linnaeus's *Philosophia botanica*, but otherwise does not include smut diseases, or Linnaeus's ideas on living contagion.

In part, our investigation further illustrates that the route to understanding the past is sometimes determined by what in the past has been investigated. An English translation of *Exanthemata viva* was not available until 1995, and *Mundum invisibilem* has only recently been translated (Antonovics and Kritzinger 2016). This late attention to works from near the height of Linnaeus's career speaks to the neglect of early considerations of contagion, at least by English-speaking scholars. The omission of Linnaeus's tentative attempts at classifying disease-causing micro-organisms from posthumous editions of *Systema naturae* may further have obscured ideas which he clearly had posited in the spirit of encouraging further investigations.[43] We hope that this paper, by providing a detailed analysis of the development of Linnaeus's ideas on infectious disease, will correct some of this imbalance.

ACKNOWLEDGEMENTS

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We dedicate this paper to the memory of Arthur Cain (1921–1999), an outstanding scholar and evolutionary biologist. Our discovery of his earlier involvement in this topic came as a pleasant surprise.

NOTES

[1] The general events in the life of Linnaeus are based on biographies of Stoever (1794), Blunt (1971), Goerke (1973) and Koerner (1996) .

[2] Throughout, unattributed translations are by the authors.

[3] C. Linnaeus (hereafter CL) to J. F. Gronovius, 1 September 1735 (L0044). Throughout, numbers in parentheses prefixed L refer to a letter's entry in the online Linnaean Correspondence project database: URL http://linnaeus.c18.net/ (accessed 26 February 2018).

[4] The full descriptive (phrase) name was *Cucubalus floribus hermaphroditis pentagynus, capsulis unilocularibus, calycibus angularis*.

[5] Synomyms of *Silene latifolia* Poir. include *Lychnis alba* Mill., *Melandrium album* (Mill.) Garcke and *Silene pratensis* Godr. Linnaeus (1737: 171) described the healthy form of this species under *Cucubalus floribus dioicis*.

[6] In this herbarium, three sheets are labelled as referring to p. 170 of *Hortus Cliffortianus* (Linnaeus 1737) and to *Cucubalus floribus hermaphroditis*, but the plants are all healthy males with normal anthers. So the specimens described by Linnaeus have been lost or replaced. Linnaeus re-organized his collections several times (Gardiner and Morris 2007; C. Jarvis to J. Antonovics, pers. comm., 26 August 2010).

[7] CL to Albrecht Haller, not dated [1737] (L0228).

[8] Floras of the period, including van Royen (1740), Dalibard (1749) and Crantz (1766), cited Linnaeus's entry but provided no independent descriptions. Böhmer (1750) subsumed hermaphrodites as a variety. Willig (1747) added that he has never found hermaphrodites.

[9] Library, Linnean Society of London: cat. no. BL71.

[10] "upsulari 1752 … in Aire … Jumkihl": the rest of the note is illegible (Figure 3), but the first line is possibly "dolore? ad/in hermaphrodita." Other words are "dioicis" and "varietas est", probably indicating his intention to make it a variety.

[11] Blunt (1971) gave a vivid account of the pomp associated with these collecting trips. Some of the plants found near Jumkil were listed in the Linnaean dissertation *Herbationes Upsalienes* (Fornander 1753; also see Berg and Uggla 1951).

[12] The English word smut is from the German Schmutz, meaning dirt. Its initial usage in English was for the plant disease. Its use to imply something lewd is attributed to Samuel Pepys, who on 20 June 1668 wrote: "I saw this new play my wife saw yesterday, and do not like it, it being very smutty" (*Oxford English dictionary*, third

edition, online version: URL www.oed.com/view/Entry/182889?redirectedFrom=smutty#eid (accessed 1 February 2018)).

[13] However, none of these books are in Linnaeus's library in the Linnean Society, London, although Linnaeus (1737) did cite Bauhin *et al*. (1650) in his *Hortus Cliffortianus* (1737).

[14] O. von Münchhausen (hereafter OM) to CL, 9 December 1751 (L1351).

[15] OM to CL, 7 October 1752 (L1495); 7 May 1753 (L1593); 26 September 1754 (L1802).

[16] From Aymen's description, it is clear that he is not describing anther smut (caused by *Microbotryum*), because he says that the anthers are unaffected. He was probably describing the ovary smut, *Sorosporium saponariae* (Vánky 1994).

[17] J. B. Aymen (hereafter JBA) to CL, 12 April 1753 (L2647). Aymen himself did not find out about smut on *Lychnis* until he was informed by Bernard de Jussieu the previous year (Aymen 1939).

[18] For translation to English, see Antonovics and Kritzinger (2016). Roos probably was told about the letters by Linnaeus.

[19] Münchhausen did not specifically mention *Ustilago Hordei* (smut on barley), and judging from the details in his book and correspondence he was probably looking at stinking bunt of wheat (*Tilletia caries*) and not barley smut (*Ustilago hordei*).

[20] JBA to CL, 25 August 1753 (L1627). The next extant letter from Linnaeus was written five months later (CL to JBA, 10 January 1754 (L1703)) and made no mention of smut; the normal time for a reply was one month.

[21] JBA to CL, 18 March 1755 (L1885).

[22] CL to OM, 7 October 1766 (L5911).

[23] Referring to the forthcoming thesis of Roos (1767).

[24] CL to Peter Collinson, 28 October 1766 (L3807); CL to Domenico Vandelli, October 1766 (L3806); CL to Royal Swedish Academy of Sciences, 28 October 1766 (L3808); Johan Otto Hagström to CL, 2 November 1766 (acknowledging letter dated 31 October 1766 (L3829); CL to Abraham Bäck, 16 November 1766 (L3823).

[25] "Quis, nisi vidisset, crederet", an aphorism repeated by Roos (1767: 389).

[26] Linnaeus may have corresponded with Münchhausen shortly before *Der Hausvater* was published. Thus, Münchhausen (1766a: preface) wrote: "One of the questions posed to me by the Noble Linnaeus causes me … to address the most important here." Münchhausen then described two types of smut (now known as *Tilletia* and *Ustilago*). Linnaeus may have asked him if there were several kinds of smut.

[27] J. Ellis (hereafter JE) to CL, 5 December 1766 (L3837). Although Linnaeus had written to many others about his observations, somewhat surprisingly he appears not to have written to Ellis.

[28] CL to JE, 1 January 1767 (L3871).

[29] CL to JE, 8 September 1767 (L3960); October 1767 (L3964). Roos (1767) wrote that Linnaeus showed him the "worms".

[30] L3967, L4002, 8 December 1767. The following year Ellis repeated his doubts that fungal spores produce "animalia infusoria" (JE to CL, 17 January 1768 (L4026)) and suggested that Linnaeus, and Münchhausen too, should try a good microscope to examine these "many new scenes of nature" (JE to CL, 15 March 1768 (L4054)).

[31] When Ellis again suggested that he "shall now endeavour to get some of the Ustilago to try that experiment fairly" (JE to CL, 19 August 1768 (L4101); Smith 1821: 234).

[32] Linnaeus thanked Münchhausen for *Der Hausvater* on 7 October 1766 (L5911), referring to "Vol. 1 & 2, second edition" (Münchhausen 1766a, 1766b). However, the first volume consisted of three parts, with part 1 published in 1764 (Münchhausen 1764) and parts 2 and 3 in 1765 (Münchhausen 1765). These latter are in the library of the Linnean Society (catalogue numbers BL1210) as separate and differently stitched volumes in paper covers (Janet Ashdown (Library conservator) to J. Antonovics, pers. comm. 1 October 2015). Linnaeus must have received these early editions before 1766 because on 7 February 1765 (L3534) Münchhausen wrote: "I have attached another part of my work to these letters, the third will appear very soon", implying that Linnaeus had already received parts 1 and 2. On 20 June 1765 (L3524), Münchhausen referred to a specific page (p. 349) in the second part in relation to the origin of moisture in the soil, showing that he assumed that Linnaeus had already received a copy; he added that he was sending the third part. In an undated letter (CL to OM, [1765] (L5906)) Linnaeus in turn thanked Münchhausen for sending this third part. The second edition of the first volume of *Der Hausvater* (Münchhausen 1766a), as well as the second volume (Münchhausen 1766b), referred to by Linnaeus on 7 October 1766 (L5911), are in the Linnean Society Library (catalogue numbers BL1210 and BL1211, respectively).

[33] OM to CL, 9 December 1751 (L1351). Although Linnaeus had been made aware of Needham's work by Münchhausen, there is no evidence that he corresponded with Needham. There is no mention of such "eels" in the tenth edition of *Systema naturae* (Linnaeus 1758).

[34] D. Solander to CL,13 May 1762 (L3072). The letter was in Swedish, but Solander provided a Latin description; he also referred to these nematodes as having been described by Needham and Baker.

[35] Because of his claim to have seen fungal spores germinating into animalcules, there has been a tendency to discount Linnaeus's abilities as a microscopist (Ford 2009). It is likely that Münchhausen, with his "hundreds" of experiments, may also have seen *Anguina.* Protozoans would have been hard to see with his hand-held microscope, shown in the frontispiece of *Der Hausvater* (Münchhausen 1764, 1766a,1766b), while nematodes would have left a strong impression. Münchhausen referred to it as a Culpeper microscope, but the classic Culpeper microscope (Clay 1925) does not resemble the one illustrated in *Der Hausvater*. What is surprising is that Ellis never posited that Linnaeus might have been looking at the same worms that he and Solander had seen a few years earlier.

[36] During this period, taxonomic confusion over the various types of plant diseases is exemplified by the interactions of Roffredi (1775, 1776), Rainville (1775), Needham (1775) and Bonnet (1781). Their discussions included the observations in *Mundum invisibilem* and of smutted "Lichnis" (Linnaeus's *Cucubalus floribus dioicis*), but they seem not to have corresponded with Linnaeus on this topic; nor do they posit any relevance to human diseases.

[37] *Chaos* appeared in the tenth edition of *Systema naturae* (Linnaeus 1758: 821), but as a species epithet for the alga *Volvox*.

[38] Münchhausen (1766b) was cited here; like Pasteur, he argued that fermentation was caused by living organisms.

[39] Linnean Society Library (catalogue number BL 891/1): on the title-page Linnaeus crossed out "duodecima" and wrote "decima tertia".

[40] One later dissertation on cures for intermittent fever (or malaria) (Tillaeus 1771) made no mention of contagion, and simply reiterated Linnaeus's own thesis that malaria is caused by turbid water and stagnant air.

[41] A reprinting in Vienna in 1767 of the Stockholm twelfth edition was published as a thirteenth edition, but the contents are identical; it is sometimes labelled as edition 12a.

[42] Holland (1857). The title of the chapter on contagion now has "animalcules" rather than "insects."

[43] The general issue of why microscopy at this time never took off as a singular discipline has been discussed at length by Ruestow (1996: 280), but without any clear resolution: "The desultory use of the microscope in the eighteenth century is indeed something of a puzzle."

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