Commentary

A History of the Ecological Sciences, Part 19: Leeuwenhoek's Microscopic Natural History

There were five outstanding microscopists in the second half of the 1600s: Robert Hooke (1635–1703), Nehemiah Grew (1628–1711), Marcello Malpighi (1625–1694), Jan Swammerdam (1637–1680), and Antoni van Leeuwenhoek (1632–1723). All except Swammerdam had close ties to the Royal Society of London. Leeuwenhoek was the least educated but most persistent of them (Wilson 1995, Fournier 1996, Jardine 1999). The others published their findings during several decades, but by 1700 he was the only one still at it, and he continued this research until his death.

Fig. 1. Antoni van Leeuwenhoek at middle age.

Leeuwenhoek's father was a prosperous basket-maker in Delft who died when Antoni was six. In 1648 Antoni was apprenticed to a cloth merchant in Amsterdam. He returned home about 1654, married, and opened a shop to sell cloth, buttons, thread, and other goods.

He became a respected citizen and held several civic posts, and his close contacts included physicians and others better educated than he (Dobell 1932, Schierbeek 1959, Heniger 1973). His next-door neighbor was a physician, Cornelius 's Gravesande, who became the city's anatomist; Leeuwenhoek began attending his dissections in 1668, and in 1681 when Cornelius de Man painted a group portrait entitled "The Anatomical Lesson," he portrayed Leeuwenhoek standing behind 's Gravesande (Leeuwenhoek 1939–1999, III:Plate 1, van Berkel 1982:190–191).

Leeuwenhoek saw a copy of Hooke's *Micrographia* (1665) and—though he could not read the English text—became intrigued with the illustrations of microscopic investigations. He began making his own lenses and microscopes in 1673, and another Delft physician, Rainier de Graaf, wrote to the Royal Society of London (during the third Dutch–English war) on 28 April 1673 to inform its members that Leeuwenhoek made microscopes that excelled others available. His single-lens microscopes were more powerful than the double-lens ones then in use (Van Zuylen 1982). Along with de Graaf's note were Leeuwenhoek's first written observations, which the Society's first secretary, a German living in London, Henry Oldenburg, translated into English and published in the Society's *Philosophical Transactions*.

Fig. 2. Delft's main street; in the distance is the tower of Old Church, where Leeuwenhoek is buried (Dobell 1932:Plate 4).

Leeuwenhoek's first of several different observations were on mold on skin, flesh, and other things. In this he had been preceded by Hooke, who not only described mold as seen under his microscope in greater detail than Leeuwenhoek, but also illustrated it (Hooke 1665:125–127). Additionally, Leeuwenhoek described louse anatomy and several parts of bee anatomy (and provided illustrations of bee stings), both of which Hooke had also described and illustrated (Hooke 1665:163–165, 211–213). Hooke could have argued that Leeuwenhoek's finds were redundant and therefore unworthy of publication, but instead the Royal Society not only published them, but also sent encouragement for him to continue his researches. With that encouragement he went on to become first of the founders of microbiology. All the other contemporary microscopists studied the microscopic structure of macroorganisms, as did Leeuwenhoek (Cole 1944:265–270), but he alone discovered the living world of microorganisms (Dobell 1932, Schierbeek 1959:58–79, Yount 1996). (Hooke's discovery of fossil foraminifera shells and microspores of mold pre-

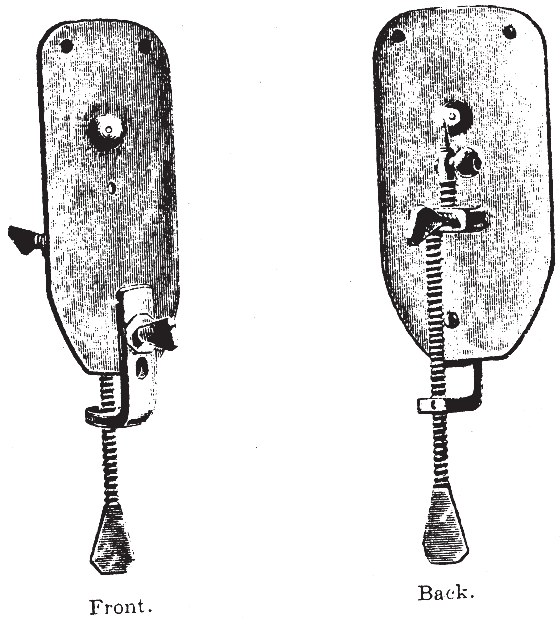

Fig. 3. One of Leeuwenhoek's single-lens microscopes, drawn by John Mayall (1886). The single lens is fastened between two metal plates, and the screws are used to position the examined object before the lens.

ceded Leeuwenhoek's investigations [Bardell 1988, Egerton 2005*a*], but one may doubt that those discoveries made him a founder of microbiology.)

Although Leeuwenhoek published letters in the *Philosophical Transactions of the Royal Society of London* for the rest of his life, the *Philosophical Transactions* did not always publish an entire letter, and it omitted publishing a few. Leeuwenhoek wrote some letters on a single topic, but most of them discussed several topics. Collected Dutch editions of his letters began to appear in 1684, and Latin editions in 1685 (Dobell 1932:390–397, Schierbeek 1959:205–209), which included letters that both did and did not appear in the *Philosophical Transactions*. About a century later, Samuel Hoole translated the published Dutch letters into English (1798–1807), but re-arranged them so that fragments of different letters on the same subject are grouped under topical headings; he did so without dating the fragments. He did provide an index, but no table of contents. Since his translation is reliable (Dobell 1950), I reprinted it in 1977, adding a brief introduction and bibliography. The various editions and translations constitute a bibliographic nightmare, but Francis J. Cole (1937) has provided an excellent guide, both to Leeuwenhoek's publications and their contents. In 1939 a committee of Dutch scientists began publishing the definitive edition of Leeuwenhoek's letters—with Dutch and English text on facing pages—and by 1999, 15 of the projected 19 volumes had appeared. Anyone having access to this set of large volumes can dispense with earlier editions for letters written by 1707, but those who lack access to it or wish to consult letters written after 1707 can use Cole's guide with either Leeuwenhoek's letters in the *Philosophical Transactions* or with Hoole's translation, or both.

In a letter to Oldenberg, on 7 September 1674, Leeuwenhoek reported that he had gone to Berkelse Lake and placed some of its water under his microscope. He discovered at least three forms of life: green streaks in a spiral (now called *Spirogyra*, a green alga), and two kinds of animalcules—apparently what we call rotifers and *Euglena viridis*. In reporting his discovery of

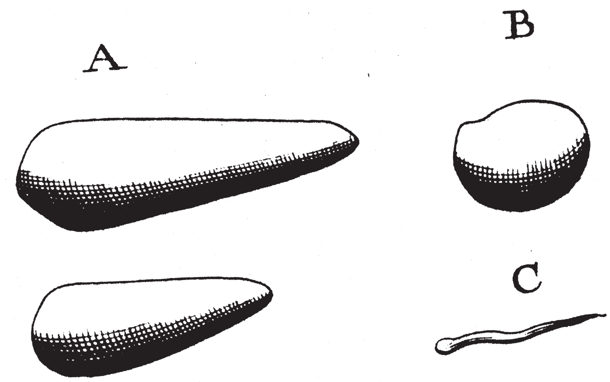

Fig. 4. Leeuwenhoek's simple illustration of animalcules from frogs, which we call protozoa. A is *Opalina dimidiate*, B is *Nyctotherus cordiformis*, and C is perhaps a larval nematode. Drawn for the Dutch edition of his letter of 16 July 1683 (Dobell 1932: Plate 23).

Fig. 5. Leeuwenhoek's Figs. 1–2: bdelloid rotifers (*Philodina roseda*), and Fig. 3, the protozoan ciliate *Coleps* (letter of 9 February 1702, originally published in 1702; reprinted from Leeuwenhoek 1939–1999, XIV:Plate II).

microorganisms, he encountered two problems that he could never handle very precisely: the naming of distinct species and their body parts. Leeuwenhoek was not a draftsman, and his brief verbal accounts aroused both curiosity and skepticism among members of the Royal Society. He hired a draftsman to illustrate his findings, and in 1683 published illustrations of protozoa (Fig. 4), which are of limited interest since the only details are their shapes.

However, by the time he wrote his letter of 9 February 1702, in which he had the ("animalcule") ciliate *Coleps* illustrated (Fig. 5), more details were drawn. He had also illustrated a rotifer (Fig. 8), and if not *Spirogyra*, at least the alga *Volvox* (Fig. 6).

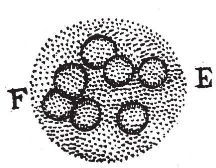

Fig. 6. Now called *Volvox*, illustrating Leeuwenhoek's letter of 2 January 1700 (*Royal Society of London Philosophical Transactions* 22:facing p. 483).

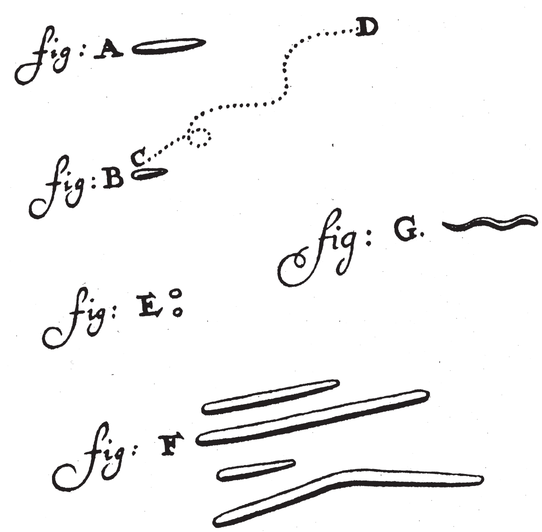

Fig. 7. Bacteria from a human mouth, letter of 17 September 1683. A is a motile *Bacillus*, B is *Selenomonas sputigena*, with C…D its path, E is Micrococci, F is *Leptothrix buccalis*, and G is a spirochaete, probably *Spirochaeta buccalis* (Dobell 1932:Plate 24 or Leeuwenhoek 1939–1999, IV:Plate 8).

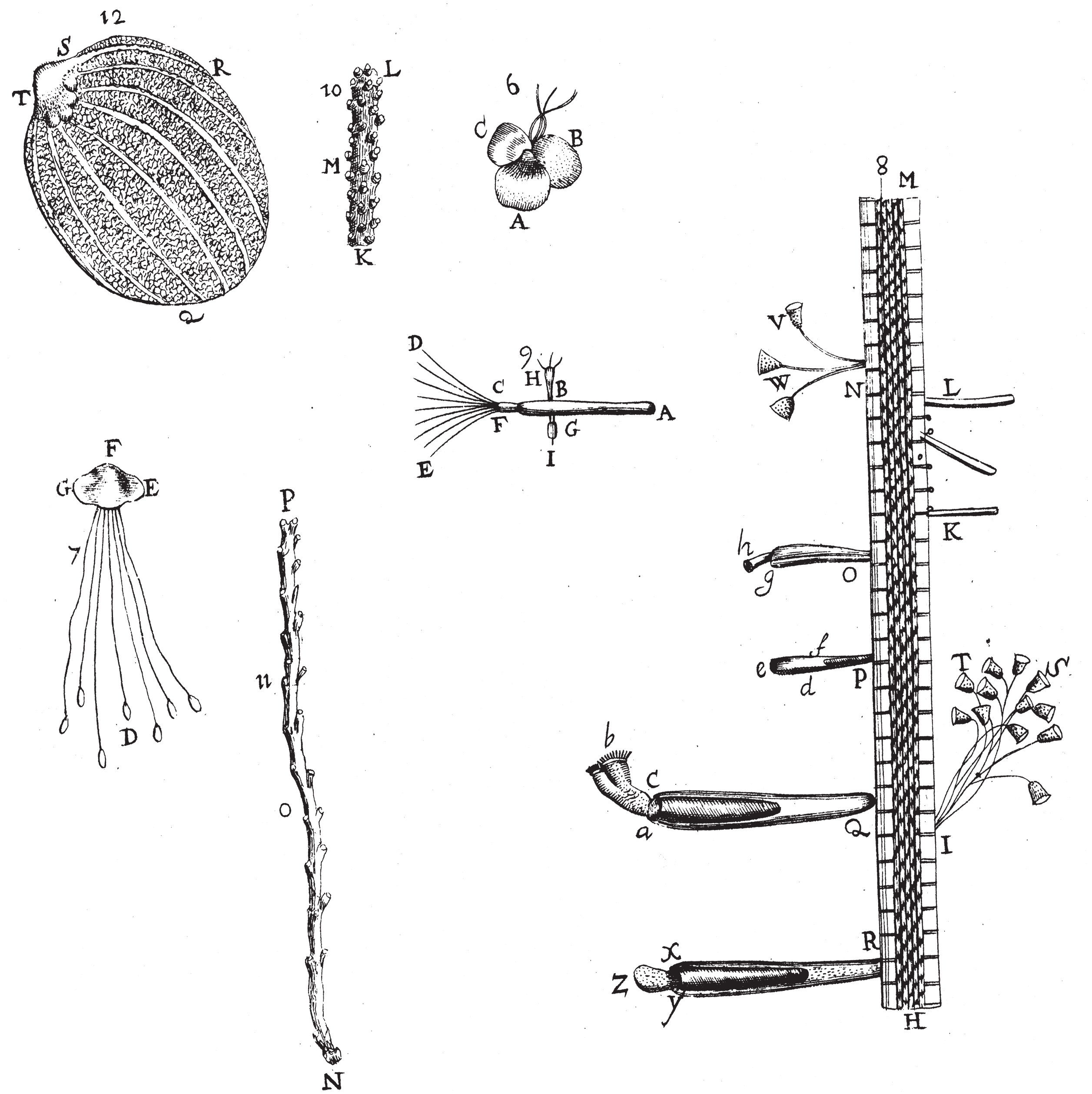

Fig. 8. Duckweed from a Delft canal with associated animalcules, from Leeuwenhoek's letter of 25 December 1702. The long structure in his Fig. 8 is part of a duckweed root, as seen under the microscope, with animalcules (rotifers, hydra, vorticellids) attached. For identifications, see Dobell 1932:277–278, Leeuwenhoek 1939–1999, XIV:Plate IX, or Ford 1982 (from *Royal Society of London Philosophical Transactions* 23:facing p. 1291).

On 14 June 1680, he reported his discovery of the incredibly small animalcules that we call bacteria; later he also had them drawn (Fig. 7). Since the bacteria came from a healthy person's mouth, he did not think they caused disease. Some biologists have doubted that he could have seen bacteria; however, some of his microscopes still exist and have been used to show that he could have (Ford 1991).

Leeuwenhoek was an important experimenter (Meyer 1937)—a worthy successor of Redi—though by modern standards his experiments seem quite simple. For example, he discovered minute "vinegar eels" (*Turbatrix aceti*) in vinegar, and also several other kinds of microorganisms in pepper water (peppercorns submerged in water). Later he added one part of vinegar with "eels" to 10 parts of pepper water and found that all the animalcules in the pepper water died, but the vinegar eels continued to flourish (9 October 1676, Leeuwenhoek 1939–1999, II:125–129). As a merchant, Leeuwenhoek learned to note the size and quantity of goods, and he took this concern into his scientific studies. He developed fairly reliable methods of measurement. He compared the lengths of some microorganisms to the diameter of hairs on cheese mites. To calculate the number of microorganisms in a drop of water, he assumed that a drop of water is the size of a pea, and that a millet seed is 1/91 as large as a pea. He then drew into a pipette a quantity of water the size of a millet seed and divided that amount of water into 30 parts along the pipette, and estimated the animalcules in 1/30 of the water. Finally, he made the calculations to obtain the number in a volume of water the size of a pea. In this case, he estimated there were 2,730,000 animalcules (23 March 1677, Leeuwenhoek 1939–1999, II:119–201).

Leeuwenhoek never tired of making discoveries with his microscopes, but he also developed theoretical interests. One of the strongest such interests, which he constantly discussed, was the idea of spontaneous generation of life, against which he collected much evidence, beginning also with his letter of 9 October 1676. Dobell (1932:136, note 1) interpreted some comments in this letter as showing Leeuwenhoek debating with himself the possibility of spontaneous generation before he reached his firm opposition to the idea seen in his later letters, and Ruestow (1984) agreed. However, Leeuwenhoek's modern editors think this is a misunderstanding of Leeuwenhoek's less than crystal-clear comments (in Leeuwenhoek 1939–1999, II:101), and Smit (1982) appears to agree with these editors, since he does not discuss any ambivalence in this letter. The occasion for Leeuwenhoek raising the question of spontaneous generation was his discovery of microorganisms in rainwater that had stood in a cask for several days. A later example of Leeuwenhoek's observations discrediting spontaneous generation is in a letter written 9 February 1702, stating that on the previous 25 August he had found animalcules (rotifers) in water from a house gutter, in which he observed that they became dry for a time, and then when wet again, their bodies swelled and they swam off.

He thought that if one did not know that they were dormant in the dry matter and then it became wet, one might think they arose spontaneously in the wet matter.

Another of Leeuwenhoek's strong theoretical interests was in reproduction. This interest was sharpened by the discovery of spermatozoa ("animalcules" to him). A medical student, Johan Ham, told him in the summer of 1677 about his discovery of animalcules in the semen of a man with venereal disease; he believed they arose from the putrefaction of the semen. Leeuwenhoek refused to accept Ham's idea on their origin, since that implied spontaneous generation. His study of his own semen (from his marriage bed, he informed the Royal Society) showed that spermatozoa are natural to semen. He reported his observations to the Royal Society in a letter written in November 1677, and in a subsequent letter of 18 March 1678 he included drawings of both human and dog sperm (Leeuwenhoek 1939–1999, II:280–293, 346–349, Plates 16–17). During his lifetime, he described sperm from 30 kinds of animals: 7 mammals, 2 birds, 1 amphibian, 7 fish, 11 arthropods, and 2 mollusks (Cole 1937:8). He soon concluded that sperm are embryos, and he rejected his townsman de Graaf's conclusion that embryos arise after intercourse when eggs from mammalian ovaries enter the Fallopian tubes (Lindeboom 1982, Ruestow 1983). Leeuwenhoek thought ovaries are nonfunctioning in females, just as nipples are nonfunctioning in males. In a letter dated 13 June 1679, he rejected an Aristotelian report that mice reproduce by parthenogenesis (Leeuwenhoek 1939–1999, III:73–83), but in a long letter written on 10 July 1695, he reported (Leeuwenhoek 1939–1999, X:269–301) his discovery of parthenogenesis in aphids. He returned to this subject in subsequent letters (Cole 1930:90, 1937:224, Egerton 1967:6–16). After discovering parthenogenesis, he should have rethought his belief that embryos are contained in sperm. On other occasions he admitted his mistakes, but concerning parthenogenesis he went to extremes to avoid doing so (Cole 1937:12–13, Schierbeek 1959:105–106).

Still another of Leeuwenhoek's persistent interests was in parasites. We saw in Parts 17 and 18 (Egerton 2005*b*, *c*) that this interest was fairly common among contemporary naturalists and physicians—focused on the natural history of parasites and interactions with hosts, without the parallel development of a theory of parasitology. In those days, most people had some first-hand knowledge of fleas and lice, and we have already seen that in his first letter to the Royal Society he had included observations on louse anatomy. He reported further on lice in a letter dated 15 February 1677, which is lost. In his letter of 5 October 1677, he reported observations on the development and metamorphosis of fleas. He had put several in a container and found that a flea can lay 15 or 16 eggs in 24 hours. He then carried enclosed eggs in his pocket and found they hatched in 8 or 9 days. He described the external anatomy of a larva and compared it to that of silk worms. He thought Swammerdam had mistaken flea droppings for eggs (Leeuwenhoek 1939–1999, II:245–253). Neither of these microscopists distinguished the different species of fleas they studied (Van Bronswijk 1982). In autumn Leeuwenhoek observed larvae spin cocoons, and a few days later he opened some cocoons and found inside weak fleas, which he thought were affected by the cold, indicating that they would not have come out by themselves until the winter ended (14 January 1678, Leeuwenhoek 1939–1999, II:319). On 12 November 1780, he sent observations on flea sperm (Leeuwenhoek 1939–1999, III:327). He reported further on flea anatomy and physiology in letters of 22 January 1683, and 15 and 27 October 1693. A goal of his flea studies was to determine the time period for each stage in the life cycle from egg to adult, which he finally achieved in his letter of 15 October 1693 (Leeuwenhoek 1939–1999, ?:211–227). He allowed fleas to suck blood from his hand in order to see the effect of food on egg laying.

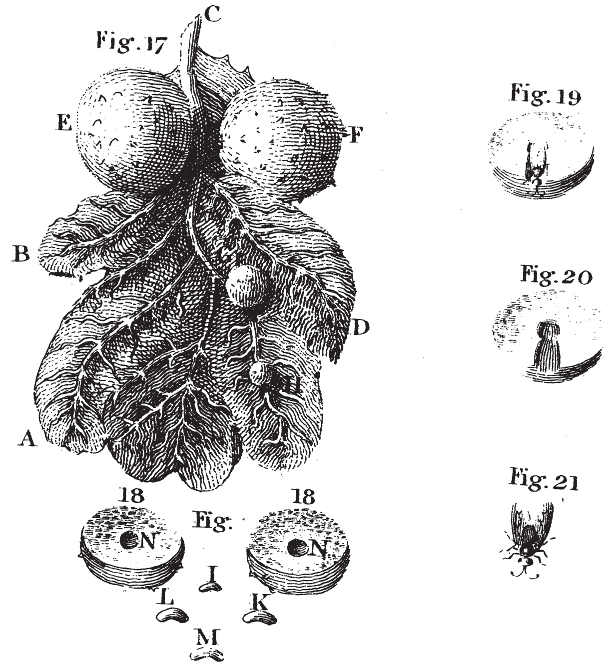

Fig. 9. Oak leaf with galls, cross-sections of a gall, four larvae, and adult fly (Leeuwenhoek, Hoole I:Plate 5, Figs. 17–21).

Leeuwenhoek examined flatworms (flukes) from the livers of diseased sheep under a microscope and suspected that the sheep got the worms from drinking rainwater that collected in fields (21 February 1679, Leeuwenhoek 1939–1999, II:417–419). He pursued the subject no further until 1698, when he and Professor of Medicine Goderfridus Govard Bidloo (1649–1713) of Leiden University (van der Pas 1978) discussed liver flukes in sheep. Both then wrote up their observations for publication, with Leeuwenhoek sending his to the Royal Society and Bidloo sending his to Leeuwenhoek, who had them published in Delft. Bidloo sent with his letter an overly precise drawing of a fluke, which shows two eyes, a heart, a circulatory system, and intestines that existed only in his imagi-

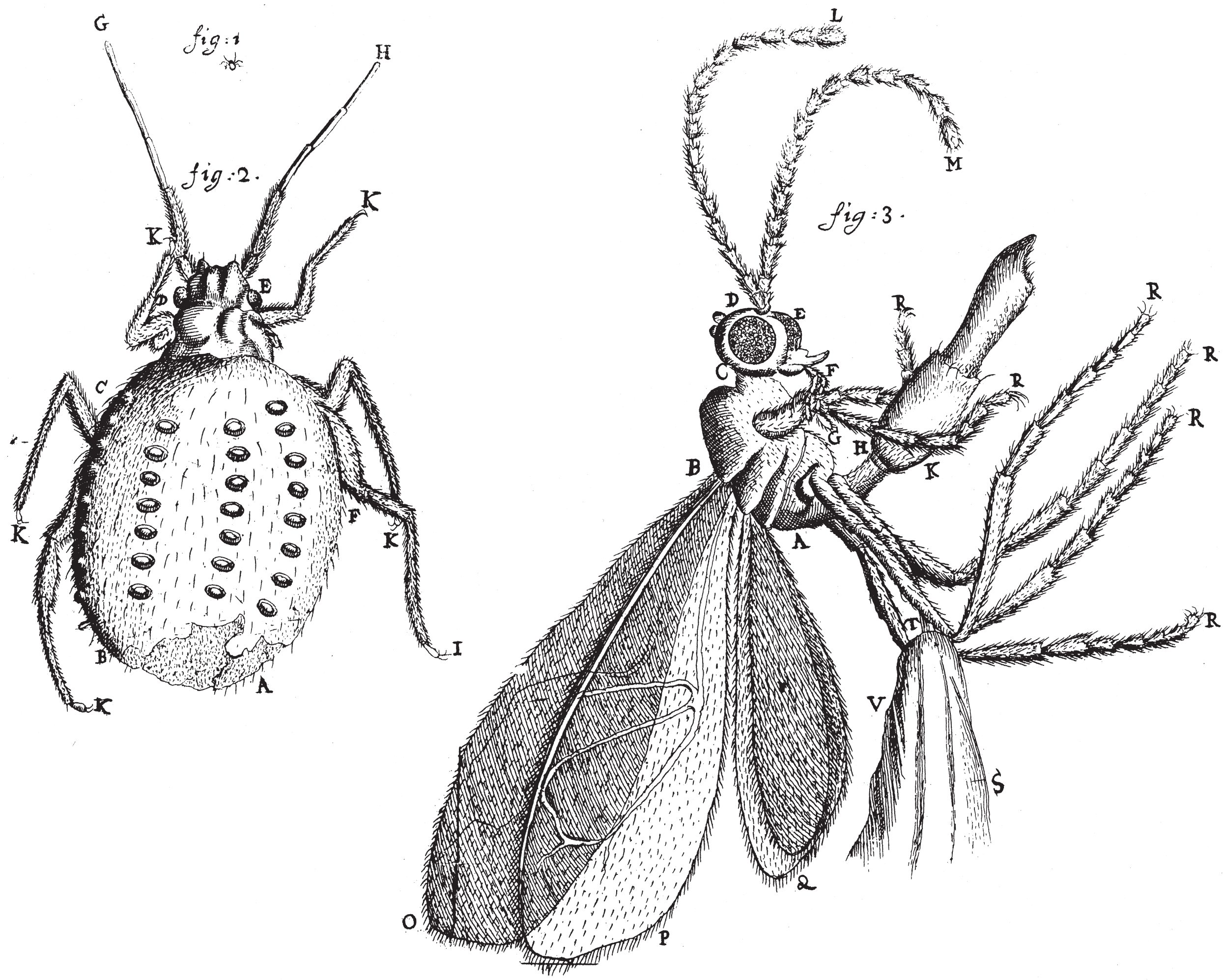

Fig. 10. Leeuwenhoek's Fig. 1 is a "green louse" (aphid) natural size; his Fig. 2 is an aphid shell seen under a microscope, from which a fly had emerged at the bottom; his Fig. 3 is a parasitic fly that emerged from an aphid (26 October 1700, Royal Society of London Philosophical Transactions 22:facing p. 655).

nation. Nevertheless, Bidloo did recognize the eggs and concluded correctly that the species is hermaphroditic. He also generalized from his observations that these worms seem to cause disease in sheep and that worms probably also cause disease in humans (Bidloo 1698, 1972). Leeuwenhoek went out and attempted to find fluke eggs in fields and ditches, where they might have been deposited in sheep feces (2 January 1700, 1939–1999, ?), but he had no way to identify them if he had found them. The fluke life cycle is so complex that it was not fully understood until the mid-1800s (Reinhard 1957).

Once when Leeuwenhoek had loose stools, he examined his feces under a microscope and described to the Royal Society the microorganisms he found (protozoa and spirochaetes or *Spirillum*), and he did not find them in his feces when he did not have diarrhea (4 November 1681, Leeuwenhoek 1939–1999, III:367–371), but he drew no conclusion about animalcules causing diarrhea.

In Holland, "gall-nuts" were imported from Aleppo, Syria for making dye. Leeuwenhoek assumed from the name that they were actually nuts, until he saw a local variety on oak trees and realized that they must be stimulated by an insect.

> *These galls were formed upon the large fibers, or vessels in the leaves, which were burst or broken, in the places where the galls were formed; so that I concluded that some insect had wounded or gnawed those vessels, and that the juices of the tree, flowing out of the wounded part, had extended themselves in globules and vessels, and thus, at length caused the formation of the gall-nut.* [14 May 1686, Leeuwenhoek 1977, I:137]

He cut open some galls and found inside a living white worm. By continuing to open others periodically, he discovered that the worms became flies. He also studied "thistle-nuts," which people carried in their pockets as health charms. He had a draftsman illustrate both kinds of galls and the associated insects (Fig. 9).

In 1700, fruit trees in Delft were infected with a great many flies, but when Leeuwenhoek examined them, he found they were associated with even more green lice (aphids), whose parthenogenesis he had discovered in 1695. The flies laid their eggs in the aphids, and later flies emerged from an aphid shell (Fig. 10).

Leeuwenhoek wanted to know not only the size and quantity of organisms he studied, but for some he eventually wanted to determine their age. He first explained briefly at the end of his letter dated 12 January 1680 (Leeuwenhoek 1939–1999, III:185) the use of annual rings to determine the age of trees, and six years later he discussed it again and sent the Royal Society an illustration of a tree seen in cross-section (Fig. 11). We saw in Part 18 (Egerton 2005*c*) that Ray explained age determination in trees in his Cambridgeshire flora (1660), but Leeuwenhoek would have been unable to read that book in the unlikely event that he ever saw it.

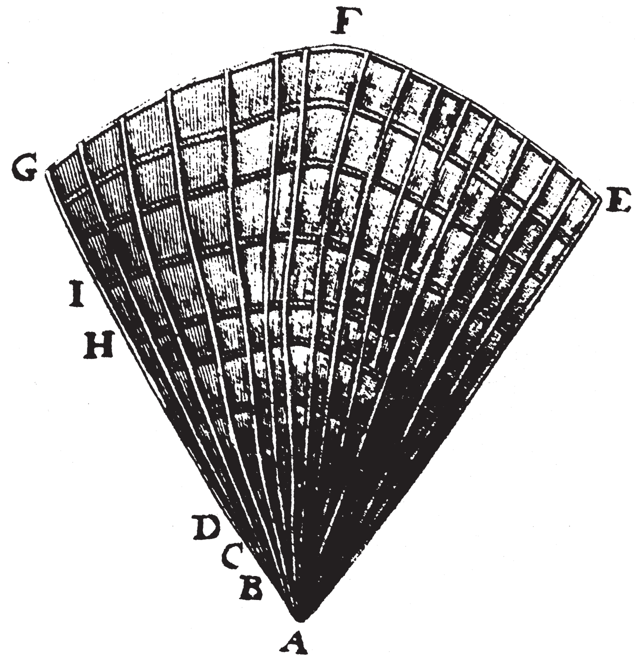

Fig. 11. Leeuwenhoek's cross-section drawing of an oak trunk was given as a pie-shaped wedge rather than in full circle as is the modern custom; he said the oak tree was 12 years old and 4 2/6 inches in diameter (written 10 July 1686, but not published until the September–October 1694 issue of the *Royal Society of London Philosophical Transactions* 18:facing p. 193).

He became interested in fish scales initially because Jews thought they could not eat eels and burbot, because each supposedly lacked scales and was therefore forbidden by Scripture. Using a microscope, he showed that they do have scales. When he examined an individual scale under a microscope he saw concentric dark lines, which he interpreted correctly as annual rings. The scale that he had drawn was thus seven years old (Fig. 12), and he assumed that this was also the eel's age.

We now know, however, that eel scales only appear at age three, and therefore the eel would have been age

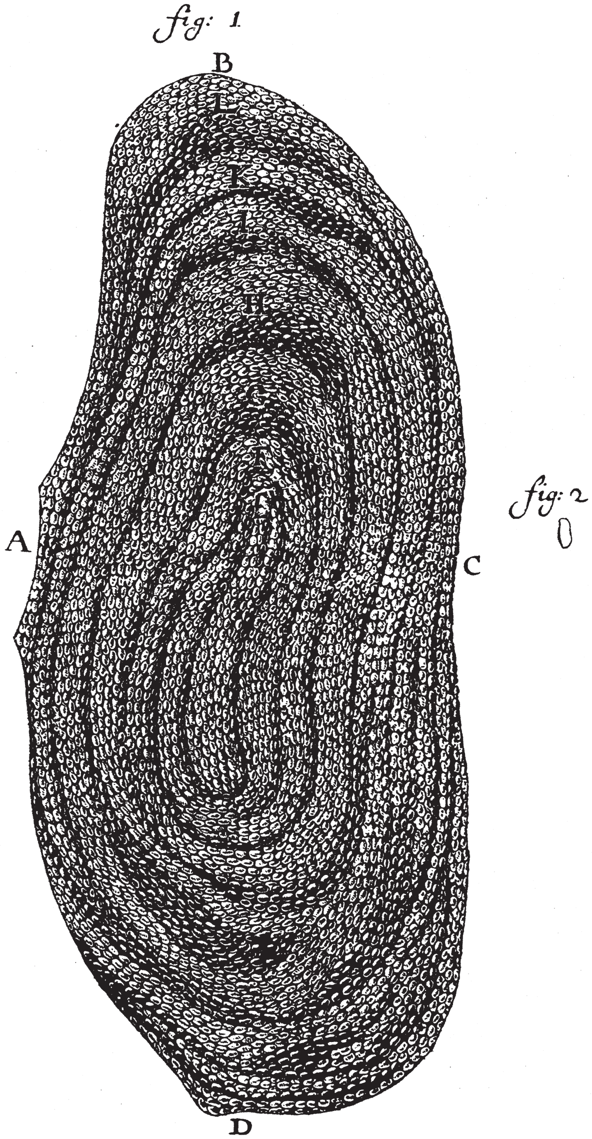

Fig. 12. Eel scale; Leeuwenhoek's Fig. 1, as drawn with a microscope, and Fig. 2 represented the actual size (written 25 July 1684, Royal Society of London Philosophical Transactions 15: facing p. 883 (1685) or Leeuwenhoek 1939–1999, IV:Plate 27).

10 or 11 (Leeuwenhoek 1939–1999, IV:293–297, and note 48). Later, he attempted to determine the age of other fish, and an elephant's tooth (Egerton 1967:9). When he turned to shellfish, he discovered that the layers of the shells were too numerous to be annual rings, and he speculated that they were laid down monthly, with the new moon (Palm 1982:159).

As a businessman and prominent citizen, Leeuwenhoek had an interest in the practical application of his investigations, and many of them were undertaken to clarify practical problems. His studies of insect life histories are examples (Bodenheimer 1928–1929, I:367–379, II:363–367, Schierbeek 1959:Chapter 6). His study of the grain weevil *Calandria granaria* in 1687 had the dual motive of studying an important pest, and also providing another opportunity to discredit the idea of spontaneous generation. On 13 March, he obtained some calandars and put 6, 8, or 9 in three vials along with 6, 10, or 12 wheat grains and carried them in a leather case in his pocket. He saw them mate on 27 March, and discovered that they lay few eggs. Comparing this to silkworms, which lay many eggs in one or two days and then die, he concluded that calandars must live longer as adults in order to lay eggs several times. He saw that females lay only one egg in a wheat grain, and he suspected that frequent stirring of stored wheat could prevent them from depositing their eggs (Leeuwenhoek 1939–1999, VII:31–33).

In the same year he also studied reproduction in a fly, probably *Calliphora erythrocephala*, which laid about 144 eggs. He followed the progress of eggs laid on 9 September and found that they emerged from pupae as adults on 12 October. He then calculated that the theoretical rate of increase over three months, assuming no mortality, resulted in 746,496 flies (written 17 October 1687, Leeuwenhoek 1939–1999, VII:81–133). This was an important step for animal demography, the first example of what Royal Chapman much later called "biotic potential" (1931:182), and Birch called "the intrinsic rate of natural increase of an insect population” (1948). Later, he calculated the potential rate of increase for other species, and speculated on factors that limit their increase, usually food or climate (Egerton 1967:14–19). He was also one of the earliest investigators of a food chain—an aquatic one that involved haddock eating shrimp and cod eating haddock (10 September 1717, Leeuwenhoek 1798–1807 and 1977, I:283–285). In an earlier letter (2 June 1700, Leeuwenhoek 1939–1999, XIII:92–95) he had discussed what shrimp ate, but he did not link that information to his 1717 letter.

Leeuwenhoek lived almost 91 years and devoted the last 50 of them to science, primarily to biology, with an impressive number of his discoveries being on natural history, many of these on what we call ecological topics. His research and publications made him famous throughout Europe, and he was highly esteemed by leading scientists of the time.

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