Contributions

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History of Ecological Sciences, Part 52: Symbiosis Studies

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Symbiosis is a term that identifies persistent relationships between species, according to Surindar Paracer and Vernon Ahmadjian (2000:6). Their textbook discussed three kinds: commensalism, mutualism, and parasitism. Other kinds that some authors have identified, phoresis and inquilinism, they considered forms of commensalism. They also mentioned that some investigators have considered predation as a kind of symbiosis; they do not mention competition, which is often a persistent relationship within and between species. They also provided an outline: "Historical Landmarks of Symbiosis" (Paracer and Ahmadjian 2000:235–238), which skips from 1500 BC (Ebers papyrus) to AD 1200 (Albertus Magnus). Two small, not-quite textbooks entitled *Symbiosis* appeared in America in 1970, the much smaller by William Trager, Rockefeller University, and the much larger by Thomas Cheng, Lehigh University. Also in 1970, Clark Read, Rice University, published *Parasitism and Symbiology: an Introductory Text*.

"Symbiosis is the most relevant and enduring biological theme in the history of our planet" (Stanley 2006:857). This is a modern echo of Pyotr (Peter) Kropotkin's claim of 1890 (see below). Although non-predatory species interactions are a major aspect of ecology (Henry 1966–1967, Margulis 1998, Paracer and Ahmadjian 2000), I am unaware of any general ecology textbook that reflects Stanley's claim for the importance of symbiosis in its organization. Some of Stanley's claim rests upon endosymbiosis—microorganisms living mutualistically within larger organisms—which Paul Buchner surveyed in detail (German 1953, revised in English, 1965)—and symbiogenesis of organelles within cells (Khakhina 1992); the latter is only indirectly within ecology's domain. Many types of symbiosis are inconspicuous and were overlooked until the later 1800s or during the 1900s, and some types still seem under-appreciated.

Paul Buchner (1965:3–74) wrote a detailed history of studies on endosymbiosis of microorganisms with plants and animals, beginning in the mid-1800s. Jan Sapp wrote (1994) a useful history of symbiosis, with many more examples and details than are included in the present survey. He discussed symbiosis more briefly in his *Genesis: The Evolution of Biology* (2003:234–249). My organization of this essay differs from Sapp's, and I explore some topics he did not. For example, everyone knew that fruits contain seeds, and that seeds are the source of new plants. It was equally obvious that humans and various birds and mammals ate fruits. When did naturalists first comment on the fact that animals eating fruits are important disseminators of plant seeds? Sapp's history, which discussed symbiosis between plants and animals, included neither this aspect of it, nor even pollination. Whoever wishes to write a history of mutualism studies concerning seeds can begin with Henry Howe and Judith Smallwood's bibliographic guide, "Ecology of Seed Dispersal" (1982). A complexity is that some animal dispersal agents are also seed predators (Janzen 1971). Lee Dugatkin's *The Altruism equation: seven scientists search for origins of goodness* (2006) is comparatively narrow in scope, but scientists he discussed are important for symbiosis studies.

450 BC–AD 1858

The most fundamental symbiotic relationship is animals eating plant material and animal physiological wastes becoming fertilizer for plants. This was such a basic awareness in agrarian societies that it never received any special name or comment. Another symbiotic relationship so basic among agricultural societies that it received no special comment was human maintenance of domesticated animals. This could be seen as symbiotic only after the concept of symbiosis was defined.

In antiquity, there were isolated examples of symbiosis described, plus an organizing concept, the balance of nature. Parasitism was the first symbiotic relationship recognized. The Egyptian Ebers medical papyrus (ca. 1550 BC) contained a prescription for killing intestinal round worms (quoted in Clendening 1942:4, Hoeppli 1959:5).

The earliest contribution in antiquity to the balance of nature concept was by the Greek traveler–historian Herodotos (died ca. 425 BC), with his argument that Divine Providence had contrived to have predatory animals produce fewer offspring than their prey, thus preventing predators from eating all their food (Herodotos 1926–1938, volume 2, pages 135–137, book 3, section 108–109). Isolated examples of mutualism were reported in antiquity, beginning with Herodotos' report (1926–1938: volume 1, page 98, book 2, section 68) of Egyptian Plovers (*Plovianus aegypticus* or *Hoplopterus armatus*) picking leeches from inside the mouths of Nile crocodiles (*Crocodylus niloticus*), who, in "appreciation" for this service, never harmed the plovers. This also seemed to illustrate the balance of nature (Egerton 1973:326, 2001*a*:95–96, 2001*b*:151).

Zoological works attributed to Aristotle (384–322 BC) were more scientifically sophisticated than Herodotos's *History*, though Herodotos was an Aristotelian source. Aristotle's *Historia Animalium* reported (1965–1991:547^{b} 6–17) that clam *Pinna* and crab *Pinnotheres* lived together. (Current understanding: the clam receives no benefit, and *Pinnotheres* eats some food the clam might have eaten had the crab not been there.) Apiculture began in ancient Egypt, Mesopotamia, and perhaps elsewhere (Townsend and Crane 1973:387–389). *Historia Animalium* contained a guide to apiculture (Aristotle 1965–1991: volume 3, 623^{b}15–628^{b}22) and stated that when a bee visited one kind of flower, that was the only kind further visited until it returned to the hive. External parasites were discussed as a group,

Fig 1. Egyptian plover (*Plovianus aegypticus*) cleaning leeches from Nile crocodile (*Crocodylus niloticus*). Drawing by Kathryn H. Delisle. Sapp 1994:cover.

"which though not carnivorous live on the juices of living flesh—insects such as lice, fleas, and bugs" (Aristotle 1965–1991:volume 2, 556^{b}21). Although copulating insects were observed, insects were supposedly generated also spontaneously from putrefying matter, excrement, or in a diseased body. In compensation, "people with lousy heads get fewer headaches." The kinds of external parasites found in different kinds of animals were itemized, such as: "Sheep and goats have ticks, but no lice. Pigs have lice, large hard ones." Fish lice "resemble the many-footed woodlice, except that they have a flat tail" (Aristotle 1965–1991: volume 2, 557^{a}22–23). A brief comment on the remora is part of this treatment of external parasites (Aristotle 1965–1991:volume 2, 557^{a}30–31

> *In the sea between Cyrene and Egypt there is a fish called "louse," which dogs the dolphin; this fish gets extremely fat owing to the bountiful supplies of food available for its benefit when the dolphin is out hunting.*

Two species of remora inhabit the Mediterranean Sea (Thompson 1947:68). *Historia Animalium* also reported that the cuckoo *Cuculus canorus* lays eggs in the nests of other birds and disposes of the parasitized bird's own eggs (Aristotle 1965–1991: volume 2, 563^{b}29–564^{a}7).

Historia Animalium (563^{b}14–564^a 6, 618^{a}8–30) and *Generatione Animalium* (750^{a}11–15) reported brood parasitism in the cuckoo (*Cuculus canorus*; Schultze-Hagen 2009), along with uncertainty about whether cuckoos can become transformed into hawks.

Theophrastos (ca. 371–ca. 287 BC) was Aristotle's successor as head of the Lyceum in Athens and author of the first two botanical treatises, *Historia Plantarum* and *De Causis Plantarum*. In the former, he distinguished between adverse environmental conditions and diseases (HP, IV:14, 1916:391–393)

> *They say that wild trees are not liable to diseases which destroy them, but that they get into poor condition, and that most obviously when they are smitten with hail when either they are about to bud or are just budding or are in bloom; also when either a cold or a hot wind comes at such seasons: but that from seasonable storms, even if they be violent, they take no hurt…. Cultivated kinds, however, they say, are subject to various diseases….being worm-eaten….also a "knot" (which some call a fungus, others a bark-blister)…*

Further examples from both works are quoted by Ainsworth (1981:12–13). Theophrastos knew that mistletoe is a distinct kind of plant, though he did not call it a parasite (CP II:17, 1976–1990:333–335)

> *…some plants are unable to sprout—either the seeds or the plants—in the ground, as the ixia [mistletoe, Loranthus europaeus], the stelis [Viscum album], and the hyphéar, stelis being the Euboean word, hyphéar the Arcadian, and ixia the word in general use.*
>
> *Some assert that all of them are a single natural entity, but because they grow on different plants they are also considered to be different: so the hyphéar occurs on the silver-fir and pine, and so too the stelis, whereas the ixia occurs on oak, terebinth, and a number of other trees.*

Roman authors on agriculture also discussed plant diseases, but without advancing beyond

Theophrastos (Ainsworth 1981:14).

Ainsworth (1981:41) and Paracer and Ahmadjian (2000:235) cite a description of (parasitic) mistletoe by Albertus Magnus (about 1200–1280) as a landmark, but without citation or details. Albert wrote *De Vegetabilibus et plantis* after 1250 (Egerton 1983, I:448). Albert did not know the botanical works by Theophrastos, which discussed mistletoe's growth on trees (Greene 1983, I:146 and Egerton's note 57 on pages 462–463). Albert's observations on oak galls are quoted in Egerton's history, part 9 (2003:88).

History of parasitism of both plants and animals, 1700–1900, was discussed in parts 29, 30, and 44–46 of this history (Egerton 2008*b*, *c*, 2012*b*, 2013*b*) and is not repeated here. Carl Linnaeus (1707–1778) provided students at Uppsala University with information for writing doctoral dissertations, which dissertations he had published under their names, but these dissertations are now attributed to Linnaeus. A landmark dissertation, "The Oeconomy of Nature" (Latin thesis defended by Issac Biberg, 1749, English 1759) was the first paradigm of ecology, and it included a section (number 7) on dissemination of seeds. Biberg/Linnaeus explained that some plants have seeds that winds disseminate, but others have seeds disseminated by animals (Linnaeus, English edition 3, 1775:64–65)

> *Berries and other pericarps, are by nature allotted for aliment to animals, but with this condition, that while they eat the pulp they shall sow their seeds; for when they feed upon it they either disperse them at the same time, or, if they swallow them, they are returned with interest; for they always come out unhurt.*

Linnaeus then provided a variety of examples, including plants sprouting from manure applied as fertilizer, mistletoe being deposited by thrush droppings on tree limbs, crossbills dispersing seeds from fir cones, and swine turning up the earth while rooting for seeds.

English physician Edward Jenner (1749–1823), remembered for his experiments leading to his establishment of smallpox vaccination (published in 1798), was also an early experimenter on bird behavior (Jenner 1788, Le Fanu 1951, Fisk 1959:86–96, Wilson 1973, Bircham 2007:113–116). He studied the parasitic cuckoos at the request of his former medical-surgical teacher, John Hunter. Jenner observed three species which cuckoos parasitized: titlark, water-wagtail, and hedge-sparrow. He found an egg which a cuckoo hatchling had expelled from the nest of the parasitized parent bird and restored it into the nest and noted its second expulsion. He commented that "The smallness of the Cuckoo egg in proportion to the size of the bird is a circumstance that hitherto, I believe, has escaped the notice of the ornithologist" (1788:227).

A new aspect of symbiosis and balance of nature that developed in the mid and late 1700s was the study of pollination. It was obvious that bees and butterflies visited flowers to collect food, but the benefit to the plants was not obvious. Arthur Dobbs (1689–1765), an Irish Protestant member of the ruling class (governor of North Carolina, 1754–1765 [Chichester 1921, Snapp 1999, Calhoon 2004]), discovered the mutualism of pollination. His report appeared in the *Philosophical Transactions of the Royal Society of London* (1750). His attention might have been attracted by a swarm of busy bees, and he then consulted Réaumur's *Mémoires pour servir à l'histoire des insectes* (volume 5, 1740) for additional information. Or, perhaps he read Réaumur first and was then inspired to observe bees. At any

Fig. 2. Edward Jenner. Fisk 1959:book jacket.

rate, although highly praising Réaumur's work, when he read Réaumur contradicting Aristotle's claim that when a bee visits a particular kind of flower, it visits no other kind until it returns to the hive, Dobbs found that his observations supported Aristotle, and so he sent his observations to the Royal Society of London. Dobbs's observations were adequate to make his claim, and his article was quite clear, but it attracted no attention at the time (Grant 1949).

German botanist H. L. Hermann Müller (1829–1883), younger brother of zoologist Fritz Müller, wrote an encyclopedic *Befruchtung der Blumen* (1873), updated and translated into English (1883), with posthumous preface by Darwin. Müller's book has a good historical introduction (1883:1–29, 1977), though he was unaware of Dobbs's 1750 article. It began therefore, with Christian K. Sprengel's *Das entdeckte Geheimniss der Natur im Bau und in der Befruchtung der Blumen* (1793), an encyclopedic survey (Egerton 2008:170–171). Sprengel (1750–1816) was rector of a Lutheran school and an amateur botanist (King 1975). He concluded that some flowers cannot be fertilized without the assistance of insects, and that the function of flowers and nectar is to entice them into performing this task. He explained his initial discoveries on page one of his book, which Fredrick Bodenheimer translated into English in his history of biology (1958:333–340). Sprengel then proceeded to study flower morphology to learn how it guides insects to ensure fertilization. He observed that while gathering nectar, insects carry pollen from the anthers of one plant to the stigma of another, but he failed to wonder why cross-fertilization seemed necessary. Müller thought that this omission was why Sprengel's monograph attracted little attention from botanists. Subsequently, three botanists published studies indicating that cross-fertilization was necessary for producing healthy plants (Knight 1799, Herbert 1837, Gärtner 1844–49). However, it took the new context provided by Darwin's *Origin of Species* (1859) to attract general interest in pollination studies.

Another new aspect of symbiosis and balance of nature during the later 1700s was the identification, first, of different kinds of gases, and second, the discovery that animals need one gas (oxygen), which plants emit, and plants need another gas (carbon dioxide), which animals emit. This discovery emerged from the chemical–plant–animal investigations that Joseph Priestley, Jan Ingen-Housz, and Jean Senebier conducted during the 1770s–1780s (Egerton 2008*a*:164–169).

Studies on plant diseases and on animal diseases and parasites made substantial progress during the 1700s, but without breakthrough establishment of a germ theory of disease (Egerton 2008*b*, *c*).

The blood-sucking habit of vampire bats was known to the Mayan and other Central and South American Indians before the arrival of Europeans in America, and the entourage of Hernando Cortés (1485–1547), conqueror of Mexico in the early 1500s, received reports of about it (Villa and Canela 1988). In March, 1800, Alexander von Humboldt (1769–1859) encountered them on the plains (llanos) of Venezuela, attacking his horses (Botting 1973:95), and Charles Darwin (Darwin 1838:25) collected a new species attacking his horses in Brazil in April, 1832.

Cowbirds *Molothrus* in America and cattle egrets *Bubulcus*—initially only in Africa, now also in the Americas—associate with large hoofed mammals that flush insects as they move about; these birds catch those insects. This is at least a commensal relationship, though large mammals might derive benefit from reduced insects in the grass, which would make this a mutualistic relationship. Cowbirds are also brood parasites. In her monograph on *Cowbirds and Other Brood Parasites*, Catherine Ortega (1998:47) commented

> *Foraging conditions and foraging modes may have favored parasitism in some groups. Many brood parasites are nomadic, following food resources. Cuckoos wander around assessing local foraging conditions, becoming numerous during local population outbreaks of caterpillars. Honeyguides also wander in search of beehives, and cowbirds presumably used to follow roaming herds of Bison. These three groups of brood parasites, therefore, are nomadic, and becoming sedentary for the time required to set up a territory, construct a nest, incubate eggs, and raise young would be problematic.*

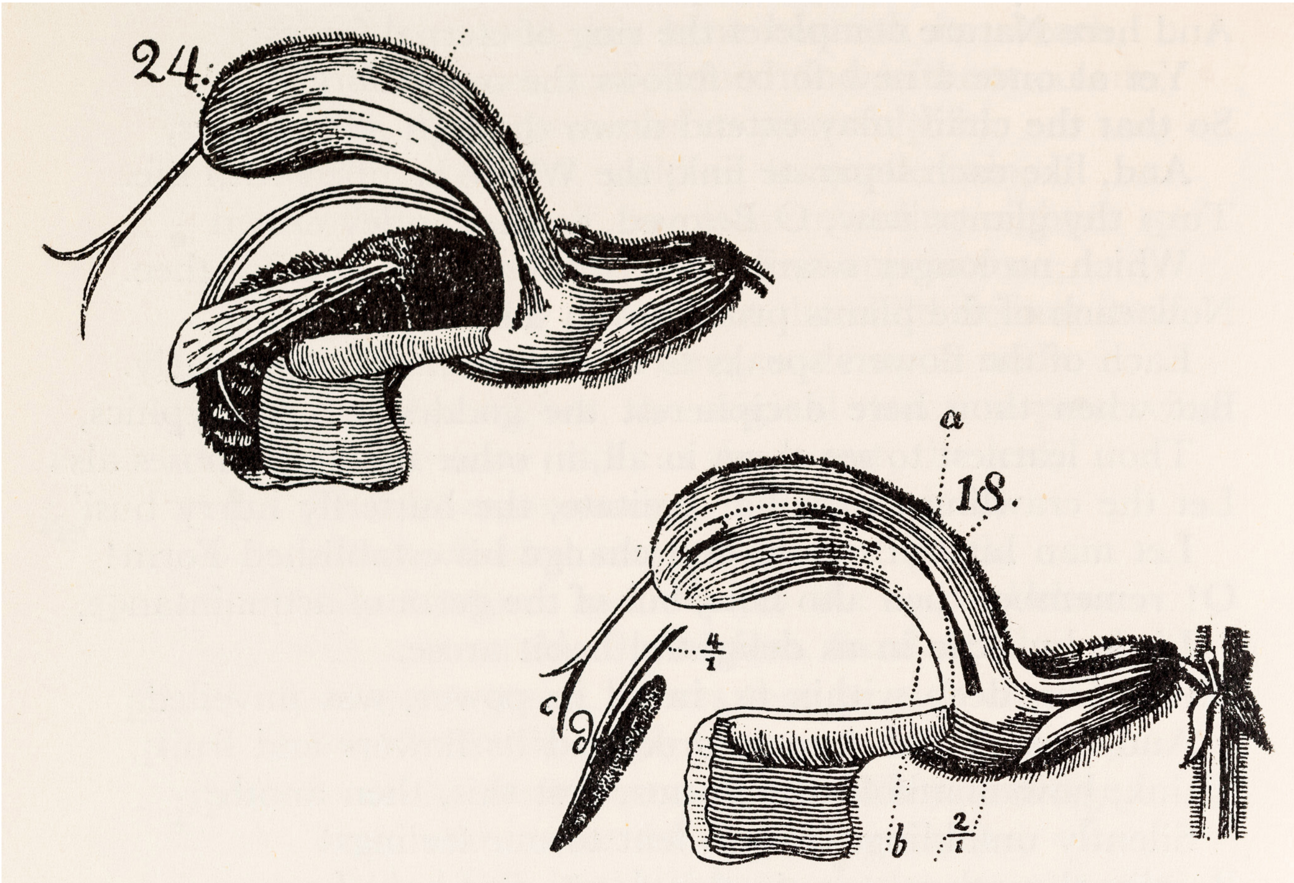


Fig. 3. Pollination of *Salvia pratensis*. Sprengel (1793). From Bodenheimer 1958:338. Sprengel's drawing of bee pollination of *Nigella arvensis* is reproduced in Egerton 2008*a*:170.

No need to speculate about cowbirds and bison. The Lewis and Clark Expedition (1804–06) into America's northwest (Egerton 2009:440–448) in their journals called cowbirds "buffalo-pecker," which ornithologist-editor Elliot Coues (1893, 1965:1081) explained came from a habit of these birds of picking ticks off the backs of bison. Alexander Wilson (1766–1813) was not the discoverer of parasitism in cowbirds *Molothrus ater*, but he was a careful observer of them and published the first detailed account of them in volume 2 (1810) of his *American Ornithology*, showing a parasitized Maryland Yellowthroat parent feeding a young cowbird. Having grown up in Scotland (Egerton 2009:454–459), he was previously aware of brood parasitism in European cuckoos.

American naturalist Henry Thoreau (1817–62) had an ecological outlook on nature and sought connections between species (Egerton 2011*a*). His insightful essay, "The Succession of Forest Trees" (1860, 1980), discussed squirrels planting oak trees by burying more acorns than they ever dug up, and

Fig. 4. Cowbirds *Molothrus ater*: 1. Male, 2. Female, 3. Young being fed by parasitized parent, 4. Maryland Yellowthroat. Wilson 1808–1814, II, plate 18.

wood mice doing the same with chestnuts. He also acknowledged that Linnaeus had said that “while the swine is rooting for acorns he is planting acorns” (1980:90). Thoreau was citing Linnaeus from memory and did not quite convey details correctly, but did capture the explanation’s essence.

Darwinian revolution

Darwin’s theory of evolution by natural selection (1859) emphasized struggle for existence and is logically incompatible with Linnaeus’s economy of nature (Limoges 1970:151, Egerton 1973:341). However, that incompatibility was overlooked by Darwin and his contemporary followers. Darwin himself noted what we call symbiotic relationships, such as dependency of mistletoe upon insects for pollination and birds for disseminating its seeds (Darwin 1859:3), and reciprocal dependence of flowers on pollinating insects and of insects on flowers making pollen and nectar (Darwin 1859:92–93). “Darwin influenced pollination ecology more deeply than anybody else during the nineteenth century” (Müller 1883:4–11, Faegri and van der Pijl 1971:3). His hypothetical food chain—clover, bees, mice, cats (Darwin 1859:73–74)—illustrates symbiotic relationships (clover–bees, bees–mice), though some links in the chain have limited validity (McAtee 1947, Egerton 2007:52–53). In *On the Origin of Species* (Darwin 1859:3361–363), Darwin discussed the dissemination of seeds at the biogeographical scale and pointed out that some fruit-eating birds can fly 35 miles an hour, and even faster when caught by a gale, and so they can often defecate viable seeds far from where they ate their food. Darwin’s focus concerning seed dissemination was not symbiosis, but he took that fact for granted. Darwin’s studies on orchid fertilization by insects (1860–1861, 1862) was a detailed study of symbiotic relationships within an evolutionary context. My previous illustrated discussion of this subject is online (Egerton 2011*b*:359–363).

Among difficulties with his theory, which Darwin cited in the *Origin*, was how could natural selection account for the evolution of such social insects as honeybees and ants which have sterile workers in their hives or colonies, differing morphologically from the fertile members? He decided (1859:237)

> *This difficulty, though appearing insuperable, is lessened, or, as I believe, disappears, when it is remembered that selection may be applied to the family, as well as to the individual, and may thus gain the desired end.*

This was a one-sentence response which could easily be lost from memory as one continued to read his various complex resolutions to other questions.

The significance of Darwin’s work in general and the *Origin* in particular for symbiosis studies lay less in the particular examples that he discussed than in the new paradigm that he provided, with which it became possible to view symbiotic relationships as having evolved over time. Early participants in Darwin’s revolution were fellow Englishmen Henry Walter Bates (1825–1892) and Alfred Russel Wallace (1823–1913), who left England in 1848 to explore Amazonia. Bates stayed until 1859, seven years longer than Wallace (Bates 1863, McKinney 1970, 1976, Dickenson 2004, Egerton 2012*a*:42–49, Drouin 2014:151–157). He returned to England just before Darwin published the *Origin*, and became an immediate convert to Darwin’s theory when he read that book. When Bates in 1861 read to the Linnean Society of London his paper on *Leptalis* butterflies mimicking color patterns of Heliconiidae butterflies (published 1862), he was among the earliest to provide new evidence for Darwin's theory of evolution by natural selection (Blaisdale 1992:63–141). Batesian mimicry occurs when a palatable species evolves to resemble an unpalatable species. Remarkably, Wallace (1865:18–22) found a parallel case of mimicry among the Papilionidae of Malaya (Blaisdale 1992:144–156), which he reported to the Linnean Society in 1864 (published 1865). On the basis of his and Bates's studies, Wallace announced laws of mimicry, which German zoologist Fritz Müller (1822–1897) challenged on the basis of his own studies (Blaisdale 1992:186–197). Müller, older brother of botanist Hermann Müller, had received a Ph.D. degree at Berlin under Johannes Müller in 1844 (McKinney 1974). He permanently immigrated to southern Brazil, where he wrote *Für Darwin* (1864, English 1869), which earned him Darwin's lifelong friendship. Müllerian mimicry (1879) differed from Batesian mimicry in that both species of butterflies were about equally distasteful to predators, and by coming to resemble each other, predators learned more quickly of their distastefulness. Several species of Euglossini orchid bees exhibit Müllerian mimicry (Dressler 1982:375).

In contrast to Bates's ready acceptance of Darwin's theory of evolution, Yale University geology professor James Dana (1813–1995), who had readily accepted Darwin's theory of coral reefs in the 1840s, and later had only minor changes to suggest (Dana 1885), was a tardy convert. Dana had corresponded with Darwin—and had received an autographed copy of the *Origin*—and was friends with evolutionist Asa Gray. However, Dana struggled until ca. 1874 before accepting Darwin's theory of evolution by natural selection (Sanford 1965, Stanton 1971:553). Dana's version of evolution was a mixture of Darwinism and Lamarckism. All scientific revolutions have immediate defenders and slow converts.

Recent times

Intraspecific cooperation

Intraspecific cooperation is sometimes considered an aspect of symbiosis, though not by Paracer and Ahmadjian (2000). That social species—wolves, lions, many primates, elephants, many hoofed mammals, meerkats, aquatic mammals, some fish, ants, honey bees, termites—engage in cooperation was common knowledge since antiquity. Alfred Espinas (1844–1922) was a French philosopher, author of *Des Sociétés Animales* (1878, English 1935), who wrote his doctoral dissertation in Paris (Mitman 1992:65–66, Brooks 1998:97–133, Egerton 2014*a*:59–60). His understanding of evolution came from Herbert Spencer. Espinas's book was the first comprehensive survey of animal mutualism within species: coral, social insects, fish, reptiles, birds, mammals, and humans.

Darwin's emphasis upon struggle for existence was carried to an extreme by his "bulldog," Thomas H. Huxley (1888), which prompted a Russian prince, naturalist, geographer, and exiled anarchist, Pyotr (later, Peter) A. Kropotkin (1842–1921), to publish "Mutual Aid among Animals" (1890), and articles on mutual aid among humans, all of which he collected into a much-read book, *Mutual Aid* (1902); both versions drew upon his own Siberian observations (Naumov 1973, Miller 1976, Mitman 1992:66–67, Sapp 1994:20–23, Dugatkin 2006:12–36, 2011, Borrello 2010:30–38, Hale 2014:227–235). He acknowledged that his awareness of this issue came from a lecture by St. Petersburg University Professor of Ichthyology Karl Fiodorvic Kessler, "Mutual Aid among Animals" (1880), in which Kessler said:

“Mutual aid is as much a law of nature as mutual struggle; but for the *progressive* evolution of the species the former is far more important than the latter” (quoted in Kropotkin 1899:498; Miller 1976:173, Todes 1987:545–546). Kropotkin’s autobiography did not mention Espinas.

Kropotkin grew up in luxury in, and sometimes near, Moscow, and he developed an early fondness for nature. His very conservative father unknowingly hired two young radicals as tutors of his three children, one a student at Moscow, the other a Frenchman, who taught about the French Revolution along with the French language (Kropotkin 1899:15–18). Pyotr’s hero became Alexander von Humboldt, whose *Cosmos* he read, and he wanted to explore Siberia just as Humboldt had explored tropical America. At age 15 he was sent to the emperor’s Corps of Pages, in St. Petersburg, for education as a government administrator or army officer. Pyotr found it very boring, and at the end of five years he did not ask for assignment to any of the positions most coveted by other students. Rather, he wanted to go to the Amur River Valley in Siberia (Kropotkin 1899:154–157). Nature in Siberia met his expectations. He took five expeditions to explore and sometimes to map regions that had never been mapped. However, he felt that government was a burden to the people rather than an aid to them.

After five years in Siberia, Kropotkin returned in 1867 to St. Petersburg and spent the next five years partly at its university, studying mathematics, science, and especially geography, and also much time at the Russian Geographical Society (Kropotkin 1899:224–225, Miller 1976:72–73, Dugatkin 2011:18–19). Yet he was distracted by anarchist politics and joined a group that gave books and assistance to the working class. These activities landed him in prison, from which he escaped after a year, in 1876, and he went to England, where he could speak his mind. A trip to France, however, also landed him in prison, but influential allies in France and England applied pressure to the French government, causing his release back to England. Kropotkin saw the same impulse for cooperation in humans that he saw in nature, and he thought that if social species of animals live without government, so could humanity.

One of America’s two leading entomologists in the early 1900s was Milwaukeean William Morton Wheeler (1865–1937), who mainly studied ants, which eventually led to a special interest in social insect species (Evans and Evans 1970, Mallis 1971:362–368, Shor 1976, Burgess 1996:110–112). (The other leading entomologist was John H. Comstock, 1849–1931 [Egerton 2013*a*:55–58]) Wheeler’s broader interest was encouraged by an invitation to lecture before the Lowell Institute in Boston in 1921. Those six lectures then became chapters in his book, *Social Life among the Insects* (1923), on beetles, wasps, bees, ants, parasitic ants and ant guests, and termites. The fifth chapter, on parasitic ants and ant guests, shows how intraspecific cooperation can lead to interspecific relationships. Wheeler argued that an ant colony can be considered as an organism (1911) or superorganism (1928) (Wheeler 1911, 1928; Evans and Evans 1970:255–256, 263–266, Wilson 1971:317–318, Borrello 2010:28–29). The revival of the latter term occurs in the title of Bert Hölldobler and Edward O. Wilson’s *The Superorganism: the Beauty, Elegance, and Strangeness of Insect Societies* (2009).

Indianian W. Clyde Allee (1885–1955), a Quaker, attended a Quaker college, Earlham (B.S., 1908), and was a graduate student in zoology at the University of Chicago under Victor Shelford (M.S, 1910, Ph.D., 1912). After having several positions elsewhere, he returned to the University of Chicago in 1921 (Engel 1983:172–183, Kimler 1990, Mitman 1988, 1992, 1999, Sapp 1994:137–139, Burgess 1996:11, Sterling 1997*a*, Dugatkin 2006:37–60). Allee acknowledged that his pacifism influenced his choice of

Fig. 5. Pyotr A. Kropotkin, age 22. Kroptkin 1899:facing 210.

Fig. 6. William Morton Wheeler collecting ants in a New South Wales national park, Australia, 1931. Archives of Museum of Comparative Zoology, Harvard University.

research topics, but claimed his research was nevertheless objective. He studied animal aggregations, a social formation intermediate between individuals and communities. He published books on it—*Animal Aggregations* (1931), *Animal Life and Social Growth* (1932), *The Social Life of Animals* (1938)–and he interested students in conducting research on it. His ally at Chicago was zoologist Alfred E. Emerson (1896–1976) from Ithaca, New York, who earned his degrees at Cornell University under Comstock (B.S., 1918, M.S., 1920, Ph.D., 1925). (Park 1967, Wilson and Michener 1982, Burgess 1996:39–40). He became the leading world authority on termites, and he wrote the chapters on insect societies in their *Principles of Animal Ecology* (Allee et al. 1949: chapters 24, 31–35).

Englishman William Donald Hamilton (1936–2000) majored in genetics at Cambridge University, where Sir Ronald Fisher was located, but had few contacts with him (Grafen 2004, Dugatkin 2006:86–106). Nevertheless, Fisher's *Genetical Theory of Natural Selection* (1930) became his bible. He had an early interest in the biology of altruism. Discouraged by those he hoped to interest in it, he moved to London for graduate study, but continued working mostly alone. Yet, "Hamilton's graduate student life is the period of his greatest scientific work" (Grafen 2004:113). He was not a mathematician in the same league with Fisher, but he could build upon Fisher's foundation to develop his own mathematical models: "inclusive fitness was a major conceptual advance in biology wholly original with Hamilton" (Hamilton 1963, 1964, Cronin 1991, Grafen 2004:116). E. O. Wilson (1875:118) summarized his achievement

> *The modern theory of genetic theory of altruism, selfishness, and spite was launched…by William D. Hamilton in a series of important articles (1964, 1970, 1971a, b, 1972). Hamilton's pivotal concept is inclusive fitness: the sum of an individual's own fitness plus the sum of all the effects it causes to the related parts of the fitnesses of all its relatives.*

He made two trips to the Congo Valley to study HIV virus, contracted malaria on the second trip and died shortly after returning home, age 63.

Harvard University Professor Edward O. Wilson (b. 1929) wrote that Hamilton's "seminal theory of kin selection" (Wilson 1994:315) was the most important "element" in sociobiological theory, but that he could not accept it upon first reading. Wilson is not only a world authority on ants, as Wheeler had been, but also a leading ecologist and evolutionist. His *The Insect Societies* (1971) discussed in most detail intraspecific cooperation; chapter 19 is on symbiosis between ant species, and chapter 20 is on symbiosis between ant species and other arthropod species.

Wilson broadened the scope of his investigations in *Sociobiology: the New Synthesis* (1975), which attracted about the same degree of controversy as Darwin's *Origin* had (Ruse 1979, Segerstrâle 2000). Subsequently, intraspecific cooperation was investigated by sociobiologists (Wilson 1975:120–129, 1994:315–327). University of Louisville Professor Lee Dugatkin (b. 1962) provided a recent synthesis, *Cooperation among Animals: An Evolutionary Perspective* (1997), limited to intraspecific relationships, but in his *Principles of Animal Behavior* (Dugatkin 2009 [edition 2]:326–332) he also discussed mutualism between species. Stanford University Professor Joan Roughgarden (b. 1946) challenged both Richard Dawkins, *The Selfish Gene* (1976) and aspects of sociobiology in *The Genial Gene: Deconstructing Darwinian Selfishness* (2009). A controversy between defenders of "selfish" vs. "genial" genes may be long lasting.

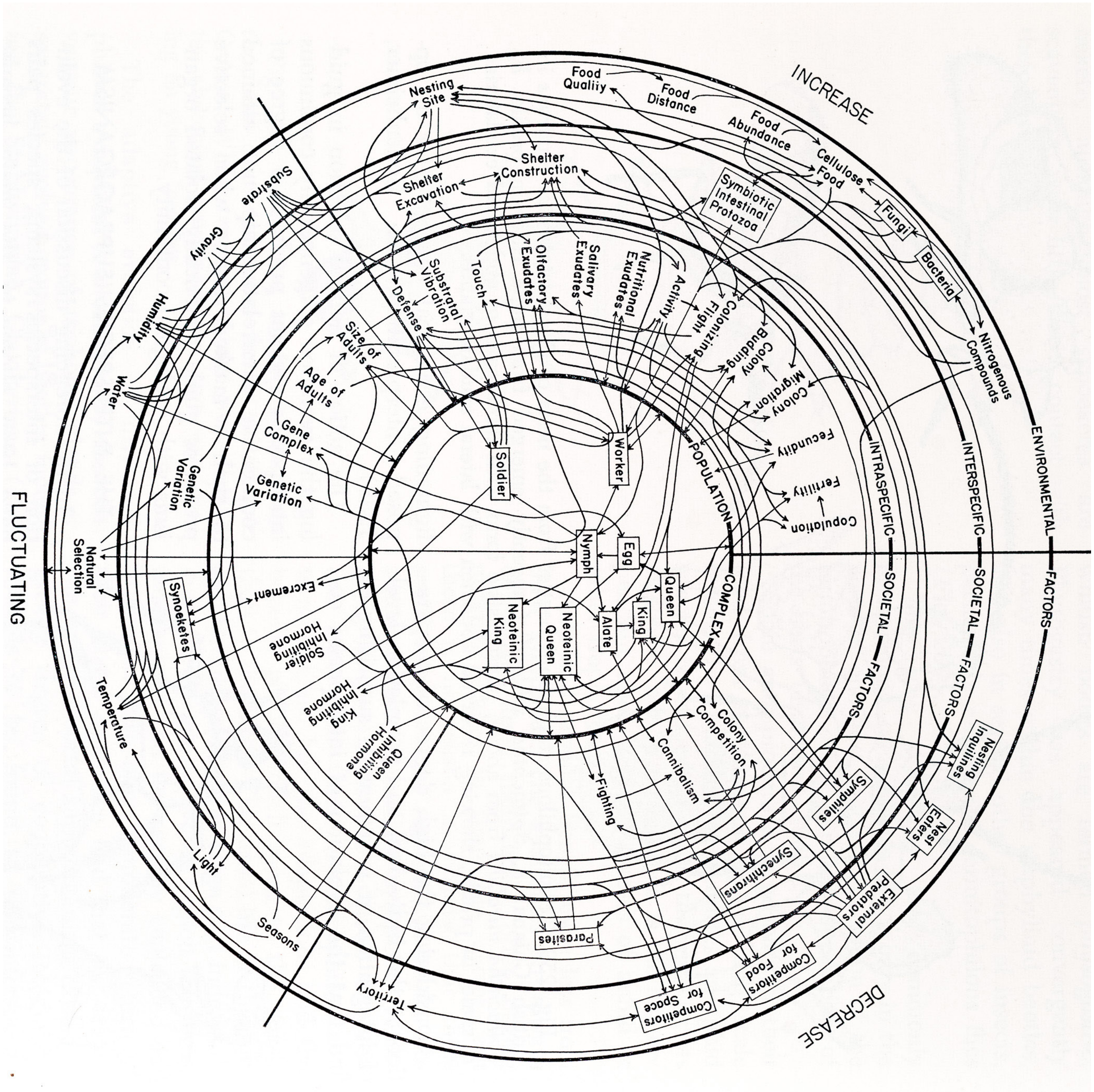


Fig. 7. Diagram of the factoral complex influencing the population of typical termites of the family Rhinotermitidae. Arrows indicate direction of effects. Allee et al. 1949:722.

One aspect of intraspecific cooperation that has received recent attention is assistance in raising young offspring ("cooperative breeding"), seen in some species of both birds (Woolfenden and Fitzpatrick 1984, 1996:16–17, Skutch 1999, Dugatkin 2006:120–121) and mammals, including wolves (Allen 1979:260–264). However, the human ability to cooperate on large scales, as Frans de Waal (2014) and Gary Stix (2014) argue, was a huge asset in human rise to world dominance.

Predation?

Since predation has been commonly observed before the Greeks and ever since, it is impracticable to survey such studies. What seems practicable is to mention studies that provide significant new insights. Should an insect eating a plant leaf be called a predator? That seems preferable (to me) to calling them parasites. Ehrlich and Raven might disagree.

In 1964, while they were both on the faculty at Stanford University, zoologist Paul Ehrlich (b. 1941) and botanist Peter Raven (b. 1936) collaborated on a notable study, "Butterflies and Plants: a Study in Coevolution." Joel Kingsolver and Robert Paine put their study in historical perspective (1991:313)

> *The idea that plant secondary compounds evolved as defenses against insect herbivores had been suggested by Fraenkel (1956, 1959); and much of Ehrlich and Raven's paper is a comprehensive survey of patterns of host plant use by different taxa of butterflies. To explain these patterns, they define the process of coevolution….*

Ehrlich and Raven referred to these butterflies as "phytophagous or parasitic organisms" (1964:600). But if a caterpillar eating a leaf is a parasite, so is a deer eating a leaf, which is absurd. Yet, the deer is not a predator either. Maybe Ehrlich and Raven "define the process of coevolution," which is not the same as defining coevolution. They used the term without defining it (Ehrlich and Raven 1964:586, 605), and did not use the term in their summary. Herbert Hanson's *Dictionary of Ecology* (1962) does not contain the term. Michael Allaby's *The Concise Oxford Dictionary of Ecology* (1994) does.

Parasitism

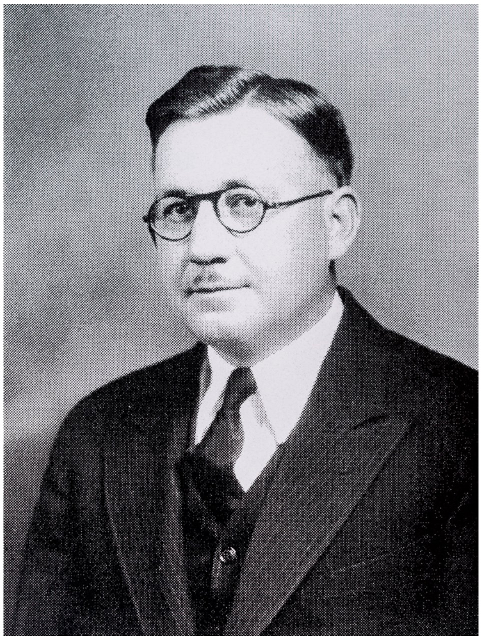
During the 1800s, great advances occurred in the understanding of parasitism and diseases of both plants and animals, leading to a breakthrough, a germ theory of disease (Egerton 2012*b*, 2013*a*, *b*). Histories of animal parasitism (Foster 1965, Philip and Rozeboom 1973, Kean et. al. 1978, Penso 1981, Grove 1990), of phytopathology (Böhner 1933–1935, Ainsworth 1981, Campbell et al. 1999), of biological control (Thompson 1939:1–27, DeBach 1974), and of microbiology (Bulloch 1938, Winslow 1943, Brock 1961, Clark 1961, Waterson and Wilkinson 1978, Wilkinson 1992) describe progress to germ theory by the 1870s. During the 1900s the fields of plant parasitology and animal parasitology expanded greatly, in numbers of parasitologists, in university education, in societies, and in journals. G. Ainsworth, *Introduction to the History of Plant Pathology* (1981) and Lee Campbell et al., *The Formative Years of Plant Pathology in the United States* (1999) continue their surveys into the 1900s. Histories of animal parasitology by Foster (1965), Kean et al. (1978), and Grove (1990) cover the 1900s down to their publication dates, but all three are organized by parasitic diseases, not by chronology.

With the rise of four ecological sciences by the early 1900s (Egerton 2013*d*, 2014a, b, c), followed by ecological societies founded in Britain and North America, it becomes less essential to follow here the overall development of animal and plant parasitologies. Therefore, only a few (mostly American) aspects of that story are told here.

Part 45, on entomology during the 1800s, ended with discussion of Leland Howard's promotion from Assistant Entomologist to Chief Entomologist at USDA in 1894 and his study on parasitism in white-marked tussock moths (Howard 1933, Mallis 1971:79–86, Hatch 1972, Sterling 1998*c*, Egerton 2013*a*:73–74). That species was a native, and he found that its increase to plague proportions was soon followed by increases in its native parasite species, which quickly reduced its numbers. A similar cycle was less likely when foreign pests were introduced and increased to plague numbers, such as gypsy moths and brown-tail moths. He and W. Fiske, head of the Gypsy Moth Parasite Laboratory, Melrose Highlands, Massachusetts, reported on the control of these foreign tree parasites by introducing their native European parasites (Howard and Fiske 1911). Their landmark monograph included a 69-page history of previous introductions of foreign parasites to combat foreign insect pests. It proved impossible to eliminate these foreign moths, but their level of forest destruction was reduced to the level that occurred in Europe (Schwerdtfeger 1973:381).

Vladimir Alexandrovitch (called Anatol) Kostitzin (1882/83–c.1963) was a Russian mathematician and scientist who participated in revolutionary ferment in Moscow in 1905; afterwards he went into exile in Austria, France, and Switzerland (Scudo and Ziegler 1976:396). He returned to Russia before World War I and fought in the Russian army and participated in the Russian Revolution. His early interests were in physical sciences, but he married a parasitologist who moved to Paris in the mid-1920s, and he followed by 1927. In 1930, he heard the prominent Italian mathematician Vito Volterra lecture in Paris on "the mathematical theory of the struggle for life," and in 1931 he was junior coauthor with his wife (J. Kostitzin) of a mathematical analysis of the relationship between hermit crab *Eupagurus curanensis* and its barnacle parasite *Chlorogaster sulcatus*. That study became an example in his *Symbiose, parasitisme et évolution (étude mathématique)* (1934). That book, in turn, was absorbed into his more general *Biologie mathématique* (1937, English 1939).

In the United States there are state veterinary medical associations. The one in Oklahoma was established in 1907, and its centennial was celebrated with a centennial history (Ewing 2006). The Helminthological Society of Washington was organized in 1910 (Anonymous 1960), the *Journal of Parasitology* was founded in the United States in September 1914, and the American Society of Parasitologists (APS) was founded on 30 December 1924 (Kiger 1962). ASP had 281 members in 1927 and 550 members by 1931. Henry B. Ward edited the *Journal of Parasitology*, volumes 1–18, with 4238 pages; volumes 19–39 published 11,162 pages. Many states also support veterinary medicine schools within state land-grant colleges. Iowan parasitologist Wendell Krull (1897–1971) was founding head of veterinary parasitology when the veterinary medicine school opened at Oklahoma A and M College (now Oklahoma State University) in 1948. His biography was written by his successor, Sidney Ewing (2001). In 1956, American veterinary parasitologists organized the American Association of Veterinary Parasitologists, with Krull as its first secretary-treasurer, and later, as its president. Although Krull and Ewing emphasized livestock and companion animal parasitology in teaching and research, Krull's "The



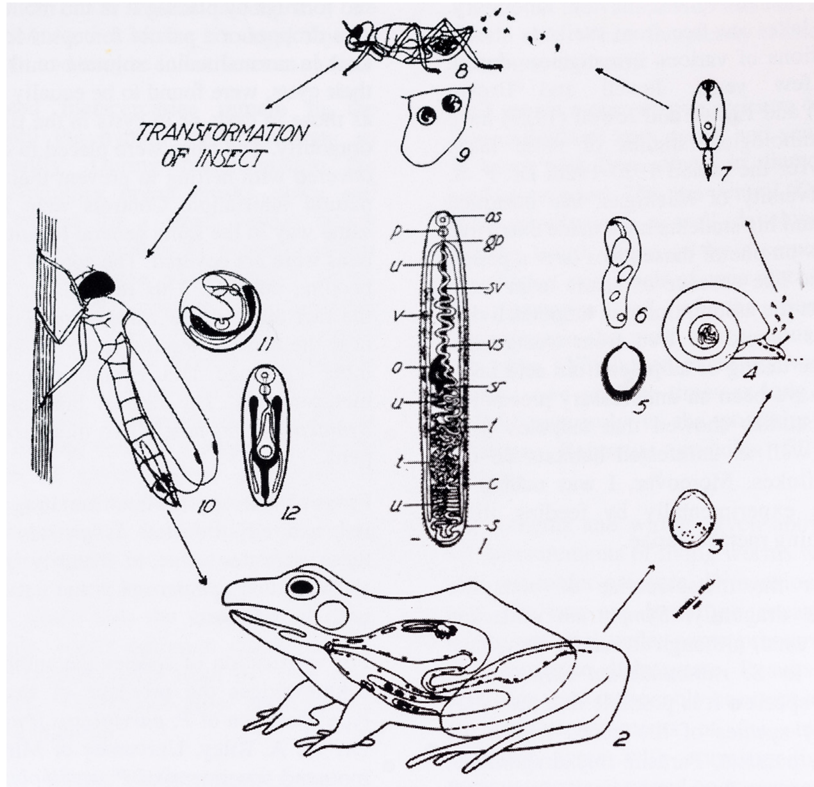


Fig. 8. (a) Wendell Krull, 1931. (b) Life cycle of trematode *Pneumonoeces medioplexus*, involving three hosts: leopard frog *Rana pipiens*, snail *Planorbula armigera*, and dragonfly *Sympetrum obtrusum*. Krull 1930. Krull's caption explained each numbered illustration. From Ewing 2001:44, 48.

Life History of Two North American Frog Lung Flukes" (1930) was on wildlife.

Midwestern ecological parasitologist Gerald Esch wrote a history of field parasitology and stated that (Esch 2004:97)

> *Field parasitology in North America, from the standpoint of both teaching and research, had its beginning in the University of Michigan Biological Station (UMBS) close to Douglas Lake, and near the tiny village of Pellston in the northern tip of lower Michigan. Research in field parasitology at UMBS began in 1914, with the work of William Walter (Will) Cort.*

Cort (1887–1971) began publishing his research on Douglas Lake parasites with two papers in 1915, and he published 20% of the 350 parasitology papers coming from that station by 2004 (Stoll 1972, Esch 2004:97) . He began teaching helminthology there in 1927. The Douglas Lake Biological Station was also an important center for limnological research and teaching (Chandler 1963:100–102, Egerton

2014*b*:45), which provided ecological and environmental knowledge relevant to understanding aquatic parasites. Incidentally, Cort and Krull were great friends.

North Dakotan Edward Steinhaus (1914–1969) was the son of a farmer and store-owner father and a schoolteacher mother (Knipling 1974, Steinhaus 1975:158–160, Steinkraus 1999). His career orientation was influenced by reading Paul de Kruif's *Microbe Hunters* (1926). He developed strong interests in both entomology and bacteriology, choosing the latter for his major at North Dakota Agriculture College (now North Dakota State University, B.S., 1936), and at Ohio State University he majored in bacteriology and minored in entomology (Ph.D., 1939). There, he met and married bacteriologist Mabry Clark (1940). He joined the U.S. Public Health Service at its Rocky Mountain Laboratory in Montana, 1941–1944, where he published his first book, *Catalog of Bacteria Associated Extracellularly with Insects and Ticks* (1942). Eventually, he decided his research was insufficiently valued and resigned (Steinhaus 1975:148–150). He went to the University of California, Berkeley, 1944–63 (Steinhaus 1975:152–158); in 1963 he became the first Dean of Biological Sciences at the new University of California campus at Irvine (Steinhaus 1975:258–266). Steinhaus established insect pathology as a separate science (Cameron 1973:298–299) and published *Insect Microbiology* (1946), followed by *Principles of Insect Pathology* (1949). He led an effort to found the *Annual Review of Entomology* (1956) and co-edited it for seven years (Steinhaus 1975:410–415). In 1959 he was among the first to receive the Founders' Memorial Award from the Entomological Society of America, and in 1963 he served as its president. He founded the *Journal of Insect Pathology* in 1959 (Steinhaus 1975:416), which he changed in volume 7 (1965) to the *Journal of Invertebrate Pathology* (Steinhaus 1975:383). "Biologist, educator, author, entomologist, administrator, editor, bacteriologist, virologist, Steinhaus was one of the most productive scientists of his time and trained many of the most important living scientists in this discipline" (Steinkraus 1999:639).

Midwestern field parasitologist John Janovy, Jr. (born 1937) perhaps brought the natural history essay tradition to animal parasitology, with his *Keith County Journal* (1978). Janovy did not write only about parasites, but he used his 13 natural history essays to place animal parasites within a broad context. His books may interest other parasitologists, but are written for a broader audience. His *Yellowlegs* (1980) discussed parasites of lesser yellowlegs *Tringa flavipes*, which he studied during a sabbatical, within the context of the natural history of this sandpiper. *Back in Keith Country* (Janovy 1981) continues his memoirs, as does *Dunwoody Pond: Reflections on the High Plains Wetlands and the Cultivation of Naturalists* (Janovy 1994). There are snippets of his career in *On Becoming a Biologist* (Janovy 1985), but he wrote that book for biology majors in college. He has continued publishing books on his later career, which, along with a bibliography of scientific papers, are listed at his web site. None of the above-cited books excepting *Biologist* have indexes or bibliographies; some books contain illustrations from his pen.

Midwesterner Gerald Esch (born 1936) does not mention being inspired by Janovy's essays to write his own, but he does include a very positive account of Janovy's research and teaching in *Parasites, People, and Places* (2004:136–156). The scope of Esch's essays are much broader than Janovy's, not being limited to his own research. He identifies himself as an "ecological parasitologist." What exactly is ecological parasitology? Traditional parasitology has focused upon finding the life cycle of a particular parasite, as in Krull (1930). At Wake Forest University, Esch and his students often conducted research at Charlie's Pond, where they were interested in its fauna of fish, frogs, insects, and parasites. One such parasite was a hemiurid *Halipegus occidualis*, which Krull had studied, and its life cycle was

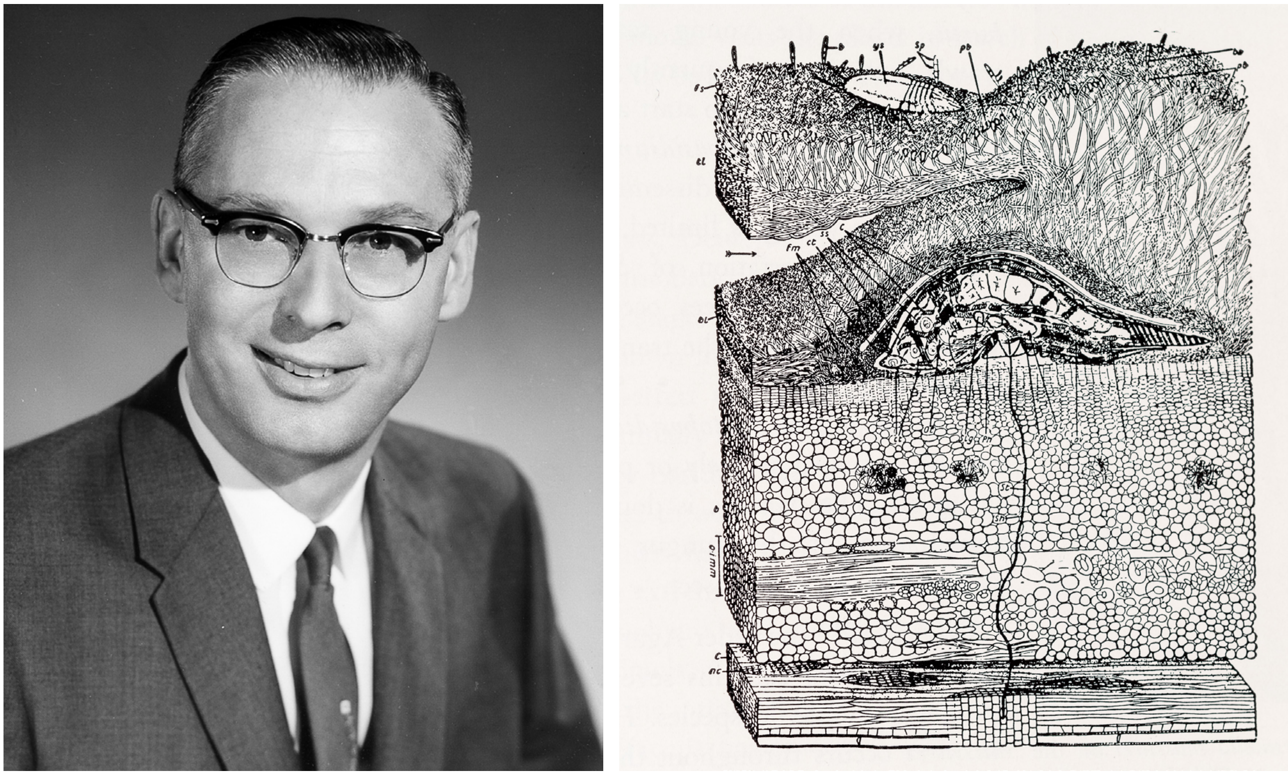


Fig. 9. (a) Edward Arthur Steinhaus. [color photo at web site]. (b) Sectional view of symbiotic association between fungus *Septobasidium burtii* and scale insect *Aspidiotus osborni*. Insect sucking tube extends through bark of tree into cambium. Young scale insect crawls over surface of fungus. Couch 1938. From Steinhaus 1946:391.

thus already known. This species lives in the mouth of the green frog *Rana clamitans*, and these recent parasitologists discovered that they can lift a frog's tongue and count its parasites without having to kill the frog (Esch 2004:77). Instead, they clip a toe to be able to identify it again at a later capture. This technique enabled them to assess the population of the pond's frogs and parasites. One student, Derek Zelmer, wrote a Ph.D. dissertation on the population dynamics of this parasite (Esch 2004:78–79).

Instead of writing a historical survey of particular parasitic diseases, as earlier historians of parasitology had, Esch wrote case histories of particular ecological parasitologists and their research. There are six chapters of such case histories in his first collection of essays (Esch 2004, 235 pages). Since that collection was well received, he wrote another, longer one (Esch 2007, 355 pages). The second collection, *Parasites and Infectious Disease: Discovery by Serendipity, and Otherwise*, is divided into two parts. The Prologue has 17 biographical sketches (with photographic portraits), based upon interviews that Esch conducted with each of these parasitologists (104 pages); and 15 chapters on particular parasitic infections, this part being in the tradition of the earlier histories of parasitology cited above. Some of those who were interviewed reappear in later chapters.

Brood parasitism has been known since antiquity in European cuckoos (see above); during the 1800s, it was discovered in cowbirds of the Americas (see above); and during the 1900s in African finches (Ortega 1998, Davies 2000). In 1868, New Zealand shepherd James MacDonald discovered a kea parrot *Nestor notabilis* attacking a sheep and eating some of its flesh (Garstang 1895, Wikipedia). Similar reports followed, including reports of it attacking rabbits, dogs, and horses. A bounty was established and tens of thousands killed. Doubts were expressed until it was videotaped feeding on a sheep in 1993. It is now a protected rare species, but some are still being shot. The Laysan Finch *Telespyza cantans*, in westernmost Hawaiian Islands, behaves similarly on the wings of albatrosses (Mitchell 1990:169).

Pollination

Although most of Hermann Müller's *Die Befruchtung der Blumen durch Insekten und die gegenseitigen Aupassungen beider* (1873, English 1883, discussed above) described flower mechanisms to ensure proper pollination, he also studied insects attracted to particular kinds of flowers and devoted a 38-page chapter to insect pollinators. Paul E. O. W. Knuth (1854–1900) received a doctorate from his hometown university at Greifswald (1876), and then became a high school teacher, first at Iserlohn, and later at Kiel (van der Pas 1973). Inspired to surpass Müller's monograph, he took a leave of absence and studied at the tropical botanical garden in Buitenzorg, Dutch East Indies, November 1898–March 1899, which had facilities for visiting scholars (Dammerman 1945:66). There, Knuth studied pollination of over 200 species of tropical plants (and other subjects) in preparation for his *Handbuch der Blütenbiologie* (three volumes, 1898–1905, English 1906–1909).

No one has tried to outdo Knuth's encyclopedic treatment. F. Faegri and L. van der Pijl instead wrote *The Principles of Pollination Ecology* (1966, edition 2, 1971) as a guide for educators (not expecting its adoption as a textbook). It is unclear (to me) why a second edition was needed, though it cited a book published in 1965 and one in 1970 not cited in their first edition. The second edition is slightly longer, but with shorter pages. Philip Regal studied the "Pollination by Wind and Animals: Ecology of Geographic Patterns" (Regal 1982), and also studied patterns of frequency of these different modes of pollination for the "most exposed layers of vegetation: trees in the case of forests, and the dominant shrubs for shrub communities" in North and Central America and in Australasia (Regal 1982:498). First, he described the ecogeographic trends for different regions and then discussed the possible reasons for the trends. Much causal uncertainty remained, but he provided guidance to the existing literature and pointed to further research opportunities. Olle Pellmyr's "Pollination by Animals" (2002) is a synthesis focused on evolutionary dynamics.

Lichens

During the 1800s, botanists steadily increased their knowledge of both algal and fungal species (Ainsworth 1976:26–197), and mycologist–phytopathologist H. Anton de Bary (1831–88; on him: Paracer and Ahmadjian 2000:231–233, Egerton 2012*c*:314–315) in his textbook on the morphology and physiology of fungi speculated that gelatinous lichens are (de Bary 1866:291, translated in Mitchell

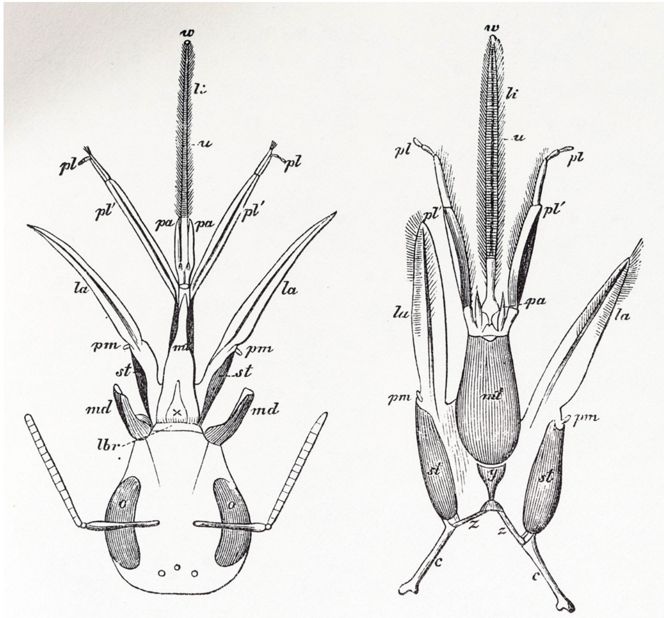
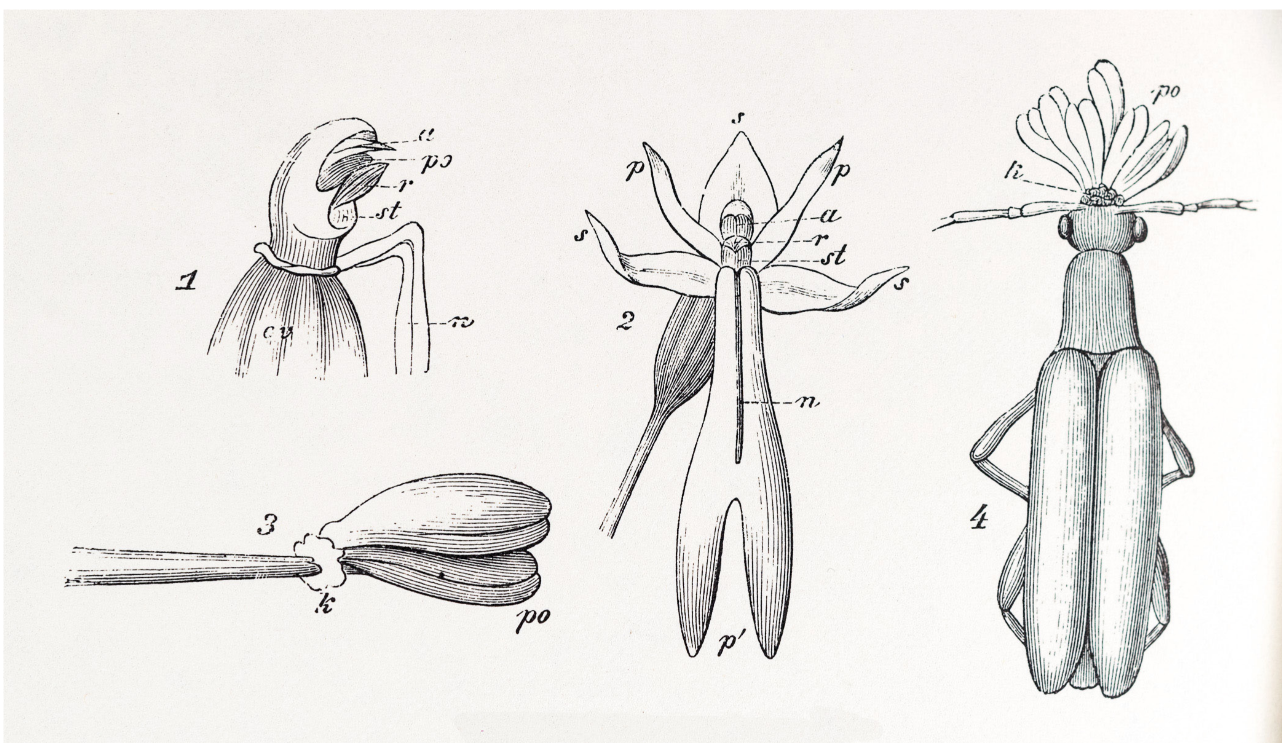


Fig. 10. (a) Diagrams of heads of humble bee (*Bombus*) and mouth-parts of hive bee (*Apis*). (b) Mechanism for pollination in orchid *Listera ovata* (Figs.1–3) and pollinating beetle *Grammoptera lavis* with pollinia on forehead (Fig.4). Müller 1883:59, 530.



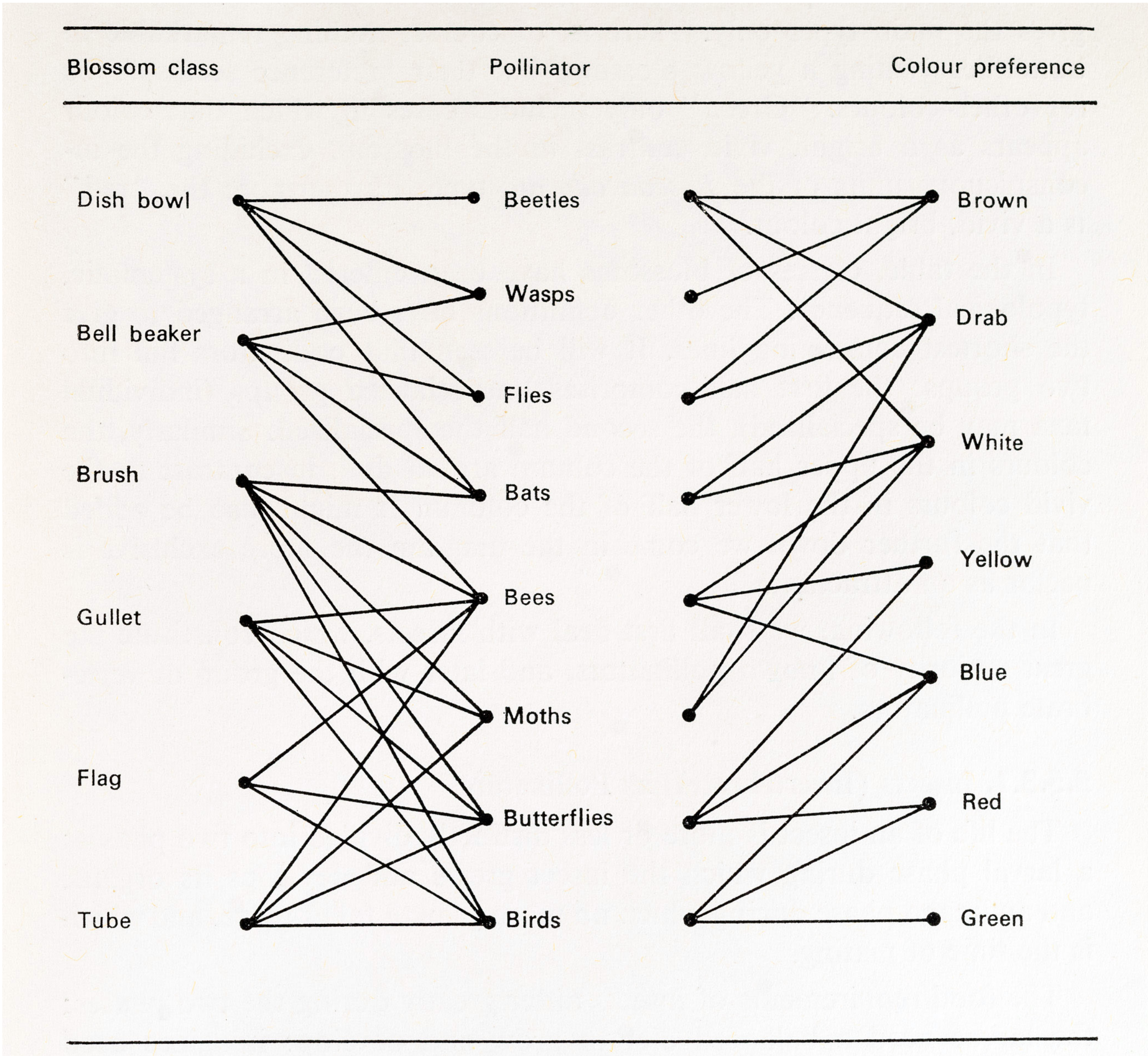


Fig. 11. Table 4. “Harmonic” relations between pollinators and blossoms. Faegri and van der Pijl 1966:83, 1971:111.

2002:195)

> *either the fully developed, fruiting condition of plants whose immature states were included until now in the algae as Nostocaceae and Chroococcaceae, or those families are typical algae that assume the form of* Collema, Ephebe *etc. as a result of penetration by certain parasitic ascomycetes.*

The next year Swiss botanist Simon Schwendener (1829–1919) briefly announced that lichens have a dual nature, combining algae and fungi (Schwendener 1867, Sanders 1975, Ainsworth 1976:97–99, Cittadino 1990:27–31, 52–55). In 1868 he elaborated on his conclusions (summarized in English, Schneider 1897a:24–25). A year later, he claimed that lichens are "ascomycetes parasitic on algae" (Schwendener 1869:38–39, translated in Mitchell 2002:195).

Simultaneously, in 1867, Russian botanist Andrey S. Famintsyn (1835–1918), and Ukrainian botanist (Josif) O. V. (or W.) Baranetsky (1843–1905), both of whom had studied under de Bary (Mitchell 2011:124–125), studied a cross-section of a lichen thallus and observed green cells (then called gonidia, now, phycobionts) fall out, and they cultured them separately and concluded that they "completely resemble the form *Cystococcus* described by Nageli" (translated in Khakhina 1992:21). However, they concluded that the alga *Cystococcus* was an immature stage of a lichen. They published their findings in French and German articles (Fanintsyn and Baranetsky 1867*a*, *b*). Baranetsky next found that lichen gonidia are "physiologically independent organisms" (1868, translated in Khakhina 1992:22). De Bary thought that it might be possible to make an artificial lichen synthesis by "inoculating free-living gonidia with spores of the species concerned" (1868, translated in Mitchell 2011:126). His student Max Reess (1845–1901) attempted this with some success (1872).

The dual theory of lichens met resistance from lichenologists who had invested much thought on lichens as a distinct group comparable to algae, fungi, and mosses. Most notorious of these lichenologists was William Nylander (1822–99), a Finn living in Paris, most of the time in poverty (Collander 1966:23–28, Lawrence 1974, Vitikainen 2000), just as mycologist Persoon had in the early 1800s (Egerton 2012*b*:303–304). Nylander attacked the dual theory beginning in 1870, and he ended all contact with Schwendener's supporters. He urged others, including his English colleague and correspondent James Crombie (c.1831–1906), later author of *A Monograph of Lichens Found in Britain* (1894) and related works (Mitchell 2003, Seaward 2004), to do likewise. With that encouragement from a leading lichenologist, clergyman Crombie complained in 1874: "a theory has been started which, should it be accepted, would virtually deprive lichens of the position which had hitherto been assigned them in the vegetable kingdom" (quoted in Mitchell 2002:198).

If lichens have a dual nature, how do they reproduce? De Bary's student, Ernst Stahl (1848–1919), sought sexual organs and found them in *Collema microphyllum* (Stahl 1874, translated in Mitchell 2006:153)

> *...lichen spermatia are to be regarded as productions physiologically equivalent to the spermatozoids of other cryptogams. The projecting continuation of the ascogonium is to be seen as the female receptive organ; the fertilizing effect becomes transferred to the ascogonium through the multicellular tube.*

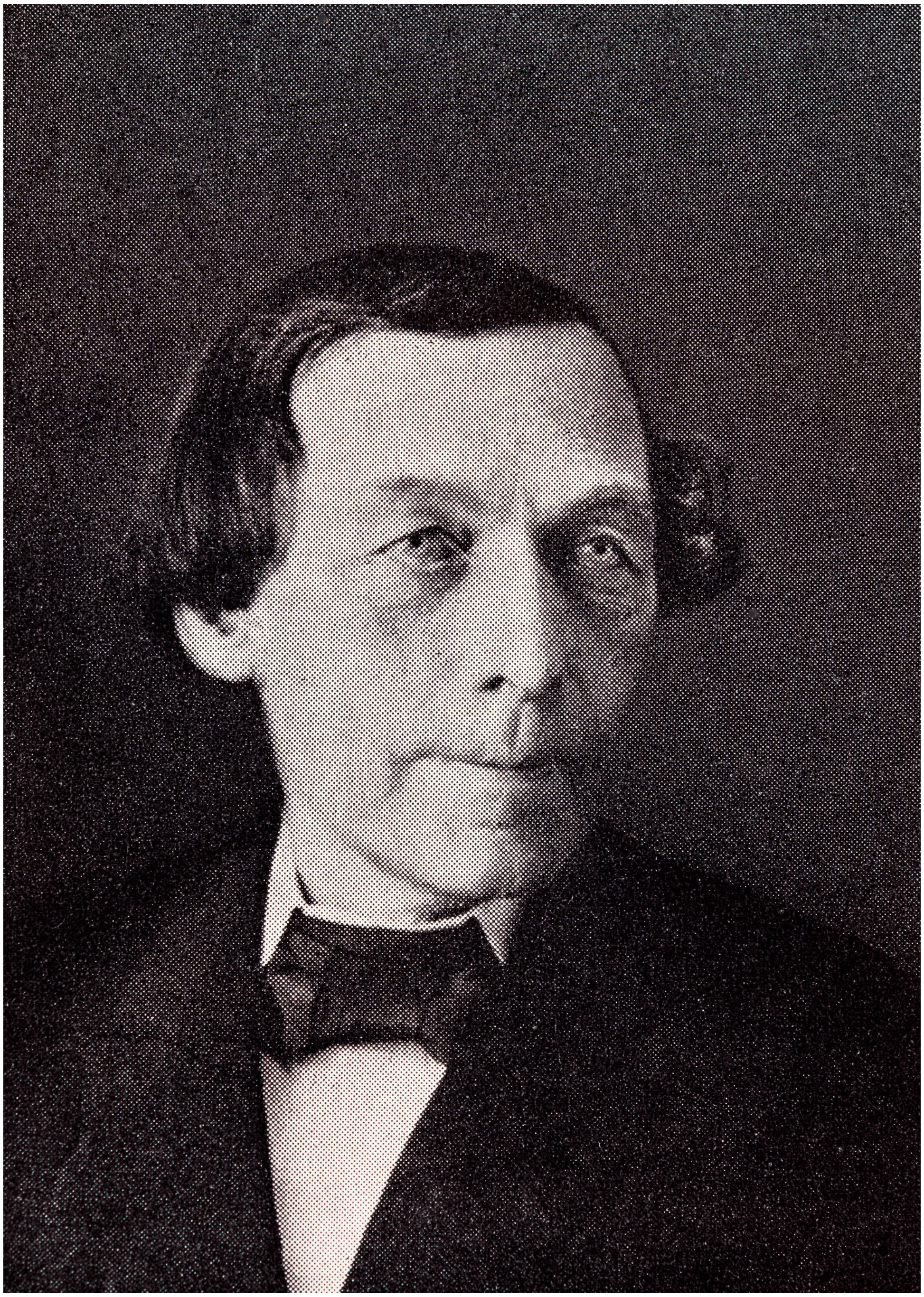


Fig. 12. William Nylander. De Virville 1954:198 or Collander 1965:facing 32 or web.

Stahl saw a similarity with fertilization in red algae and borrowed a phycological term, “trichogyne,” to indicate the upward extending ascogonium. However, other botanists questioned Stahl’s discovery of sexuality in lichens. Some viewed his “spermatia” as asexual propagules, and others thought spermatia could function as either sexual cells or asexual propagules. Lichenologists have not achieved a consensus on this question (Mitchell 2006:153–162). Both de Bary (1866) and Schwendener (1867) had initially suggested that lichens were algae parasitized by fungi. University of Göttingen botanist Johannes Reinke (1849–1931) suggested (1872) that the parasite might be the algae; E. Janczewski came to the same conclusion: “endophytic *Nostoc* is a chlorophylous parasite that depends on the *Anthoceros* thallus for its raw nutrients” (1872, translated in Mitchell 2007:111). However, Reinke (1873) changed his mind and suggested that long, healthy lives of lichens indicated that it was not a parasitic relationship, and suggested “consortium” to describe the relationship (Ainsworth 1976:98). German plant physiologist Albert B. Frank (1839–1900) suggested instead (1877) the term “Symbiotismus” (Frank 1877:195, translated in Sapp 1994:6)

> *…where two different species live on or in one another under a comprehensive concept which does not consider the role which the two individuals play but is based on the mere coexistence and for which Symbiosis is to be recommended.*

In an address given before the Association of German Naturalists and Physicians in 1878, de Bary adopted the term “Symbiose,” defining it as “the living together of unlike named organisms” (Bary 1878, 1879*a*, translated in Sapp 1994:7). Since he taught at Strassbourg University, on the (recently changed) French–German border, he also published it in French (Bary 1879*b*). Reinke apparently changed his mind yet again, for Michael Mitchell quotes him (Mitchell 2011:131, in translation) commenting in 1895: “Acharius’ perception of lichens as constituting a class of plants comparable to algae and fungi remains, for the most part, correct,” which Mitchell calls a “reactionary notion.”

Although isolated papers relevant to lichen ecology appeared in the 1870s–1880s, “the study of lichen ecology was pioneered by Bruce Fink (1861–1927)” (Mitchell 2011:130) in the 1890s, concerning Minnesota lichens. While at the University of Minnesota, Conway MacMillan (Egerton 2013*d*:358) headed the Minnesota Botanical Survey, and in summer he hired Fink, from Upper Iowa University (where Krull had earned his B.A. degree), as a survey member; he identified Minnesota lichens, and seems also to have absorbed MacMillan’s ecological perspective. Fink published a series of five “Contributions to a Knowledge of the Lichens of Minnesota,” the fifth of which considered “lichen formations of the region, causes of their peculiar make-up, and comparisons with similar formations within and outside the area” (Fink 1899:283). In his judgment, his was the first paper to consider lichen ecology (separate from considering symbiosis between fungus and alga), and lichenology’s historian agrees that this was “the earliest attempt to assess the influence of environmental factors on lichen colonization” (Mitchell 2011:131). Fink identified 19 taxa within a *Pyrenula* lichen formation of trees with smooth bark, 17 taxa within *Lecanora* formation of exposed granite, and 7 taxa within *Endocarpon hepaticum* formation of exposed earth. Fink reached out to other lichenologists in “Ecologic distribution an incentive to the study of lichens” (1902) and in “Some common types of lichen formations” (1903). Fink’s message influenced Copenhagen high school teacher Olaf Galløe (1881–1965), who published “Danske Likeners Økologie” (Galløe 1908, Mitchell 2011:132). Eugenius Warming (1841–1924) also discussed lichen

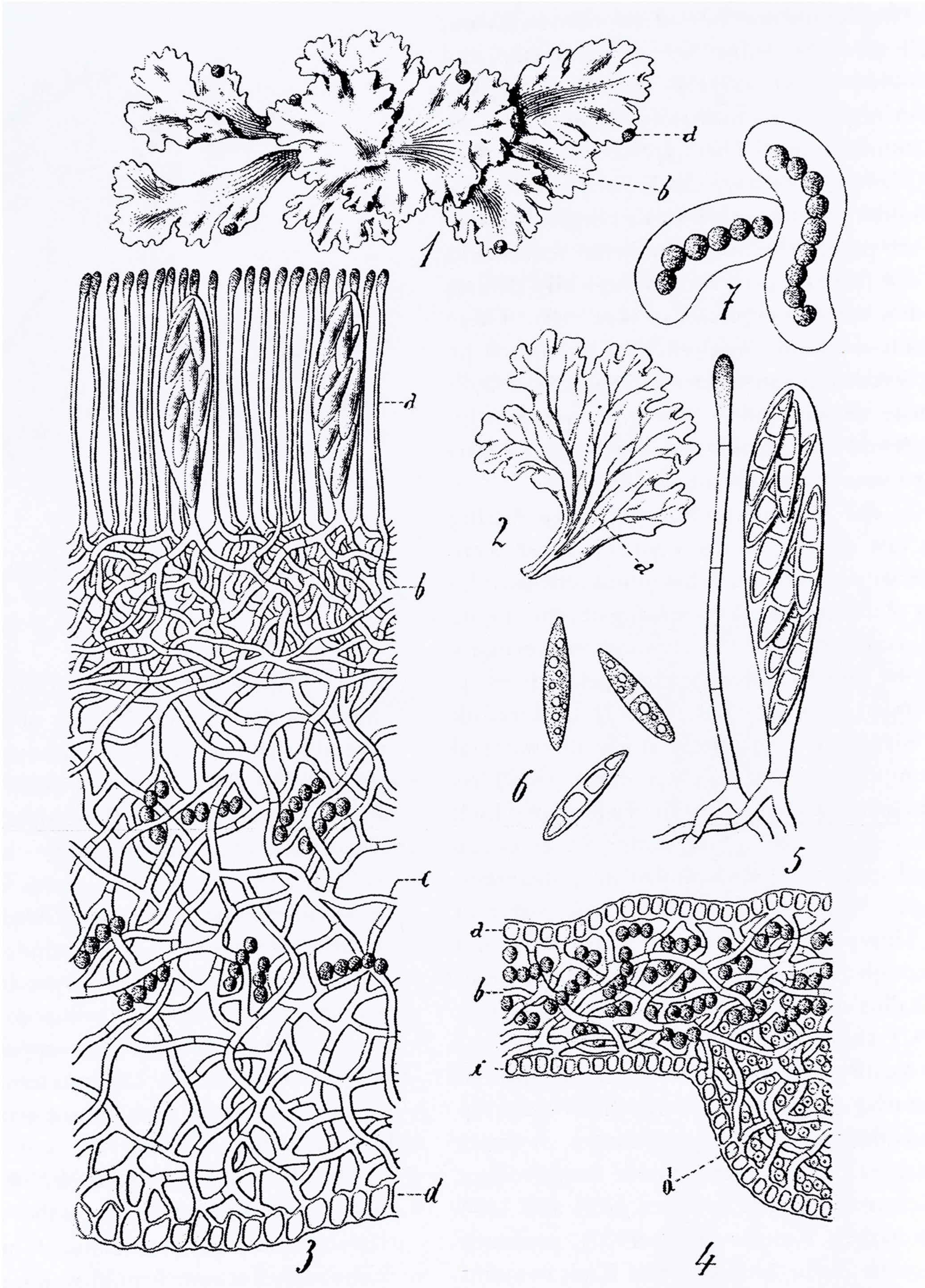


Fig. 13. *Hydrothyria venosa*. Schneider 1897, plate 64. From Mitchell 2009:18.

formations in the English version of his book, *Oecology of Plants* (1909:see index; Mitchell 2011:132). Particularly significant was his account of lichen coastal communities or zones (1909:224, 1977)

> *Spray cast up by the breakers, and particles of salt deposited by foam and wind on the plants, introduce a floristic modification into the rock-vegetation, so that there is an admixture of halophytes or it is purely halophytic. There thus come into being communities, including those composed of lichens, which display a zonal distribution. On granite rocks at Bornholm (in Denmark), at Kullen (in Sweden), and elsewhere on the northern coasts, the vegetation is arranged in several belts. Lying lowest, where the rocks are very frequently wet, is Verrucaria maura, a very thin black scaly lichen divided into small pieces; this lichen is widespread along the coasts of northern and arctic seas. Higher up, the rocks are reddish yellow with* Placodium murale*, which is accompanied by* Xanthoria partietina*. Above this follows a belt of* Ramalina scopulorum*; here the action of the saltwater is reduced to little or nothing. In the first two lichen-belts cracks in the rock entertain halophytic* Spermopghyta *including* Matricaria maritime*,* Aster tripolium*, and species of* Atipleax*. A little higher the action of the salt water vanishes, and the vegetation on littoral rocks is identical with that on inland rocks.*

His study was supplemented by M. C. Knowles, "The Maritime and Marine Lichens of Howth," in Ireland (1913; Mitchell 2011:132).

In the United States, Illinois native Albert Schneider (1863–1928) began his career as a very promising lichenologist, but after four publications he switched to pharmacology (Cattell and Brimhall 1921:604, Sapp 1994:32–34, Mitchell 2011:129). He had received his B.S. degree at the University of Illinois, and M.S. degree from the University of Minnesota, where he taught cryptogamic botany for two years before moving to the Brooklyn Institute in order to obtain a Ph.D. at Columbia University. His first article, "Mutualistic Symbiosis of Algae and Bacteria with *Cycas revoluta*" (1894) was not about lichens, but about a symbiotic relationship of a vascular plant species and symbionts in its roots. Such relationships had been known since the 1880s, but not previously reported for this species. The alga involved was *Nostoc commune*, and as a symbiont it could live underground. Bacteria involved included at least three species of *Rhizobium*: *mutabile, curvum*, and *Frankii*. Schneider turned his doctoral dissertation into *A Text-book of General Lichenology* (1897), followed by *A Guide to the Study of Lichens* (1898). He also wrote a general article, "The Phenomena of Symbiosis" (1897), covering animals as well as plants, though he published it in a botanical journal, where few if any zoologists would have read it. He recognized a range of relationships (1897b:930–931)

- *I. Incipient Symbiosis (Indifferent Symbiosis).*
    - *1. Accidental Symbiosis.*
    - *2. Contingent Symbiosis (*Raumparasitismus*).*
- *II. Antagonistic Symbiosis.*
    - *1. Mutual Antagonistic Symbiosis (Mutual Parasitism).*
    - *2. Antagonistic Symbiosis (Parasitism).*
        - *a. Obligative Antagonistic Symbiosis.*
        - *b. Facultative Antagonistic Symbiosis.*
    - *3. Saprophytism.*

a. Faculative Saprophytism.
b. Obligative Saprophytism.

III. Mutualistic Symbiosis

1. Nutricism (Semi-mutualistic Symbiosis).
2. Mutualism.
3. Individualism.
a. Semi-individualism.
b. Complete Individualism.

IV. Compound Symbiosis.

Schneider defined all of these terms. He coined the term "nutricism," which he defined as when "one symbiont nourishes the second symbiont without receiving any benefit in return" (1897b:940). He also provided a chart indicating how he thought these stages of symbiosis evolved (1897*b*:932).

Lichens are modest components of existing ecosystems, but Professor Andrew Watson, University of East Anglia, and his former graduate student and current collaborator, Tim Lenton, think that lichens played a more prominent role in life's invasion of dry land than they do now that they share the land with bacteria, plants, animals, and fungi (Morton 2007:216–217). During the Proterozoic Era when they arose, they were more effective at leaching nutrients out of rock and sands and spreading themselves than were bacteria; lichen growth increased the flow of phosphates into the oceans and ultimately "paved the way" for plants to make their way onto land.

Thomas Jensen (2002:84) provides a recent summary of lichen diversity

> *These are symbiotic relationships between fungi and algae including the cyanobacteria. There are about 15,000 to 20,000 known species of lichens with about 520 having both a blue-green and a green component (Rai 1990). About 1,600 species of lichen have a blue-green photobiont. The fungi are Ascomycetes, Blasidiomycetes and Fungi Imperfection, and a wide variety of blue-greens.*

Commensalism and mutualism

Invertebrate zoologist Pierre-Joseph van Beneden (1809–94) had fought for Belgian independence in 1830. He became Belgium's foremost zoologist, at Catholic University, Louvain (Kemna 1897, Florkin 1970). In a discussion on "La Vie sociale des Animaux inférieurs" (1873) he introduced the terms "commensalism" and "mutualism" (Boucher et al. 1982:317, Dajoz 1984:83–84, Sapp 1994:7–8, 18–20). He expanded and popularized his concepts in *Les commensaux et les parasites dans le règne animal* (1875, English 1876). He defined a commensal individual as requiring "a simple place on his vessel, and does not partake of his provisions" (Beneden 1876:1). Mutualists are (Beneden 1876:68)

> *…animals which live on each other, without being either parasites or messmates; many of them are towed along by others; some render each other mutual services, others again take advantage of some assistance which their companions can give them; some afford each other an asylum…*

Beneden concluded that there was an "almost insensible gradation of differences between parasite, messmate, and free animals" (Beneden 1876:56), and he provided numerous examples of these

Fig. l4. Pierre-Joseph van Beneden. KU Leuven file at van Beneden web page.

relationships. De Bary (1879*a*:21, 1879*b*:306–309) thought that different kinds of lichens also showed this gradation of relationships. Later, "commensalism has been expanded to include all those ecological unions in which, although both parties do not benefit, as in mutualism, neither one is harmed…" (Allee et al. 1949:243).

In late 1860s or early 1870s, English amateur naturalist Thomas Belt (1832–1878), in Nicaragua, discovered that small stinging ants *Pseudomyrma bicolor* live in hollow thorns on the bull's horn acacias where, in exchange for safe places to nest and feed, they protect acacias from depredations of other vegetarian animals (Belt 1888, 1985:218–222, Brown 1960, Van Ripper 2004, Egerton 2013*a*:40–42). In his account of foraging or army ants *Eciton predator*, Belt (1888:20) mentioned that birds follow these ants and snap up any insects that take flight to escape the ants, but he did not mention which species of birds he observed. Perhaps he saw different species at different or even at the same times; Edwin Willis and Yoshika Oniki (1978:246) listed 50 species that regularly follow army ants. Another of Belt's discoveries was that leaf-cutting ants *Oecodoma* use the leaf parts to grow fungi, which they ate, in underground rooms. Wheeler, discussed above, published "The Fungus-growing Ants of North America," in which he acknowledged (1907:677) Belt's publication (1874) of this discovery.

Nebraskan lawyer–botanist Roscoe Pound (1870–1964) introduced to many American naturalists the concepts of "Symbiosis and Mutualism" (1893). He misdated de Bary's *Die Erscheinung der Symbiose* (1879), and his interpretations of symbiosis and mutualism met with some disapproval by Sapp (1994:30–31). Pound left botany in the early 1900s, but he did exert some influence upon his collaborator, Frederic E. Clements (Tobey 1981, Egerton 2013*d*:358–360).

Professor Paul Portier (1866–1962), University of Paris, wrote *Les Symbiotes* (1918), probably the first synthesis since Beneden's (1875). Portier was an animal physiologist with broad interests (Monnier 1975). His concept of symbiosis involved bacteria being symbionts of all multicellular organisms (Buchner 1965:70–71, Sapp 1994:77), which Maurice Caullery challenged in the French edition (Caullery 1922, 1952) of his *Parasitism and Symbiosis* (explained in the English edition [Caullery 1952:280]). Portier's idea never carried the day; nevertheless, it was similar to later ideas on symbiogenesis/endosymbiosis. Invertebrate zoologist Caullery earned his doctorate in Paris in 1895, taught in Lyons and Marseille, and returned to Paris as head of the department of evolution at the Faculty of Sciences in 1909 (Tétry 1971). He also became head of Station Zoologique de Wimeraux, at the Straits of Dover. Sapp (1994:142) summarized his perspective

> *Caullery's aims were to rid accounts of teleology and anthropomorphism; to show that all cases of mutualistic symbiosis could be accounted for in terms of individual life struggle, domination, and control; and to show that no natural distinction could be made between parasitism, mutualism, and commensalism.*

In Germany, Paul E. C. Buchner (1886–1978), from Nuremburg, went to the University of Munich in 1907 to study botany, but lectures by Richard Hertwig persuaded him to switch to zoology (Sapp 1994:110–111). He published numerous works on endosymbiosis of animals with microorganisms, emphasizing insects (listed in Buchner 1965:843–845). He began in 1911 with a series of 10 articles that culminated in *Tier und Pflanze in intrazellularer Symbiose* (Berlin 1921, 464 pages). After publishing

14 more articles, he published a second edition of his book, with a slightly abridged title, but twice as many pages: *Tier und Pflanze in Symbiose* (Berlin, 1930, 900 pages); more articles and books followed, culminating in *Endosymbiose der Tiere mit pflanzlichen Mikroorganismen* (Basel, 1953, 771 pages), which was translated into English and expanded (New York, 1965, xviii + 909 pages).

Perhaps the first synthesis in English on symbiosis was in Allee, Emerson, Park, Park and Schmidt, *Principles of Animal Ecology* (Allee et al. 1949:243–262, 710–721), preceded and followed by Caullery, *Parasitism and Symbiosis* (French 1922, 1950, English 1952). Caullery's English edition did not cite Allee et al.'s *Principles*, and they did not cite his French edition (1922). Caullery's list of journals included *Zeitschrift für Morphologie und Oekologie die Tiere*, but not Elton's *Journal of Animal Ecology*, and Caullery's English editor, Munro Fox, did not catch it. About 10–15% of titles in Caullery's 608-title bibliography in the English edition had post-1925 publications, which represents what he considered anew since the French edition. Read's *Parasitism and Symbiology* (1970), with almost the same title as Caullery's English edition, did not cite Caullery but did cite Allee et al. (1949). Douglas Boucher, Sam James, and Kathleen Keeler compiled a bibliographic guide to "The Ecology of Mutualism" (1982), and there are at least four multi-authored collections of symbiosis studies (Henry 1966–1967, Cheng 1971, Boucher 1985, Seckbach 2002). Although Carlos Herrera and Olle Pellmyr subtitle their edited collection "An Evolutionary Approach," their *Plant-Animal Interactions* (2002) can still be considered mostly studies in symbiosis. (Herrera described himself as an "evolutionary ecologist.")

Sometimes, a species of plant and a species of animal have developed a tight bond of mutual dependence. Such a bond Stanley Temple (1977) hypothesized between the Mauritius extinct dodo *Raphus cucullatus* and the tambalacoque tree *Sideroxylon grandiflorum*, whose seeds are within hard-shelled fruits, which only dodos could supposedly open. Andrew Mitchell repeated Temple's hypothesis (without citation and naming the tree *Calvaria*) in *The Fragile South Pacific: an Ecological Odyssey* (1990:131). However, the basis for Temple's hypothesis was subsequently discredited (Witmer and Cheke 1991, Hershey 2004, Cheke and Hull 2008:37).

A parallel relationship which Mitchell (1990:130–131) discussed is between the critically endangered Samoan tooth-billed pigeon *Didunculus strigirostris* and the *Dysoxylum* trees. This pigeon is the national emblem of Samoa and appears on some of its money. Titian Ramsay Peale (1799–1885), discussed in parts 33 and 38B (Egerton 2009:462–464, 2011:154–156), discovered it during the U.S. Exploring Expedition of 1838–1842, while the expedition was in Samoa in October 1839 (Peale 1848, Stanton 1975:132–133). Corey and Shirley Muse's account of this pigeon (Muse and Muse 1982:95–96) includes Norman Adams' color painting and mentions it eating wild yams *Dioscorea bulbifera*, but no mention of *Dysoxylum*. The *Dysoxylum* genus includes many species, some widely distributed.

A better documented case in which both species co-evolved in ways that worked to their increasing benefits is Ronald Lanner's argument in *Made for Each Other: A Symbiosis of Birds and Pines* (1996). Lanner is Professor Emeritus of Forest Resources at Utah State University, Logan. It was obvious how pine species with small seeds and large wings dispersed—by wind. But what about species with large seeds and little or no wings, such as white-bark pine *Pinus albicaulis* and several species of pinyon pine in western North America (Lanner 1996:14–15)? These species participate in a pine–corvid mutualism. Lanner focused particularly upon the white-bark pine–Clark's Nutcracker relationship, but he also

Fig. 15. Clark's Nutcracker in a white-bark pine. Lanner 1996:cover.

surveyed the knowledge for similar large-seed pine–corvid relationships for comparable mutualistic relationships in other American and Eurasian pine forests. In western North America, there are four jays that establish mutualistic relations with pines: Clark's Nutcracker, Pinyon Jay, Scrub Jay, and Steller's Jay. Each jay has a different-sized beak that determines the pines with which it can maintain a mutualistic relationship. Only Clark's Nutcracker *Nucifraga columbiana* has a beak large enough to open white-bark pine cones, which it stores underground in caches for later use. A single nutcracker has been known to harvest 129,000 seeds in one year, of which 76% were stored in caches (Lanner 1996:68). Where western pines are growing in an isolated clump, they indicate a cache which a corvid never recovered. Howe and Smallwood (1982:202–203) listed earlier studies on seed dispersal by animals.

One might expect that Lanner's findings would soon be picked up in general studies; I checked a

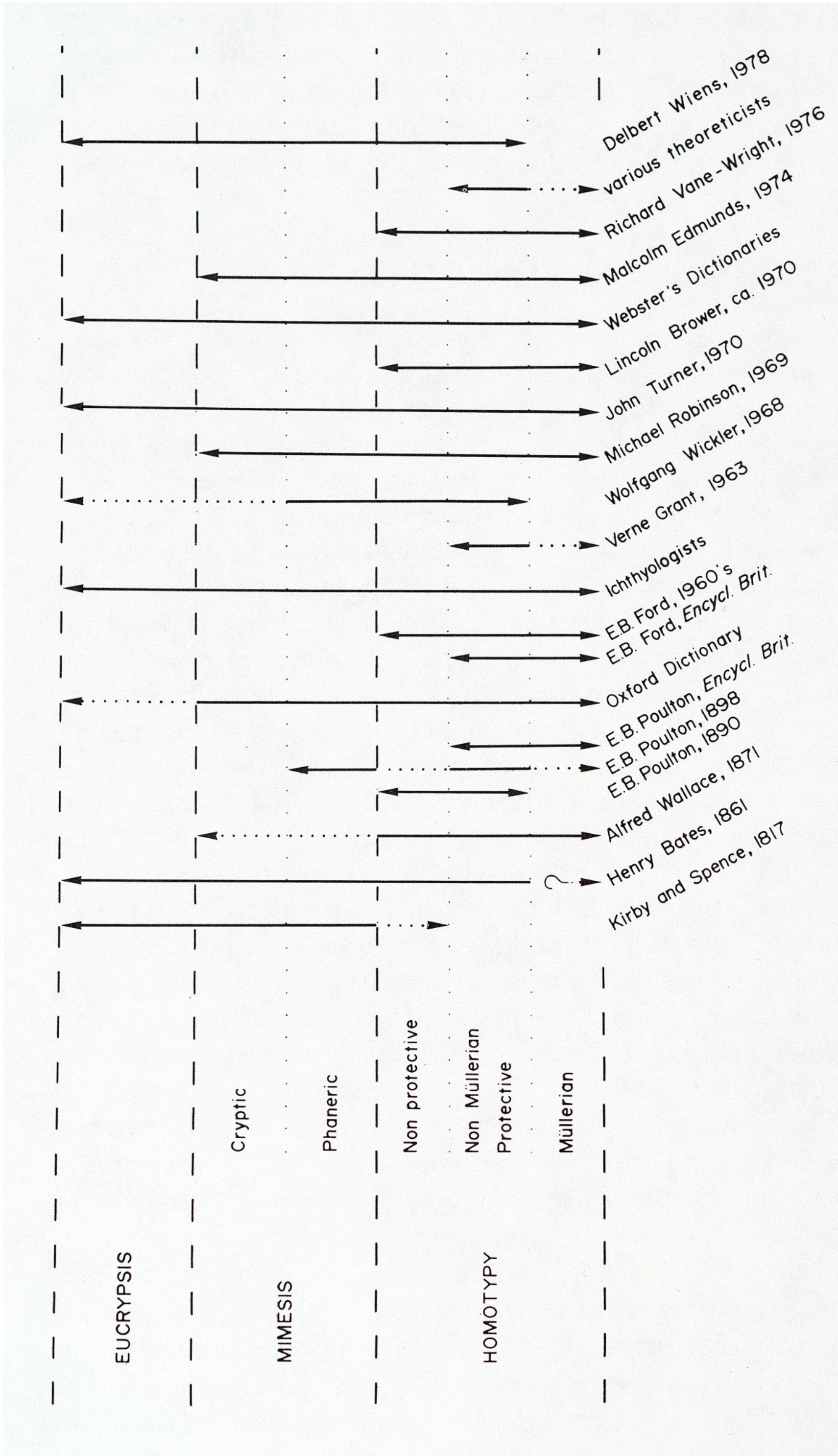


Fig. 16. Chart of historical landmarks in mimicry studies, 1817–1978. Pasteur 1982:172.

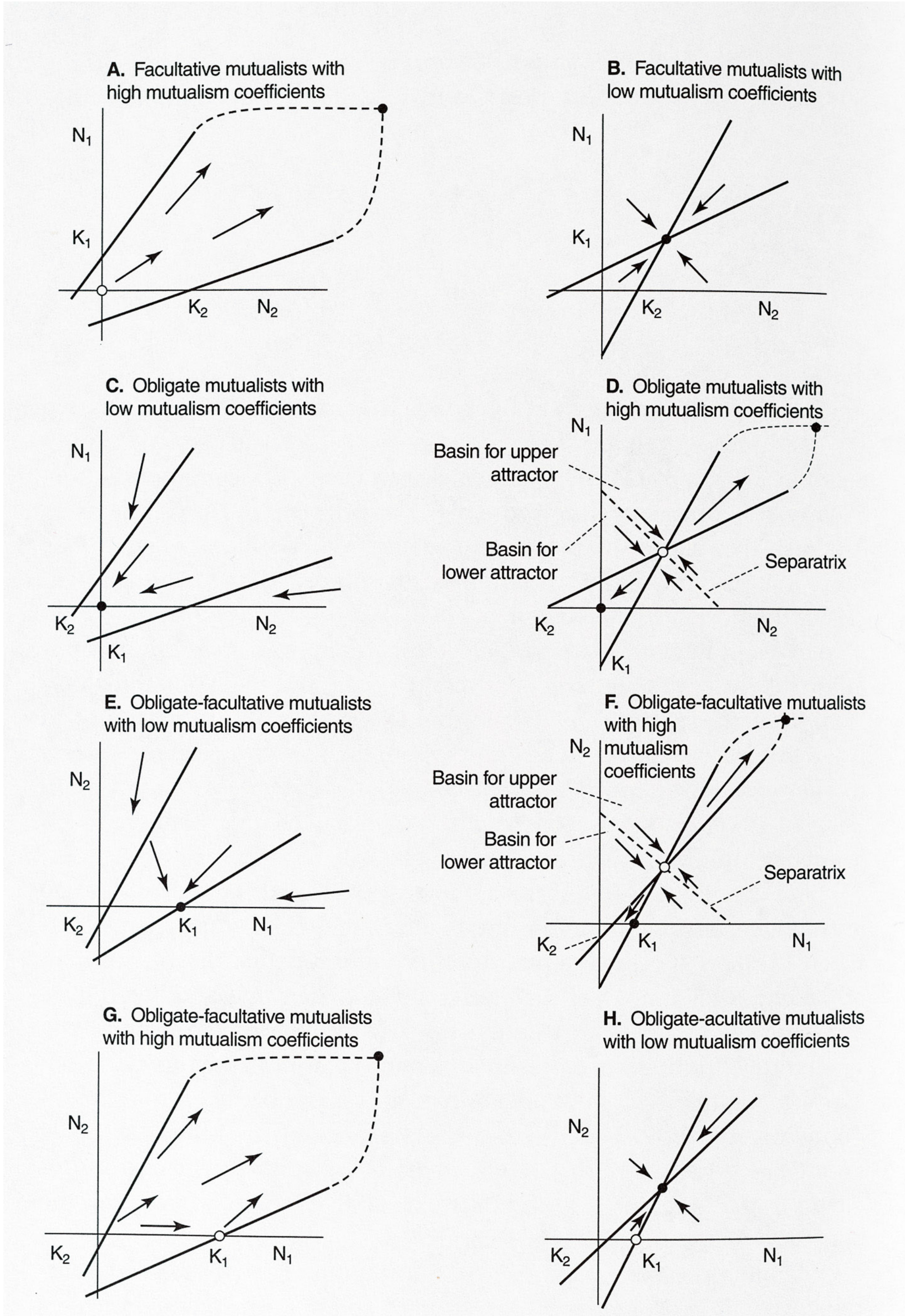


Fig. 17. Eight possible cases of mutualistic interactions among species. The label for diagram H should read "Obligate-facultative…" Vandermeer and Goldberg 2003:238.

sample of two. Spaniard Carlos Herrera's "Seed Dispersal by Vertebrates" (2002) did not cite Lanner. Canadian Graham Powell's *Lives of Conifers* (2009) is a large, attractive monograph, with one chapter on seeds and another on cones and reproduction, but with no hint of mutualistic assistance in seed dispersal.

There has not been a continuous chronological tradition of mimicry publications since the time of Henry Bates (1861), but later researchers have been aware of earlier studies, and so there is continuous intellectual progress. Georges Pasteur's "Classificatory Review of Mimicry Systems" (1982) was not organized historically, but it provided an extensive discussion and bibliography to supplement history of mimicry sources cited above. He also provided a historical chart that indicated the landmark publications since Bates (1961), with mention also of Kirby and Spence's isolated discussion in 1817.

Egbert Leigh, Jr. (1999:212) thinks "mutualism is the central problem of evolutionary biology." He is a tropical rain forest ecologist in Panama who sees a connection between the intense competition found among species in those forests and mutualism: mutualism is a strategy for surviving competition.

University of Michigan ecologists John Vandermeer and Deborah Goldberg's textbook, *Population Ecology: First Principles* (Vandermeer and Goldberg 2003:235–240), contains a discussion of mutualism and its influence upon population dynamics of species involved. They explained eight possible mutualistic relationships, cited real examples, and also provided a diagram of hypothetical impacts upon species involved (Fig. 17).

Algal mutualisms with animals

Algae form mutualistic relations with some species of animals. When Abraham Trembley discovered green hydra in 1740, he was unsure whether they were plants or animals (Egerton 2008:416–417). Unknown to Trembley at the time, Antoni van Leeuwenhoek had discovered brown hydra in 1702. Green or brown, they captured and consumed food like animals (though having some similarities to sundew and Venus fly-traps catching insects). Other green animals, including protozoa and freshwater sponges were subsequently discovered, but no progress was made in understanding the situation until after French chemists Pierre-Joseph Pelletier and Joseph-Bienaimé Caventou studied the green pigment in vascular plant leaves in 1817 and named it chlorophyll (Egerton 2012*b*:203–204). In 1851 Max Schultze determined that the green pigment in *Stentor, Chlorohydra*, and *Dalyellia* was chlorophyll (Buchner 1965:3–4). In 1879, Scottish biologist–reformer Patrick Geddes (1854–1932) reported that the green marine planaria *Convoluta* expired oxygen like plants (Radick and Gooday 2004). He argued (1882) that the alga involved was not a parasite and the relationship was one of mutual benefit. In Berlin, Karl Brandt (1854–1931) in 1881 came to a similar conclusion (Mills 1989:43–76, Sapp 1994:11). Ernst Haeckel followed in their footsteps in his discussion of symbiosis in the protozoan order Radiolaria (1887, Egerton 2013*a*:234–236).

Coral reefs are impressive, with their multicolored variety and abundance of life. Yet mutualistic coral reefs are adapted to nutrient-poor environments (Muscatine and Porter 1977), and algae are more important reef builders than scleractinian corals (Goreau 1963). Coral reefs can flourish because they function at every trophic level: algae are primary producers, and the corals are: primary consumers when utilizing photosynthetic products; secondary and tertiary feeders when ingesting herbivorous and carnivorous zooplankton; direct-deposit feeders when taking up dissolved organic substances from sea water; and saprophytes when taking up dissolved organic substances from sea water (Muscatine and Porter 1977:454–455). With such symbiotic versatility, one might expect that corals are also environmentally flexible, but sadly, not so. Global warming leads to ocean water acidification, which is fatal for corals (McCalman 2014).

Historically, the most contentious issue concerning coral reefs was not their physiology or the relative contributions of coral versus algae, but Darwin's theory of reef formation on the sides or tops of sinking volcanoes. Skepticism over his claim was expressed ever since his book appeared in 1842, but a prominent controversy only arose after John Murray posed an alternative (1880). Since this controversy was not about symbiosis, it was discussed in part 51 on marine ecology (Egerton 2014*c*:384–385).

Bacterial and fungal mutualisms with plants

Fungi not only developed mutualistic relations with algae in lichens, but also with vascular plants. As previously explained (Egerton 2012*b*:213), Albert Frank (1885) coined the term "Mykorrhiza," and later (1887) distinguished ectotrophic mycorrhiza of trees from endotrophic mychorrhiza of Orchidaceae and Ericaceae (1887; Ainsworth 1976:100–101). Hermann Hellriegel and Herman Wilfarth—also discussed earlier (Egerton 2012*b*:213)—discovered (1888) that other vascular plants, especially legumes, established mutualistic relations with bacteria that can obtain nitrogen from air for metabolism, which vascular plants without bacteria cannot obtain (Wilson and Fred 1935).

However, not mentioned in part 43 was the Dutch microbiologist–botanist Martinus Beijerinck (1851–1931) who published in 1888 his research on root-nodules of *Trifolium repens* and *Vicia faba*, in which he named the nodule bacterium *Bacillus radicicola*. In portions of Beijerinck's article, which Thomas Brock translated from German into English (Brock 1961:220–224), previous studies by Brunchorst and by Frank were mentioned, but not Hellriegel and Wilfarth (1888), which appeared about the same time. Was this a case of simultaneous discovery? Yes, to some undetermined extent. Beijerinck's research was certainly done independently (Hughes 1978), but he might have known that Hellriegel had discussed his and Wilfarth's research at the annual meeting of the German Society of Scientists and Physicians in Berlin in 1886 (Schadewaldt 1972:237).

The area of mutualism between vascular plants and fungi or bacteria is called the rhizosphere; in 1972, Wayne Bell and Ralph Mitchell coined the term "phycosphere" to indicate the area of mutualism between algal cells and bacteria. Phycospheric interactions can be stimulative or inhibitory for either bacterium or alga (Cole 1982:296–307).

Bacterial and protozoan symbiosis in animals

Some bacteria and protozoa form mutualistic relations with animals by living in their guts and aiding digestion, often in special anatomical adaptations, such as a rumen or cecum (Buchner 1965, Howard 1967, McBee 1971, Janzen 1985:53–56, Dyer 2002, Ohkuma 2002).

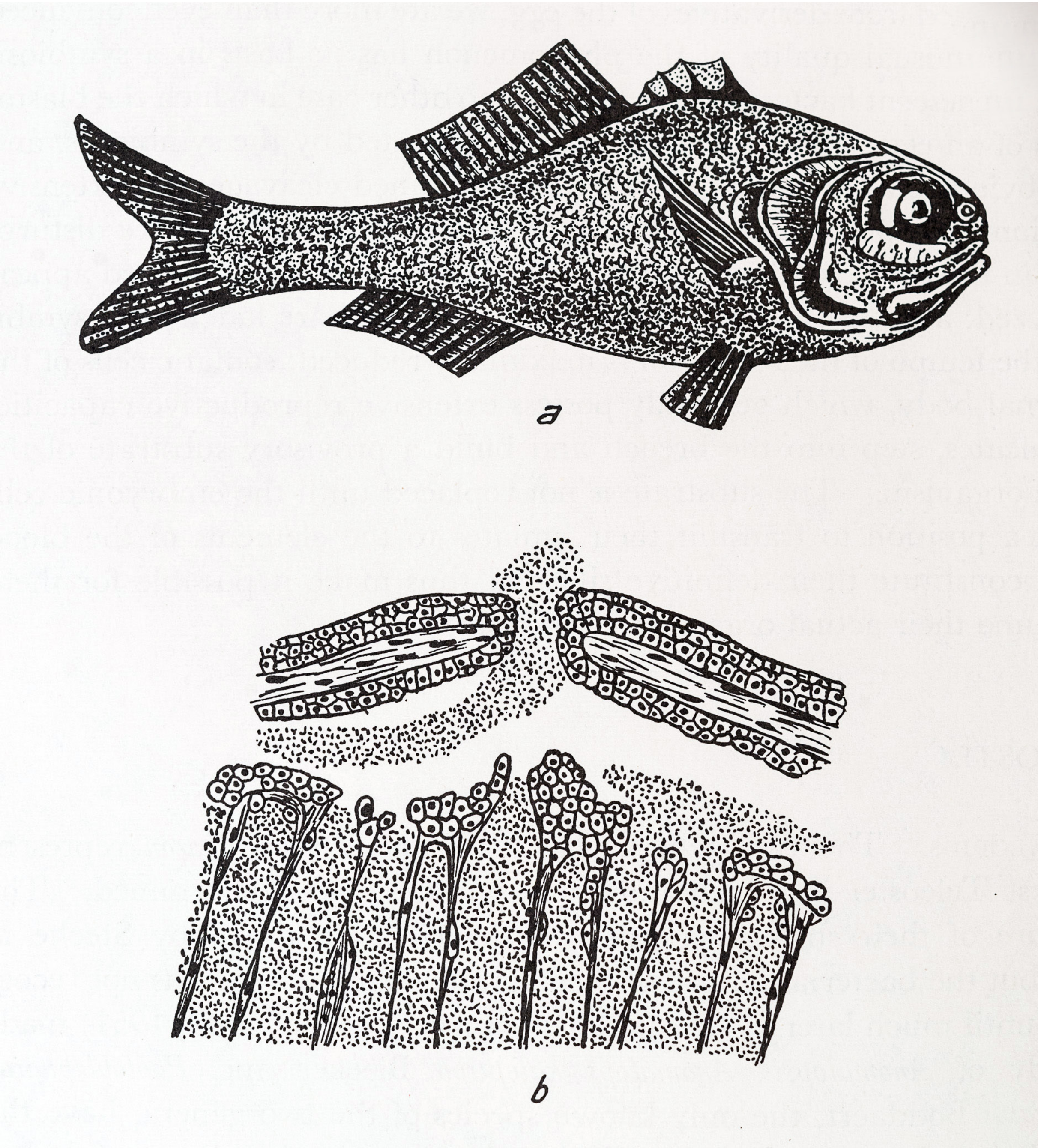


Fig. 18. (a) Luminous organ under the eye of *Anomalops katoptron*, which lives in atolls of the Banda Islands. (b) Section of the organ, showing bacteria. Steche 1909. From Buchner 1965:590.

Fig. 19. Three examples of cleaning symbiosis of fish: a bluehead *Thalassoma bifasciatum* cleans a smooth trunkfish *Lactophrys triqueter* (top), a neon goby *Elecatinus oceanops* cleans a black anglefish *Pomacanthus paru* (middle), and a violet-spotted Pederson shrimp *Periclimenes pedersoni* cleans a longjaw squirrelfish *Holocentrus marianas* (bottom). Limbaugh 1961:cover.

Luminescent bacteria, *Beneckea* and *Photobacterium*, are found in some marine fish and cephalopods having luminescent organs. Other luminescent bacteria live saprophytically on dead fish. According to Buchner (1965:589), O. Steche published his discovery of luminescent fish in 1909, and Newton Harvey (1921) explained that the light came from luminescent bacteria.

Deep sea exploration often reveals highly specialized animals adapted to a severe environment. An example is the tube worm *Riftia pachyptila*, which R. Hessler discovered at a depth of 2600 m northeast of the Galapagos Islands in 1977 (Childress et al. 1987:114, Scott and Fisher 1995, Shillito et al. 1999). It attains a length of a meter and has no alimentary canal. It lives at hydrothermal vents that spew hydrogen sulfide into the sea. The worm has no capacity to directly use this compound to produce energy, but it contains sulfide oxidizing bacteria residing in its trophosome that do so.

Cleaning symbiosis among animals

Herodotos' ancient report of plovers plucking leeches from the mouths of Nile crocodiles (discussed above) was not a unique cleaning relationship. German biologist Franz von Wagner (1892) suggested pseudoscorpions ride on larger arthropods to remove parasitic mites. Caullery (1952:16) itemized other cleaning relationships

> *…ungulates and certain birds which follow the herds, sometimes resting on the animals and picking off the ticks and the oestrid larvae that infest the hide. Starlings do this, also some wagtails (*Motacilla flava*) and magpies in France,* Crotophagus *in America, and* Buphagus*, the ox-pecker, in Africa.*

Randall Breitwisch (1992) observed both red-billed and yellow-billed oxpeckers in Kenya's savannas, whose symbionts include zebras, impalas, giraffes, wart hogs, Cape buffaloes, rhinoceros, and Masai cattle. However, he saw waterbucks and hartebeests intolerant of oxpeckers' probings. Oxpeckers sound an alarm if predators of their "customer" approach, which Breitwisch suggests could be motivated by oxpeckers being unable to operate when a symbiont moves quickly, and if large mammals trust oxpeckers as lookouts, they can relax while being searched.

Cleaning symbiosis seems known most extensively among marine animals (Feder 1966). Zoologist C. William Beebe (1877–1962), from the New York Zoological Society (Sterling 1997*b*), at small Eden Island (west of Indefatigable Island) in the Galapagos Islands saw a red crab remove three red ticks, *Amblyomma darwinii*, from a sunbathing marine iguana (Beebe 1924:121–122, map facing 10), and saw several small wrasse cleaning parrotfish (1928:147)

> *During the period of verticality, and internal mastication, if such it was, a school of little wrasse darted out and thoroughly cleaned cheeks, lips, teeth and scales of all particles of organic coral debris, the parrotfish remaining quite motionless all the while. It was an aquatic parallel of crocodile and plover, cattle and egret, rhino and tick-bird.*

Mexican fishermen in Gulf of California call an angelfish *Holacanthus passer* a barber fish because it grooms other fish.

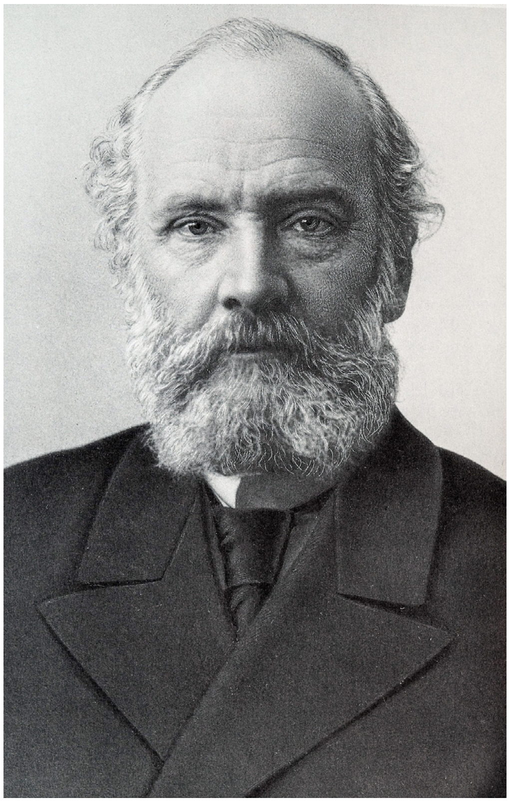


Fig. 20. (a) Andre Famintsyn. (b) Konstantin Merezhkovsky. (c) Boris Kozo-Polyansky Khakhina 1992:18, 35, 63.

Fig. 21. (a) James Lovelock. (b) Lynn Margulis. New York Times 24 November 2011 (online)

Chief diving officer Conrad Limbaugh (1924–60), Scripps Institution of Oceanagraphy, discovered new examples of cleaning symbiosis in spring 1949 while skin diving along the southern California coast; he observed a small kelp perch *Brachyistius frenatus* cleaning a walleye perch *Hyperprosopon argenteum* twice its size (1961:42), though Limbaugh did not realize at the time what he was watching. He drowned in 1960 in an underwater French cave, without ever seeing his last articles in print (Price 2008).

Symbiogenesis

Endosymbiosis describes an independent organism living mutualistically inside another organism. Symbiogenesis describes a formerly independent organism living as an organelle inside another organism's cell. Studies on symbiogenesis occurred almost simultaneously with two Russian botanists, Andrey Famintsyn (1835–1918) and Konstantin Merezhkovsky (1855–1921). Famintsyn established Russia's first laboratory of plant physiology, in St. Petersburg, where he was also an outstanding teacher (Khakhina 1992:17). He was impressed by Schwendener's evidence for the dual nature of lichens (1868), and he suggested that all organisms were "consortiums" (1907). By then, Famintsyn had a substantial series of publications on symbiosis in Russian (Khakhina 1992:124–125), German, and French (Famintsyn and Baranetsky 1867*a*, *b*, Famintsyn 1889, 1892). Merezhkovsky was curator of the zoology library at Kazan University, and he lost that post in 1914 (Khakhina 1992:34–36). He was aware of Famintsyn's early work and wrote to him for either copies of his papers or references to them. Merezhkovsky published mainly in Russian (Khakhina 1992:130–131), but he also published his first study on symbiogenesis in German (1905). In 1910, Merezhkovsky coined the term "symbiogenesis" (Khakhina 1992:36, Sapp 1994:51). Famintsyn and Merezhkovsky engaged in a priority dispute, but Sapp (1994:48–52) cited European and American publications on symbiogenesis preceding both of their studies.

Boris Kozo-Polyansky (1890–1957), whom Liya Khakhina (1992:62) judged a "fine botanist-theoretician," was of a later generation than Famintsyn and Merezhkovsky. He focused on expanding Darwin's theory of evolution by natural selection. His writings on symbiogenesis during the 1920s and 1930s were ignored by contemporary Russian botanists—they considered symbiogenesis theory as "unscientific fantasy"—but were appreciated later. Kozo-Polyansky saw symbiogenesis, including the creation of lichens, as evidence of Darwinism, when some skeptics still thought evidence of natural selection was questionable.

Gaia

This subject will be discussed in more detail in part 64 of this history, on the biosphere, but it is also relevant here. The Gaia theory was introduced and developed by English chemist James Lovelock (born 1919), who worked on medical research during World War II and later worked for NASA (Lovelock 2000*a*:69–240). In 1965 at the Jet Propulsion Laboratory in California he had the idea that "the Earth controls its surface and atmosphere to keep the environment always benign for life" (Lovelock 2000*a*:241). He pondered this idea until 1972, when he published a 1.7-page letter to the editors of *Atmospheric Environment*, entitled "Gaia as Seen through the Atmosphere." He named his hypothesis "Gaia" after the Greek name for Mother Earth. Despite its brevity, his letter had eight references, including one he co-authored and one by ecologist G. E. Hutchinson, "The Biochemistry of the Terrestrial Atmosphere" (1954). Lovelock's hypothesis was that life within the biosphere behaves like a world organism, that it controls the gases in the atmosphere, and that if life died out, the atmosphere would change in ways that would no longer support life.

Lovelock has devoted his career since 1972 to turning his hypothesis into a theory and collecting evidence supporting it. He elaborated his findings in *Gaia: A New Look at Life on Earth* (1979). It was accepted by some environmentalists and popular writers, but met scientific opposition. As his investigations continued, so did his publications, which can be taken as interim reports: *The Ages of Gaia: A Biography of Our Living Earth* (1988), *Gaia: The Practical Science of Planetary Medicine* (1991), *Homage to Gaia: The Life of an Independent Scientist* (2000*a*), *The Revenge of Gaia: Earth's*

Climate in Crisis and the Fate of Humanity (2006), and *The Vanishing Face of Gaia: A Final Warning* (2009). For those who would not read his 440-page autobiography, he also published a 15-page summary (Lovelock 2000*b*). There have also been critical assessments by others of his Gaia theory. An early supporter was American biologist Lynn Margulis (1938–2011), whose research on endosymbiosis she found compatible with Lovelock's Gaia theory (Mann 1991, Margulis 1998; Weber 2011). Scientists have held two symposia to evaluate Lovelock's Gaia theory, and MIT Press published their findings (Schneider and Boston 1991, Schneider et al. 2004). There are at least four books devoted to Lovelock and Gaia: Lawrence Joseph, *Gaia: The Growth of an Idea* (1990); Tyler Volk, *Gaia's Body: Toward a Physiology of Earth* 1998), Jon Turney, *Lovelock and Gaia: Signs of Life* (2003), and John Gribbin and Mary Gribbin, *James Lovelock: In Search of Gaia* (2009), and ecologist Tim Flannery discussed Gaia favorably in *Here on Earth: A Natural History of the Planet* (2010). I think Gaia is a new version of the balance of nature concept. Philosopher of science Karl Popper claimed that scientific theories cannot be proven, just disproven, and that theories that are not potentially falsifiable are not scientific (Popper 1962:36–37). Certainly, Gaia has been neither proven nor disproven, and it seems not falsifiable, at least in some versions (Ruse 2013).

Concluding observations

Symbioses are relationships important for the survival of most species, yet their manifestations are commonly so subtle that they are easily overlooked. Three examples of symbiosis were known in antiquity (crocodile–plover, pinna–pinnotheres, remora attachments), but these reports were merely natural history novelties, which maybe illustrated the balance of nature. Linnaeus's economy of nature concept was a version of the balance of nature that he used to organize examples of mutualism in support of his economy of nature concept. Thoreau was attracted to Linnaeus' idea and added at least one example of his own: squirrels burying acorns, some of which germinate and become trees. The next significant step after Linnaeus was Darwin's theory of evolution by natural selection, which placed symbiosis within a theoretical context presumably evolving over time, from casual contacts to more significant contacts. Since around 1870, many lines of research developed that later contributed to current understanding of symbiosis. Kropotkin's *Mutual Aid* (articles 1890, book 1902) swept together a synthesis on one aspect, and later attempts to synthesize symbiosis knowledge into a coherent branch of ecology have been ongoing at least since Maurice Caullery's *La Parasitisme et Symbiose* (1925, English 1952). The next synthesis seems to have been in Allee et al., *Principles of Animal Ecology* (1949). Multi-author collections on symbiosis began with Henry (1966–1967), and by 1970 there was at least one textbook and other educational books, which are perhaps signs of a mature science. James Lovelock's Gaia concept showed that novel perspectives were still possible around 1970. Joan Roughgarden's *The Genial Gene* (2009) showed that some debates concerning symbiosis can be long lasting.

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