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Commentary

A History of the Ecological Sciences, Part 30: Invertebrate Zoology and Parasitology During the 1700s

During the 1700s, most studies on "invertebrates" (Lamarck had not yet coined the term) concerned species of economic importance: insects and parasites (including also some insects). Previous parts of the present history for the 1700s discuss relevant achievements by Leeuwenhoek, Réaumur, Linnaeus, and White (Egerton 2006*a*, *b*, 2007*a*, *b*), and mention Réaumur's disciples. However, entomology was advanced so extensively that only the most important contributions can be discussed here. A more thorough survey is F. S. Bodenheimer's general history of entomology (1928–1929), which extends to midcentury, as does his article on the history of insect parasitism (1931). S. L. Tuxen (1973) briefly surveys the history of entomology during the 1700s. Part 2 of Jean Théodoridès' comprehensive but brief survey of the history of parasitology includes the 1700s (1966:191–195, 206–208). There are also two much longer works, but of slightly narrower aspects of the history of parasitology, a history of helminthology by David Grove (1990), and a sourcebook of tropical medicine and parasitology by Kean, Mott, and Russell (1978). Both of these include the 1700s, as does Edward G. Reinhard's article on the history of liver fluke studies (1957:213–215). Georg Sticker's article on the history of parasitology (1926), despite its title, spans the years 1626 to 1722.

Conveniently, a French physician opened the century with a 468-page treatise on the generation of worms in the human body (Andry 1700 [edition 3, 1741; English translation, 1701]). Nicolas Andry de Boisregard (1658–1742), because of his important book, was invited to join the faculty of medicine at the Collège de France, and rose to become dean of faculty and a crusader against barbers performing surgery. He also published the first book on orthopedics in 1741, and coined that term; today, all the choices at the Nicolas Andry web site concern orthopedics (such as Kohler 1995). But he deserves to be remembered for his first book as well as his last (Hoeppli 1959, Foster 1965:10–12, Théodoridès 1966:191, Grove 1990:37–38, 783). His stimulus to write the book came from his experience with a 30-year-old male patient in June 1698 who passed a very long tapeworm.

Fig. 1. Nicolas Andry, by Jean-François de Troy.

He then read about parasitic worms and decided that (1701, from Hoeppli 1959:86)

> *…worms cause most of the diseases which attack mankind and even those who have diseases which one calls venereal, nourish in their bodies an infinite number of invisible insects* [a broader term then, than now] *which corrode and bite everything they find and cause all the destruction which one knows…*

He agreed with those who denied spontaneous generation in the gut (Egerton 2005). This was a judgment, not a matter of proof (Andry 1701, from Grove 1990:37)

> *Worms breed in the bodies of men and other animals, by means of a seed that enters there, in which those worms are enclosed. For all animals…are bred of a seed which contains them…this Seed of Animals, contains in no little Bulk, the Animal that is to be formed in it, and that Microscopes discover them to us sometimes quite formed.*

Andry believed the embryo contained a miniature adult that had only to increase in size. Since the possibility of spontaneous generation was hotly debated throughout the 1700s (Hoeppli 1959:113–156, Farley 1977:18–30, Egerton 2008*c*), he also quoted from letters to him on the subject, written in 1699, from two respected authorities, Niklass Hartsoeker and Giorgio Baglivi, supporting his views (partly quoted in Kean et al. 1978, I:6). Another hot debate at the time was whether animals are fully formed (preformation) in the egg (ovists) or sperm (animaculists, including Leeuwenhoek), or whether it developed gradually after fertilization (epigenetists) (Gasking 1967). The above quotation shows that Andry was a preformationist (Farley 1977:20).

Although Andry seems enlightened about the origin of internal parasites and their importance as a cause of disease, some of his other speculations seem less so. He thought that body humour helped determine the sort of parasite that developed from an egg (1701, from Grove 1990:37)

> *…a Man, whose body abounds with a certain sort of Humour, will produce Worms of a certain sort, whilst he who abounds with another Humour, will produce Worms of another; and he who has no Humour proper for the Eggs of Worms, will produce none, and so be free of them.*

He also thought that parasites change with age, "some become like frogs, others like scorpions, others like lizards" (1701, from Hoeppli 1959:99). In his history of parasitology, Foster (1965: Plate 3) reproduces one of Andry's illustrations (1718) showing a worm-like parasite with two legs and a horse-shaped head. Edward Tyson (1683) thought that what we call genital pores of tape worms were mouths; Andry disagreed—he thought they were pulmonary openings for air (Grove 1990:359).

We met Maria Sibylla Merian (1647–1717) in part 21 (Egerton 2006*b*:221) because Réaumur cited her remarkable account of tropical ants. She also deserves to be discussed here, and fortunately there is now an excellent biography of her (Todd 2007) and an essay review of three reproductions of her work (Valient 1993), which facilitate this. Merian was the daughter of a prominent Frankfurt publisher who produced well-illustrated books with pictures and maps, including a natural history encyclopedia. He died when she was three, and her mother married a painter and art dealer. She went to school,

Fig. 2. *Taenia saginata*. Andry 1718: Plate 19. First illustration of a human tapeworm showing the scolex.

probably until she was 14, and she also learned to paint with watercolors and to engrave pictures for publication. At 13 she raised silkworms, watched their life history, and painted them. She was encouraged to draw flowers, decorated with caterpillars. She obtained a copy of Johannes Goedaert's *Metamorphosis Naturalis* (1662), which contained uncolored illustrations without the plants with which they were associated (Bodenheimer 1928–1929, I:388–395). She aspired to do better, using color and plants. In 1665 she married a former journeyman, Johann Andreas Graff, or Graffin (1637–1701), and they returned to his native Nuremburg, where he worked as a painter–engraver–publisher and she worked as an artist, naturalist, and art teacher (Wettengl 1998 *b*, *c*, *d*). They had two daughters (whom she taught her own skills), and, using her married name, Graff published her *Neues Blumen Buch* (1680; in English, 1999, under her maiden name) and the first two of her three volumes, entitled *Der Raupen wunderbare Verwandlung, und sonderbare Blumen-nahrung* (The Caterpillar's Wondrous Metamorphosis and Particular Nourishment from Flowers,1679, 1683, 1717). Her *New Book of Flowers* is in three sections, with all the flowers in Section 1 having insects on or near the plants, but the emphasis is on the flowers (Segal 1998). In the caterpillar volumes, the emphasis is reversed. There are fifty uncolored plates with text in each volume (Merian 1978, 1991). Although she depicts eggs, caterpillar, cocoon or chrysalis, and adult, she emphasized the caterpillars, because that was the stage that consumed the plant with which it is associated in her illustration (Bodenheimer 1928–1929, I:401–407, II:373–379, Ludwig 1998). She did not provide scientific names, but her illustrations and texts were so precise that Linnaeus used them to describe her species (Stearn 1978). In her books on insects and plants (Todd 2007:74)

> *The reader encounters not merely an object to be examined, but a drama in miniature proportions. In each picture, a caterpillar appears on the plant it eats, along with its pupa, its cocoon, if it makes one, and the resultant moth or butterfly. Sometimes, the butterfly is laying eggs on a leaf or along a stem. Often the caterpillar's predator, a fly that will emerge from the cocoon after killing its host, appears also, with many of its life stages.*

Merian left Graff in 1685 and joined a religious colony until 1691, when she moved to Amsterdam, a world center of trade, wealth, scholars, and private museums. Her husband divorced her and she regained her maiden name. She may never have met Leeuwenhoek, but she read his letters, and also the works of Swammerdam and others who wrote on insects. In 1699 she offered for sale 255 of her paintings to fund a trip to the Dutch tropical colony, Surinam, in northeast South America.

For two years she and her younger daughter, Dorothea, 21, lived in Paramaribo on the Surinam River, observing and collecting plants and animals, taking notes and making sketches for a book that could turn this risky adventure into a profitable scientific success (Davis 1998). In spring of 1700 she traveled up the Surinam River beyond the last sugar plantations to explore the rain forest, with slaves cutting a trail for her, and cutting down a palm tree so she could search its leaves for insects. She did collect enough specimens, notes, and sketches for a book, yet had hoped to stay longer. Illness, the heat, and humidity forced her to return to Amsterdam (Wettengl 1998*e*, *f*). Leeuwenhoek's letters inspired her to study her insects with a magnifying glass, and she reported on details she discovered by doing so. She was especially interested in the drama of parasitism and predation. Her *Metamorphosis Insectorum Surinamensium* (1705) had 60 folio colored plates of her paintings—large enough to portray her insects life size (Fig. 4). Peter the Great went to the Netherlands in 1716, and on January 13, 1717 (the very day of her death) he purchased two volumes of her paintings for 3000 Dutch guilders. The agent who

Fig. 3. Maria Sibylla Merian with samples of her subjects, paintings, and books. Engraved by Georg Gsell. Merian 1717.

arranged the purchase, Georg Gsell, was Dorothea's husband; the Gsells accepted Peter's invitation to go to St. Petersburg, where they painted at court and taught art.

Her books and her art remained popular during her lifetime (Rücker 1998) and for the rest of the century (Bürger 1999:88).

> *Nine editions of Maria Sibylla Merian's three works were published during her lifetime, between 1675 and 1717. With the dissolution of her estate and the Gsells' departure for St. Petersburg, the heirs sold all the copperplate engravings to the publisher Johannes Oosterwijk. Thereafter, between 1718 and 1771, a total of 10 further posthumous editions of the book of caterpillars and the Surinam book were published in Latin, Dutch, and French, in Amsterdam, The Hague and Paris.*

Fig. 4. Emperor moth (*Arsenura armada*) feeding on leaves of the coral tree (*Erythrina fusca*). Merian 1705: Plate 11. Peter the Great and Sir Hans Sloane both purchased original watercolor paintings from which this engraving was made, now in the Natural History Museum, London (which was founded with Sloane's collections) and reproduced in Rice 1999:91 and in the Archives of the Academy of Sciences, St. Petersburg, and reproduced in Wettengl 1998*f*:228–229. The published illustration is a mirror image of the paintings.

One example of her influence is August Johann Roesel von Rosenhof (1705–1756), an Austrian nobleman (though born in Arnstadt, now in Germany), who in 1720 was apprenticed to an artist uncle (Geus 1975). In 1728 he was sick in Hamburg for a month and a friend gave him a copy of Merian's *Metamorphosis insectorum Surinamensium*, which quickly turned him into a zoologist. Being an artist, he took up the challenge of Merian's illustrations to do as well. He, like her, also focused mainly on insects (Bodenheimer 1928–1929, I:461–475, II:405–412), but he also became interested in amphibians and reptiles and published *Historia naturalis ranarum* (1753–1758) on German frogs and toads.

In 1709 a wave of a cattle epizootic of rinderpest swept from Central Asia into Russia, then into Poland, Hungary, and Dalmatia, and by 1711 it reached northern Italy. The Venetian Senate asked the medical faculty at the University of Padua for help. Its leading professor, Bernardo Rammazzini (1633–1714) advised cleanliness, isolation of sick animals, and fumigation of stables. Like Fracastoro (Egerton 2004:27–28), who undoubtedly influenced him, Rammazini believed in contagious inanimate "seeds of disease." In his oration to faculty and students in 1713, he compared rinderpest to smallpox because of a similarity of pustules in the infected victims and the prevalence of death from the fifth to the seventh day. He predicted that the violence of the epidemic would diminish in cold weather and that it would not infect humans, since it did not infect horses, pigs, or wildlife (McDonald 1942). The Pope's physician, Giovanni Maria Lancisi (or Lancisio [1654–1720]), was a Roman who had studied medicine there (Castellani 1973). He was already studying the epidemiology of influenza and malaria, and his publication suggested quarantine, isolation, and slaughter of infected cattle, which was effective when rinderpest reached the Papal States (1715). Following Fracastoro and Rammazzini, he believed in inanimate agents of infection (Wilkinson 1984, 1992:38–44). In another work, *De noxiis paludum effluviis* (1717), Lancisi recommended draining swamps to eliminate both noxious air that caused malaria and "maligna insecta" (Futcher 1936:547–548, passages translated in Kean et al.1978, I:22).

Antonio Vallisneri (or Vallisnieri, 1661–1730) studied zoology and medicine under Malpighi, and he began his own researches repeating some of the observations published by Malpighi and by Redi (Franchini 1931, Montalenti 1976).

He then published an article on his studies of insect reproduction in 1700 that was impressive enough for him to be appointed to the medical faculty of the University of Padua. In 1713 he published a book on the subject, and a part of it that discusses four species of flies that parasitize rosebushes is now translated into English. The species he discussed in most detail was the garden–rose sawfly (now named *Arge pagana*). On 6 May he observed a female land on a tender young shoot and insert what he called a "hooked sting" (ovipositor) into the shoot and saw a slit, into which she laid her eggs. He cut off this shoot and took it inside to observe egg development. On 20 May, three larvae hatched, and on 21 May, all the others did. He watched them eat and grow and shed their skins several times before spinning cocoons in the bottom of their box under leaves. He then dug around the base of his rosebushes and found cocoons [pupal cases] of the other larvae like the ones in his box.

After 18 days, nymphs [pupae?] emerged from his cocoons, and a few days later adult flies emerged from the nymph skins. He wondered why God bothered to put these insects through such a complex series of stages, and decided it was "to confound our human pride" (Vallisneri 1932:300). He capably described the natural history of these flies in detail, including their predators, but that alone did not

Fig. 5. Antonio Vallisneri in 1715. Engraved by Ant. Luciani. From Vallisneri 1932:facing 320.

motivate his modern translators. The climax of the translated discussion is entitled “Reflections on Prevailing Beliefs concerning the Origins of Insects,” in which he took to task Francesco Redi and others for believing that insects can arise by any means besides eggs of the same species. We saw in Part 17 (Egerton 2005:136–137) that Redi discredited the belief that flies arise from putrid meat, but that he still believed insects within fruit arose there from the plant’s “vegetative principle.” When others discredited this claim, he acknowledged his error but never published a recantation. Vallisneri and his translators apparently were unaware of Redi’s acceptance of the new information.

Vallisneri made important contributions to entomology (Bodenheimer 1928–1929, I:407–415), and just as diligently, or more so, he studied parasites of animals and people (Savelli 1961). In 1713 he also published a book on the *Ascaris* and *Neoascaris* worms of humans and cattle. He described and illustrated the sex organs of both sexes, but he misinterpreted what he saw. He concluded that what is now called the female *Ascaris* was hermaphroditic, and that what is now called the male was a different species. His illustrations were reprinted by Daniel Leclerc (1715; Hoeppli 1959:100, 105). Vallisneri was sure that these worms arose from eggs, but how? He accepted the current *emboîtment* theory, that Eve’s ovaries contained all of humanity, with each generation being in the eggs of the previous

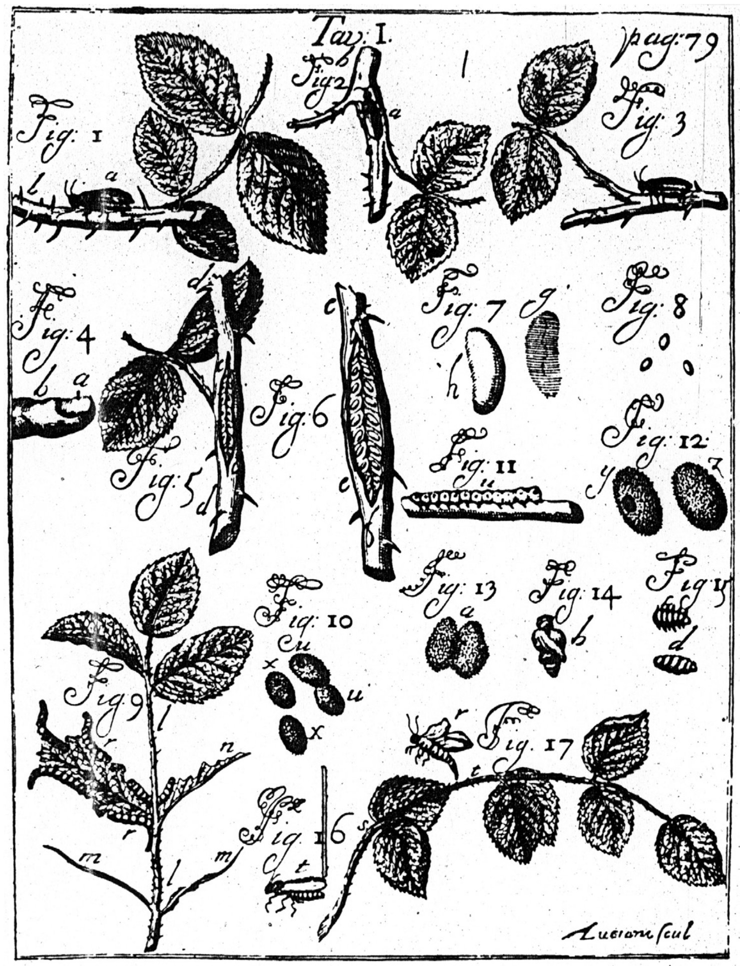

Fig. 6. Life history of the garden rosebush fly (Vallisneri 1713*a*: Plate 1). From Vallisneri 1932: facing page 321.

generation, like nested boxes, and he decided that God implanted these parasites in Eve's ovaries after the Fall (Hoeppli 1959:97, 401), or that they were benign residents before and became parasitic afterwards (Farley 1972:101–102, 1977:21), and that they could be transmitted from mother to child through placenta or breast milk (Grove 1990:38). In 1721 he published a book on spermatozoa (partly reprinted in Cristofolini 1968:107–130) in which he postulated that they were "independent organisms or parasites, believing that they have the task of preventing the clotting of the semen" (Bodenheimer 1958:57). In addition to writing numerous publications on insects and parasitism, Vallisneri also wrote on these topics in his voluminous correspondence (1991–1998) and biological notebooks (Vallisneri 2004), only now being published. Vallisneri received numerous letters concerning insect reproduction from Giacinto Cestoni (whom we met in Part 17 [Egerton 2005:138]), written from 1697 to 1718, which are also published (Cestoni 1940–1941).

While Vallisneri studied flies and intestinal worms, one of his former students pondered the rinderpest disaster. Carlo Francesco Cogrossi (1682–1769) studied medicine under Rammazzini and Vallisneri at Padua, and then returned home to Crema to practice. In 1713, he wrote out his thoughts on the epizootic and sent them to Vallisneri, who accepted his conclusions. Cogrossi's *Nuova idea del male contagioso de'* *buoi* (1714) “presents the first clearly reasoned and thoroughly argued defense of *contagium animatum* theory” (Belloni 1961:12–14, Wilkinson 1992:45). His discussion (1714, 1953:4–5, 2005:103–104) began with a review of past achievements: Redi’s discovery in 1668 that flies lay eggs on putrid meat, which eggs hatch into maggots; Bonomo’s discovery in 1687 that a contagious disease, scabies, is caused by the itch mite (Egerton 2005:138); and then he quoted Vallisneri’s statement (1713*b*) that “all insects are generated from their proper parents, feed on food proper to them, and dwell in surroundings proper to them”(Cogrossi 1714, 1953:7). Cogrossi had heard that the Turks did not suffer from the itch, and he speculated that “this immunity derives from their habit of bathing, which does not allow these skin-dwelling worms to establish themselves on the skin” (1714, 1953:9). He further speculated that the itch could be eliminated from a population by isolating people with the disease and treating them and their clothing to eliminate it. From these observations and arguments, he concluded (1714, 1953:12) that cattle rinderpest “proceeds from invisible insects [with broader meaning then than now] dangerous only to them…” As supporting evidence, he cited Leeuwenhoek’s discovery of microscopic animalcules and Athanasius Kircher’s report of tiny worms in blood (Egerton 2005:134–135, 2006*a*). Vallisneri supported Cogrossi with his own observations (Belloni 1961:14–16, Vallisneri 2005:122–154).

Scientific journals of the 1700s carried descriptive accounts of nonparasitic invertebrates, mostly marine, which cannot be fully enumerated here. A controversy developed over whether corals were plants or animals. The Italian naturalist Luigi Ferdinando Marsigli (1658–1730) argued they were plants, and the French physician-naturalist Jean André Peyssonnel (1694–1759) argued they were animals (Marsigli 1725, Peyssonnel 1752, Lorch 1965, Plantefol 1974, Rololico 1974, McConnell 1990). Réaumur (1729) agreed with Marsigli that corals were plants. The account of noninsect invertebrates that attracted most attention was the discovery of regeneration in fresh-water “polyps.”

Leeuwenhoek, in a letter written on Christmas Day 1702 and published in 1704, first described and illustrated a brown one (*Hydra vulgaris* or *H. oligactis*), which he found living on the roots of duckweed (*Lemna*). His account explains their reproduction by budding, and he was fascinated by their tentacles, which he illustrated separately, more enlarged than his illustrations of the whole animals (all reproduced in Egerton 2006*a*:51); however, he called them horns and failed to discover their function.

Regeneration in hydra was discovered by a Genevan scholar living in The Netherlands, Abraham Trembly (1710–1784), whose interest in zoological research was awakened by reading Réaumur’s memoirs on insects (Baker 1952:16, 1976, Lenhoff and Lenhoff 1986:28–29, Buscaglia 1987:272–283, Dawson 1987:87–88). Réaumur had also published observations and experiments on the regeneration of crayfish limbs (Réaumur 1712, 1718, Skinner and Cook 1991:25–36).

When Trembly discovered a green hydra (= *Chlorohydra viridissima*) in June 1740, he was unaware of Leeuwenhoek’s account of a brown hydra, and since his was green, he was uncertain whether it was animal or plant. He thought he could decide by cutting it in half and seeing if it died like an animal or regenerated like a plant. It did regenerate, but its behavior left him uncertain. On 26 September, he initiated a correspondence with Réaumur that lasted until Réaumur’s death in 1757 (Trembley 1943). After Trembley sent him live specimens, Réaumur assured him that they were animals. By the time Trembley sent an account to the Royal Society of London (1743), word of his sensational discovery had arrived several times (Lenhoff and Lenhoff 1991:58–59). Trembley described hydras capturing and consuming prey as well as their regenerating and their usual mode of reproducing by budding. The

Fig. 7. Abraham Trembley in 1778 (Trembley 1783:frontispiece).

book he published on his experiments in 1744 explained more than 50 discoveries, including green hydras moving towards light despite the lack of eyes. He was highly praised both for his techniques and conclusions (Goldstein 1965:1–31, Dawson 1991:309–314). The illustrations were drawn and engraved by his friend and fellow naturalist, Pierre Lyonet (1706–1789), whose own anatomical studies and illustrations of insects made him the worthy successor of Swammerdam and Malpighi (Van Seters 1962, Pierson 1973, Richards 1973:186, Tuxen 1973:100–102). In 1768 Lazzare Spallanzani, whom we met in Part 29 (Egerton 2008*c*), announced that snails could regenerate another head after the first one was severed. This also created a sensation among naturalists and intellectuals (Carozzi 1985).

Charles Bonnet (1720–1793) was from the Geneva area and developed an early interest in insects (Bonnet 1948:42–43). After reading the first volume of Réaumur's *Mémoires*, he sent him his own observations on ant–lions, and Réaumur suggested that he try to verify Leeuwenhoek's claim that aphids can reproduce without fertilization of eggs.

Beginning in 1740, Bonnet conducted careful studies on the life cycle of aphids, which became the main subject of his *Traité d'insectologie* (1745). This book established his reputation as a naturalist (Pilet 1970, Buscaglia 1987:283–299). He showed that aphids can indeed produce several generations without males fertilizing eggs. Parts of his observations were printed in English before the book (Bonnet 1743), and other parts are now reprinted in German (Bodenheimer 1928–1929:I, 476–486) and in English (Hall 1951:174–176). He also studied parasites, and in his memoir on *Taenia* (1750) he mistakenly described and illustrated a *Diphyllobothrium latum* tapeworm body with a *Taenia* scolex. Later, he discovered his

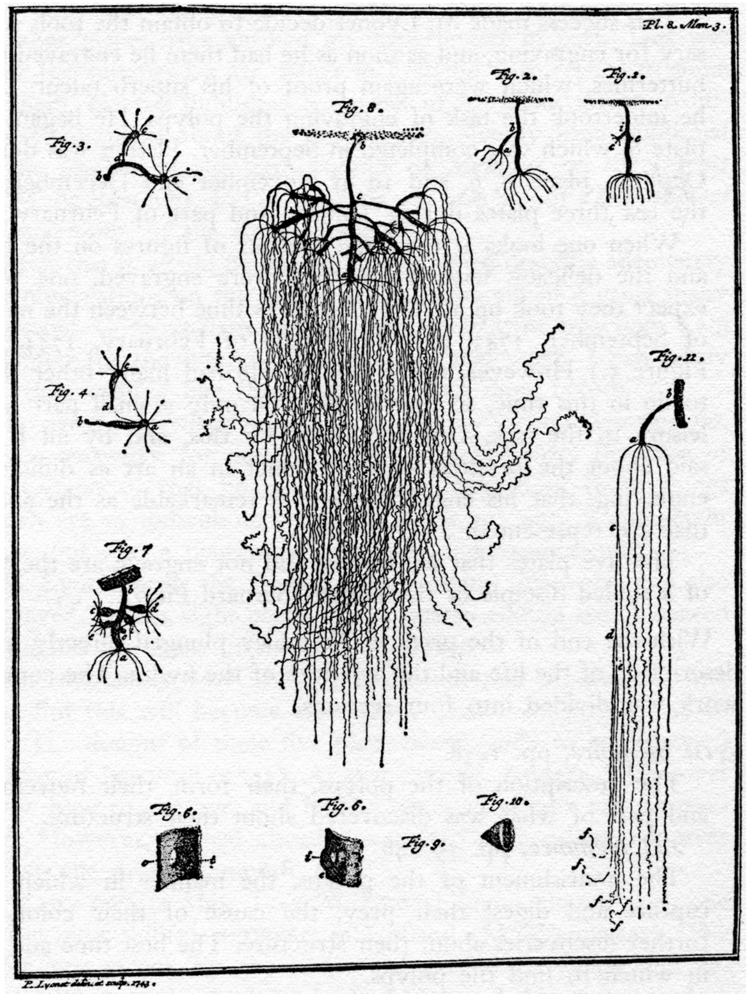

Fig. 8. Hydra drawn by Pierre Lyonet (Trembley 1744: Plate 8).

error, and in 1777 he published a correction (both accounts are abstracted in English translation, with illustrations, by Kean, Mott, and Russell [1978, II:L654–657]). He dismissed the ideas of spontaneous generation and emboîtment within a host as absurd, and he therefore reluctantly concluded that eggs enter from outside the host (Farley 1972:105–106). As mentioned in Part 28 (Egerton 2008*b*), his eyesight gradually failed, and he switched for a while to botany, but as his sight further declined, he concentrated on theoretical and philosophical biology (Glass 1959:164–170, Gasking 1967:117–129, Bonnet 1971, Anderson 1982, Bowler 1989:60–63). He used his observations on parthenogenesis to support arguments for emboîtment in *Contemplation de la nature* (1769, extract in English [Hall 1951:377–381]).

Carl Linnaeus (1707–1778), in the first edition of *Systema Naturae* (1735:28, 1964), under "Observations on the Animal Kingdom," paragraph 10, listed three intestinal worms in humans:

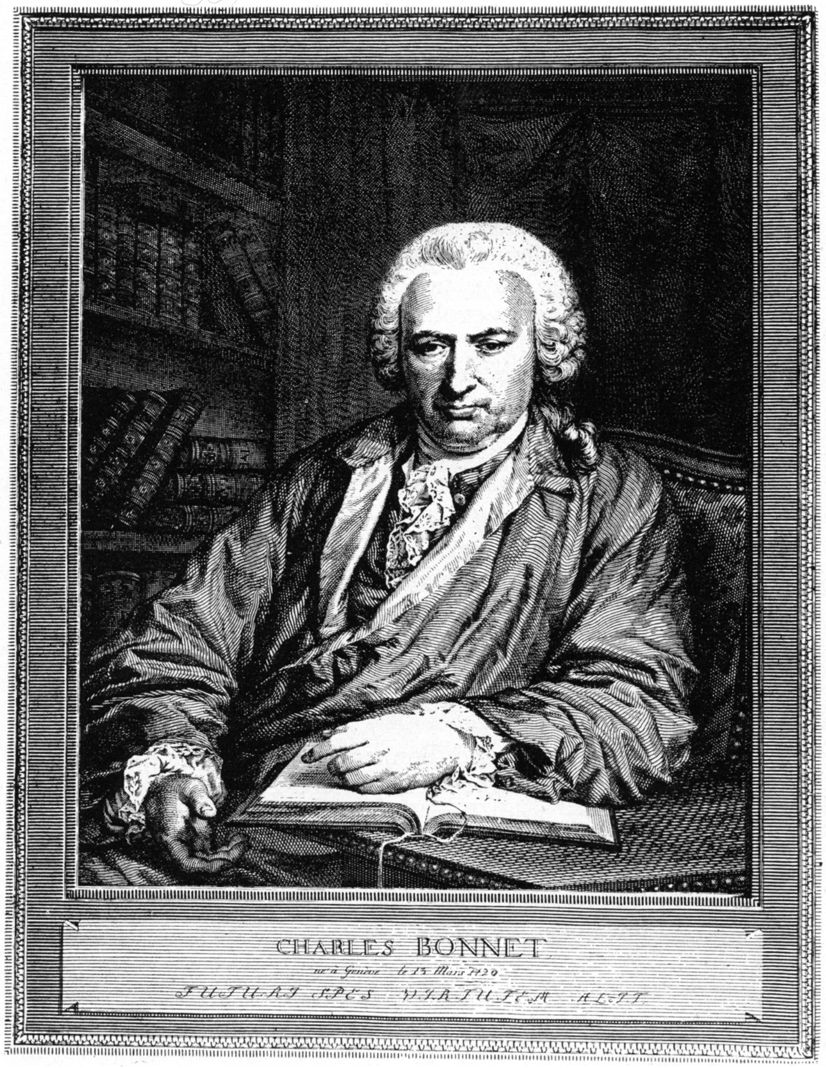

Fig. 9. Charles Bonnet, 1777, by Jens Juel.

Lumbricius ("the same species as the ordinary earthworm"), *Ascaris* ("identical with those very small worms…one finds anywhere on marshy spots"), and *Taenia* ("from man, dogs, fishes, etc."). He and student Godofred Dubois published a dissertation in 1748, *Taenia*, describing four tapeworms, including the first accurate description of *Taenia latum* (now *Diphyllobothrium latum*; 1751 reprint is translated in Kean et al.1978, II:654). By the time Linnaeus published the 10th edition of *Systema Naturae* (1758), he listed and described 25 species of intestinal parasites (Linnaeus 1894:647–651, 819–820, Grove 1990:4–5). Furthermore, he followed Leeuwenhoek in believing that internal parasites enter the body with food or water (Egerton 2006*a*:53–54). He found a supposedly free-living tapeworm (there are none), a free-living planaria, and a free-living *Rhabditis*, that he believed were the early stages of *Diphyllobothrium latum*, *Fasciola hepatica,* and *Enterobius vermicularis* (Grove 1990:40). In 1764, he and student Daniel Weser published a dissertation, *De Hirudine*, on leeches; and in *Systema Naturae*, edition 12 (Volume 1,

1766) Linnaeus described 14 species of leeches (Smit 1979:124, 133).

Linnaeus' strong interest in insects is discussed briefly in Part 23 (Egerton 2007:84–85), but more can be added here. In the first edition of *Systema Naturae*, he enthused: "The curious investigator, who wants to examine the *properties* of insects, can hardly have a greater pleasure anywhere" (Linnaeus 1964:27). In 1739 he elaborated on the properties of insects in a Latin oration (reprinted 1751) that advertised the intellectual and practical rewards of their study (English translation: Linnaeus 1781:309–343, 1977). He had five students publish dissertations on insects, largely written by himself (English translations: Linnaeus 1772, 1781:345–456). Over 2000 insects are named and described in the 10th edition of *Systema Naturae*, and the leading entomologist of the second half of the 1700s, Fabricius, studied for two years under Linnaeus. Linnaeus' contributions to entomology were, therefore, substantial (Bodenheimer 1928–1929, II:275–296, Usinger 1964, Essig 1965:687–690, Tuxen 1973:105–109).

Linnaeus was so impressed by experimental confirmation that *Acarus scabiei* caused scabies that he considered other diseases, like dysentery, whooping cough, smallpox, and plague were probably caused by acarus-like insects (Leikola 1982:48–49). He pointed out that diseases could be spread by clothing, furniture, and other things. Eggs of mites could remain dry for many years and then develop (Linnaeus 1757). He also thought that Harvey, Redi, and Leeuwenhoek had refuted spontaneous generation.

Charles de Geer (1720–78) was a fellow Swede, though he had grown up in The Netherlands. He returned to Sweden in 1739 to claim his inherited estates, which included munitions works. He managed his enterprises so well he became the wealthiest man in Sweden, a member of parliament, and a baron. But all that was a sideline; entomology was the continuous thread in his life, from the time he was given silkworms at age six until the day he died (Bryk 1952, Landin 1972). He had hardly reached Sweden before being elected to the Swedish Academy of Sciences, at age 19. He began publishing articles on insects in Swedish in the Academy's transactions in 1740. His first article, on the life history of the spittle cicada (*Aphrophora salicis*) he had written at age 17.

De Geer greatly admired Réaumur's *Mémoires pour servir à l'histoire des insectes* (1734–1742), and although they never met, he followed in Réaumur's footsteps with similar studies, and even used the same title and language for his own seven volumes (1752–1778). It included life histories of 1446 species, which he illustrated on 238 plates. Unlike Réaumur, he drew his own illustrations. He dedicated his first volume to Queen Lovisa Ulrika, who shared his interest in insects. However, after publishing it, he was accused of merely rehashing Réaumur, and he was so offended that 19 years passed before he resumed publication. His estate was only six miles from Uppsala, and 18 letters he wrote to Linnaeus survive. However, he only began using Linnean binomials in his third volume (1773). His own interests were in life cycles, not systematics (Essig 1965:601–602). The German naturalist Rev. Johann August Ephraim Goeze (1731–1793) translated de Geer's volumes into German (1776–1783) and annotated them.

Bodenheimer (1928–1929, I:476–486) republished extracts from Goeze's translation. De Geer's insect collection is now in the Swedish Museum of Natural History, Stockholm.

Entomology continued to be advanced by those interested in practical problems. For example, Henri-Louis Duhamel de Monceau (1700–1782) and Mathieu du Tillet (1726–1791), whom we met

Fig. 10. Charles de Geer.

in Part 29 (Egerton 2008*c*:232, 236), concerning fungal diseases of plants, also collaborated in a study of the grain moth (now *Sitotroga cerealella*) in the Angoumois region of France. It sometimes attacked wheat in the field, but was mainly a pest in granaries. Their *Histoire d'un insecte qui dévore les grains dans l'Angoumois* (Paris, 1762) is rated by one applied entomologist turned historian, George Ordish (1976:94), as "excellent." Ordish explains why.

> *It accurately gives the moth's life history, destroys many canards about it and suggests a remedy. It also has three good explanatory plates—of the insect in all stages, the damage it does and the method of controlling it. The cure was to heat the grain carefully to a temperature of "55 to 75 degrees on M. Réaumur's thermometer," which destroyed eggs, larvae and adults.*

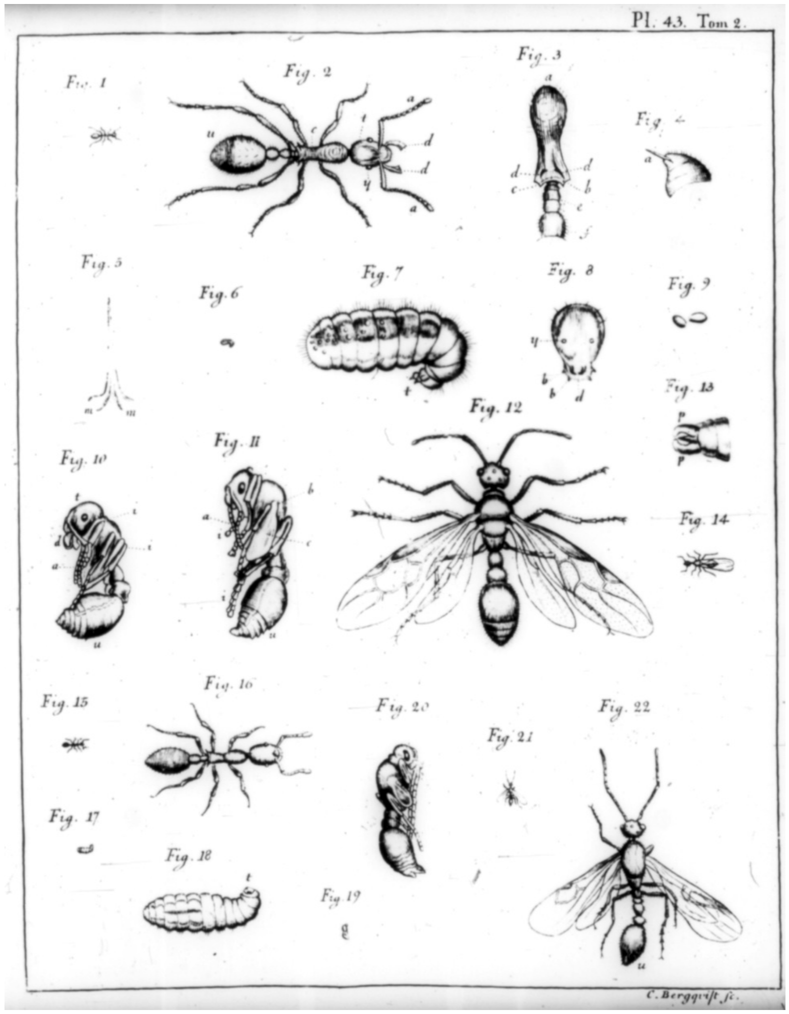

Fig. 11. De Geer 1752–1778, II: Plate 43. Ants. Each figure is explained on pages 1174–1175.

Also in 1762, a prominent Viennese physician, Marco Anton Plencic (or Plenciz, 1705–1786), published his *Opera medico physica*, which included "perhaps a more closely reasoned discussion of [contagious diseases] than any other contemporary treatise" (Wilkinson 1984:145). There were actually four treatises in his *Opera*, the first expounding his contagion theory, and the second and third applying it to the diseases of smallpox and scarlet fever (Kruta 1975). He had studied medicine at Vienna and then at Padua, where he received his M.D. degree in 1735. If he arrived at Padua before 1730, he could have heard of Cogrossi and Vallisneri's ideas on contagion directly from Vallisneri, but even if he arrived there after Vallisneri died, chances are that the latter's ideas were still being discussed. Plencic emphasized, perhaps more than anyone previously, the importance of microorganisms that Leeuwenhoek had discovered—a drop of water might contain two or three million—and the rapidity with which they could multiply. Yet, despite the lucidity of his presentation, animate contagion lingered as a minority opinion.

Otto Frederik Müller (1730–1784) was from Copenhagen and attended its university before becoming a tutor for the son of a noble family (Spärck 1932, Snorrason 1974). He traveled with the family around Europe, became interested in natural history, and became a member of several national scientific societies. In 1773 he married into wealth and had the leisure to devote his time to publications, culminating in his *Zoologiae Danicae* (two volumes by him, 1779–1784, and two by later naturalists, 1806). He had studied theology in college and studied nature within a natural theology context. His *Fauna insectorum Fridrichsdalina* (1764) described 858 insects, spiders, and centipedes on the Frederiksdal estate where he tutored. He next described 1100 species in *Flora Fridrichsdalina* (1766). From 1773 until his death he studied a wide variety of invertebrates, especially microorganisms and other neglected phyla, and became known as the Danish Linnaeus. Müller's studies on marine biology will be discussed in Part 34.

We met Johann Christian Fabricius (1745–1808) in Part 29 (Egerton 2008*b*), concerning his treatise on plant diseases (1774). He studied for two years under Linnaeus in Uppsala and considered those years formative of his outlook and understanding (Jespersen 1946:35). Although Danish, in 1775 he became professor of natural history at the University of Kiel, now in Germany, where he remained for the rest of his life (Landin 1971). He had a global interest in insects, and his research took him yearly to other universities and museums in western Europe to study specimens and literature unavailable in Kiel (Armitage 1958). His vast entomological publications, in German or Latin, were mainly descriptive and systematic: he named and described some 10,000 species (Essig 1965:622–625, Tuxen 1973:109–111). The first of these publications, *Systema entomologicae* (1775), replaced Linnaeus' classification based on wings with a more natural one based on mouthparts, which Linnaeus had actually suggested in *Systema naturae* (edition 2, 1740). One biographer thinks that Fabricius' *Philosophia Entomologica* (1778), patterned after Linnaeus' *Philosophia Botanica* (1751), was his "most important book of all and one of the most important books in entomology of all times" (Tuxen 1967:5). By 1781, Fabricius was an evolutionist to the same extent that Linnaeus and Buffon were (Jespersen 1946:44–46). That is, he thought species can change through hybridization or by changing location and being modified by the new environment. He developed these thoughts further in his *Resultate Natur-Historischer Vorlesungen* (1804), but in doing so, Jespersen suggests (1946:53), he may have drawn upon Lamarck's *Recherches sur l'organisation des corps vivans* (1802).

Peter Simon Pallas (1741–1811), whom we met in Part 27 (Egerton 2008*a*) as an explorer in Russia, was the son of a professor at the Berlin Collegium Medico-Chirurgicum, and he studied there and in three other universities, 1754–1759, and in 1760 received a doctorate in medicine at the University of Leiden with a dissertation on parasitic worms (Esakov 1974, Wendland 1992). In it Pallas listed the known species of helminths and revised Linnaeus' classification of them. Foster (1965:13) considers this dissertation his major contribution to parasitology, but if so, it was certainly not his only significant contribution. In an 18-page article on bladder worms, included in his 200-page *Miscellanea zoologica* (1766), he also made two important contributions, as Grove explains (1990:323–324)

> *Firstly, by classifying 'hydatids' into non-adherent and adherent forms, he managed to separate cystic worms from serous cysts, respectively. Secondly, he renewed awareness of the morphological similarities between cystic worms and the heads of tapeworms.*

However, he thought that all cystic worms were of a single species, *Taenia hydatigena*, and that they assumed different forms, depending on the species of their host. Pallas also described the parasites of Russian birds, mammals, and fish in his travel volumes (Théodoridès 1966:193). In 1781, he reported an experiment in which he inserted the eggs of tapeworm *Dipylidium caninum* into the abdomen of a puppy and a month later obtained short tapeworms from the pup. Parasitologists who repeated this experiment did not confirm it (Grove 1990:41, 364–365). Nevertheless, Pallas clearly stated that parasites enter the body as eggs with food, and that some kinds move out of the alimentary canal through blood vessels to other locations within the body (Leuckart 1886:26).

Scientific societies during the 1700s played very important roles in advancing the understanding of invertebrate life histories (Bodenheimer 1928–29:II, 79–133). Lepidopterists in England formed the world's first Society of Aurelians by 1740 (Allen 1978:14–15, Salmon 2000:30–35, 398). We saw in Part 28 (Egerton 2008*b*:170) that insect pollination discoveries began in 1750, but aroused little interest among naturalists. Parasites did arouse interest. In 1780 the Academy of Science of Copenhagen announced a prize for the best essay "Concerning the seeds of intestinal worms; whether tapeworms etc., are inborn in animals or enter from the outside" (Foster 1965:15). There were two winners, of a gold and a silver medal, and both winners believed that internal parasites arose spontaneously inside their hosts. The gold medal went to a Berlin physician, Marcus Eliesar Bloch (1723–1799), whose *Abhandlung von der Erzeugung der Eingeweidewürmer* (Treatise on the Generation of Intestinal Worms, 1782), with 10 plates, was translated into French in 1788. Bloch also published *Allegemeine Naturgeschichte der Fische* (General Natural History of Fish, 12 volumes, 432 color plates, 1782–1795), so he must have been interested in parasites of fish as well as of humans. His *Abhandlung* provided 12 arguments supporting the idea of spontaneous generation of parasitic worms within their hosts (quoted in English, Farley 1972:106–107), even though he knew they produced eggs, and he could have known that Spallanzani had discredited the idea of spontaneous generation of microorganisms (Egerton 2008*c*:235). Bloch classified tapeworms according to whether they had hooks on the head ("armatae") or not ("inarmatae") and described 16 species of the former and 4 of the latter (Grove 1990:387).

The silver medal went to Rev. Johann Goeze of Quedlinburg, Germany, whom we just met as translator of de Geer's *Mémoirs*. Goeze had a microscope. His *Versuch einer Naturgeschichte der Eingeweidewürmer Thierischer Köper* (Attempt of a Natural History of Intestinal Worms in Animal Bodies, 1782) was a longer work than Bloch's, having 471 pages and 43 plates. Pallas had suspected that echinococci were related to tapeworms, and Goeze confirmed it by describing scolices of echinococcal cysts and their similarity to heads of tapeworms (Grove 1990:324). He named it *Taenia visceralis socialis granulosus* (=*Echinococcus granulosus*). He also reported that the opening at the side of each proglottid was not a mouth or an airway but was for reproduction (translated in Keanet al.1978:II, 621–622)

> *On the mature lower segments the marginal openings in part project so far that the protrusion and the indented osculum can be seen with the naked eye. I inserted a horse hair, and afterward I pulled off the surface with fine instruments until I saw with pleasure under the magnifying glass that the hair was in the transverse canal that led to the ovary.*

Since all the tapeworms he examined had eggs, he wondered if they were hermaphroditic.

There had been an epidemic at Göttingen in 1761 (probably cholera), and during an autopsy of a girl, a medical student opened her caecum and several worms crawled out. They were given to Dr. Johannes George Roederer (1726–1763), who described them as a new species, "trichuris," to the Göettingen Academy of Science, which published his account and illustration (in English, Kean et al.1978:II:361–362). Roederer described the two sexes, but thought they were different species, and he mistook the head for the tail. In 1771 Linnaeus named it *Ascaris trichiura* (now *Trichuris trichiura*) and Goeze identified correctly the head and tail (Grove 1990:457).

Fig. 12. Johann Christian Fabricius, published 1797.

Physicians were sometimes asked to see if they could cure sick livestock, but eventually that casual approach seemed inadequate. The first veterinary school was founded in 1762 at Lyon, France, by a bored lawyer, but enthusiastic horseman, Claude Bourgelat (1712–79), and he organized another school near Paris in 1766.

Rinderpest was a problem in Scandinavia in 1763, which inspired the Swedish government to send one student of surgery and two of medicine on scholarships to Lyon. One of the medical students was Peter Christian Abildgaard (1745–1801), who returned to found the Danish Veterinary School in Copenhagen in 1773 (Stamm 1932, Wilkinson 1992:65–70). There, he conducted research in parasitology, and in 1789 he founded the Danish Natural Science Society. In the first volume of the journal he founded (1790), he announced that a cestode worm that lives in the intestine of sticklebacks had no reproductive organs and resembled tapeworms he had found in mergansers. He suspected that these worms in sticklebacks might be immature tapeworms that also lived in the ducks, so he tested this idea (translated in Kean, Mott and Russell,1978:II, 7).

> *I collected a great number of stickle-back fishes (small fishes) and for three days I fed those to two ducks. After another three days I killed the ducks and opened their intestines. In one of the ducks' intestines I found 63 pieces of the tapeworm from the fish; they were all living and more active and faster in their movements than those taken from the belly of the fishes. They had the same length and shape as in the before-mentioned seabirds. In the other duck I found only one tapeworm which was living, but not as active in its movements as the ones from the first duck…*

Unfortunately, his Danish publication did not attract the attention it deserved.

The century ended as it began, with a treatise on parasitic worms that repudiated the spontaneous generation of internal parasites. Valeriano Luigi Brera (1772–1840), professor of medicine at the University of Pavia, wrote a treatise on parasitic worms as causes of human illnesses (1798, German 1803, French 1804), which apparently first suggested that people become infected from their food (Foster 1965:8, translated from the French edition, p.125): “Perhaps in time more happy observers will discover the eggs of the principal human worms in the bowels of the animals from which we take our daily food.” He also rejected the idea that parasites might be normal or harmless or necessary for health. In other respects his book was little advanced from Andry’s and Vallisneri’s at the beginning of the century. He still believed that the worms or their eggs might be transmitted to a fetus in the uterus or in breast milk to infants, and he believed, incorrectly, that tapeworms possess their total number of segments in their earliest stages and do not add segments later (Hoeppli 1959:106). Brera was a prolific author of medical books and probably was taken seriously.

Some naturalists during the 1700s studied “invertebrates” out of fascination with species they encountered—Leeuwenhoek, Merian, Marsigli, Trembley, Muller, Fabricius. Other naturalists were motivated partly by fascination and partly by practical concerns—Réaumur, de Geer, Bonnet. However, the very substantial European investment in the study of insects and animal parasites made during the 1700s was strongly motivated by agricultural and medical problems. Connections were even made between agricultural and medical problems, especially when livestock and humans seemed to suffer from similar diseases. Medical schools have existed since antiquity, but veterinary schools first arose during the 1760s, in France. Veterinary schools benefited both from progress in human medicine, and contributed to it by encouraging studies on parasites of livestock that had human implications. Many aspects of a germ theory of disease were explored during the 1700s, but it remained a minority opinion. Six more decades of evidence were accumulated in the 1800s before the germ theory became firmly established. Nevertheless, naturalists during the 1700s produced an extensive literature that provided a foundation for that eventual achievement.

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