



CONTRIBUTIONS

Commentary

A History of the Ecological Sciences, Part 21: Réaumur and His History of Insects

On 21 November 1877, Thomas Henry Huxley gave a talk at Cambridge University, occasioned by the presentation of an honorary LL.D degree to Charles Darwin, in which he commented (Huxley 1900, I:480): “I know of no one who is to be placed in the same rank with [Darwin] except Réaumur.” Had he spoken a few years later he could have added Louis Pasteur to that tiny group of our greatest biologists. The range of sciences that Réaumur investigated was as broad as Darwin’s, and his lifelong productivity may have been comparable (Wheeler 1926:263–274, Torlais 1961, Grasse 1962, Gough 1975, Drouin 1995), though Réaumur is credited with no scientific theory like Darwin’s theory on evolution by natural selection. Réaumur is remembered for his thermometer (1731), but one historian of meteorology thinks “his work on thermometry was far below the standard of much of his other scientific work” (Middleton 1966, 1979). Perhaps so, but his thermometer nevertheless dominated France until replaced in revolutionary France by the Centigrade thermometer in 1794 (Birembaut 1958). His thermometric studies may have piqued his interest in the relationship between temperature and the rate at which insects develop. His primary fame and importance rests on his *Mémoires pour servir à l’histoire des insectes* (six volumes, 1734–1742), which is also where his significance for ecological sciences lies. Because of his studies on insect behavior, Wheeler (1926, 1936) considered him a founder of ethology.



FIG. 29.—RÉAUMUR, 1683–1757.

Fig. 1. Réaumur as a young scientist.

René-Antoine Ferchault de Réaumur (1683–1757) was from a prominent La Rochelle family, and he probably attended Catholic schools there and elsewhere before going to Paris in 1703. In Paris he studied mathematics under Pierre Varignon, who nominated him for membership in the Académie Royale des Sciences, to which he was admitted in 1708. During his career he was its director 12 times and its subdirector 9 times. French iron and steel production was backward compared to some other European countries, and the government generously supported his experiments to improve this technology. His book on iron production (Réaumur 1722) is translated into English (1956), as are his *The Art of Hatching and*

Bringing Up Domestic Fowls (Réaumur [French edition] 1749, [English edition] 1750), his incomplete memoirs on ants (1926), and part of his memoirs on bees (1800). In French, there is an excellent, if unillustrated, modern anthology of his writings compiled by his biographer, Jean Torlais, that includes extracts from incomplete memoirs on ants, spiders, beetles, frogs, and toads (Réaumur 1939:213–255). (Amphibians and reptiles fell under his concept of “insects.”) His early papers on geometry (1708–1709) were outstanding (Taton 1958), and in 1740 he drew upon mathematics in discussing the construction of honeycombs by bees (Réaumur 1734–1742, V:389, Drouin 1995:206–207). In 1709 he began studying the growth of shells of aquatic animals, and he subsequently investigated a wide range of natural history topics, including the silk of spiders (1710), making purple dye from mollusks (1711), regeneration of crustacean legs (1712), and the production of artificial pearls (1717). His movement toward entomology was gradual, and did not involve abandonment of other investigations.

Réaumur’s first notable study on insects was on the clothes moth (1728), and this led to his study of caterpillars in the first volume of his history of insects. He had already written at the beginning of the introduction to Volume I (Réaumur 1734–1742, I, 3; translated by Wheeler in Réaumur 1926:29):

I am not in the least inclined towards a precise enumeration of every kind of insect, even if it could be undertaken. It seems to me sufficient to consider those kinds which prove to us that they deserve to be distinguished...the many hundreds and hundreds of species of gnats and very small moths which exhibit nothing more remarkable than a few slight differences in the form of the wings or legs, or varieties of coloration or of different patterns of the same colours, may be left confounded with one another.

He was right about the countless species of insects, but John Ray’s approach of trying to identify and study those in one’s locality was a good strategy. Fortunately,

Réaumur’s volumes are well illustrated. Like Leeuwenhoek, he was no draftsman, but hired one or more women who were competent. His species were identified and named by Carl Linnaeus (1758:362–618) and later restudied by Vallot (1802) and Bodenheimer (1928–1929, I:415–448 and II:379–399). A few determinations remain debatable (Müller and Wheeler 1982), but that probably would have been true even if Réaumur had been more concerned with naming them himself.

Hawkmoth caterpillars refused all food except leaves of spurge. He put some of its milky juice on his tongue and soon his mouth was on fire, and washing did not relieve it. Yet hawkmoth caterpillars drank it with no ill effects. When he put caterpillars of the cabbage moth (*Mamestra brassicae*) and the common dagger-moth (*Acronycta* sp.) with young cabbages, the next day he failed to find them. Yet the cabbage leaves were gnawed. When he searched the earth in the pots with cabbages, he found them. He returned at night with a candle and found them feeding on the leaves (Miall 1912:254–255).

The first memoir of the second volume concerns the effect of temperature on the time needed for insects to develop, a topic that Swammerdam and Leeuwenhoek had briefly explored. Pupae kept in hot-houses in winter produced moths long before others kept in cool places. He also froze some caterpillars in 1736 and later discovered they were still alive when thawed (Rostand 1962a, b). Realizing that insects develop faster in warm weather, Réaumur (1734–1742, II:322–315) attempted to estimate the annual rate of increase for a butterfly, which he knew developed in about a month in warm weather. He had seen adults of the species throughout the year, but since he knew it would develop slower during the winter, he estimated that there were probably seven generations per year. Since females laid 9 to 14 eggs, he used 10 eggs in calculations. Using Leeuwenhoek’s method of calculation (Egerton 1967:2006), he showed that from one breeding pair, 156,250 individuals could be produced in the seventh generation, and that the year’s total was 195,310. Since no such rate of increase was

Pl. 2. pag. 120. Mem. 2. de l'Hist. des Insectes Tom. 2.

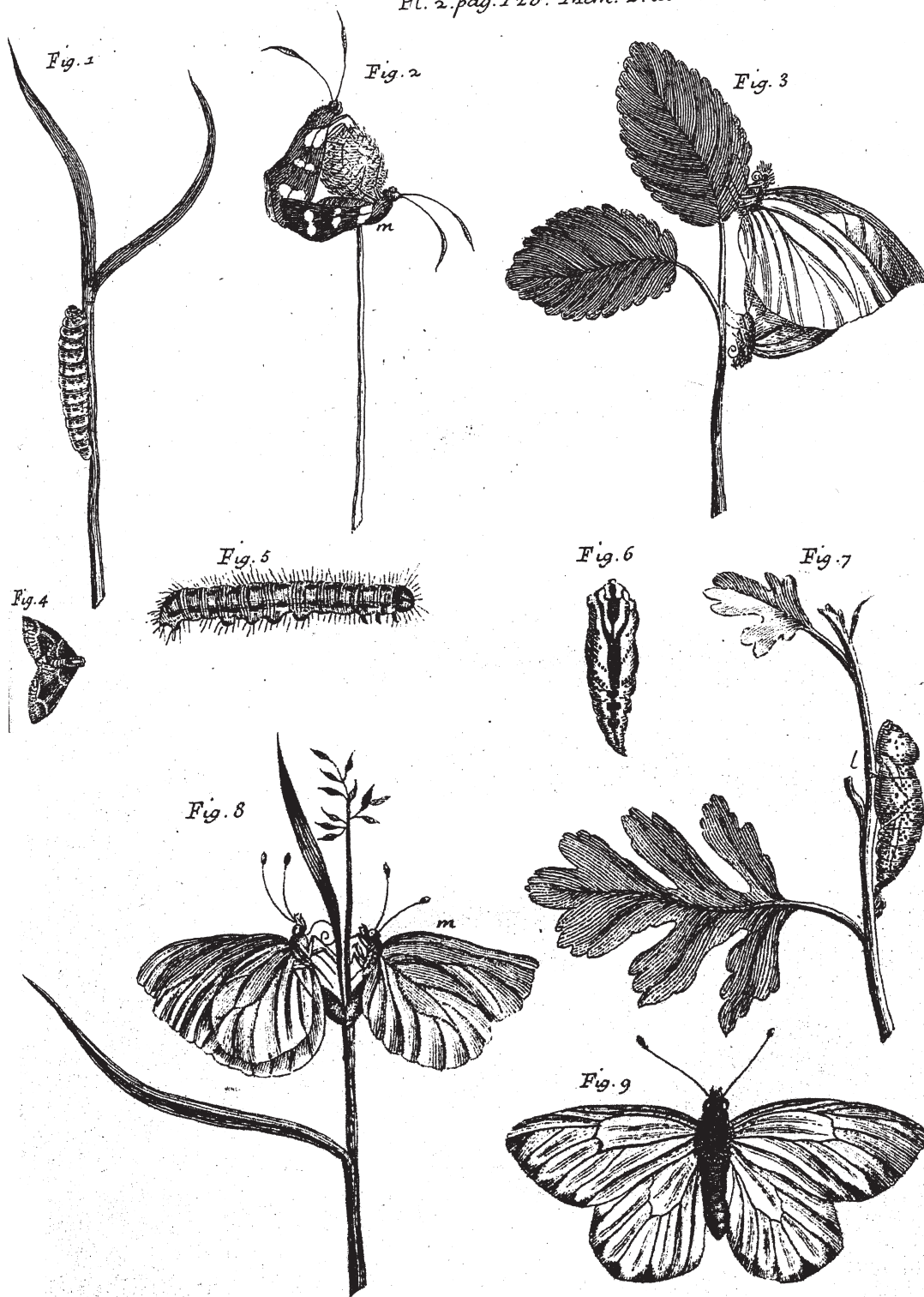


Fig. 2. Caterpillars, chrysalises, and butterflies, showing specific species attracted to specific plant species. Réaumur 1734–1742, II:Plate 2.

achieved, he concluded that a worm he described limited the increase by eating immature forms.

In a following memoir, Réaumur (1734–1742, II:335–339) discussed a plague of caterpillars (*Plusia gamma*) that had erupted throughout France in June and July 1735. The butterfly involved produced only one batch of eggs in its lifetime. The first generation of the season developed in the spring from eggs that had overwintered. This generation then produced another generation that laid the eggs that next overwintered. A female laid about 400 eggs, which meant that if there were only 20 individuals hatched in a locality in the spring, the second generation could potentially produce 800,000 eggs to overwinter. He then concluded that it was not as important to explain why a plague erupted occasionally, as to explain why it did not happen more often. First, every species of butterfly has parasites and predators, which greatly limit its numbers. Diseases and weather likewise restrict their increase. A plague year would therefore occur when weather favored the butterfly but not its diseases, parasites, or predators. This explanation was in accordance with the fact that caterpillars had been very numerous in autumn 1731, spring 1732, and in 1737. But a plague of the proportions of 1735 had not occurred during those three years because flies that lay eggs in the caterpillars had also been numerous. Réaumur repeated from Richard Bradley's *A General Treatise of Husbandry and Gardening* (1721–1724, II:221) the plausible but inaccurate statement that killing two butterflies in August before they reproduced was as good as killing 8000 caterpillars the following June.

Memoir 5 in Volume II is on leaf rollers and leaf folders. He explained that one can watch these caterpillars at work by cutting off leaves that are rolled or folded, expelling the caterpillars, and then placing them on other leaves of the same plant. They quickly work to conceal themselves using these leaves, securing their abode with silk threads.

The same leaf that provides shelter is also eaten. Tortrix caterpillars are common on oaks in summer,

and sometimes completely strip the trees of leaves. In its rolled leaf, it is screened from view by outer turns of its green case, and can eat inner turns at leisure. It must have a way to escape an enemy. It moves with great agility and often escapes at an open end of its tube, and then drops off the leaf on a silk thread; when all is quiet, it climbs back to its leaf, coiling the thread and eating it. When it outgrows one tube, it builds another; the last one becomes the chrysalis in which it changes to an adult (Miall 1912:264–265). Réaumur devoted Memoir 11 in Volume II to the enemies of caterpillars, describing in detail many of their predators and parasites. He stressed knowing which species were harmful (believing there were only about a dozen in France), and which animals attack them.

Réaumur made substantial contributions to the knowledge of parasites, studying parasitic fungi, worms, mites, and insects (Bodenheimer 1931:412–414, Théodoridès 1959a). In the preface to Volume II (1736) he reviewed claims for spontaneous generation of insects, and then agreed with Redi, Swammerdam, and Leeuwenhoek that such ideas were undermined by careful study: “No species of insect generates any insect of a species other than its own.” (Réaumur 1734–1742, II:xl). He explained that what we call entomophagos parasites arise in three ways: (a) by the parasite's eggs introduced from plant leaves, (b) by the parasite fixing its eggs on the body of the caterpillar, and (c) by the parasite laying eggs in the body of the caterpillar. He provided a clear illustration of larvae of the ichneumonid fly *Apanteles glomeratus* inside a pierid (Whites family) caterpillar (Réaumur 1734–1742, II:Plate 34, reproduced in Théodoridès 1959a: xv). Eventually he observed the flies coming from the worms in the caterpillars (Réaumur 1734–1742, II:440–442). In some larval entomophagos endoparasites he discovered ectoparasites (hyperparasites, pp. 444–445) and species that lay their eggs in the eggs of butterflies (oophagos parasites, p. 448).

Leeuwenhoek had discovered that aphids are parthenogenic (Egerton 2006), which attracted great interest. In Volume III, Memoir 9, Réaumur claimed that both

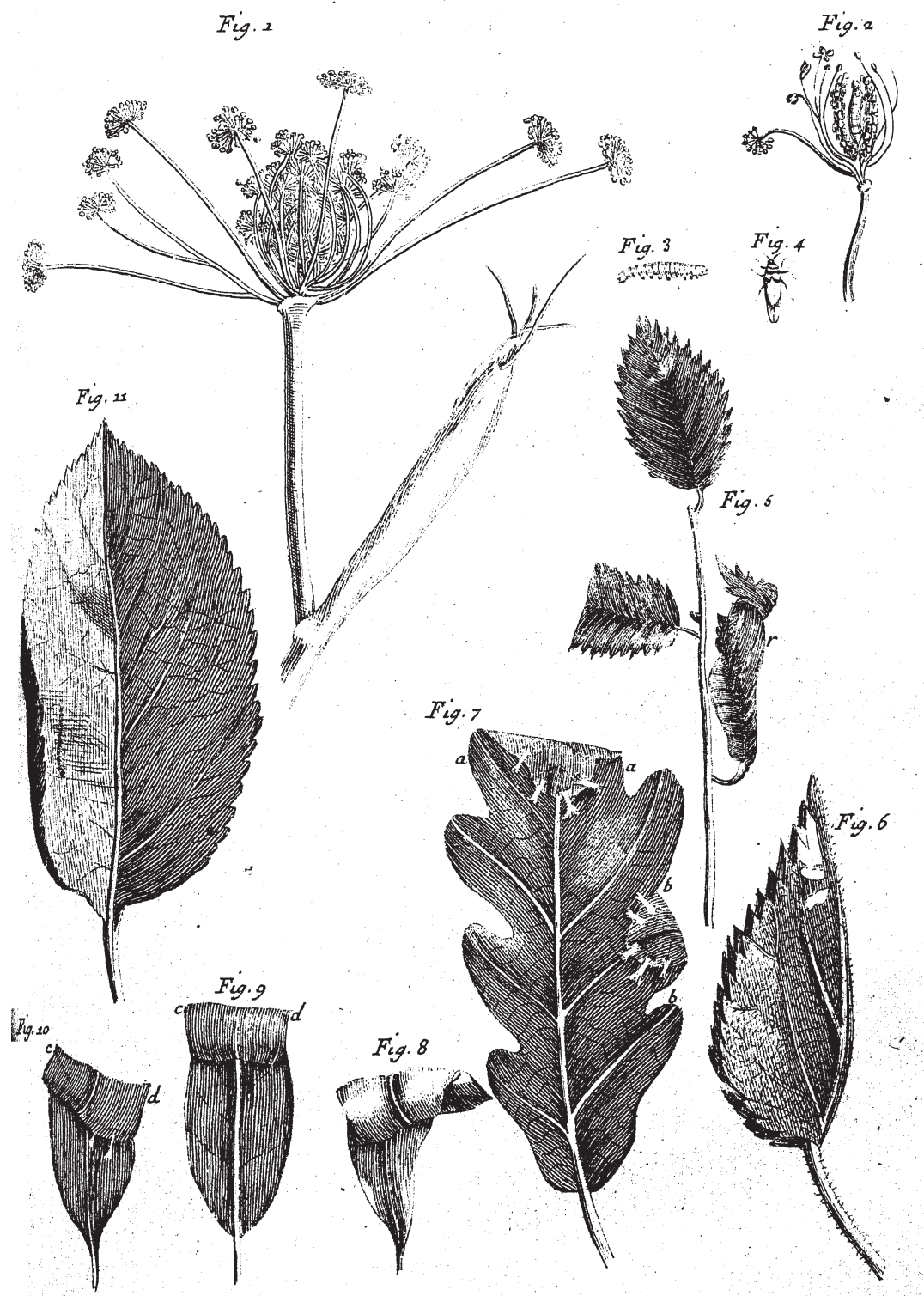


Fig. 3. Leaf rolling and folding caterpillars. Réaumur 1734–1742, II:Plate 16.

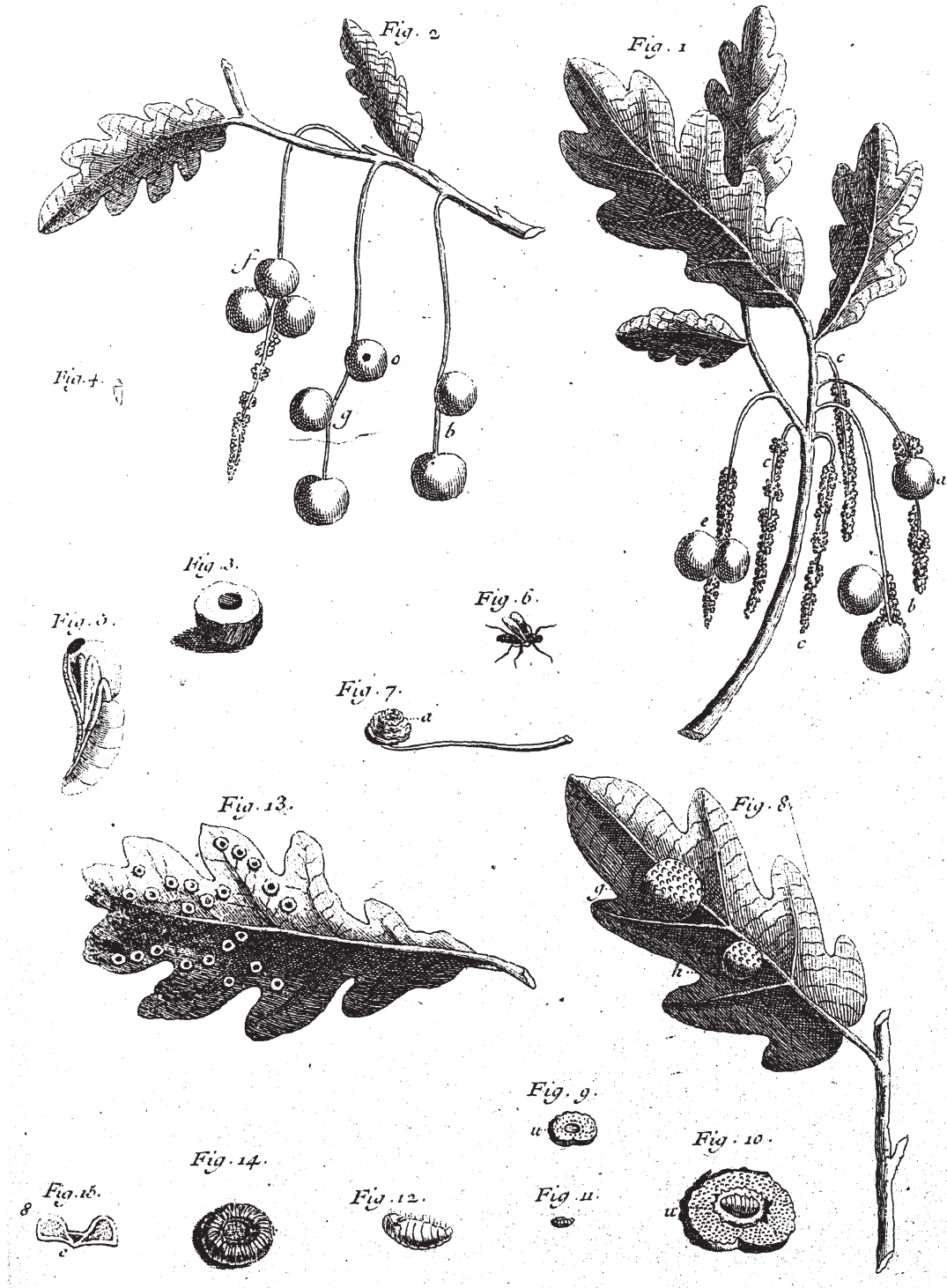


Fig. 4. Insect galls had already been studied in detail by Redi, Leeuwenhoek, and others before Réaumur, yet the subject was vast enough for him to make new discoveries. Réaumur 1734–1742, III:Plate 40. Captions (pages 521–522 for Plate 40) describe all the figures in detail.

winged and wingless aphids are adults, since both are viviparous. Leeuwenhoek had thought the wingless ones were immature and would later acquire wings. Leeuwenhoek had also concluded that ants prey on aphids (they do, rarely, on injured ones; Réaumur 1926:158), but later naturalists had concluded that ants merely drink the honeydew produced by aphids, and Réaumur agreed. He discovered red ants (probably *Formica rufa*) that live underground with grey aphids (Miall 1912:270).

Robert Hooke (1665:185–191), as we have seen (Egerton 2005:95), laid a good foundation for mosquito studies using his microscope, and Réaumur followed his example. When he had the thorax and head of mosquitoes drawn, he and his draftsman also used either a microscope or magnifying glass (Fig. 5). It is one of six excellent plates he devoted to them. Of course, at the time, no one knew that female mosquitoes transmit deadly microorganisms when they bite, so their status was that of an annoying pest rather than a dangerous one. Nevertheless, three authorities on mosquitoes commented: “Réaumur, in his classic work [1734–1742, IV:615–622], gives a detailed and most interesting account of the egg-laying process in the common house-mosquito, *Culex pipens*. The account of this wonderful observer is so faithful that we reproduce it here...” (Howard et al. 1912:140). They quoted it in English translation, but it is too long for me to repeat.

Réaumur's Memoirs 5–13 in Volume V (1740), more than 500 pages, constitute the most important treatise on bees published in the 1700s (Miall 1912:271–274, Théodoridès 1959a:71–74 and 1968:27–31). It is partly translated into English (Réaumur 1800). It includes description and illustrations (reproduced in Théodoridès 1959a:xvi) of *Braula caeca*, a dipterous ectoparasite of bees, which he called a “pou” (louse) (pp. 711–712 and Plate 38, Figs. 1–3). In the first memoir of Volume VI he reported that inside the bodies of bumble bee (*Bombus*) queens he found and illustrated (Plate 4, reproduced in Théodoridès 1959a:vii) clusters of worms. Sometimes the cluster was as large as a small cherry, and at first he thought

they were the “germs” (sperm) that enter the eggs, but further study showed they were eel-like worms that live at the expense of the female. Furthermore, they prevented her eggs from developing (Réaumur 1734–1742, VI:22–23). Théodoridès (1959a:vi) tells us that this nematode (*Sphaerularia bombi*) was only officially named and described in 1837 by Léon Dufour.

Réaumur described in detail, and had illustrated in detail, flies that lay eggs on or in the skin of mammals (illustrations reproduced in Théodoridès 1959a:xvii–xxiii). Particularly innovative was his illustration of fly larvae and pupae that infect the pharynx of deer (Fig. 6).

Réaumur had intended to publish a seventh volume of his insect histories, and he made a good start on it (Réaumur 1939:213–255). His seven memoirs on beetles for this volume were virtually complete, with 21 plates having numerous illustrations, yet the volume remained unpublished until 1955. It merits the detailed attention of a historian of entomology, but I pass over it here in favor of his incomplete memoir on ants, which is briefer, but has the advantage of being about social insects, which have more general appeal than species having solitary habits, and is available in both French and English versions. The reason William Morton Wheeler chose to translate Réaumur's manuscript on ants rather than the one on beetles is obvious: Wheeler was a leading authority on ants (Evans and Evans 1970).

Réaumur wrote “Histoire des fourmis” for Volume VII, probably between October 1743 and the end of January 1744 (Wheeler 1926:xiv), though he set it aside before he completed it. Wheeler first edited and published it with annotated translation in 1926; the “Histoire des fourmis” and part of his treatise on bees remain Réaumur's only substantial writings on insects in English. Much of the treatise on ants is of ecological interest. His experiments on ants were innovative and among his best (Drouin 1987:42–44). Réaumur wrote that John Ray had found only five species of ant in England; Réaumur said (without naming them) that France had all five plus many more species.

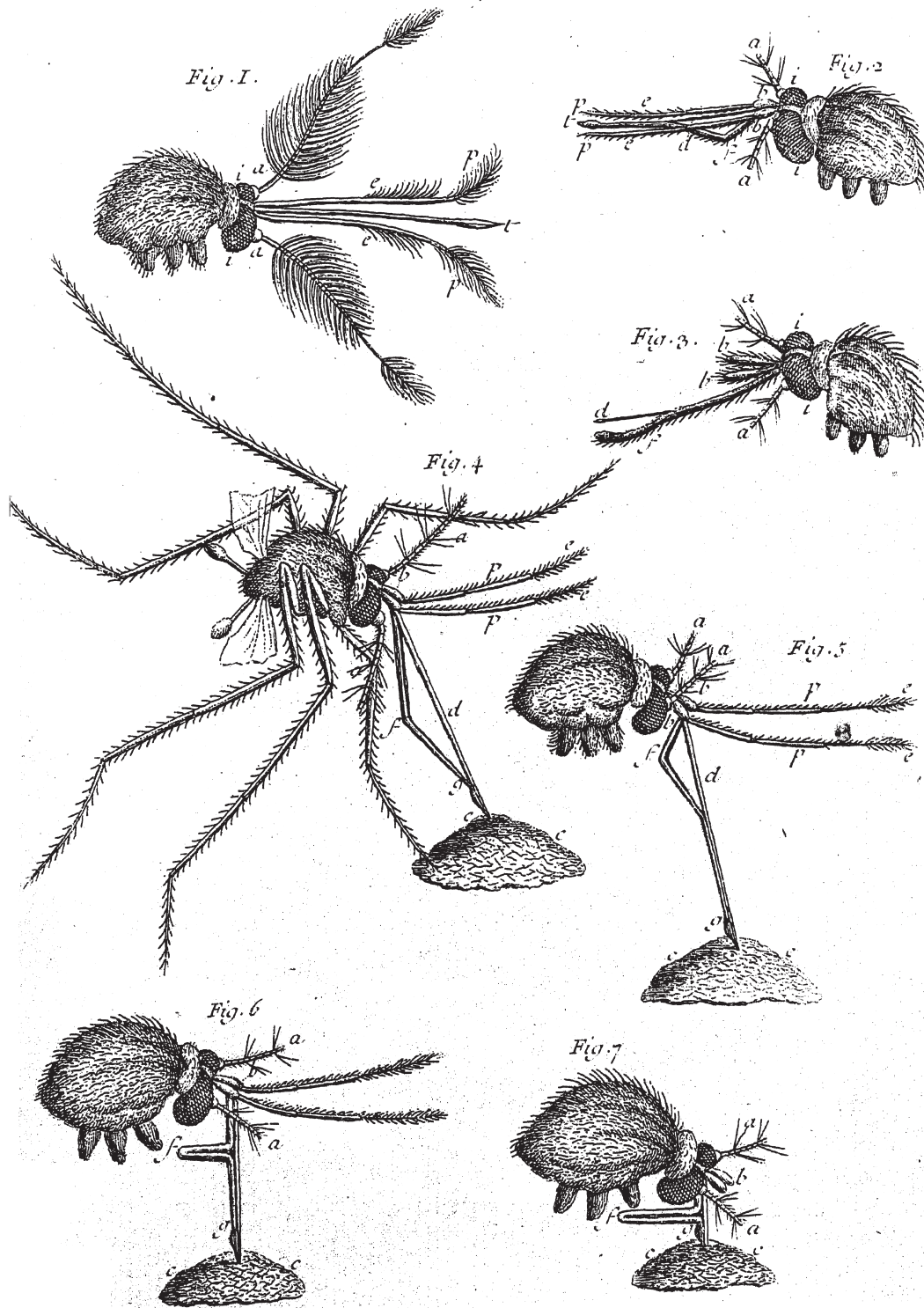


Fig. 5. Thorax and heads of mosquitoes. Réaumur 1734–1742, IV:Plate 41, Fig. 1 male, Figs. 2–7 biting females.

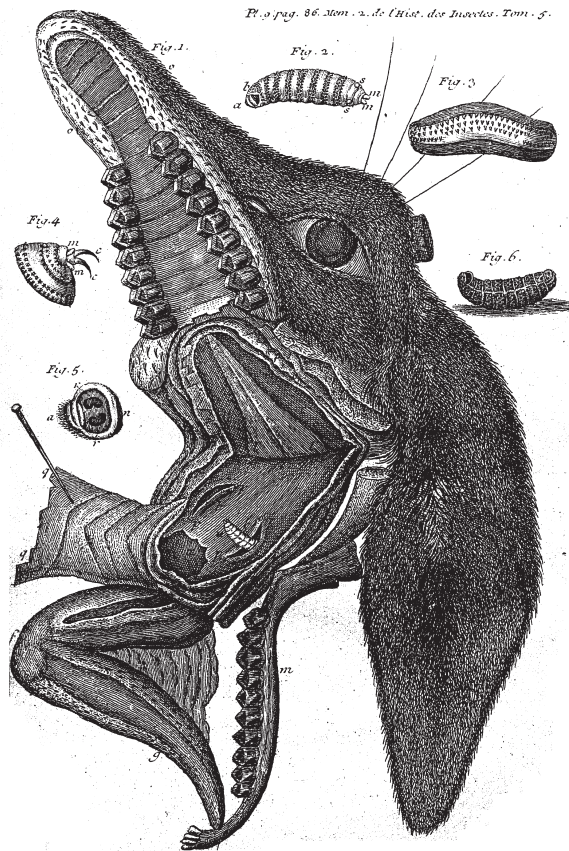


Fig. 6. Deer head dissected to reveal fly larvae and pupae. Réaumur 1734–1742, V:Plate 9.

Réaumur's approach of concentrating on conspicuous species did allow him to make some generalizations. There were no known species of solitary ants, like the solitary bee and wasp species (still true when Wheeler commented on this). Some ant species have permanent abodes and other species have only temporary abodes. Even those with permanent abodes abandon it when a drought or excessive rain makes it unsuitable. Some species build formicaries (ant hills) with little pieces of dead wood, others live in hollow trees, others burrow tunnels in the ground, and still others hide their formicary under rocks or flower pots (Réaumur 1926:135–140). He dismissed as folklore the ancient story of industrious ants storing up grain for the winter, because he had never discovered such stores when he excavated formicaries, and he even

ran experiments with enclosed ants that were given grain and nothing else to eat; they starved (Réaumur 1926:147–149). Wheeler (1926:230, note 29) pointed out that Réaumur was correct about ants in northern France that hibernate, but there are species around the Mediterranean Sea that do store grain.

In the country, the trees usually had lines of ants going up and down, and Réaumur found they usually did no harm, for they sought the excretions of aphids and scale insects. However, he discovered that a dark-brown moderate-size species did gnaw the flowers, buds, and young fruit of apricot trees. Sometimes different species, or different colonies of the same species, fight for possession of a tree (pp. 155–156). Ants like honey, and if they find egg cells of solitary bees with honey stored in them, they can force the female to abandon the site. He cited the French translation (1743) of Richard Bradley's *The Gentleman and Gardener's Kalendar* on how to destroy ants that become pests: chop up an earthworm on a flat dish, place it near them, and when it is covered with ants they can be killed. Ants kill caterpillars placed on their formicary and sometimes also ones they encounter on elm trees. The best way to clean a skeleton is to bury the animal in a formicary. Several species of spider lay eggs on folded tree leaves, and the mother stays close by to protect them. Réaumur drove away a spider and placed the leaf with eggs on the ground, and in a few hours ants had eaten the eggs (pp. 157–159).

No one before Réaumur had reported on ants mating. Swammerdam had thought that all winged ants were male, but in September 1731 Réaumur saw flying swarms of insects, which he discovered were mating ants, male and female. He saw them, after mating, return to the formicary they had left. He realized that they only needed wings for mating and that they later shed them (Drouin 1987:39–42). However, a question he could not answer was whether ant colonies (Réaumur 1926:177)

...are founded, like those of the wasps, by a single mother, without the aid of any worker; or whether they are founded by one or several fe-



Fig. 7. Réaumur in his later years.

males that are accompanied by several workers for the purpose of taking charge of operations.

Wheeler (1926:247, note 71) said both types of colony formation occur among different ant species. On 10 June 1720, Réaumur found a formicary that at night had all entrances except a small one stopped up; the others were opened in the morning (Réaumur 1926:213). He discovered that larvae and nymphs can only be found in formicaries during warm months, and that they are located more or less deeply within them according to the hour of day and the weather, and that workers stay busy moving them about. If the formicary is disturbed, workers quickly carry them to safety. Some species do not spin cocoons, but many do, and

a larva completes a cocoon in about 29 hours. It soon metamorphoses and remains dormant one or two days before shedding its skin to become an adult. Formicaries normally increase in population, because ants are produced more rapidly than they die. This causes a constant enlargement of the formicary as long as it is practicable, but after that, a swarm probably leaves to make a new formicary. One can distinguish between a migrating colony and normal ant traffic to and fro, because a migrating colony goes in only one direction and carries its larvae and cocoons. Sometimes adults even carry other adults, in which case the pair lock mandibles; generally, larger ones carried smaller ones, and he suspected that the ants being carried were males (Réaumur 1926:189–194).

Réaumur (1926:187–188) cited the remarkable *Metamorphosis insectorum Surinamensium* (1705, 1980; see Bodenheimer 1928–1929, I:401–407, Ruckler and Stearn 1982, Rice 1999:90–119), by the equally remarkable Maria Sibylla Merian (1674–1717), for her gorgeous color illustrations (Wettengl 1997), and account of tropical ants occasionally swarming into houses. People had learned to tolerate them, because they cleaned out the cockroaches and other insects and spiders before leaving. She also reported that leaf-cutting ants sometimes defoliate a tree. Some of them climb up and cut the leaves from the branches, and when they fall to the ground, others take them to the formicary, apparently as food for larvae. Later, Thomas Belt (1874:71–84) reported that the leaves were used within the formicary as compost on which to grow fungal food for both adults and larvae (Wheeler 1926:250–251, note 90).

Réaumur's natural history of insects was widely read and appreciated, and it inspired other naturalists to make similar studies. He carried on an extensive correspondence with some of them, and many of those letters are published. These are the most notable examples. Pierre Lyonet read Réaumur's work and began his own investigations in 1736 on the anatomy of insects (Miall 1912:291–293, Van Seters 1962, Piereson 1973). In 1737 Charles Bonnet read Réaumur's work and began a correspondence that resulted in his

studies on parthenogenesis in aphids and other subjects (Miall 1912:284–291, Bodenheimer 1928–1929, I:476–486, Savioz 1940, Pilet 1970, Dawson 1987). In 1739 Abraham Trembley read Réaumur's work; he began his famous investigations on hydra in June 1740 and reported his findings to Réaumur in October (Miall 1912:279–284, Trembley 1943, Baker 1952, 1976, de Beer 1960, Dawson 1987). Jacques François Artur, a physician in the French colony of Cayenne (French Guiana), began corresponding with Réaumur in 1741 and sent many observations that Réaumur used in his *Memoires* (Chaïa 1968). Charles de Geer was elected to the Swedish Academy of Sciences at age 19 in 1739, and he initiated his correspondence with Réaumur in 1744 (Landin 1972). De Geer so admired Réaumur that he gave his own seven-volume work (1752–1778) the same title as Réaumur's. August Johann Roesel von Rosenhof was inspired by Maria Sybilla Merian's book to study insects, but then turned to Réaumur's work for scientific guidance (Miall 1912:293–303, Bodenheimer 1928–1929, I:361–367, Geus 1975); I am unaware of any correspondence between him and Réaumur.

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