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The History of Avian Medicine in the United States IV. Some Milestones in American Research on Poultry Parasites

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SUMMARY

Most of the major contributions of Americans to knowledge of poultry parasites have been made in the last 100 years. Factors responsible for this tardiness differed somewhat according to the disease. The first parasitic diseases to receive attention were usually those with distinctive characteristics as well as serious consequences, such as "gapes" and lousiness. Since helminths could usually be readily observed, whereas protozoa could be observed only by persons skilled in microscopy, disorders attributable to the former usually received attention earlier than did protozoan diseases. The control of ectoparasites, before the use of modern insecticides, became vastly simplified as mechanical incubators and brooders replaced the hen, and as the birds were provided with better housing. The major contributions of Americans to our understanding of parasitic diseases of poultry are detailed for five disorders attributable to helminths, and two attributable to protozoa. The latter are histomoniasis of turkeys and coccidiosis of chickens. No attempt has been made to evaluate the impact of contemporary research.

INTRODUCTION

With few exceptions, the enduring contributions of Americans to knowledge of poultry parasites have been made in the last 100 years. Many factors contributed to that circumstance. To appreciate the impact of some of those factors over much of Europe one has only to read Beeck's account of the development of poultry husbandry in Germany (9). Most of our immigrants came from

Europe, bringing with them many of the practices, prejudices, and traditions of their homelands, where agriculture still demanded of them long days of arduous effort. Add to this the additional hardships imposed on them by having to clear forests, or break the stubborn prairie sod for farming, and one can begin to understand why poultry received so little attention. Moreover the new land afforded the early settlers an abundance of game (39), a situation that prevailed to various degrees almost until the opening of the twentieth century. Small wonder, then, that the rearing of poultry in confinement and on a large scale was virtually unthinkable, except perhaps near the large eastern cities, where large numbers of fresh eggs could be marketed at a profit.

A careful study of poultry growers' inquiries directed to the editors of early periodicals dealing with agriculture, poultry in particular, discloses that the first parasitic diseases of chickens to attract specific attention were those with symptoms so characteristic as to be easily recognized: gapes and lousiness. Bennett's "The Poultry Book" (10), the earliest comprehensive American treatise that did not merely paraphrase European literature, says of gapes, "This is the most common disorder of poultry and all domestic birds." It is also the first to receive consideration. As for lousiness, Bennett deals with it in the closing section of his chapter "Diseases of Poultry," having dealt first with diseases affecting internal organs.

GAPES

As early as 1797, a letter to the *Medical and Physical Journal* from a Baltimore physician and Professor of Anatomy, Dr. Andrew Wiesenthall, reported finding worms in the trachea of chickens and turkeys that displayed difficulty in breathing and might die gasping for breath. The report did not appear in print until 1799 (67). Only later was the same disorder reported in chickens in England. Dr. Wiesenthall did not concern himself with the taxonomic position of the worms but did report success in removing the parasites by twisting a feather, stripped of its barbs almost to the tip, in the trachea and withdrawing it slowly, with the worms adherent. This method, sometimes used with variations, and often with less skill than it had been by its originator, remained a controversial means of treatment for well over a century.

Both the disease and the worms that caused it received intermittent attention over the decades that followed, mostly in Europe. In the process, the worm was given at least two generic names in various combinations with even greater numbers of specific names. But despite much publicity, including an offer of prizes for the best essay on the parasite's life cycle, the next really substantial contribution was, again, made by an American, more than 80 years after Dr. Wiesenthall had described the disease and identified its cause.

In the summer of 1883, another physician, Dr. D. H. Walker of the small town of Franklinville, N.Y., south of Buffalo, started studying birds with gapes, brought to him by neighbors whose poultry were dying. In those days, the family physician served in many capacities. Dr. Walker, gifted with insight, curiosity, and creativeness that could easily make him the envy of many a parasitologist of a later era, knew his point of attack: the source of the infection must be determined. He wrote to Dr. Joseph Leidy, well known as America's first and (then) most distinguished student of parasitology and protozoology (not to mention his first claim to fame, paleontology). Dr. Walker enclosed with his inquiry a specimen of the worms found in the trachea. Here is Dr. Walker's own account (62):

"On August 15, 1883, I received his reply as follows: 'The source of the gape worm (*Syngamus trachealis*), of the chickens, has not been discovered. If you have an opportunity of investigating and determining its origin, you may do much service to science. It would be found only in the embryonic or larval condition, in some intermediate host.' "

This sagacious assertion was based entirely on Dr. Leidy's tremendous capacity for reasoning beyond, and ofttimes in spite of, existing concepts. One of Europe's foremost authorities, Dr. J. P. Mégnin, had declared positively that no intermediate host was involved — true *under certain conditions*. But to Dr. Leidy, these conditions were not satisfied frequently enough in nature to account for the prevalence of the disease. With this, Dr. Walker was in complete accord.

To Dr. Walker, the busy small-town physician, the field was entirely new, but he accommodated the concept of an intermediate host as comfortably as if he had been a working parasitologist throughout his professional life. The way in which he determined his course of study and the experiments he devised to implement it cannot be presented in this brief article, but they could well serve as models for parasitologists of this day. To all but the most skeptical, the transmission of the gapeworm by earthworms was established.

Even as recently as the late 19th century, many American scientists still looked to Europe for solutions to their problems. And so it was that the views of the prominent European parasitologist Mégnin prevailed for some time over those of the unheralded country doctor from Franklinville. Indeed, a translation of Mégnin's article, declaring that no intermediate host "can be incriminated," was just appearing in the First Annual Report of the Bureau of Animal Industry, a publication that was to be widely circulated.

Disappointed at not having a full report of his findings presented in the succeeding issue of the same publication, Dr. Walker published his results in the *Bulletin* of the Buffalo Society of Natural Sciences, in 1897 (62). There, one can read the entire story of one of the more remarkable contributions of American investigators to knowledge of poultry parasites. To what extent the progress in the control of this serious disease of various galliform birds was retarded by the reluctance of some scientists to appreciate the implications of Dr. Walker's findings, can probably never be known. Indeed, even today, many parasitologists seemingly fail to appreciate what Dr. Leidy, paleontologist first and parasitologist second, recognized throughout: the survival of some parasites through the vicissitudes of geologic time demanded better means of transmission than those so often used in laboratory studies.

OTHER HELMINTHS

A recent checklist of helminths of poultry in the United States and Canada lists more than 60 species and is still not complete (8). Nearly half of the entries are nematodes. Cestodes are in second place. Most of the more important genera were discovered and first described by European workers. The majority of poultry helminths are transmitted by invertebrates, and earthworms are the sole or most important source of infection with *Heterakis gallinarum* and at least two species of *Capillaria*. American parasitologists were the first to show such transmission for all three of these parasites.

Dr. James E. Ackert of Kansas State College discovered that *Heterakis* was transmitted by earthworms (1). J. W. Scott's earlier report of such transmission actually involved what we now know as *Ascaridia galli* (47). Ackert, like Scott, was uncertain whether the transmission was merely mechanical or if the annelid was a true intermediate host. As we know now, *Heterakis* actually hatches in the earthworm and migrates to positions where it will not be voided, being liberated only as the earthworm is eaten by a suitable galliform host. As Dr. Ackert was conducting his studies, the role of *Heterakis gallinarum* in transmission of the protozoan that causes blackhead in many galliform birds was quite unknown, and Dr. Ackert's chickens were not necropsied early enough to have displayed conspicuous signs of the disease. It seems unlikely that all would have escaped infection with the blackhead parasite, because large numbers of earthworms were fed, and, as we shall see in a later section, blackhead had been troublesome in turkeys in the vicinity of Kansas State College for at least a decade.

As for Scott's earlier studies on the transmission of *Heterakis perspicillum* (= *Ascaridia galli*), the earthworms were, indeed, merely mechanical conveyors of the unhatched eggs, or, if hatching did take place, of larvae still in the digestive tract (3).

W. A. Riley and L. G. James of Minnesota were apparently the first Americans to study in detail the life history of *H. gallinarum* (45). Although their article appeared in May 1921, at the time it was prepared they were not aware of Graybill and Smith's report (25) announcing the production of fatal blackhead in turkeys after they were fed embryonated eggs of the common cecal worm. Riley and James worked only with chickens, but some of their birds almost certainly developed blackhead. Like the earlier European workers, however, they attributed the diarrhea and cecal disturbances to the heterakids. The next major articles on the life cycle of this nematode were all by North American workers: Graybill (24), C. Uribe (61), and H. P. Dorman (21), all of the United States, and A. B. Baker (4) of Canada. Baker was the first to point out explicitly that the presence of blackhead profoundly influenced the growth of the cecal worms and often drastically reduced their numbers.

Capillaria annulata, frequent inhabitant of the crop of chickens, turkeys, pheasants, bobwhite, and some other galliform birds, had long been known in Europe before it was first reported in chickens in this hemisphere, by A. B. Wickware (66) of the Poultry Pathology Laboratory at Ottawa (1922). E. B. Cram of the USDA found the same parasite in her chickens at Beltsville in in 1925 (14). Later (1931), she reported that she had been unable to transmit this nematode experimentally by feeding embryonated eggs (16) — a method that was successful for many other poultry nematodes including *Syngamus trachea* and *Heterakis gallinarum,* both of which commonly depend on some earthworm to get into their definitive host. E. E. Wehr, also at Beltsville, confirmed Cram's findings and conducted experiments entailing the feeding of various invertebrates that were commonly eaten by free-ranging poultry. Earthworms (*Helodrilus foetidus* and *H. caliginosus*) transmitted the capillarids, he reported in 1936 (63). Some species of *Capillaria* apparently required no intermediate host. *C. caudinflata,* like *C. annulata,* however, required earthworms, though not all genera and species of these annelids served equally well. Wehr and R. W. Allen at Beltsville (2,64) and N. F. Morehouse (37) at Iowa State College studied the transmission of *C. caudinflata.*

Some significant contributions to studies of poultry parasites were not primarily discoveries but were the work of patient scientists who gave guidance to others. In 1892, Dr. Albert Hassall of the USDA started an animal-parasite collection and an index to the world's literature on animal parasitology. Both have continued to the present; and out of those humble beginnings has arisen the internationally known *Index-Catalogue of Medical and Veterinary Zoology* (31), a tool that no serious investigator in parasitology can ignore. Also, the parasite collection, early enhanced by the substantial contributions of such ardent collectors as Leidy, C. W. Stiles, and Hassall himself, soon became, and remains, the most comprehensive and thoroughly documented parasite collection in existence. Other contributions were of a similar nature. As early as 1896, Stiles (51) published the most extensive paper concerning tapeworms of poultry that was to appear in this country until a decade later, when B. H. Ransom brought the subject up to date (42). Monumental compilations by Stiles and Hassall (52), Cram (15), and others either featured helminths of poultry exclusively or gave them a prominent place. The above achievements are given an early position in this history because, originally, contributions in helminthology dominated both the literature and the collections.

ECTOPARASITES

As indicated in the introductory passages, ectoparasites of poultry were prominently mentioned as among the most troublesome poultry disorders in this country during the 19th century. But I shall not dwell on this subject. Substantial contributions have been made by entomologists, arachnologists, and epidemiologists in this country. In the field of control, especially, much of the more important research has been quite recent — in the last 3 or 4 decades. But long before that period, some developments profoundly affected the prevalence of ectoparasites. Lousiness was no longer the scourge that plagued our pioneer farmers after artificial incubation and brooding interrupted the cycle that had hitherto bestowed on the young chicks or poults the unwelcome heritage of the brooding hen. Also, by the opening of the 20th century, designs were readily available for well-lighted and well-ventilated poultry houses that could be constructed at moderate cost. With suitable floors, roosts, nests, and other facilities, effective disinfection of the houses became possible. Mites caused problems only sporadically or, in some years, not at all, as I recall our small-scale operations in the early decades of this century.

PROTOZOAN DISEASES

Protozoan diseases of poultry were not recognized as early as those caused by the more obvious parasites. Only two such diseases figured prominently in the development of our poultry industry in this country: blackhead (histomoniasis) of turkeys and coccidiosis, especially among chickens. Of these, blackhead was later in becoming established in birds in this hemisphere but was the first to be clearly identified and receive the attention of some of our most able investigators. I shall therefore consider it first even though, from the economic standpoint, it is no longer a threat to commercial poultrymen in North America.

Blackhead in turkeys. Frederick Rice, Veterinarian, Rhode Island Agricultural Experiment Station, was apparently the first to report this disorder in our scientific literature (44). He gave the disease no name. He mentioned the discoloration of the heads of affected birds and warned that the ravages of this disease could lead to extermination of the state's profitable turkey industry. His brief note of a dozen lines, appearing in 1892, was given no attention in the scientific literature for nearly 80 years. In the same publication in which Rice's brief warning appeared, the

President of the Board of Managers, Mr. C. O. Flagg (who was also Director of the Station), reported (22) that on February 12, 1891, the Board had voted to establish a Poultry Division and had "arranged with the Apiarist of the Station, Mr. Samuel Cushman, to take charge of the work. Considerable experience in the raising of thoroughbred fowls qualifies him for the enterprise." A recent account (30) refers to that appointment as creating the first "full-time" college poultryman, but Cushman actually served in the dual capacity of "Apiarist and Poultry Manager," and remained so in their listing.

In September 1893, Cushman published the most comprehensive of the reports he was to make during his 5 years as Poultry Manager: a bulletin on the production of turkeys (19). It necessarily drew heavily on the observations of the many growers that Cushman had very wisely consulted during his earlier orientation period. The disease the growers called "Black Head" or Blackhead" was given prominent attention, as were growers' views concerning suspected causes and the circumstances that favored or discouraged its prevalence. In his report for the year 1893 (20), published early in 1894, Cushman first used the term "Black Head," which, in a brief appeal to growers for cooperation, he attributed (by implication) to their own usage. By that time, Cushman and his colleagues were as alarmed as Rice had been 3 years earlier. But Rice had long since left the Station, his report on the "Disease among Turkeys" having been a part of his last report as Veterinarian on the Station Staff.

Cushman served well, but he was not trained as an epidemiologist or pathologist. Consequently, in the fall of 1893 he very wisely sent the viscera of a diseased turkey to the Bureau of Animal Industry, where they were received for study by Dr. Theobald Smith, one of the ablest pathologists of his time. In April 1894, Cushman sent Smith the viscera of another affected turkey, and in June, those of a third. In one of the most concise and challenging statements ever to introduce an important contribution in parasitology, Smith wrote of these three specimens:

"The changes induced by this affection were so peculiar and yet so uniform in these three cases that a specific infectious disease could not but suggest itself on even superficial examination. A careful study of this material convinced the writer that the cause of this disease was a protozoan parasite not hitherto recognized" (48).

Armed with the above convictions, Smith spent 3 weeks in Rhode Island in August 1894, collecting and examining 46 turkeys of various ages, all obviously ill. Of these, 16 had blackhead, the disease that Smith was to term "infectious entero-hepatitis." Before actually making his classic report, in 1895, Smith examined three more turkeys, one obtained locally and two others sent by Cushman, bringing to 52 the total number of birds examined. Of these, 19 had involvement of one or both ceca and the liver, and two others had only cecal involvement. Smith's records were so precise that even today his data tell us much about the circumstances of the time in the light of information developed only in the past two decades. His description of the pathological changes that characterized the disease was adequate for decades to come; and despite numerous challenges, the specific protozoan that he designated as the causal agent is almost universally accepted. The generic name has been changed. Originally, Smith tentatively called the organism "*Amoeba meleagridis,*" largely because of "its simple structure" and the resemblance of the disease to amoebic dysentery in man. Many years later, when he had better equipment available and his early designation had been heavily criticized by a small body of workers who confused blackhead and coccidiosis, Smith reopened his studies. He had to retract nothing, but conceded that the generic name tentatively assigned in 1895 might need to be changed (50).

From 1900 to 1906, Dr. Cooper Curtice, a parasitologist, was employed by the Rhode Island Agricultural Experiment Station to study blackhead. At first he had neither facilities nor turkeys, and he had an assistant only in his final year. But despite those difficulties, he made important contributions to our knowledge of the transmission of blackhead (17,18). He attributed its spread to the association of turkeys with chickens, the latter birds carrying and disseminating the blackhead parasites without showing evidence of the disease. He also showed that earthworms from soil contaminated by chickens occupancy transmitted the blackhead parasite to turkeys. No one knew of the role of the cecal worm, *Heterakis gallinarum,* at that time. Curtice also provided very persuasive evidence that the blackhead parasite was not transmitted by the birds' eggs.

Hardly had Curtice left the Station before his successors, L. J. Cole and P. B. Hadley, pronounced blackhead a form of coccidiosis, and Smith's organism a stage in the life cycle of the coccidian (11), a view that had already appeared in some texts in Europe. Smith, then at Harvard, was incensed, resumed his studies on blackhead, and retaliated with a scathing denunciation of Cole and Hadley for confusing the two diseases and their causal

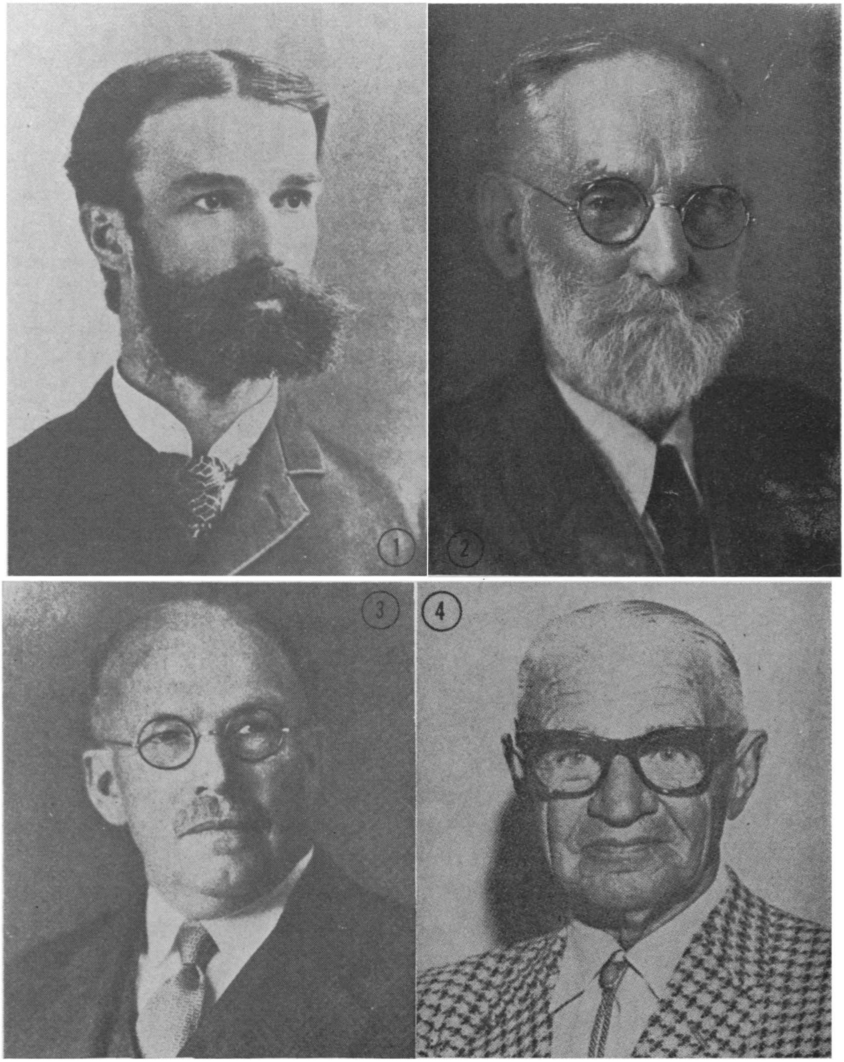

Fig. 1. The "Big Four" in the control of blackhead in turkeys. 1) Theobald Smith, 1889; 2) Cooper Curtice, about 1930; 3) E. E. Tyzzer, 1929; 4) William A. Billings, about 1958.

agents (49). Cole, a geneticist and having only a minor role in the regrettable confusion (although nominally in charge of the poultry work at the Rhode Island Experiment Station as the episode started), quietly withdrew (12), being comfortably settled in his own specialty elsewhere. Hadley, a microbiologist, remained at Rhode Island from 1908 (when the first startling announcement of the supposed identity of the two diseases was made) until 1920, much of the time attempting to defend the coccidial theory of the etiology of blackhead, or, when that became untenable, the trichomonad theory of its etiology (26–29).

The long (136 pages + plates) article "Blackhead in Turkeys: A Study in Avian Coccidiosis" (13), published in 1910 as Rhode Island Agricultural Experiment Station Bulletin 141, although quite erroneous in thesis, must actually be classed as something of a milestone in poultry-parasite research in this country. In 1907 the authors made an extensive inquiry into the prevalence of blackhead by a circular letter sent to "nearly all the experiment stations in the United States and Canada." Blackhead was known in at least 28 states from Florida to New Hampshire and along the entire Pacific coast, as well as in several provinces in Canada. So widely spread although the first reported recognition of the disease had been only 15 years earlier! How could that be? We must consider the question, though not until the contributions of a few other Americans have been noted.

As already indicated, the earliest of Cole and Hadley's reports confusing blackhead and coccidiosis provided Smith the incentive to reopen his studies on blackhead, and the 1910 bulletin provided still further stimulation. Between 1908 and 1921, Smith alone published three articles on blackhead, while four others were coauthored by a very able colleague, H. W. Graybill, who made several contributions in his own right. Graybill is best known for his role in having incriminated the cecal worm in the transmission of blackhead. That important discovery, announced in a paper by Graybill and Smith in 1920 (25), is believed by some to have been Graybill's, but there can be no question that having the paper co-authored by Smith greatly enhanced the interest shown in the newly revealed association of the parasites. The authors were not certain just how the cecal worm was involved in the transmission of blackhead, but that was to be revealed to a considerable extent by another able researcher who had also taken exception to the confusion of blackhead and coccidiosis.

Dr. E. E. Tyzzer, also at Harvard, and also a pathologist of no mean ability, was in charge of the school's cancer research program. He had, however, made some studies of the coccidia, especially those of rodents. He also had at his disposal one of the best libraries on this continent, and he knew the literature in protozoology. Unlike Smith, he was not under attack personally, but he deplored the confusion of two diseases that in his concept were sufficiently individual to make such confusion unjustified. So he turned his attention to learning more about each.

Between 1919, when Tyzzer reported on the developmental stages of the blackhead parasite (53), and 1936, when he explored immunization with organisms attenuated *in vitro* (58), he published (alone or with students or colleagues at Harvard) more than 20 articles. In those he reported his explorations into almost every phase of blackhead research that had yet been pursued, excluding only those requiring such recent developments as electron microscopy and fluorescent antibody techniques. Even today, a report on histomoniasis would be difficult to write without acknowl-

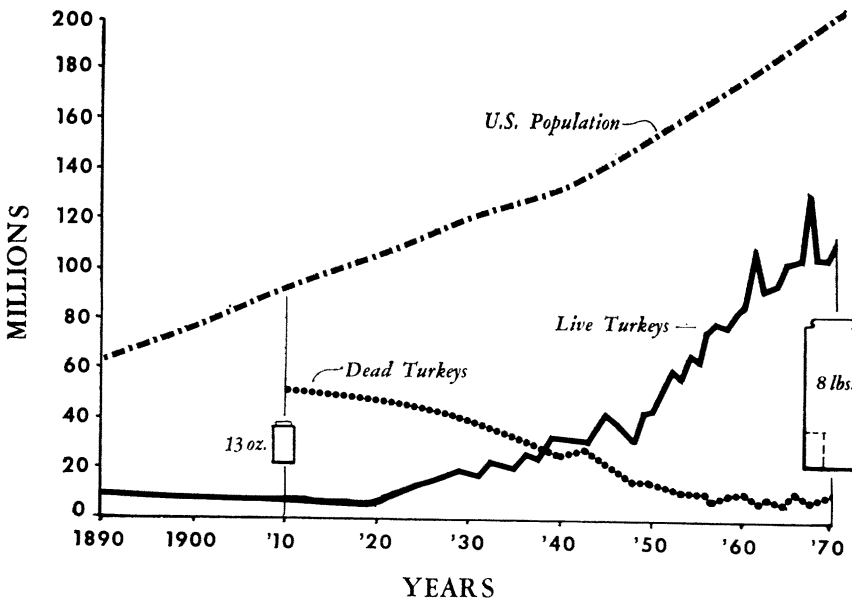

Fig. 2. Eighty years of turkey production in the United States.

edging some contribution that Tyzzer's laboratory made to implementation of the study if not to actual shaping of the concept developed.

It was Tyzzer, after pondering for years the natural transmission of blackhead, who demonstrated experimentally that *Histomonas meleagridis* (renamed as a flagellate [54]) was actually brought into the birds by the embryonated eggs of the cecal worm, *Heterakis gallinarum* (59). So conclusive were Tyzzer's experiments that they dispelled the doubts of all except those skeptics who wanted to *see* the histomonad in the embryonated egg, which Tyzzer was never able to show although that has now been accomplished by Gibbs (23) and others.

It may seem that with all of that accumulated knowledge, the control of blackhead should not have eluded the growers for so long. But the reports of Smith, Curtice, Graybill, and Tyzzer did not *reach* the growers. One man they did reach went far in correcting that. A young veterinarian from Cornell, William A. Billings, joined the University of Minnesota staff in 1919. He read everything on turkeys that he could get his hands on, and for two years he experimented with rearing poults away from chickens, on clean soil, and exercising every precaution against infection that his studies had suggested to him. It was 1923 by the time he sallied forth to enlighten the turkey growers, armed with an enthusiasm and a flair for evangelistic work that must have reminded many an early grower of the methods employed by Billy Sunday, who had been stumping in the rural Midwest so vigorously for a dozen years. The story of Dr. Billings' early efforts has been told and retold, in farm journals and even in the pages of *The Readers Digest,* in "The Man Who Saved the Turkey Dinner" (43). When Dr. Billings went to Minnesota, mortality among domestic turkeys was still about 50%, with an estimated nine-tenths of that being due to blackhead. Among some flocks that mingled with chickens, mortality rose to 75% or more. A growing population of about 105 million persons had to content itself with fewer than 10 million turkeys (Fig. 1). One estimate (41) placed the 1920 production at fewer than 4 million! Millions of children, of whom I was one, had never tasted turkey, nor were we to do so for many years to come — not at Thanksgiving, Christmas, or any other time. Bled and largely picked, but otherwise unaltered, a few turkeys for the holiday trade might land in the local butcher shop, priced at 55, 60, and even up to 70 cents a pound. As a laborer, my father would have worked from 7 o'clock Monday morning until late Thursday afternoon to have earned the price of such a bird for Thanksgiving. In one generation, the turkey industry was snatched from the brink of oblivion and converted to such a thriving state that I can well recall how my children winced as they encountered turkey so frequently on the school lunch program. And as a member of the school board, I knew precisely why we were serving it so often.

No one person has been accorded more credit for turning the turkey industry around than "Doc Billings," as he was affectionately known. If I were to list the four greatest contributors in conquering blackhead, they would have to be Smith, Curtice, Tyzzer, and Billings (Fig. 2). The first three were scientists of world renown. Tyzzer, more than any other individual, ushered in the era of modern research on two of the greatest parasitic scourges of poultry in our time, blackhead and coccidiosis. Billings never sought the role of the polished scientist, but he carried a down-to-earth message that could not be misunderstood. As I have said so often in short talks I used to give at Thanksgiving time, "What Billings said may not always have sounded good in the hallowed halls of Harvard, but in the ears of turkey growers everywhere, few voices rang more nobly." Were you to go to visit the Poultry Hall of Fame, you would not find there the portrait of Smith, Curtice, or even Tyzzer, great though his contributions. But the crusty veterinarian who stumped the Minnesota countryside preaching the gospel of rearing turkeys in spite of blackhead — his portrait is there for all to behold. Discovery is not enough. The implementation of knowledge to the benefit of humanity at large is a prized accomplishment.

Most recent of American achievements that had spectacular success in the control of blackhead has been the development of safe and effective antihistomonal drugs that can be used conveniently and at a cost compatible with profitable commercial production. A search for such a drug had been going on since Tyzzer's time, but he was never able to find one that was entirely safe to use and economically priced (55). During the late 1930's and throughout the 1940's, the search intensified, doubtless stimulated by the spectacular successes scored in developing effective coccidiostats. Although phenothiazine had been shown to be effective against the cecal worm (65), control of which would ultimately result in the control of blackhead, such an indirect approach was too slow for the needs of the times. During the difficult years of World War II, millions of persons had discovered that turkey was an excellent table item at any time of the year and, being unrationed, spared the ever-too-scarce red points required to purchase the so-called "red meats." Despite shortages in equipment and labor, turkey production had at least doubled since 1930 (Fig. 1). True, there was a brief lull in the demand as rationing was lifted, but in 1950 the demand was still brisk. Then, through the efforts of many researchers, at first two, and later more, antihistomonal drugs were developed and marketed. Growers, mill owners, and bankers, all with new confidence in the ability of the enterprises to avoid excessive losses, responded to enable the industry to produce turkeys in unprecedented millions. The chart shows the results. In recent years, overall mortality among commercially grown turkeys has usually not reached 10%, but tending to hover near 7.5 to 8%. Mortality from blackhead has been less than 0.5%, and some growers say they have not seen a case in years.

Coccidiosis in chickens. Unfortunately, the spectacular success achieved against blackhead has not been matched with coccidiosis, by all odds the number-one parasitic disease of chickens. The lack of success is despite the fact that the total effort against coccidiosis has been much greater. There are reasons, of course.

Neither blackhead in turkeys nor coccidiosis in chickens was here in pre-Columbian times. The turkey was a native of the Western Hemisphere, but the histomonad was not here, and *Heterakis gallinarum* also may have been absent. Chickens, like their cousins the pheasants, were natives of the Eastern Hemisphere, and it was these birds that introduced both *Histomonas meleagridis* and their own species of coccidia. Because of the exacting requirements of the life cycle of the blackhead parasite, it did not become established sufficiently to attract attention by losses among susceptible birds (domestic turkeys) until about 1880. That story is too long to detail here, but several technological developments, rapid westward expansion, and the depletion of much of our natural game resources all contributed to the development of conditions favoring the ultimate establishment of blackhead.

Not so with coccidiosis. Although infections were self-limiting, reinfection was possible from oocysts voided but a few days before their ingestion by the same or other individual birds of the same species. No cecal worms, earthworms, or hosts with differing degrees of susceptibility to the disease were required. Why did the disease not become so rampant as to attract attention very early? Coccidiosis was hardly known in this country when Rice and Cushman were becoming alarmed over the ravages of blackhead. Our early poultry books did not mention coccidiosis as a specific entity. Salmon's "The Diseases of Poultry" (46) mentioned it under the caption "Psorospermic Enteritis," and actually distinguished between the intestinal form, attributed to infection with *Eimeria dubia*, and the cecal form, caused by *Coccidium tenellum*. At that time, all of the early work on the condition had been done in Europe. In this country, growers were confusing the disease with others that caused diarrhea. But that was not the only reason that the disease had not been recognized as frequently as blackhead would have been. There were several species of coccidia in chickens, and some actually did little harm. Moreover, until almost a quarter of the 20th century had passed, the gradual ingestion of relatively small numbers of infective stages was common, and in many instances such ingestion increased the birds' resistance sufficiently to protect them. Thus it was that chickens, if not closely confined, escaped most forms of coccidiosis without serious losses.

After World War I, two laboratories in our Pacific Coast states, where coccidiosis was quite prevalent, made contributions that stimulated work on the disease. J. R. Beach at California clarified the distinction between coccidiosis and bacillary white diarrhea of young chickens (5). He also advocated feeding milk to control coccidiosis. The recommendation proved somewhat controversial, although scarcely as much so as the view that Beach and J. C. Corl expressed later: that the severity of a case of coccidiosis had little relation to the number of oocysts ingested (6). W. T. Johnson, in Oregon, could not accept that view. He considered it contrary to what appeared to be happening in farm-grown poultry (34). He arranged experiments in which he showed that, despite many other influencing factors, the progressive ingestion of small numbers of sporulated oocysts actually increased the resistance of many birds, so that responses to infection were not severe (34,35). Johnson was probably also the first to publicize the use of potassium dichromate (he used 2½%) for the sporulation of oocysts. He credits Hadley with having given him the idea by telling him in a personal communication that such a solution was suitable for prolonged storage of sporulated oocysts (35). Johnson was apparently also the first (1923) to suggest that turkey coccidia were of a different species from chicken coccidia, the shapes of the oocysts being different (32). Also, at the invitation of the editors of *Poultry Science,* Johnson contributed some of the clearest photomicrographs of various stages of the coccidia of chickens that had appeared anywhere (33). Those illustrations were a great aid to persons seeking to diagnose the disease.

But, as with the research on blackhead, Tyzzer made the monumental contributions that marked the opening of a new era of research on coccidiosis of poultry. As early as 1902, he had published on the coccidia of rabbits and, as Cole and Hadley's confusing report appeared, Tyzzer was studying certain cryptosporidia of mice. He knew the world's literature in the field, had personal experience with the coccidia of mammals, and had seen blackhead in various galliform birds. As we have noted, he did not rush into print with his results on the study of blackhead; he was even more deliberate in publishing on coccidiosis in poultry. In December 1926, at the Second Annual Meeting of the American Society of Parasitologists, in Philadelphia, he gave the select few in attendance a glimpse of what his caliber of study would yield (56). Three months later, the half-page abstract appeared in print. He could now state positively, with support from morphologic and pathologic evidence, that: 1) *Eimeria tenella,* producing severe responses, was a different species of *Eimeria* from that (or those) found in the intestine of chickens; and 2) the species that he recovered from turkeys (which he called *Eimeria meleagridis,* n.sp.) would not infect chickens. He thus showed that Johnson's view was correct.

Two years later, in 1929, Tyzzer published that enduring classic "Coccidiosis in Gallinaceous Birds" (57), 115 pages replete with magnificent plates (two in color) with more than 50 figures, some of which have not been excelled to this day for accuracy of portrayal of the regions involved, tissues invaded, and developmental stages of the parasite. In all, Tyzzer carefully described *Eimeria tenella,* three new species of the same genus from the intestine of the chicken, one from pheasants, one from bobwhite, and two from turkeys. He demonstrated host-limitation (often called "host-specificity"), self-limitation, and the development of acquired resistance. The last he showed to be of appreciable consequence only with the species that penetrated the cells most deeply, *E. maxima* and *E. tenella*. He found no cross-immunity and no acquired passive immunity.

Tyzzer was to publish in 1932, with two associates, a sequel to the above contribution (60), and he had released only two short articles on coccidiosis in the interim. But his place in the annals of coccidiosis was assured. When the New York Academy of Sciences staged its comprehensive program "Coccidiosis" (all hosts), in 1949 (38), Dr. E. E. Tyzzer was Honorary Chairman. Then approaching 75, he understandably did not appear to deliver his brief opening comments, but the leadership that he had shown on this important poultry disease was recognized by even the youngest of a new generation of investigators.

One more landmark should not be overlooked. It is one of those contributions that, although not directly applicable to the alleviation of growers' troubles, determine the direction of research efforts for decades to come. This was P. P. Levine's paper "The effect of sulfanilamide on the course of experimental avian coccidiosis" (36). As the author stated, "this report is not intended to convey the impression that sulfanilamide is of practical value in the control of coccidiosis under farm conditions." He then expressed the view that some derivative might be found that would have "the same coccidiostatic action as sulfanilamide but with less toxicity for the host."

So stimulating was the above report that, according to a survey that I made, 238 published articles during the next 20 years (1940–1959) dealt with what I considered "newer" treatments, whereas only 21 dealt with the older type (skimmilk, lactobacilli, and similar substances). All except a half dozen of the reports on the latter types of treatments were based on studies made before Levine's work had appeared. To be sure, not all of those 238 reports of newer treatments could claim successes, but they represented efforts that ultimately produced a considerable number of effective coccidiostats. And that was fortunate because, among the many ways in which the coccidia differ from the histomonads is their ability to adapt themselves to a new situation. We should have suspected it. Some years ago, one catalog of the coccidia (40) listed 562 species of the genus *Eimeria* alone, and 130 of the genus *Isospora*. Even if many are duplicates, undescribed species probably considerably outnumber duplications. Organisms as plastic from the evolutionary standpoint as are the coccidia would surely show enough variability that some could cope with concentrations of drugs that the hosts could tolerate well. In contrast, we know today of only two kinds of histomonads, a remarkable example of evolutionary stability for organisms so old. And *Histomonas meleagridis* is virtually as susceptible to the first effective antihistomonal drugs as it was a quarter of a century ago, when they were originally used. Thus, we can better understand why coccidiosis is so difficult to stamp out, despite enormous research efforts.

OUR GENERATION'S HERITAGE

I have omitted much, and in doing so I may have offended many. With very few exceptions, I have not mentioned contributions by contemporary researchers. It is not easy to determine the impact of relatively recent research, and I am no prophet. The work of my generation I leave to some future historian. There is a category of contributions that I must acknowledge — that of our devoted educators. I shall give only two examples. Dr. E. R. Becker's timely monograph on coccidia and coccidiosis (7) doubtless encouraged many a young parasitologist to select a problem for which he might otherwise have found his source material too elusive to make his choice attractive. Dr. Becker, alone or with various of his students, wrote more than 20 other articles on coccidiosis, principally on species found in mammals. However, some of his students made valuable contributions in the field of protozoan parasites of poultry.

My other example is Dr. James E. Ackert's influence. Aside from his many contributions in the field of helminths of poultry, some of Dr. Ackert's students have so distinguished themselves as to be known to all of us who read our scientific literature on poultry diseases. And now the students of some of Dr. Ackert's students are reporting on poultry parasites, and will doubtless set milestones in their eras and areas of research. Indeed, even now, one can almost see the emergence of some of these concepts with real impact.

But lest I be tempted to prophesy, I close with complete satisfaction that the period of discovery is not over. It is upon us, around us, and so close to us that we sense its presence but cannot perceive its dimensions. That is the stuff that progress is made of.

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