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## The wonderful lives of Joseph Leidy (1823–1891)

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Except in Philadelphia where his greater-than-lifesize statue adorns the entrance to the great Academy of Natural Sciences, and the University of Pennsylvania biology department is housed in the building that bears his name, Joseph Leidy (1823–1891) is virtually unknown today. Yet his myriad contributions to science are important and entirely trustworthy. Although Leidy was one of America's greatest naturalists, his biographer, Leonard Warren [9], found it necessary to devote an entire chapter to Leidy's lack of reputation (Chapter 16, "The eclipse of Leidy"). In his fascinating new book of great interest to microbiology Warren writes (p. 251): "In the course of his career, Leidy examined tens of thousands of organic forms and described and named over a thousand new ones—fossils, protozoa [*sic*], parasites of many forms, insects, molluscs, and helminths—a feat virtually without precedent. What did this busy investigator have in mind? ... Without question he gathered his knowledge because it gave him pleasure." A precise tabulation of Leidy's contributions was published more than 100 years after his death [2]. In 1923, more than 30 years after he died, Leidy was commemorated by one of his many admirers: "Dr. Leidy's vision covered all nature, from the mammals and gigantic reptiles of the past to the world of small things which are revealed to the eye by the highest powers of the microscope; and I never knew anyone who carried on so varied a series of observations without confusion." Leidy is considered "the founder of American vertebrate paleontology, parasitology, and protozoology and America's foremost anatomist, the person who revealed the

power and versatility of the microscope..." (p. 252 [9]). Not only was he the first in North America to discover the dinosaur but he was the first in the world to discern what wood-dwelling "white ants" (termites) eat. His impatient curiosity led him to investigate the dwellers of a decaying log in New Jersey. He reported that a squeeze of intestinal fluid revealed ("like citizens leaving a crowded meeting hall") a flurry of live "parasites" [5]. When he documented the bacilli, trichomonads, prysonymphids and hypermastigotes that exuded from the "termes" hindgut he named his 1850 paper, "On the existence of endophyta in healthy animals as a natural condition" [4].

Leidy discovered benign, indeed requisite cellulolytic protists responsible for the ingestion of wood by termites. He was also the first to recognize the *Trichinella* nematode as the cause of trichinosis caused by undercooked pork. He gave binomial names in use today to hundreds of New World animals, fungi, protists and bacteria. Leidy's descriptions and drawings of amoebae (rhizopods) are still without parallel. "A driven man, he seemed possessed by a sustained frenzy," or as one acquaintance put it, "absorbed in his new discoveries of rhizopods in the cracks of the city pavements" (p. 251 [9]). "How can life be tiresome as long as there is still a new rhizopod undescribed?" (p. vi [9]) is the way Leidy himself stated his passion in his sparse and appropriate style.

Disdaining speculation, Leidy always remained close to his original material. None of his observations has been shown to be mistaken or exaggerated. He may also be claimed

to be the founder of the forensic use of the microscope: a murderer confessed that blood was really human, and not from a chicken as he had claimed, after Leidy noted that its red cells lacked the requisite nuclei of avian red blood cells. Leidy in 1851 transplanted human tumor tissue under the skin of a frog, and determined, five months later, that the tumor had acquired a new blood supply and was thriving. His keen microscopy skills ended the current medical theory that hay fever, asthma, colds and other respiratory disorders were caused by an infusorian (an old name for ciliates), "*Asmathos ciliaris*". He showed "*A. ciliaris*" to be no more than deformed ciliated epithelial cells in the mucus of patients! Trained as a physician, Leidy practiced medicine for only a few years until returning to his interest in science and teaching. Warren's saga explains clearly how Leidy always preferred his curiosity-driven self-determined research. His collections, teaching charts and museum specimens ranged from mineral collections to large mammals to drawings of microbial communities.

Although he never lacked national and international colleagues, as well as correspondents, Leidy had not a single scientific co-author in his entire career. In their quantitative analysis of Leidy's immense contribution to the identification and classification of extant and extinct organisms new to science, Glassman et al. [2], provide us with a dichotomous table. Two kinds of organisms are listed: "Animals" (and, by name, the many new genera and species names Leidy conferred) and "Plants". Remarkably, especially as we recall that this paper was published in 1993, under the heading of "Plants" Leidy's contribution is listed: "Many plants, including fungi". Unfortunately, most members of the public still today recognize only these two great kingdoms of organisms. In the public eye, of course, all "microbes" are germs, enemies of people that do not count as life even enough to be classified as either animal or plant. This animal-plant dichotomy, a gross misconception that obviously persists even among today's scholars, aggravates the continued undervaluation of Leidy's contribution. Here we consider only one, but one of special interest to microbiologists: Leidy's discovery of the natural habitat of *Bacillus cereus*. This account is derived from the splendid archives of the Academy of Natural Science in downtown Philadelphia, Leidy's publications [4, 5] and our own work [6].

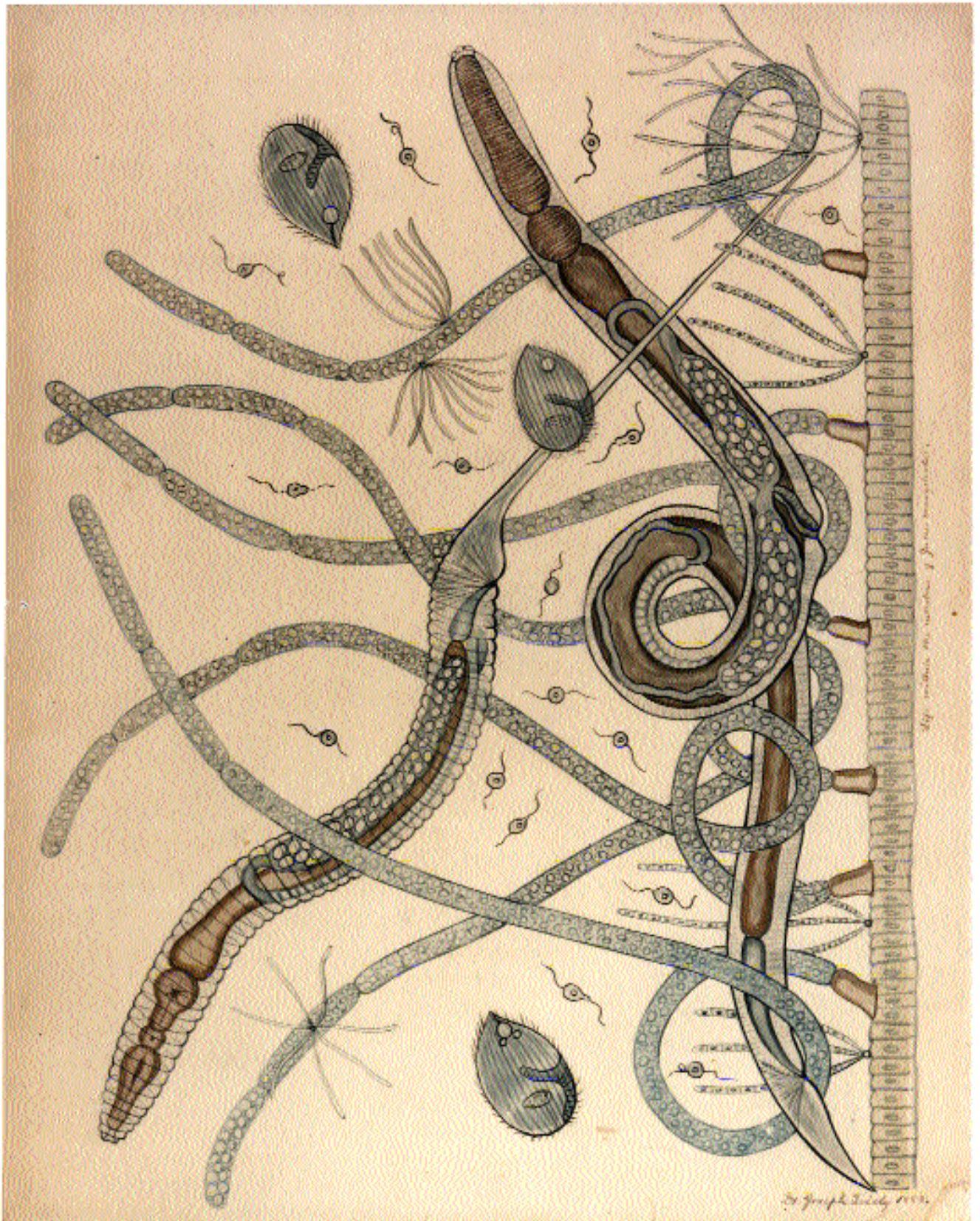
Hundreds of Leidy's original drawings reside in the Academy's cabinets —among them his exquisite microscopic analyses. As the "last man who knew everything" and a superb teacher, Leidy always generously shared his time and energy with motivated acquaintances, friends, colleagues and students. For the benefit of his admiring students he arranged his painstaking and accurate drawings for us as gorgeous wall charts, one of which is highly reduced here (Fig. 1). The microbial community of the intestine of the millipede *Julus marginatus* is revealed. Both the *Trichomyces* and the thinner *Arthromitus* are "rooted" in the chitinous intestinal epithelium

of this arthropod. Of course by Leidy's and subsequent reckoning these attached gut microbes are "non-photosynthetic plants".

The detail and accuracy of Leidy's drawings of the epibionts permits us to recognize without a doubt microorganisms we know from our own long experience with termites, millipedes, roaches and sowbugs. The attached filamentous spore formers have also been found by many other microscopists in the intestines of other animals: ducks, rodents, humans and many other kinds of arthropods. Our work has mostly involved those in the intestines of subterranean and dry wood-eating termites [7] and *Porcellia scaber*, the sowbug [3]. Recently we found Leidy's "non-photosynthetic plant", this filamentous spore former, in the great tropical Caribbean cockroach *Blaberus giganteus* [1]. In these publications we prove that these intestines are the natural habitat of an organism that, in culture, is familiar to all microbiologists as *Bacillus cereus*. Leidy would probably be delighted to know that it was he who discovered *B. cereus* in its "natural condition". His careful work permits us to understand why, in culture, this bacillus retains a great predilection for high concentrations of food, a sensitivity to light, a tendency to form spores on exposure to dryness or air, and to be motile in young cultures. We now understand why these bacteria form filaments and settle down to attach or at least, when the cultures are mature, to make sticky exudates. Most of all, we have a context for their incredible resistance to environmental insults of desiccation, acidity and anoxia.

Here magnificent unpublished photomicrographs by the superb electron microscopist, the late David G. Chase (in addition to the others in our papers referenced below [6, 8]) verify how observant was Leidy; they display at high power the attachment of the spore formers to the gut and the differentiation of the spores within the filaments. These bacilli are not, as widely touted, "soil organisms", since, in the soil they are dormant as spores. Rather they are normal inhabitants of animals. The filamentous spore-forming "non-photosynthetic plants" of Leidy are cyclical symbionts whose defecated spores persist in the soil. They grow as motile bacilli and short filaments when contingencies provide them with

**Fig. 1** One of Leidy's many beautiful wall charts archived at the Academy of Natural Science of Philadelphia. This one depicts the intestinal epithelial cells of the millipede *Julus marginatus* at the bottom. Besides the three swimming ciliates and the unidentified mastigotes, one recognizes an attached nematode replete with eggs and six trichomes of *Trichomyces* sp., the obligate symbiotrophic fungus. We added arrows to *Arthromitus* sp., with and without spores, attached to the *Trichomyces* sp. or directly to the epithelium. The branched *Arthromitus* sp. at the bottom right was seen in termite preparations by Harold Kirby (1900–1952) and by us [6]. The branched Gram-positive bacterium is clearly a bacillus. It resembles the *Arthromitus* sp. observed in the sowbug, *Porcellia scaber* [3], which in culture is *Bacillus cereus*. No taxonomic description of it has ever been made in either the botanical or the microbiological literature. The actual size of the wall chart is approximately 2 × 3 m





**Fig. 2** “*Arthromitus*” attached to the chitinous gut wall of the California termite, *Reticulitermes tibialis*. Portions of the termite epithelial cells are seen at the bottom and right side of the transmission electron micrograph. The attachment structure seems to be composed of exudate from the bacterium and local thickening of the insect chitin at the region of attachment. The dark bodies just inside the chitinous layer are termite mitochondria. This protograph, taken by David G. Chase in about 1984, reveals in detail the “*Arthromitus*” intestinal attachment first described by Joseph Leidy. (Magnification, ca. 50,000 $\times$ )

of moisture and food. The short flagellated filaments course through the intestines looking for “docking sites”. They find them, usually at the surface of the chitinous epithelium, as documented by electron microscopy (Fig. 2). They attach,

differentiate, and some even form “spore attachment filaments”. Then they release spores, usually from their distal free ends. By peristaltic action the spores are expelled from the anus to reside, until further opportunities for sustenance arise, in the soil. Modern microbiologists, especially those who work with genes involved in differentiation of *B. cereus* still have much to learn from the legacy of the Philadelphian doctor. As wise naturalist and superb artist his major lesson for microbiologists is that they, like him, should be students of life in nature, life under “natural conditions”, before they incubate their objects of study in the artificial environment of the research laboratory.

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