

CONTRIBUTIONS

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History of Ecological Sciences, Part 46: From Parasitology to Germ Theory

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Progress in parasitology and microbiology during the 1800s is one of the great triumphs of science. The consequences for humanity and domestic animals have been momentous, yet this story is not widely known in any detail. It is a story that was built upon achievements of the 1700s (Egerton 2008*a*, *b*) and parallels progress in phytopathology during the 1800s (Egerton 2012). In retrospect, it might seem like a rather small step from the accumulated evidence about plant and animal parasites during the 1700s to the establishment of germ theory in the 1870s–1880s. But that illusion is only plausible when one forgets that there are vitamin-deficiency diseases, scurvy, beriberi, goiter; genetic diseases, diabetes; and optically invisible viral diseases, small pox, yellow fever, which defenders of a germ theory could not explain to skeptics during the 1800s (Carter 1977, 1980). Disease causation was a very contested terrain, and Casimir Davaine seems to be the only investigator who contributed significantly to both parasitology and bacteriology. The discoveries within parasitology and microbiology during the 1800s came too thick and fast to be comprehensively surveyed here. This part surveys the high points and is divided into three sections: parasitology, microbiology, and the discovery of arthropod vector-transmission of disease. Discoveries in vector transmission were aided by the great progress made during the 1800s in entomology (Egerton 2013).

Parasitology

We saw in part 44 (Egerton 2012:309–311; also Théodoridès 1966:195–196) that Italian Agostino Bassi (1773–1856) in 1835 first demonstrated an animal disease (of silkworms) caused by a parasite (a

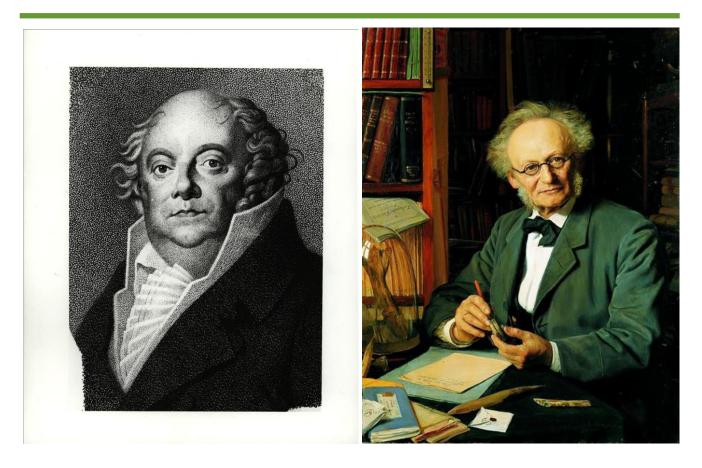


Fig. 1 (a) Karl Asmund Rudolphi. Humboldt University Library. (b) Japetus Smith Steenstrup.

fungus), and in the early 1840s, immigrants to Paris, David Gruby (1810–1898) and to Berlin, Robert Remak (1815–1865), published on fungal diseases on human skin. French physician and biologist Charles-Phillipe Robin (1821–1885), who joined the Faculty of Medicine in Paris (Grmek 1975), published an important synthesis, *Des végétaux qui croissant sur l'homme et sur les animaux vivants* (1847), which he re-titled in a much-enlarged second edition, *Histoire naturelle des Végétaux parasites* (1853). Considering how relatively unimportant fungal parasites on animals are, it seems curious that this subject achieved such early prominence in parasitology during the 1800s. Although silkworm muscardine was fatal, most of the other fungal diseases of animals were not.

Early advances concerning animal parasites came in helminthology, the study of worms. Karl Asmund Rudolphi (1771–1832), considered the father of parasitology, was son of a Stockholm school teacher, studied medicine at Greifswald, where he wrote a dissertation on intestinal worms (1794). He completed a course at the Berlin Veterinary School (1801) and taught at Greifswald until 1810, when he accepted the chair of anatomy and physiology at the new University of Berlin (Foster 1965:17–19, Théodoridès 1966*a*:199, Kruta 1975, Penso 1981:255–256, Grove 1990:8–10, 816, et passim). His *Entozoorum, sive vermium intestinalium* (two volumes, 1808–1810) synthesized the knowledge on internal parasites, describing 457 species, with 629 references in a bibliography of 172 pages (Foster

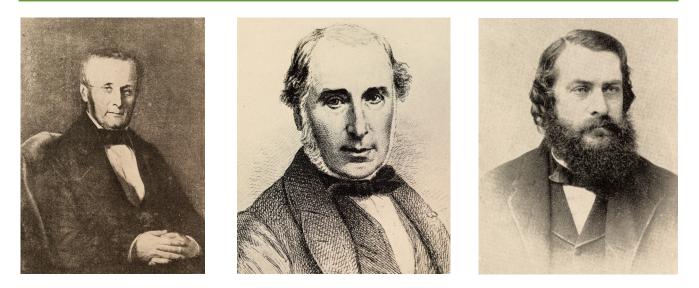


Fig. 2. (a) Félix Dujardin. Huard and Théodoridès 1959:74. (b) Casimir Joseph Davaine. Foster 1965: Plate 5. (c) Joseph Leidy. Reinhard 1958: Fig. 2.

1965:18). His *Entozoorum synopsis* (1819) described 552 distinct species and 441 names of what he considered dubious species. He thought parasites were "generated by disease in the body of the host" (Kruta 1975:592). He dedicated *Entozoorum synopsis* to Viennese museum curator Johann Gottfried Bremser (1767–1827), who also in 1819 published *Ueber lebende Würmer im lebenden Menschen*, with color plates superior to Rudolphi's black-and-white ones (Foster 1965:19, Farley 1972*a*:108–110, Grove 1990:9–10).

Japetus Steenstrup (1813–1897), from northern Jutland, taught school until he published two scientific works in 1842 that brought him fame and appointment as professor of zoology at the University of Copenhagen (Müller 1976). One work, a lengthy paper, discussed what one could learn from layers of dead vegetation in peat bogs, and became a foundation for paleoecology (Egerton 2009:49–52). The other was a book on the alternation of sexual and asexual generations in some invertebrate species, "one of the most illuminating generalizations in the history of biology" (Reinhard 1957:216–220, Foster 1965:20–23 + plate VI; Farley 1972*a*:117–119, 1977:58–60, Grove 1990:44–45). Alternating generations had previously been discovered in jellyfish, which he verified in *Scyphistoma-strobila* (Steenstrup1845:11–25). Steenstrup also studied this phenomenon in free-living claviform polypes (*Coryne*) and salpae (*Proles*) (1845:26–51), and in three species of parasitic trematodes, including the liver fluke of sheep (1845:52–93, partly reprinted in Kean et al. 1978:11–13). He demonstrated what had been previously suspected, that an alternate generation of the fluke lives in snails. His book had three plates with many figures, explained in great detail. Steenstrup, son of a vicar, corresponded with Darwin, but never accepted Darwin's theory of evolution.

Félix Dujardin (1801–1860), from Tours, had broad scientific interests, and turned to parasitology in 1837–1851 (Huard and Théodoridès 1959*b*, Foster 1965:23–24, 40, 113, Théodoridès 1966*a*:197, 199, Geison 1971, Grove 1990:10, 796, et passim). His *Histoire naturelle des Infusoires* (1841, 700 pages, 22

plates) was a major contribution to protozoology. He studied a variety of parasites, making important discoveries which were mostly synthesized in his *Histoire naturelle des Helminthes ou vers intestinaux* (1845, 650 pages, 12 plates), which was the beginning of nematology, the study of a particular group of worms parasitic on both plants (Raski 1959:386, Egerton 2012) and animals. (Nonparasitic nematodes in soil apparently consume bacteria.) Casimir Joseph Davaine (1812–1882), from St.-Amand-les-Eaux, conducted biological research while practicing medicine in Paris (Foster 1965:24, 46, Théodoridès 1966*a*:196, 201, 1968, 1971, Grove 1990:13–14, 794, et passim). He made important contributions to both parasitology (example in English translation: Kean et al. 1978:349–350) and bacteriology (see below). He summarized his parasitology in *Traité des entozoaires et des maladies vermineuses de l'homme et des animaux* (1860, edition 2, 1877, partial English translation, 1863). Davaine also contributed to phytopathology, as another founder of nematology (Egerton 2012:320).

Many worthy investigators described the life histories of multicellular parasites throughout the rest of the 1800s (see literature guide, below). However, dissecting the bodies of victims of parasites was insufficient for revealing the life cycles of many parasites having more than one kind of host. Experimental parasitology had begun in the later 1700s (Egerton 2008:424–425), but had not become standard practice. Parasitologist Ernst Friedrich Gustav Herbst (1803–1893), at the University of Gottingen, somewhat accidentally revived the practice in 1850 (Reinhard 1958:113–114, Foster 1965:72–73, Grove 1990:578–579). He dissected cats and dogs, searching for spiral fleshworms, *Trichina* (now, *Trichinella*) *spiralis* and afterwards fed the flesh to a caged badger. When the badger died, he dissected it also and found many *Trichina* in its muscles, which gave him the idea of feeding the badger's remains to puppies. Months later he dissected them and found *Trichina* in their muscles (Herbst 1851).

James Paget (1814–1894), a London medical student in 1835, saw specks in the muscle of his cadaver and wanted to examine them under a microscope (Reinhard 1958:109-111, Foster 1965:69, Grove 1990:572-575, 813, Peterson 2004). Since St. Bartholomew's Hospital lacked one (!), he went to the head of the Natural History Department of the British Museum, who also lacked one, but advised that the Museum botanist, Robert Brown, had one. With Brown's microscope Paget discovered that each speck contained a spiral worm, which he sketched, and then gave an oral report to the medical students' Abernethian Society. London anatomist Richard Owen (1804-1892) named and described it (1835), crediting Paget as discoverer (Grove 1990:575–577, 812, et passim, Rupke 1994, 2004). In 1846, Philadelphia anatomist-naturalist Joseph Leidy (1823–1891) noticed specks in ham he was eating that resembled cysts of Trichina spiralis, which he had examined in human cadavers (Leidy 1846, Middleton 1923:104, Ward 1923:12–13, Foster 1965:74, 190, Ritterbush 1973, Grove 1990:577–578) and reported this discovery to the Philadelphia Academy of Sciences. The British Annals and Magazine of Natural History and the German Froriep's Notizen alerted Europe to Leidy's discovery (Reinhard 1958:113). However, Viennese parasitologist Karl M. Diesing (Grove 1990:3, 11, 27, et passim) decided, without seeing Leidy's specimens and probably without checking ham himself, that Leidy's Trichina must be a different species than spiralis, since it came from a pig, which he named T. affinis in his Systema Helminthum (volume 2, 1851). Since Herbst's experiment, feeding badger remains to puppies (see above) was also published in 1851, Diesing did not have a chance to learn from Herbst's experiment before misnaming Leidy's specimens. German physician Gottlob Friedrich Heinrich Küchenmeister (1821–1890), who had discovered that bladderworms were immature tapeworms (1855; Reinhard 1958:114, Foster 1965:41-42, 73, 75, Grove 1990:11-12, 579, 802-803), decided in his encyclopedia of human parasites (two volumes, 1855, English, 1857) that *Trichina spiralis* was an immature stage of the intestinal whipworm *Trichocephalus dispar* (now *Trichuris trichiura*), though he also suspected that Leidy's *Trichina* might be *T. spiralis* and not Diesing's *T. affinis* (Reinhard 1958:114–115).

Three German professors gradually cleared up this confusion by experimentation. Gissen zoology professor (Karl Georg Friedrich) Rudolf Leuckart (1822-1898) in 1856 fed muscle containing trichinae to mice, and three days later he found young worms in the mouse intestines (Foster 1965:56, et passim, Théodoridès 1966a:201, Schadewaldt 1973, Wunderlich 1978, Grove 1990:805, et passim). However, he confused himself in his next experiment, in which he fed muscle containing trichinae to a young pig, then waited five weeks before examining its intestine. In the large intestine he found about a dozen mature Trichocephalus dispar, which he assumed were mature Trichina spiralis (Reinhard 1958:116). In 1859, Berlin medical professor Rudolf Carl Virchow (1821–1902) (Risse 1976, Grove 1990:580– 581), obtained muscle with trichinae from an autopsy and fed the muscle to a dog, already weakened by a physiological experiment. Three days later, the dog died, and Virchow found Trichina worms, some containing eggs and others sperm cells. This undermined both Küchenmeister and Leuckart's conclusions. Leuckart confirmed Virchow's results and concluded that humans acquire Trichina spiralis from dogs (Reinhard 1958:118). Final clarification came from Dresden professor of pathology Friedrich von Zenker (1825–1898) (Grove 1990:579–587, 822), who in 1860 obtained from one autopsy Trichina cysts in muscle and free-living in the intestine. He wondered about the source of infection and learned that the victim had attended an employer's Schlachtfest four days before death. Zenker found the butcher who had prepared the ham and sausage for the celebration and obtained some of it, which was infested with trichinae (Zenker 1860). Virchow had continued his own experiments and had put together all the pieces of the puzzle except finding the adults in human intestine, which Zenker had done (Reinhard 1958:118–119). Virchow then demanded that all pork be inspected before being sold, and after a talk on this in Berlin in 1865, a veterinarian arose and insisted that trichinae were harmless. A physician challenged the veterinarian to eat some of Virchow's demonstration sausage; the veterinarian did and five days later became paralyzed (Reinhard 1958:121).

England's first notable parasitologist was neither Paget nor Owen, but Thomas Spencer Cobbold (1828–1886), a graduate of the Edinburgh medical school in 1851 (Foster 1965:25–28, et passim, Kean et al.1978:393–394, Grove 1990:793–794, et passim, Bynum 2004*a*). In 1857 he moved to London, and in 1872 he became professor of helminthology and botany at the Royal Veterinary College. His *Entozoa: an Introduction to the Study of Helminthology* (1864) was enthusiastically reviewed because it rivaled texts from Continental Europe. His *Parasites: a Treatise on the Entozoa of Man and Animals including Some Account of the Ectozoa* (1879) "was not a new edition of his earlier book but an entirely new work with a far wider design" (Foster 1965:28).

Microbiology

Leeuenhoek had discovered bacteria in 1683 (Egerton 2006:50–51), but had not linked them to disease. We saw in part 44 (Egerton 2012:310–311) that two European Jewish physicians, David Gruby and Robert Remak, identified fungal diseases of humans in the early 1840s. Possibly, they had read the speculations by another European Jewish physician, Professor of Anatomy and Physiology Friedrich Henle (1809–1885). He argued in his *Pathologische Untersuchungen* (1840) that contagious diseases

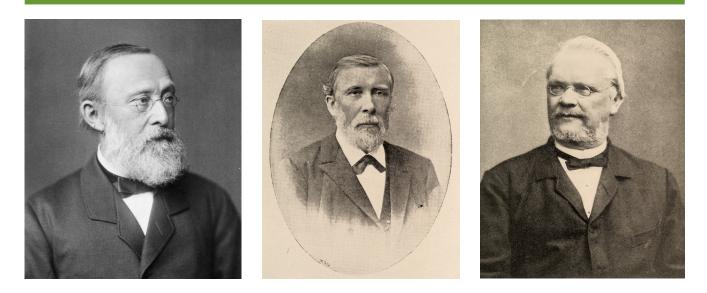


Fig. 3. (a) Rudolf Carl Virchow. Wikipedia online. (b) Friedrich von Zenker. Reinhard 1958: Fig. 4. (c) Karl Leuckart. Reinhard 1957: Fig. 7.

are caused by living beings (Henle 1938:33–53, Hintzsche 1972), but he had doubted that it was yet possible to identify these parasites. His writings exerted some influence on Robert Koch in formulating his postulates (Carter 1985*b*).

Obstetrician Ignaz Semmelweis (1818–1865) noticed in 1846 that women giving birth in one Vienna clinic, aided by medical students, had a much higher death rate from puerperal fever than did patients in another clinic, in which women were aided by midwives (Risse 1975). He suspected that the medical students were transmitting infection from dissected cadavers to the women, and when the students washed their hands in chlorinated lime water, the death rates dropped sharply. He thought decaying organic matter from dissected cadavers caused the disease (Carter 1981, 1985*a*, Semmelweis 1983:245). He did make changes that saved lives, and in 1850 he was first to claim that childbed fever had only one cause (translated in Brock 1961:80–82). His *Die Aetiologie, der Begriff und die Prophylasix des Kindbettfiebers* appeared in 1861 (Semmelweis 1983 [English version]). Subsequently, predecessors, including Oliver Wendell Holmes (Holmes 1843), pointed to their own publications on contagiousness of childbed fever (Carter 1981).

Bacteriology had two French—Davaine and Pasteur—and two German founders—Cohn and Koch. Bacteriology became a science after it was discovered that bacteria can cause disease in animals and humans. Davaine first linked bacteria to a disease, anthrax. By 1850, when Davaine began his research, it was known that anthrax was contagious and inoculable (Théodoridès 1966:156–157). He began the research with his teacher, pathologist Pierre-François-Olive Rayer (1793–1867; Bulloch 1938:391). In sheep that had died from anthrax, Rayer found "small filiform bodies in the blood, about twice as long as a blood corpuscle" (translated in Théodoridès 1966:158), but neither physician then determined whether

the filiform bodies were cause or effect of anthrax. Davaine returned to this research when (Davaine 1863, translated in Théodoridès 1966:159)

...in February 1861, M. Pasteur published his remarkable work on the butyric ferment, a ferment consisting of small cylindrical rods which possess all the characteristics of vibrios and bacteria. The filiform corpuscles that I had seen in the blood of anthracic sheep were much like the vibrios in shape and I was led to try and discover if this kind of corpuscle (or others of the same nature as those which determine butyric fermentation) when introduced in the blood of the animal would not act as a ferment.

Davaine inoculated two rabbits and a rat with blood from a sheep that had died of anthrax and they all died in two or three days. He then inoculated another rabbit with blood from a rabbit that had died, and it died after 17 hours. He described the bacterium and suspected that it caused the disease. Pustules from humans with anthrax contained the same bacterium. He was unable to give the disease to birds or frogs. Two medical professors in Paris opposed him, but his responses to them convinced the Académie des Sciences to award him a prize in 1865. In 1866, Pasteur inhibited wine spoilage by heating the wine, and in 1868 Davaine applied heat to decontaminate anthrax blood (Théodoridès 1966:161–162).

Spallanzani had apparently settled the spontaneous generation debate in 1765 (Brock 1961:13–16, Egerton 2008a:235), but Félix-Archiméde Pouchet (1800–1872) revived the debate in a brief article (1858), followed by his Hétérogenie, ou traité de la génération spontanée (1859). From Rouen, Pouchet studied medicine in Paris, then returned home to direct Rouen's Muséum d'Historie Naturelle (Crellin 1975a). He had published two noncontroversial previous books on sexual generation in mammals. He argued for the existence of a "force plastique" that seems reminiscent of Buffon's moules intérieurs and molecules organiques (Egerton 2007:147–148), about which naturalist Pouchet likely read in his younger years. His new suggestion was that life spontaneously generated as eggs, spores, or seeds (Bulloch 1938:92–95, Farley and Geison 1974:169). Chemist Louis Pasteur (1822–1895) had decided by 1852 that life was associated with molecular asymmetry, detectable by optical means, not characteristic of inorganic compounds (Sechevalier and Solotorvsky 1965:15-62, Porter 1972:1249, Farley and Geison 1974:172, Geison 1974:359-361, 1995, Salomon-Bayet 1986, Debré 1998). He therefore opposed the heterogenesis hypothesis. His studies of fermentation (1857-1860) showed that the process was not purely chemical, as Justus Liebig claimed (Holmes 1973:349), but a product of metabolism of yeast and other microorganisms Conant 1957a). This research strengthened his conviction that life does not arise spontaneously (Farley and Geison 1974:173–174). To combat the idea, he conducted experiments to show that air contains invisible germs (Bulloch 1938:96-102, Debré 1998:159-172). Spallanzani had shown that a broth heated and sealed in a container produced no forms of life, but his critics claimed the heated air prevented spontaneous generation. Pasteur needed to show that after the broth boiled it could be exposed to ordinary air with germs and still produce no forms of life. His former professor, Jérôme Balard suggested he place his broth in a flask, then heat the neck and draw it out into a swan-neck that admits atmospheric air but traps particles, including germs in the curved neck (Pasteur 1860, 1861, Conant 1957b:508-516). A committee from the Académie des Sciences presented Pasteur an award for his 1861 memoir. When Pouchet challenged Pasteur's results, the Académie appointed another committee that also favored Pasteur. Although these committees wanted to use Pasteur's results against Darwin's theory of evolution, Pasteur still deserved the prizes (Farley and Geison 1974:197).



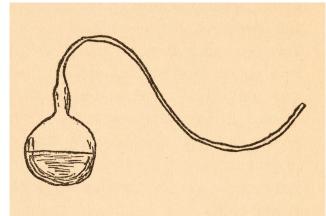


Fig. 4. (a) Louis Pasteur in his laboratory. By A. Edelfelt. Bettex 1965:181. (b) Broth in flask with J. Balard's elongated swan neck. De Kruif 1926:81.

In 1861 Pasteur examined rancid butter and discovered bacteria that, when placed in a drop of water on a glass slide, were more active at the water's center than at the edges. When he added a stream of oxygen, fermentation stopped. He called these organisms *anaerobes*, living without air, in contrast to *aerobes*, organisms that needed air (Geison 1974:363–365, Debré 1998:108–109). He also realized the significance of anaerobes in the cycle of life (Debré 1998:110, partly paraphrasing and partly quoting [in translation] Pasteur 1951, II:103)

...fermentation and putrefaction "come together to accomplish the great destruction of organized matter, which is the necessary condition for the perpetuation of life on the surface of the globe. Life directs the work of death at every stage. The perpetual return to the atmospheric air and to the mineral kingdom of the principles that plants have taken from them is correlated to the development and the multiplication of organic activity." Putrefaction restores to the atmosphere the water, the carbon dioxide, hydrogen, and ammonia without which life cannot exist. Extracting the oxygen and rejecting the carbon dioxide that will be taken up by the plants, the anaerobes are necessary to the cycle of life, for "the continual breakdown of dead organic matter is one of the necessities for the perpetuation of life."

Debré (1998:114) thinks that "Pasteur's research on fermentation created microbiology, which became the field of his next investigation."

In 1865, Pasteur accepted an appeal to study a catastrophic silkworm disease, which took six years to fully understand, and to learn about epidemics. Bassi's discoveries on fungal muscardine of silkworms (Egerton 2012) during the 1830s did not provide much guidance for understanding and combating pébrine in the 1860s. Being ignorant of zoology, Pasteur visited Jean-Henri Fabre to obtain a silkworm cocoon (Debré 1998:184–185). His investigation did not produce a straightforward understanding; he was reluctant to accept that a parasite caused pébrine (Steinhaus 1956:120–125, Geison 1974:374). Part of the problem was that there was also another disease, flacherie, that had to be distinguished from pébrine rather than being considered a stage of pébrine. Pasteur distinguished between these diseases in 1867, then accepted their contagiousness and developed ways for silkworm growers to avoid transmitting them. Eventually, it was learned that pébrine was a protozoan and flacherie a bacterial disease. The Franco-Prussian War (1870–1871) prompted Pasteur to study spoilage of beer, so France could avoid buying German beer (Porter 1972:1251–52, Geison 1974:380, Debré 1998:249–253). He extended his pasteurization process from wine to beer. The Pasteur Institute opened in 1888.

Surgeon Joseph Lister (1827–1912) was the successful proponent of aseptic surgery, who transformed surgical procedures (Dolman 1973, Fisher 1977, Worboys 2004). His concern for infections from surgery led a colleague to show him, in 1865, Pasteur papers on spontaneous generation (1861) and putrefaction (1863), which inspired Lister to successfully use carbolic acid as an antiseptic (Brock 1961:83–85, Dolman 1973:403). He also faced formidable opposition, but was more successful than shorter-lived Semmelweis had been.

Ferdinand Julius Cohn (1828–1898) was born in Breslau (now Wroclaw, Poland), son of a prosperous merchant, and allowed to attend the University of Breslau, but not allowed to take a doctoral degree there because he was Jewish (Geison 1971*a*, Hoppe 1983, Drews 1999, Matta 2007:95–151). He received his doctorate in botany at age 19, in 1847, from the University of Berlin. He returned to Breslau by 1849, supported at first by his father. He became an associate professor at the university in 1859, and in 1866 the minister of agriculture provided him with a new institute of plant physiology (Drews 1999:32, Matta 2007:146). In 1870 he founded *Beiträge zur Biologie der Pflanzen*, and he began devoting his research to bacteria. He applied to bacteriology principles developed for cryptogamic botany (Matta 2007:95). His *Ueber Bacterien, die kleinsten lebenden Wesen* (1872, English 1881) was the first general introduction to bacteria, including his dividing species into six genera, explaining that bacteria are nature's most widespread organisms. He recognized that they were responsible for the dissolution of dead organisms, allowing their material to be used again by new life, that they cause certain diseases—anthrax, diphtheria, blood poisoning, silk-worm diseases—and that they can be killed by prolonged high temperatures, but not by freezing..

However, not all biologists accepted all his conclusions. As late as 1878, Munich Professor of Botany Carl von Nägeli (1817–1891), who earlier had dismissed the work of Gregor Mendel (Olby 1974), claimed (translated in Lagerkvist 2003:63–64):

There are no true bacterial species. On the contrary, the variability of bacteria is unlimited. The same species might, during generations of growth, assume different morphological and physiological forms which over the years sometimes would cause milk to turn sour or protein to putrefy, sometimes cause diphtheria or typhus fever, cholera or recurrent fever.

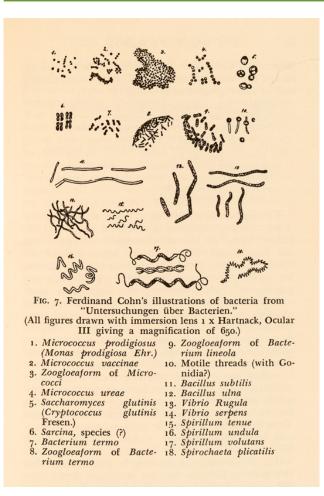


Fig. 5. Cohn's illustration of bacteria (1875). Ford 1939:85.

Although bacteriologists now know that bacteria exchange genetic material in conjugation, change does not occur on as great a scale as Nägeli imagined.

H. H. Robert Koch (1843–1910) was from a mining town, son of a mining official, whose mother and other relatives stimulated his interest in plants and animals (Dolman 1973*a*, Brock 1988, Lagerkvist 2003:59–84). He attended Göttingen University, 1862–1866, studying botany, physics, and mathematics, before switching to medicine. One of his professors was Jacob Henle, whose Handbuch der rationellen Pathologie (1846-1853) "reaffirms his previous convictions regarding the living nature of contagious agents" (Dolman 1973a:420). After practicing medicine in several places, Koch volunteered as a field hospital physician in the Franco-Prussian War. Afterwards, he resumed medical practice while also pursuing research. An anthrax epidemic focused his attention on that, and he verified Davaine's claim that rodlike organisms in sheep blood caused the disease. He invented techniques to culture anthrax bacteria in cattle blood and studied its life cycle, including spore formation and germination. He correlated his laboratory findings with seasonal prevalence of anthrax in livestock and asked Cohn for permission to demonstrate his findings to him. He did so, convinced Cohn, who had him demonstrate them to the medical faculty, then published them in Cohn's journal (1876, 1961). Koch carried bacteriological techniques beyond Cohn's, and his assistant, Julius Richard Petri, invented the Petri dish, used with agar and a nutrient to grow bacteria in a sterile environment. Koch's fame was rivaled only by Pasteur, for he discovered the bacilli for tuberculosis (1882) and cholera (1883). Koch is most remembered for his impeccable procedural postulates, for which he was partly indebted to Henle (Carter 1985b). Despite his postulates, his conclusions were not always accurate: the use of his tuberculin (introduced 1890) to treat TB was sometimes disastrous, and his claim that distinct human and bovine TBs could not be transmitted from one species to the other (1901) was proven incorrect. He was associated with four successive institutes from 1880 on (Brock 1988:251-252). He received a Nobel Prize in 1905 (Feldman 2000:242–244).

As mentioned in part 44 (Egerton 2012), in America, Thomas Burrill introduced plant bacteriology in 1879 and George Miller Sternberg (1838–1915) introduced animal bacteriology in 1880 (Sternberg 1920, Gibson 1958, Williams



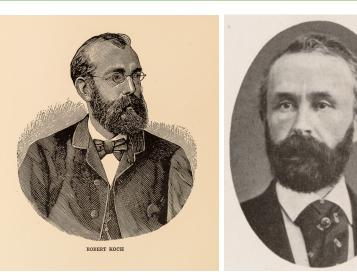


Fig. 6. (a) Ferdinand Julius Cohn. Wikipedia online. (b) H. H. Robert Koch. De Kruif 1926: facing 140. Based on photograph taken about 1883. (c) George M. Sternberg in 1869. Sternberg 1920: facing 2.

1960:125–128, Clark 1961:51–52). Sternberg had graduated from the Columbia University Medical School, but he did not learn bacteriology there. He taught it to himself while a U.S. Army physician. He also battled yellow fever at four different army posts, became infected with it at the fourth site, and barely survived. In 1879 he was appointed a member of the National Board of Health's Havana Yellow Fever Commission. Since yellow fever seemed to spread like infectious diseases, he believed it was caused by an organism, though his repeated microscope searches in the blood of victims failed to locate a causative germ. He was a skilled linguist—thanks to his mother—and he translated Antoine Magnin's textbook of bacteriology from French into English (1880), wrote an enlarged edition (1884), and finally published his own *Manual of Bacteriology* (1893). In 1880, he was sent to New Orleans to verify the European discovery of a bacterium that caused malaria. Instead, he showed that the Europeans were mistaken. He also showed that Pasteur's first announced discovery of the cause of rabies was in error. In 1893 he became Surgeon General of the U. S. Army. Burrill was "father of American plant pathology" (Campbell et al. 1999:109), and Sternberg was "father of American bacteriology" (Bordley and Harvey 1976:188).

Vector-transmission of disease

Some of the most devastating mammalian diseases are transmitted by arthropods and rodents (Busvine 1966:151–277, 1975, 1976). There were speculations in antiquity that insects were associated with diseases. Centuries later, Roman professor and papal physician Giovanni Lancisi (1654–1720) revived these speculations (Lancisi 1717) and recommended draining swamps to eliminate "maligna insecta" (Futcher 1936:546–548, Kean et al.1978, I:22, Egerton 2008*b*:413). He had both followers and

detractors, but Patrick Manson (1844–1922) ended speculations with definite evidence (Manson-Bahr and Alcock 1927, Manson-Bahr 1962, Clarkson 1974, Harrison 1978:23-34, Haynes 2001, Bynum 2004b). He was from a Scottish village where, at age 11, he shot a "savage cat" and extracted from its intestine a long tapeworm. In 1857 his family moved to Aberdeen, where he attended school and in 1860 entered the Aberdeen Medical School, from which he received an M.D. in 1866. In 1867 he followed a brother to Formosa (Taiwan), where he studied tropical diseases, about which he previously had known little. In 1871 he settled at Amoy, an important Chinese port. He became interested in elephantiasis, as he often removed tissue from infected patients (Haynes 2001:36-55). Upon returning to Britain in 1874 for a year's leave, he found at the British Museum in 1875 a publication by Timothy Lewis (1872) based upon elephantiasis observations in India. Lewis found in the tumors a parasite, Filaria sanguinis hominis, which he believed was the immature stage of a larger adult worm. Manson wondered if the infection might be transmitted by mosquitoes. He had two medical student assistants in Amoy look for Filaria in patients' blood. One student could only work at night, and he found many more Filaria in blood than did the day student. By having students investigate patients' blood extracted every three hours. Manson found that Filaria were much more abundant in blood during night than day. His gardener, infected with elephantiasis, allowed mosquitoes to feed on his blood, and Manson found the worms inside the mosquitoes. Knowing little about mosquitoes, his early publications (1877, 1878a, b) contained misconceptions about their life cycle-that humans became infected by drinking water containing mosquito larvae-which he later clarified (1880, 1899). Alexis de Abreu published the first book on tropical medicine in 1623 (Egerton 2005:133), but that isolated achievement was not the founding of tropical medicine. Rather, Manson is considered the founder for: his discovery of the

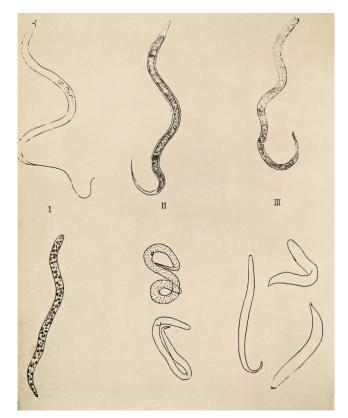


Fig. 7. Patrick Manson's drawings of embryo filaria (1877). From Foster 1965: Plate 7.

first disease transmitted to humans by an insect vector, his textbook, *Tropical Diseases: a Manual of the Diseases of Warm Climates* (1898), and his opening the School of Tropical Medicine in London (1899). He was knighted in 1903.

Parisian Charles Laveran (1845–1922), son of an army doctor, studied medicine at Strasbourg and later, like Koch, served as a physician in the Franco-Prussian War, but for the French (Foster 1965:159–163, Klein 1973, Harrison 1978:7–16). In 1878–1883 he served in the army in Algeria (as his father had) and studied malaria. In 1880 he discovered malarial plasmodia in blood from victims. He found this parasite in four forms, and

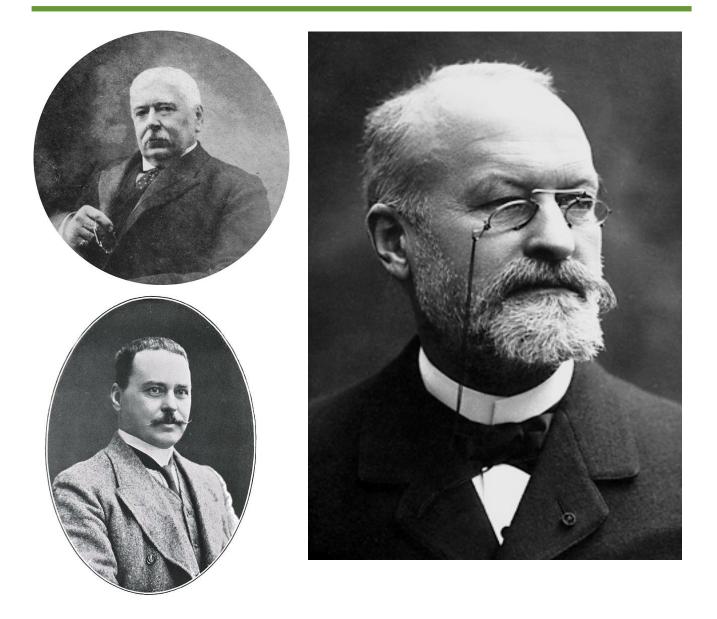


Fig. 8. (a) Patrick Manson. (b) Ronald Ross. (c, right) Charles Louis Alphonse Laveran. All Wikipedia online.

his colleague E. Richard described an un-pigmented fifth form and observed that they all existed inside red blood cells. Laveran published two notes on malaria in 1880 and a book at Paris in 1881 (Laveran [English versions 1893, 1978). He returned to France and taught military hygiene. In 1896 he resigned from the army and joined the Pasteur Institute to study blood diseases. In 1907 he received the Nobel Prize for his work on parasitic protozoa.

Meanwhile, the U.S. Department of Agriculture established a Bureau of Animal Industry in 1884 to investigate and mitigate or eradicate livestock diseases. Its head was Daniel Elmer Salmon (1850–

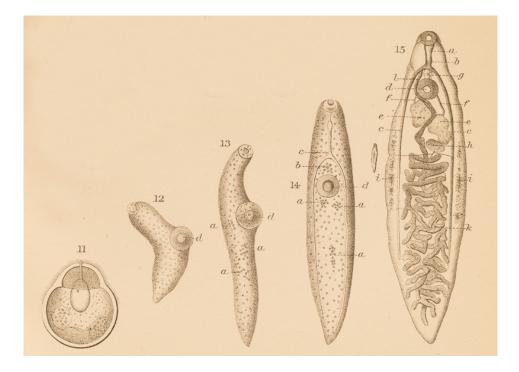


Fig. 9. Distoma lanceolatum Mehlis. Curtice 1890: Plate 17, facing 140.

1914), who had veterinary degrees from Cornell University and had worked at USDA as an investigator, 1879–1884 (Clark 1961:120–123, Foster1965:150, Dolman 1969a:3–6, et passim, Stalheim and Moulton 1987:20–25, Logue 1995:7–10, et passim). He recruited a staff that included three other Cornell graduates, who were classmates and friends, but with different majors: Cooper Curtice (1856–1939), Frederick Lucius Kilborne (1858–1934), and Theobald Smith (1859–1934). They entered Cornell in 1877 and received Bachelor's degrees in 1881. Curtice was the son of a Connecticut schoolmaster, and as a teenager he read Thoreau's writings and Darwin's Voyage and Origin of Species (Logue 1995:5-7). At Cornell University he studied natural history, paleontology, and veterinary medicine. Curtice graduated in 1881 and then obtained a D.V.M. degree from Columbia Veterinary College in New York City in 1883. Afterward, he took a summer job as a paleontologist with the U.S. Geological Survey, which turned into an occupation of three years. Kilborne majored in agriculture. Salmon hired Smith in 1884 and Kilborne in 1885. Smith was unrelated to phytopathologist Erwin Frink Smith, at a different bureau in USDA (Egerton 2012:327-329), for Theobald's parents were German immigrants named Schmitt (Clark 1959, 1961:219-235, Foster 1965:149-157, Dolman 1969a, b, 1975). Theodore Smith (who changed the spelling of his last name) was born in Albany and received a Ph.B. degree from Cornell in 1881 and an M.D. from Albany Medical College in 1883. Salmon hired him in 1884. He learned Koch's culture methods and became a skilled bacteriologist who differentiated between cholera and plague in pigs, identifying the bacteria of each, though pig cholera was later found to be viral, with the bacteria being a secondary infection. Kilborne, hired in 1885, was made head of the BAI Veterinary Experiment Station. Salmon hired Curtice at Smith's recommendation in 1886 (Dolman 1969a:3-7, Andrews 1987:113-114, Logue 1995:7-9).

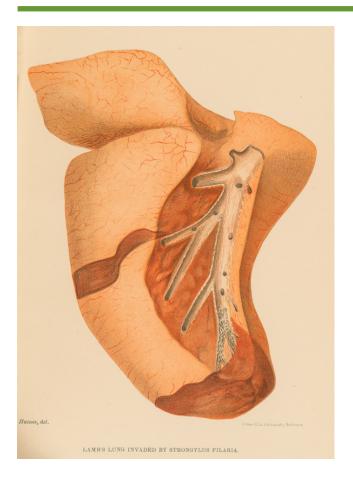


Fig. 10. Lamb's lung invaded by *Strongylus filarial*. Curtice 1890: Plate 36, facing 214.

Curtice was a parasitologist who tackled a variety of animal diseases, beginning with sheep diseases. In 1889, the United States had 42,599, 079 sheep, which justified his *Animal Parasites of Sheep* (1890), with 36 plates, which are well executed except that the black-and-white ones are rather faint. His illustration of the fluke *Distoma lanceolatum* is reproduced in Fig. 9 because it has the best contrast.

Its life cycle was not well known, but was assumed to be similar to that of the liver fluke *Distoma hepaticum* L. Four plates are in color, showing the effects of parasites on sheep lungs (Fig. 10). It is one of 11 illustrations of the genus of hair lung worms *Strongylus*, which caused verminous pneumonia. Black-and-white illustrations of species in this genus show details of anatomy not seen in Fig. 10.

The landmark case clarified by this BAI team was Texas (or southern) cattle fever. Curtice decided that it was transmitted by ticks, which he named Boophilus bovis, but no one except Dr. Mark Francis at Texas A&M took his hypothesis seriously, until he designed controlled experiments that demonstrated it (Dolman 1969a:22-24, Logue 1995:20–40). While he spent the summer of 1891 with a U.S. Geological Survey in California, Kilborne ran Curtice's experiments. Smith tackled the problem from a different direction; he studied infected cattle's blood until he isolated a parasitic protozoan that presumably caused the infection. Smith eventually accepted Curtice's tick transmission hypothesis after Kilborne ran Curtice's controlled experiments. BAI was expanding its operations and personnel, and in 1891 Salmon divided it into four divisions, each with a supervisor. He appointed Smith as supervisor of the Division of Animal Pathology, with Curtice reporting to him. A week later Curtice resigned. His biographer said it was because Curtice feared Smith would neglect Curtice's tick research and because working under Smith would destroy their friendship (Logue 1995:40-41, citing Curtice's unpublished papers). However, a Smith biographer quoted a private letter from Smith, 29 July 1896, in which Smith interpreted Curtice's resignation as "because he was not advanced," presumably to supervisor (quoted in Dolman 1969a:10).

Two years after Curtice resigned, Smith published an article "Regarded by many as the greatest contribution to biology in the 19th century" (Kean et al. 1978:14), "Investigations



Fig. 11. (a) Theobald Smith. Wikipedia online. (b) Cooper Curtice, (c) Frederick Kilborne. Logue 1995: Frontispiece, 11.

into the Nature, Causation, and Prevention of Southern Cattle Fever" (1893), which showed that the protozoa *Pyrosoma bigeminum* was transmitted to cattle by the cattle tick *Boophilus bovis*. This was the first infectious disease shown to be transmitted by an arthropod, for Manson had not yet discovered how *Filaria* was transferred between humans and mosquitoes. Smith wrote the entire report, but since Kilborne had conducted the experiments, Salmon insisted that Kilborne be listed as coauthor. This motivated Smith to resign, once he found another position. In 1895 he became a Harvard professor and headed a Massachusetts State Board of Health antitoxin laboratory (Dolman 1975:481). Possibly because Curtice knew that Smith intended to leave BAI, he returned to BAI on 15 September 1894. He was disappointed that Smith had not credited him for establishing *B. bovis* as vector of *P. bigeminum* in Smith and Kilborne's 1893 article (Dolman 1969*a*:24–25, Logue 1995:49, 75–77). Although Smith was indignant that Salmon sometimes took credit for Smith's work and Salmon had imposed Kilborne's co-authorship upon Smith's 1893 paper, he dismissed Curtice's complaint in a letter to Curtice, 4 May 1901 (Dolman 1969*a*:24–25, Logue 1995:76–77):

... I think that I am voicing a unanimous opinion and precept among scientists that the one who first successfully demonstrates, especially by new methods, a new fact, is entitled to the credit of such discovery or demonstrations. This is the case with malaria today. I worked on the mosquito theory since 1896 here in Massachusetts, but I should not think of claiming Ross's credit for 1898 ... If your animals had only died that fall you would certainly have had the credit. They probably had a mild attack but the methods for detecting it were only being worked out. I regret that the report did not state that you had believed the transfer through the bite of the young tick to be the way. But I think that the world would not pay attention to it and rightly because where would the stimulus and credit for the active worker come from who felt his territory preempted but not occupied? There is a flaw here in Smith's argument; his work on malaria was unknown to Ross and contributed nothing to Ross's success, but Curtice's work was known to Smith and did contribute to his success. However, it is also true that Curtice had quite adequately published his claims for ticks as vector of Texas (or southern) cattle fever (Curtice 1891, 1892) before Smith and Kilborne's publication. The American Veterinary Medical Association recognized Curtice's contributions by presenting to him a specially designed gold medallion in 1933 (Logue 1995, xv:119–120). In a private letter, 21 December 1933, Smith reacted to this presentation: "He got all the credit belonging to him for he published his work on the development of the tick before the T.F. [Texas Fever] report appeared" (cited from Dolman 1969*a*:26). Dr. Maurice C. Hall, who had worked with Curtice at BAI before Curtice retired, set the record straight in print concerning Curtice's contributions in "Theobald Smith as a Parasitologist" (1935), the year after Smith died.

Setting aside priority credits, there remained the challenge of using what had been discovered to eliminate Texas (or southern) cattle fever. Smith had gone on to teaching and researching bacteriology at Harvard, Kilborne had moved to Kellogsville, New York in 1894 to practice veterinary medicine (Logue 1995:52), and so Curtice addressed this challenge without them. In 1899 he met with the North Carolina Commissioner of Agriculture to develop an eradication plan, and by 1906, 12 counties had been released from quarantine that prevented cattle from movement outside those counties (Curtice 1910:255). In that year, Congress began making annual appropriations specifically for eradication. The most effective pesticide of ticks was arsenic compound sprayed on cattle or a dipping vat, the latter being more effective (Curtice 1910:260–261). He proudly announced that "There have been freed of ticks and released from quarantine 127 counties and parts of 20 counties of 929 originally infected; 90 are in varying degrees of disinfection" (Curtice 1910:257). He showed these results in an impressive map (Curtice 1910:258).

Now back to Manson; when in London in 1894, he met Ronald Ross (1857–1932), who had been born in Nepal (British India) but received his medical education in London (Crellin 1975b, Harrison 1978:17–22, Nye and Gibson 1996, Bynum 2004c). That meeting changed Ross' life. Manson published an article (1894) suggesting that mosquitoes transmitted malaria, based upon Laveran's discovery of parasites in the blood of malarial victims. Manson convinced an initially skeptical Ross to return to India and prove it. It was not an easy task, as there were a variety of mosquitoes and a variety of parasites, and he had to discover which were involved with malaria. Manson was always willing to send advice (Manson-Bahr and Alcock 1927:130-179, Harrison 1978:35-50, Bynum and Overy 1998). Ross had to learn to identify mosquito species and how to dissect their organs. Volunteers who drank water containing mosquito larvae did not become infected. It was only when he examined the stomach wall of an Anopheles mosquito on 20 August 1897 that he found the plasmodia Laveran had described. He continued studies on the plasmodia life cycle on caged birds (Harrison 1978:51-80, Ross 1988:103-105). He retired from the Indian Medical Service in 1899. The Liverpool School of Tropical Medicine was founded in 1898, and Ross was on its faculty, 1899-1912 (Crellin 1975:556, Liverpool School of Tropical Medicine web site). He won the Nobel Prize in 1902. He continued to research and publish on malaria for the rest of his career.

Australian David Bruce (1855–1931), son of immigrants from Edinburgh, went to the University of Edinburgh to study zoology, but after a year switched to medicine (Foster 1965:118–123, Dolman

1970). At his first employment as a physician in 1881 he met the daughter of a physician, Mary Elizabeth Steele, whom he married in 1883. She became his "indispensable helpmate" (Dolman 1970:527). He joined the Army Medical Service and in 1884 was sent to Malta where, inspired by Koch's discovery of the TB bacillus, he bought a microscope and investigated Malta fever. In 1886, he discovered a bacterium in the spleen of a dying patient, for which he published a name, *Micrococcus melitensis*, in 1887. In 1920 it was put into a new genus, *Brucella*, and the disease is now called brucellosis. In 1905 he was part of a commission that traced the source of the disease to goat milk. In 1889 the Bruces left Malta for Koch's laboratory, where they studied bacteriology and investigative techniques. In 1894 he was asked to investigate nagana (sleeping sickness) in Zululand. David Livingstone (1813–1873) had pointed out in his *Missionary Travels and Researches in South Africa* (1857) that it was transmitted by the tsetse fly (*Glossina morsitans*), which he illustrated and described (1865:94–95, 612), even reproducing his drawing on the title page.

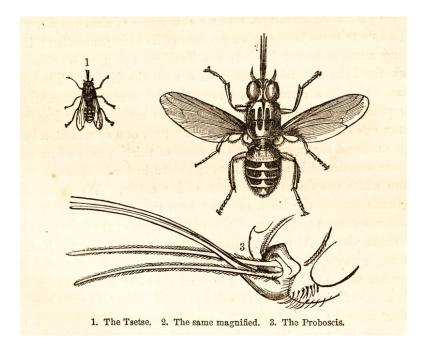


Fig. 12. Tsetse fly (*Glossina morsitans*). 1. Life size. 2. Magnified. 3. Proboscis. Drawing by J. N. Gray. Livingstone 1865:612. Why Livingstone described it in one place (Livingstone 1865:94–95) and illustrated it in another is unclear.

Nagana was known as fatal to cattle but not to wildlife, and mistakenly believed to be harmless to humans. Bruce applied his bacteriological techniques to the blood of infected cattle, but drew a blank. Instead, he found a flagellated protozoan that he thought might be a filaria, which produced the disease in dogs which he injected with infected blood (1895). He hypothesized that the common source of the



Fig. 13. (a) David Bruce. Wikipedia online. (b) Mary Elizabeth Bruce. Foster 1965: Plate 14.

parasite, which did not sicken wildlife, was wildlife, and by injecting blood from wild animals into domestic animals, he showed that wildlife were reservoirs from which tsetse flies transferred parasites to livestock. The first identified human victim was an Englishman on the Gambia River in 1901 (Foster 1965:123).

Conclusions

Knowledge of parasitic diseases, increasing throughout the 1700s and 1800s, did not lead easily and quickly to a germ theory of disease. Nor did the understanding of parasitic plant diseases. Steenstrup's insight into alternation of sexual and asexual generations in invertebrates (1842) was an important breakthrough in zoology, but it did not lead to an understanding of vector-borne diseases, transmitted by insects, mites, rats, bats, and other animals. Unfavorable environmental factors in air, water, and filth and decayed organisms seemed to be important alternative possible causes of diseases. An accurate understanding could not be achieved by abstract reasoning, but only by slow accumulation of knowledge about minute species after species. Even after bacteriology became an effective science in the 1870s–1880s, it did not clarify all diseases investigated. Rabies, smallpox, and yellow fever were well-known diseases caused by viruses, but none of their pathogens were isolated during the 1800s. First

isolated was tobacco mosaic virus in 1898, and three other presumed viral diseases were announced by the turn of the century (Waterson and Wilkinson1978:23–34). A trio of investigators at the USDA Bureau of Animal Industry in 1891–1893—Smith, Curtice, Kilborne—demonstrated that a bacterial disease of cattle was transmitted by a tick. In 1894, Manson guessed that malaria might be transmitted by mosquitoes and Bruce found a nagana parasite transmitted by tsetse flies. Once these vector-borne diseases were understood, one could hypothesize that other diseases also might fit the pattern.

Literature guide

Lisa Wilkinson's Animals and Disease: an Introduction to the History of Comparative Medicine (1992) is a fairly recent survey on the history of parasitology. Giuseppe Penso's La conquête du monde invisible: parasites et microbes à travers les siècles (1981) surveys the history of parasitology and microbiology from antiquity to recent times. It is well illustrated, but it covers the 1800s and 1900s in only 73 pages. It has a good bibliography, but does not cite other authors discussed in this paragraph except Foster. John Farley (1972a, b, 1977, 1992, Farley and Geison 1974) also surveyed both parasitology and bacteriology from the 1600s to recent times. W. D. Foster's A History of Parasitology (1965) provides good, concise coverage, with adequate, though not extensive documentation. Briefer is Jean Théodoridès' "Les grandes Étapes de la Parasitologie" (1966). P. Huard and Jean Théoridès have written Cinq parasitologistes méconnus (1959), two living in the 1700s, but the other three in the 1800s: Laennec, Raspail, and Dujardin. R. Hoeppli's Parasites and Parasitic Infections in Early Medicine and Science (1959) has good coverage of Chinese medicine, and also covers western medicine to about 1850. Edward Reinhard (1957, 1958) has written interesting histories of the study of liver flukes and spiral threadworms. J. L. Cloudsley-Thompson's Insects and History (1976) is a good general introduction to the study of insect vector diseases, and there are two good case histories: J. J. McKelvie's Man Against Tsetse: Struggle for Africa (1973) and Gordon Harrison's Mosquitoes, Malaria and Man: A History of the Hostilities since 1880 (1978). The most extensive national history of parasitology is Progress of Medical Parasitology in Japan (five volumes, 1964–1973), edited by Kaoru Morishita, Yoshitaka Komiya, and Hisakichi Matsubayashi. B. H. Kean, Kenneth Mott, and Adair Russell have compiled a valuable sourcebook, Tropical Medicine and Parasitology (two volumes, 1978), which has good coverage of the 1800s. Kenneth Warren and Vaun Newill's Schistosomiasis: a bibliography of the world *literature from 1852 to 1962* (1967) provides assistance for exploring the history of a tropical disease.

The rich literature on the history of bacteriology and microbiology provides good coverage for the 1800s. William Bulloch's *History of Bacteriology* (1938) is a classic which remains valuable. Paul de Kruif's older popularization, *Microbe Hunters* (1926), is still worthy of notice—it captures the excitement of discovery many scientists felt during the 1800s. William Ford's *Bacteriology* (1939, 1964) is brief but well documented. Patrick Collard's *The Development of Microbiology* (1976) is organized topically, with chapters on sterilization, metabolism, genetics, virology, protozoology, and more. Raymond Doetsch's *Microbiology* (1961) are good sourcebooks of primary sources, all in English. Hubert Lechevalier and Morris Solotorovsky's *Three Centuries of Microbiology* (1965) is somewhat skimpy for the 1700s but quite adequate for the 1800s. Raymond Beck's *Chronology of Microbiology in Historical Context* (2000) is a helpful reference book, but without bibliography. Ulf Lagerkvist's *Pioneers of Microbiology and the Nobel Prize* (2003) focuses mainly on Robert Koch, Emil von Behring, Paul Ehrlich, and Elie Metchnikoff. About one-third of Charles-Edward Winslow's

Conquest of Epidemic Disease (1943) discusses the 1800s, and although superseded in some respects, it contains still-useful information. James Strick's Sparks of Life: Darwinism and the Victorian Debates over Spontaneous Generation (2000) and Michael Worboys' Spreading Germs: Disease Theories and Medical Practice in Britain, 1865–1900 (2000) discuss the British shift to germ theory from several perspectives. Paul Clark's Pioneer Microbiologists of America (1961) is a substantial study, fairly well documented. Vivian Wiser, Larry Mark, and Graham Purchase edited 100 Years of Animal Health, 1884–1984 (1987), which contains two important articles that discuss parasitology during the 1800s at the U. S. Bureau of Animal Industry.

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Acknowledgments

I thank for their assistance: Professor Emeritus Sidney A. Ewing, Veterinary Parasitology, Oklahoma State University, Stillwater; Drs. Jean-Marc Drouin, Muséum National d'Histoire Naturelle, Paris, and Anne-Marie Drouin-Hans, Université de Bourgogne (both retired).