VOLUME XXII MARCH, 1924 No. 3

THE LIFE AND SCIENTIFIC WORK OF ARTHUR WILLIAM BACOT

BY MAJOR GREENWOOD.

WITH A CHAPTER BY J. A. ARKWRIGHT

(With Portrait, Plate II.)

CONTENTS.

I. BIRTH, EARLY LIFE, SOME PERSONAL CHARACTERISTICS.

ARTHUR WILLIAM BACOT was born in London on April 28th, 1866, the third son and fourth child of Edmund Alexander and Harriet Bacot.

The family is of Huguenot descent in the paternal line and an account of some of the members will be found in Samuel Smiles' book *Huguenots in England and Ireland* (p. 431). In physique, Arthur Bacot showed traces of his descent. He told me that on his first continental trip his companion would address a passer-by in voluble but anglicised French, while he himself, not having the gift of tongues, stood silent. Sooner or later there would come a conversational deadlock, the Frenchman would look round in despair and, catching sight of Bacot, his face would light up, he would begin a fluent discourse only to be plunged into deeper gloom by the discovery that this too was an Englishman.

Several of Bacot's ascendants and collaterals were members of the Medical profession; his great-uncle, John Bacot, served with distinction in the Peninsular War, and was the author of a treatise on the Venereal Diseases published in 1829. An older member of that generation, Frederick Bacot, a young Army Surgeon, fell at Seringa-Patam.

John Bacot's work on Syphilis—the title is a "Treatise on Syphilis," but it deals with the other venereal diseases too—is a favourable specimen of the more competently written manuals of a hundred years ago but is of no biographical interest; John Bacot's son, J. T. W. Bacot, also an army surgeon, published in 1869 a little volume on the Bahamas. This book does contain traces of a literary quality which Arthur Bacot's friends found in his conversation. "It was once rumoured in profane circles," says Surgeon Major Bacot, "that penitent pirates achieved even a higher degree of respectability in the old country,

https://doi.org/10.1017/S0022172400008226 Published online by Cambridge University Press

than the fighting chaplain. A story is told of a weather-beaten ruffian, who, after long absence from England, inquiring after old chums, was thunderstruck by the information that one of them, Blackburne, had become Archbishop of York." "Read," again says the Surgeon-Major, "the bright verses—

> 'Oh, who can tell, save he whose heart hath tried,
> And danced in triumph o'er the waters wide,
> The exulting sense—the pulse's maddening play,
> That thrills the wanderer of that trackless way?
> That for itself can woo the approaching fight,
> And turn what some deem danger to delight';

and then turn to wretched Blackbeard's Journal. 'Rogues a plotting! took a prize with a great deal of liquor aboard; so kept the company hot, damned hot; then all things went well again.'"

There is a characteristic Bacotian flavour in the antithesis.

As a child, Arthur Bacot was delicate and often ailing, although he was proficient at most outdoor sports, an excellent swimmer and skater (as a man he was a first-rate skater and passed the speed tests of the National Skating Association) by his eleventh year. His delicacy, called at the time "Anaemia of the Brain" was perhaps what we should now call psychoneurotic. All the children were, as Miss Bacot tells me, introspective and sympathetic to animals, a tendency encouraged and shared in by their father. Whatever we may think of its aetiology, the psychological condition led to great irregularity of school attendance and had important consequences in after life.

Psychologists tell us that the experiences of childhood are far more potent in determining what we shall become than anything which happens afterwards and certainly many of Bacot's characteristics, both trivial and important, can be very plausibly related to his childish experiences. To begin with a characteristic, which, trivial as it was, impressed all his associates, he retained into manhood most of the likes and dislikes of the average delicate child in eating and drinking. He enjoyed at the age of 50 what a boy of 5 enjoys, and it was a melancholy thing to sit next to him at a "grown-up" dinner of many courses. He was also very irritating to folk who dieted themselves on principle. To such, a man who wore no hat and lunched off bread and jam, cheese and chocolates, seemed a long lost brother, and they were very cross when they found he was not a vegetarian, in fact enjoyed roast chicken, and had no conscientious scruples against keeping a hat in his city office (he did it, he told me, because bank cashiers and city shopkeepers with tills grew nervous if a hatless man came in). They failed to perceive that he did or abstained from doing trivial things not on principle but because he had retained the tastes of a boy.

This was a trifle, more significant were two consequences.

Being often away from school and therefore thrown on his own resources, the introspection of a child, the faculty of weaving romances out of common things, was strengthened by practice and was perhaps the basis of Bacot's powers of sympathetic imagination. His attitude towards birds and beasts

https://doi.org/10.1017/S0022172400008226 Published online by Cambridge University Press

retained something childish—in the good sense—to the end. He never canted, he did not call them his "little brothers," neither did he adopt the intellectual manner of the schoolmaster abroad or treat fleas as the nicely educated young man is apt to treat a boy's brigade.

The other consequence was that Bacot had no hope of escaping from his economic environment by the usual methods. The system of education of the less prosperous middle classes even more recently than 45 years ago was bad and has been dealt with faithfully by Mr H. G. Wells. The school to which Bacot was sent was very much above the level of Kipps' academy, in fact it appears to have been an exceedingly good school of its kind and turned out several pupils beside Bacot who have made their marks in different careers, including one of the most successful novelists of our generation. But Bacot was too irregular in attendance to get the best out of the school. The methods of imparting the rudiments of mathematics, English composition and foreign languages were no doubt imperfect (they are still) but much less able men than Bacot at far worse schools than his have acquired a mastery of these rudiments. Bacot did not. He left school with no knowledge of foreign languages, and without such knowledge of the orthodox branches of science as might have enabled him to compete with a hope of success for grant-earning "Science and Art" certificates or *a fortiori* for a scholarship at the Royal College of Science.

Bacot's difficulty in acquiring languages was not wholly due to an irregular early education. His visual memory was innately more powerful than his auditory memory; it was always remarkable that while he received and interpreted visual stimuli without seeming to attend to them, no effort of voluntary attention enabled him to retain unfamiliar pronunciations. This was an individual peculiarity; other members of his family had at least normal powers of auditory memory; but, as his sister Miss Alice Bacot is an excellent artist, perhaps the family tendency is to visualisation.

A greater handicap of Bacot's early life was that although he had not acquired any facility of literary expression he had learned enough of so-called literary English to put him out. To the last this hampered him. In a private debating society, or, better still, after 70 miles of hard riding, sauntering through a little country town with a bag of chocolates or fruit, he was a brilliant talker, expressing his ideas with absolute precision and never hesitating for the apt phrase, the just comparison. A pen between his fingers effectually controlled this flow. His written language was often heavy and involved; he always gave the impression of struggling with a material which was repugnant to him; in fact, writing a formal paper was a task he particularly disliked. Sometimes in a private letter, more frequently in informal papers read to a little local debating society, one comes upon turns of expression which remind one of his talk; but they are not numerous. Had he been a citizen of an old Greek state or had a James Boswell been numbered amongst his friends, his literary reputation would stand higher.

https://doi.org/10.1017/S0022172400008226 Published online by Cambridge University Press

Bacot's initiation to the study of natural history only differed from that of any boys blessed with intelligent parents and brothers in its early date. He started butterfly hunting at five and his sister recollects that at the age of six the child was saddened by his kindergarten mistress's ignorance of butterflies and caterpillars.

Bacot's delicate health kept him out of the city until he was 16 but at 16 the hour struck and for the next 27 years he was employed in a city office. When I first met him, 23 years ago, he had been in business more than 17 years but he did not even then have above a fortnight's annual holiday and seldom reached home before 6.30. He had been a member of a local Natural History Society (now the London Natural History Society) for several years but he did not join the Entomological Society of London until much later. It would not be easy to imagine external conditions less propitious for the development of scientific ability, but between 1893 and 1909 he published more than 50 separate papers and contributed largely to Tutt's monumental treatise on the British Lepidoptera. The salient characteristics of this work are examined in the next chapter.

II. RESEARCHES ON LEPIDOPTERA.

Bacot's first published contribution to natural history was a note on the variation of larvae of *Saturnia carpini*, printed in the *Entomologist's Record* of 1893 (vol. IV, p. 199). It is very short and will bear citation in full.

In June, 1892, I took a brood of young larvae of this species on a whitethorn hedge near Thundersley, in Essex. From a male and female reared from these larvae, I got a batch of ova this spring; these hatched in about twenty days. After their first moult, the larvae varied very widely, some of them being entirely green or pale yellow, without any black, some remaining (until their third moult) quite black, with the exception of a reddish or brownish stripe along the side. The latter retained a large proportion of black in their coloration until nearly full-fed, while others, exhibiting nearly every grade between these two extremes, could be picked out of the brood. It seems strange that a brood of larvae should vary so widely after their first moult, and yet be so alike (comparatively speaking) in their last stage.

The following has occurred to me as a possible explanation. The larvae until the first moult, are quite black, and they feed gregariously until the third moult. When feeding on a hedge or bush they might easily be overlooked, as the effect of a brood of small black larvae lying close together is to blot out the leaf or leaves they are feeding on, leaving an apparent opening in the hedge, such as would be obtained if one or two leaves were picked off. If, however, the whole brood retained their black colour as they grew larger, the size of the apparent opening or hole in the hedge would become noticeable, but as they vary in colour, they match very well with the bright green leaves and dark spaces between, in fact, if they cleared a patch of leaves, the larvae would themselves (to a certain extent) present the appearance of the missing foliage. No doubt, after the third moult, when they scatter, the bright forms are, as regards colour, by far the best protected.

The second paragraph of this note distinguishes it from the ordinary natural history jotting.

Bacot's first long paper was read to the City of London Entomological and

https://doi.org/10.1017/S0022172400008226 Published online by Cambridge University Press

Natural History Society in 1895 and printed in the *Entomologist's Record* (VI, 173–181); it deals with the Genus *Smerinthus* and the technical problem which he desired to solve was the relation of the genus to allied genera. It is not the object of this memoir to appraise the technical value of Bacot's contributions to lepidopterology—I have not indeed sufficient knowledge to permit me to make the attempt—but to note features which throw light upon the habits of mind which were a foundation of Bacot's success in medical research. I therefore restrict myself to a quotation dealing with a quite subsidiary point. He is speaking of the larvae of *S. populi* and remarks:

The young larvae have very similar habits to those of *S. ocellatus*, but as they get older, the position in which they rest is very different; this is nearly always with the head downwards, and although the fore part of the body is raised, as in *S. ocellatus*, the head is curved inwards towards the leaf or twig; they will grasp the stalk of a leaf with their anal claspers only and hang down behind it, and it is quite remarkable how small a sallow leaf suffices to hide a full fed larva. On poplars I have frequently noticed them, when they have eaten half the leaf, so resting as to represent the eaten portion themselves, and they are then so well protected that, with any wind, it would I think be impossible to detect them. I have noticed that the larvae are much easier to find on misty mornings and before the sun is up. Probably the explanation of this is, that in bright sunshine the lights and shadows are much stronger, and consequently the slight difference in tint between the larva and the leaf is not so noticeable. The same fact holds good with *S. ocellatus*, and I think that, as a rule, the protective colouration of larvae is most perfect in sunlight or in full daylight.

Bacot returned to the subject of *Smerinthus* more than once, in particular to the morphology of the hybrids of *S. populi* and *S. ocellatus* which he reared.

Bacot contributed to the 10th volume of the *Entomologist's Record*, a complete morphological study of the British Liparid Moths; it is perhaps the most compact of his morphological studies and, in the precise and methodical description of the larval stages, is a good example of what may be called the school of Chapman. The late Dr T. A. Chapman, one of the most distinguished lepidopterists of our time, had an important influence on Bacot's scientific development; their long friendship was without a break and their scientific collaboration close. A quip in entomological circles that a certain treatise, we will call it Jones's treatise on Lepidoptera, should have had on the title page the explanatory words "By Bacot, Chapman and Prout," while unfair to Jones justly enough characterises the merits of a long continued collaboration of three friends. A paper of the same type but perhaps even more minutely accurate is that on the Life History of *Aglia tau* (*Ent. Rec.* XIV, 237).

From the date of his first publication to his initiation to medical entomology, Bacot's interests were balanced between morphological and genetic research. Undoubtedly the latter appealed more to him, but he probably devoted more time to the former, thereby acquiring a technical dexterity in the manipulation of small objects and a power of exact description which were to prove of great value in his later career. He perhaps owed as much to the carrying out of researches which are now interesting only to specialists, as did the greatest of British naturalists to his training on Barnacles.

Bacot's last important contribution to pure lepidopterology was however concerned with genetics; this was the paper by Bacot and Prout communicated to the Royal Society in 1909. Bacot's chief published work on pedigree breeding had been done on *Lasiocampa quercus* and *Triphaena comes*. In the former species he had found that two races from the same geographical region when crossed produced progeny which segregated into the parental forms but that this did not occur when the southern French variety, *meridionalis*, was crossed with the Scottish variety *callunae*. Working with *Triphaena comes* from Cluny, he had 60 per cent. non-melanic and 40 per cent. melanic in the first filial generation from a melanic (male) non-melanic (female) crossing. In the next generation all the offspring of non-melanic pairings were non-melanic, but from extracted melanic pairings of like parentage, in two broods there were 30 per cent. non-melanic and 70 per cent. melanic, in another brood 21 per cent. and 79 per cent. In the next generation melanic × melanic and non-melanic × non-melanic pairings bred true, but the strain was becoming weakly and died out. Prout had carried out a long series of experiments upon *Xanthorrhoë ferrugata*, which showed *roughly* Mendelian proportions consistent with the black form being recessive to the purple.

Bacot and Prout decided to experiment further with a geometrid moth *Acidalia virgularia* which offered several advantages to the breeder—its omnivorous feeding capacity, celerity of reproduction, small size and the existence of a southern French form unlike the British variety. The southern French form is distinguished by its white or cream-coloured wing ground, the London form has the ground-colour profusely dusted with dark grey atoms. The French may therefore be termed the "light" and the London the "dark" form. A complete scheme of cross-pairings was drawn up and, in all, 5531 bred specimens in ten generations were analysed.

The conclusions reached by the authors were (1) that there was no colour dominance in the light × dark cross and (2) that the obtaining of a comparatively uniform type by selective mating and the persistence of intermediates, while not decisively in favour of any one theory of inheritance were "harder to reconcile with Mendelism than with, for example, the Galtonian view." Whether the results are explicable in terms of the Mendelian doctrine as now extended by the researches of many years, is a technical point the discussion of which does not belong to a memoir of Bacot. Although he never lost his interest in the problems of genetics and indeed did more work on the descendants of the *Acidalia* strains (this was never published), he never afterwards had leisure to devote himself seriously to the subject. From the point of view of the biographer, the importance of this investigation is its marking of a stage in Bacot's scientific self-education.

Precisely what Bacot's rank as a lepidopterist really is, must be settled by specialists. What impressed an outsider was that he never suffered from the intellectual myopia to which the self-taught biological specialist is liable. I remember lunching with him and an indefatigable lepidopterist and, their conversation being mainly unintelligible to one without clear ideas as to the number of legs a caterpillar has, my attention wandered. But I pulled my wits together when Bacot mentioned the name of an eminent man of science of whom I *had* heard. Bacot spoke with praise of something the eminent man had done in entomology, but his friend shook his head sadly. "I'm afraid," he said, "you could hardly call X a *sound* entomologist, why"—speaking slowly and impressively—"fifteen years ago, X really did not know that the larva of YZ moults *n* times!" Bacot received this communication with a proper gravity, but afterwards—while carefully explaining to me why, in this particular instance, the specialist's horror was not quite so comic as it seemed—he enforced the lesson of how hard it is to see the wood if one pays very great attention to the trees. If *he* had ever experienced the temptation he overcame it.

III. BACOT'S INITIATION TO MEDICAL RESEARCH. FLEAS AND PLAGUE.

The joint research with Prout was Bacot's last important contribution to pure lepidopterology; the main stream of his intellectual life was soon to be diverted.

Before the publication of the research on *Acidalia* Bacot had made the acquaintance of some prominent workers in the field of scientific medicine. He had been introduced to Prof. Leonard Hill and Prof. Bulloch and, in 1908, gave an account of his breeding experiments in the Physiological Theatre of the London Hospital Medical College, one of a course of lectures on heredity in which members of the College staff collaborated. This was the first time he addressed a medical audience.

In 1909, I was employed by the Advisory Committee for Plague Investigations to analyse statistics of plague incidence; this commission and my appointment to the staff of the Lister Institute at the end of 1909, brought me into touch with the principal workers on the subject, Lamb, Liston, Boycott, C. J. Martin, Ledingham and Rowland. With the selfishness of youth, I was apt to inflict my very crude theories and opinions respecting the aetiology of plague upon my friends, and Bacot was a willing victim. He had by this time moved to Loughton and on our Saturday and Sunday walks he endured a good deal of verbiage about plague.

The subject is really a fascinating one; so much is known and yet there are such perplexing gaps in our knowledge. Why *did* plague disappear from England at the end of the 17th century? How can we account for long periods of intermission here and in India? These are but two of a hundred questions which everyone asked, and still asks, himself. The bacteriology of the disease was better understood than that of any other epidemic malady; the brilliant work of investigators in India had proved the rat flea to be an essential link of the aetiological chain, but the way this link fitted into contiguous links was uncertain. I used to bombard Bacot with questions about the ways of fleas and he would suggest, *inter alia*, possibilities of bridging over gaps in the time sequence. One of the first ideas he conceived was that an infection in one stage of the insect's life-cycle might be carried over into another and he surmised that a long latent period might thus be explained. The testing of this hypothesis was the topic of his first published contribution to medical entomology.

Within a few months our conversations had a practical result; I learned that the Advisory Committee were looking for someone who could study the rat flea from other aspects than the morphological, and introduced Bacot to Prof. C. J. Martin.

The gulf between the certificated professional and the amateur is not so wide in England as elsewhere, still it exists. Obviously no committee administering public funds could have been expected to invite a man of 44 whose name was unknown outside a narrow circle to throw up his means of living and become a wholetime investigator. All that could be done was to invite Bacot to take up the study of fleas in his spare time, the Committee to bear all expenses and pay an honorarium. The terms offered by the Committee were liberal, but Bacot feared that time was lacking. However, after a little hesitation, he accepted the proposal, an R.A.M.C. reservist was sent down to Loughton and with his help—he proved to be an ideal assistant—Bacot turned a derelict stable into a laboratory, collected some apparatus and a few fleas and set to work.

The time at Bacot's disposal was from seven in the evening to eight in the morning, five days a week; five hours more on Saturdays and such part of Sundays as I could not induce him to devote to forest walks. In this time he had to conquer all the difficulties of a new technic unguided by the experience of others. As I have said, he had no aptitude for languages and even if the literature had been copious it would not have helped him—as a matter of fact there was very little literature, I believe the experiments of Rösel von Rosenhoff published in 1749 were the only ones which guided him. The difficulties of his main research were sufficiently great, but in this he had only the same *kind* of obstacle to surmount as in the breeding experiments on moths from which he had learned much. But, as a side line, he took up the tracing of an infection from one stage of life-history to another, working with the house fly and *Bacillus pyocyaneus*. The tyro in a properly equipped laboratory is familiar with the difficulties of pure culturing. In an old wooden stable the omnipresence of moulds makes the work exasperatingly difficult, particularly if one has to discover for oneself all the little manipulations which the more fortunate student has had demonstrated to him by a teacher. Bacot's note on the "Persistence of *B. pyocyaneus* in Pupae and Imagines of *Musca domestica* raised from larvae experimentally infected with the bacillus," his first printed medico-entomological work (1911), is not one of his most important papers, but it cost him a great deal of patience and time.

To return to the main subject, a study of the bionomics of fleas, planned and executed under the conditions I have described, was practically completed by the autumn of 1911. The memoir finally printed in 1914 contains some additions made after 1911 but it is substantially a record of 18 months' work at Loughton in 1910–11.

The questions asked by the Advisory Committee were these. What are the effects upon each stage of the life-history of varying conditions of temperature and humidity? Under what conditions and in what phase of the cycle can fleas tide over periods of heat or cold or dryness which are unfavourable to reproduction?

Bacot answered each of these questions fully.

I will not try to summarise the memoir but merely note a few points which are characteristic.

What first impresses a reader familiar with experimental work is the success with which large stocks of fleas were kept alive, the infrequency with which any experiment failed through the death of the subjects. This success was due to Bacot's sympathetic observation of the natural habits of his captives or his intuition of what the habits were likely to be. For instance, boxes containing laying females or cocoons awaiting emergence were buried in sand, "the habit of the flea being to hide away in crevices, corners etc., where more equable conditions of temperature and humidity are likely to obtain than elsewhere." Or again his comment upon the fact that "the mainstay of the larval diet is the faeces of the adult fleas," is illuminating.

It may be that the necessity for this diet in case of larvae of a particular species depends upon the closeness of the association between the parent and the host fed upon. Fleas being chiefly, if not exclusively, nest or lair parasites, it is not surprising to find that the larvae should utilise as food the rich store of organic matter in suitable condition for assimilation that is afforded by the droppings of their parents. It is an interesting speculation as to how far the adult's habit of wasteful feeding is the direct outcome of selective action, making a special provision for the larval food supply....The other conditions provided by the nest or lair of the host in nature are also ideal for the flea larvae, or, to put it in other words, the larval requirements are adjusted to those that are most likely to obtain where the eggs are dropped. The necessary conditions of warmth and humidity are provided by the host's body, while the provision of bedding and careful choice of a dry situation all fit in with the needs of the larval stage of the parasite. When the host leaves its nest or lair the temperature and humidity fall together, but, so far as observation goes, a fall in temperature will only have the effect of slowing development; a low humidity, however, if prolonged, will be fatal even when accompanied by low temperature. *P. irritans* [the human flea] would appear to have diverged from the other nest—breeding fleas in respect of the sensitiveness of its larvae to external conditions; possibly the progressive civilization of its host has forced it to become more adaptable. Larvae of this species were successfully reared under circumstances that proved fatal to *C. fasciatus* [the common rat flea], and, for example, were able to feed satisfactorily on crushed rat faeces when the larvae of the latter species failed. Probably the trend of selective action has been in the direction of producing a race of *P. irritans* able to feed on any possible rubbish in out-of-the-way corners. Undisturbed breeding places in such immediate vicinity to its host as to receive any appreciable quantity of the parental faeces would become gradually rarer as cleanliness and comfort succeeded to the crowding and filth of primitive conditions (pp. 472–473).

The most valuable section of the memoir is that which deals with the effects of varying physical conditions on the length of the larval and cocoon stage. The general conclusion reached was that in the rat flea, *C. fasciatus*, "Extremes both of heat as well as cold produce an effect which is partly of a direct nature, and partly, perhaps, a stimulus which calls into action an inborn predisposition to prolonged rest within the cocoon under unfavourable conditions. As was found in the case of *P. irritans*, it is the *changes* in temperature which appear to be the controlling factor" (p. 539).

Bacot thought that the species contained a proportion of individuals adapted for long resting periods in the face of extreme conditions whether of heat or cold but able to respond to "warm" conditions, say a temperature of 70° F., by rapid development. The evidence upon which these conclusions were based was set out in great detail, perhaps even in too great detail. But the reader who is bored by the immense statistical tables—Table XXXVIII covers nine crown octavo pages—should remember that it is the duty of a pioneer to record all his results and that these *pièces justificatives* will be of great service to any other inquirer who decides to verify any particular result upon a larger series of experiments. It was inevitable that the number of instances in any particular experiment should often be too scanty for statistical purposes; the number requisite, depending upon the variability of the phenomenon studied, cannot be determined beforehand.

The first draft of the report on the bionomics of rat fleas was Bacot's *Habilitationsschrift* and admitted him to the circle of recognised research workers; in December 1911 he was appointed entomologist to the Lister Institute of Preventive Medicine and he began work there a few months later.

Soon after he had come to the Lister we were on our way to lunch and I asked him casually how he liked his new job. He said, "Well, you know, it doesn't seem quite real yet; it is so hard to believe that nobody will come in with a bundle of accounts that I *must* go through." The Chelsea Bridge Road is not a very romantic place, but the second which followed that remark was my golden moment in life, an authentic vision of fairy land.

The two years and six months ending in August 1914 were a time of perfect happiness for Bacot. The Lister Institute was an ideal home for him. Of course he would have been happy and respected in any society of intelligent human beings, but the staff of the Lister were precisely the kind of people to suit him. All of them had enjoyed a more regular scientific training than he, but they had been trained in different schools and many of them had seen much of the world so there was none of that donnishness which is apt to make the entrance of an "outsider" into the society of men all educated on the same lines a little irksome.

But the "Oxford Manner" would have had to bite very deeply into a man's soul to make him hostile to Bacot. To some of us it was almost comical to see how quickly Minchin and he became fast friends. Minchin loved Oxford as dearly as Matthew Arnold did; one seldom passed a tea-time with him without an anecdote of Merton. Minchin's love of precise language and dislike

https://doi.org/10.1017/S0022172400008226 Published online by Cambridge University Press

of the often barbarous jargon in which scientific papers are written were quite as real as Charles Mercier's. I remember the tone of his voice when he alluded to an eminent biologist who had the habit of pronouncing spermatozoon in four instead of five syllables. One might have trembled for the consequences of introducing him to a man who invariably gave spermatozoon only four syllables and nearly always stressed the first syllable of bacillus. But Minchin loved natural history a great deal better than correct phraseology and knew a real naturalist when he saw one.

For the first time in his life Bacot had command of good tools, and learning how to use them was a perfect joy. I think the tool that gave him most pleasure was a Zeiss binocular dissecting microscope and, with Minchin for his instructor, his progress was rapid. In ordinary microscopy, he soon became expert. Most students will know the value of a compliment I once heard C. J. Martin pay. He said, "Bacot never sees what isn't there."

Perhaps the pleasantest moments of his working day were at tea-time. Sometimes one could draw him out to talk about the ways of birds and beasts, sometimes it was a social-economic discussion in which he would play the part of Socrates but without wounding the self esteem of the victims, an effect which no doubt determined several votes at the trial of his prototype.

Bacot's judgments of the motives of large masses of his fellow citizens, or of their political leaders, were pessimistic. It would have been a good debating point in a tea-time argument to have called his attention to the discrepancy between his own practice and his theory. For he himself had a quite uncanny power of detecting a colleague's dislike of some little task and a habit of offering to do it himself in such a way that it was not till afterwards one realised that instead of conferring a favour one was accepting a service. He detected the Forsyte instinct in most political actions but he was not a Forsyte himself.

Bacot had plenty of interests outside his laboratory, or rather the habits of mind which gave him pleasure in his laboratory found happiness everywhere. He had a very good time at Loughton. Demographically it is a London suburb, inhabited by a fair random sample of middle class people. We are not really such mercenary fools as *Punch* artists and didactic novelists make out, but we do think that the owner of a Rolls-Royce is usually better worth cultivating in a social way than the push cyclist. We feel that a bearded, hatless man who strides past our Parish Church on Sunday morning at the hour of Early Communion pushing an exceptionally noisy wheelbarrow charged with manure is abnormal. When this disturber of the Sabbath Peace also supports the most extreme "socialistic" doctrines in a local debating society, those who know us only through literature would not expect him to be popular. But the practical justification that Bacot's life provided for what we regarded as his eccentricities *was* accepted. A neighbour of mine said that Loughtonians fell into two classes—those who got on with Bacot and those who did not. I have not been able to identify half a dozen members of the latter class. Perhaps after all we are subtle enough to distinguish between selflessness and affectation.

Besides being a London suburb, Loughton enjoys other advantages. It is in Epping Forest, and there are not many more beautiful places in England than Great Monkwood. Beyond Monkwood in the Wake Valley is a pond of deep water where we are allowed to bathe. These two places are always associated in the minds of Arthur Bacot's friends with his and our happiest hours. The Sunday ritual was to bathe in the pond and after breakfast to walk out through Monkwood. One remembers that ritual of many years so well; first the coming of Bacot (he was seldom in bed after five in the summer mornings) and his dog to rouse me and my dog, the chorus of the two dogs as we set out, Bacot's comments on the road (he would sometimes dismount from his bicycle, walk back several yards and point out moths or caterpillars which I only saw at the range of a few feet when he *did* point them out), then the swimming of dogs and men, the run home downhill. After breakfast, the forest again and Bacot's Fabre-like exposition of the little adjustments of life in Nature. All this is nothing in the telling, but in memory it is beautiful; most beautiful things are fashioned of very simple stuffs.

The volume of the *Journal of Hygiene* which contained Bacot's revised memoir on the bionomics of the rat-flea also contained the paper by himself and C. J. Martin on the mechanism of infection. To this paper the frequently abused term classical may fairly be applied.

As long ago as 1897 it had been inferred by Ogata that the flea was implicated in the spread of the plague. Simond in 1898 performed experiments which indicated that rats could be infected by fleas and his work was confirmed and extended by Gautier and Raybaud in 1902–3 and Verjbitzki in 1904. The workers of the Commission for the Investigation of Plague in India (1906–7) proved that fleas were the chief and perhaps the only means of transmission but were unable to decide what was the precise mechanism. Bacot and Martin set out to ascertain whether infection could be conveyed by the act of sucking. Fleas were fed on infected mice and then allowed to bite clean rats under conditions which precluded the contamination of the rat's skin with the excreta of the flea. It soon appeared that infection could be conveyed in this manner. Thus 20 fleas undoubtedly infected (all the insects used passed plague bacilli in their faeces) were given two opportunities to feed on each of 13 rats. Nine of these rats died of plague. In the course of the experiments it was noticed that although some of the fleas sucked energetically no blood entered their stomachs. On dissecting these the fore part of the stomach was found to be obstructed by a solid growth of plague bacilli. A special series of experiments was then instituted with fleas affected in this way. In a series of four experiments with specimens of *X. cheopis* (the Indian Rat flea) every rat bitten died of plague. Of six trials with *C. fasciatus* (the common rat flea) one led to the death of the host. Then two "blocked" specimens of *X. cheopis* were allowed to bite eight rats in succession;

of these, three contracted plague; in another trial two fleas infected three out of nine rats. This latter result was reproduced when two "blocked" specimens of *C. fasciatus* were used.

It was thus clear that fleas in this condition are specially dangerous and the mechanics of the process were displayed by serial sections. Owing to the blocking of the front part of the stomach by the plug of bacilli, blood cannot find its way into the stomach. The insect in its efforts to relieve its thirst continues to suck but only succeeds in distending the oesophagus. Given the opportunity "the insects suck blood again and again, and if the pharyngeal pump ceases for a moment, some of the blood will by the elastic recoil of the oesophageal wall be driven back into the wound and carry with it plague bacilli."

It might perhaps be thought that fleas in this condition could not long survive, but actually specimens were found to survive so long as 50 days under a temperature of 10–15° C. and 23 days at 27° C. When they died they were still infected[1].

This brilliant investigation is no doubt the one by which Bacot's name will be most familiarised to the scientific public. Self evidently, the credit for its planning and execution is only in part his, while the literary form of the paper is the work of a more skilful writer.

Two other papers of this period have to be mentioned as of importance to the student of epidemiology. Bacot's "Observations on the Length of Time that fleas carrying *B. pestis* in their alimentary canals are able to survive in the absence of a host and retain the power to re-infect with plague" are of much interest. Fleas were allowed to feed on infected animals, the latter being then removed from the cages, which were stored at a mean temperature of 47° F. for different periods. At the end of various intervals healthy mice were added to the cages. In one experiment where 47 days had intervened between the removal of the original sources of infection and bringing in clean stock, one of the latter died of plague within 24 days. It was thus experimentally proved that an infected fasting flea could continue to transmit disease after an interval of more than six weeks. Whether this were the maximum, could only be determined by a very long series of experiments; actually in Bacot's series no success was scored after a longer interval.

The other paper was on the survival of bacteria in the alimentary canal of fleas during metamorphosis and is an application to the flea of the principle involved in Bacot's first printed medico-entomological paper (see p. 304). In no case was Bacot able to demonstrate the persistence in the imago of an infection acquired in the larval stage, a result in rather striking contrast with

[1] In a further note published in 1915, Bacot figured a specimen in which the obstructing mass has a passage through it. This rupture does not restore the valvular action of the fore-stomach but allows blood to flow out of the stomach as freely as it enters. He remarked that such a flea was more rather than less likely to infect its host than a completely plugged flea. Presumably too such a flea would live longer, as owing to the patency of the digestive tube fresh blood can be ingested and absorbed.

https://doi.org/10.1017/S0022172400008226 Published online by Cambridge University Press

the success won by himself, by Ledingham, by Graham-Smith and by Nicholls in contaminating adult Diptera by infection in the larval stage.

In order to get into perspective the work actually done by Bacot in connection with plague and to explain what he had in mind to do, it is necessary and, I hope, not without interest to describe in some detail an incident of English medical history which the reader may have forgotten.

The scene of the events is a triangle of South East Suffolk. The eastern apex is formed by the confluence of the rivers Stour and Orwell, which are two sides of a triangle, the main line of the Great Eastern Railway being the third side. The sides are some 10, 10 and 8 miles long, the area agricultural land with a few small villages. The large city of Ipswich is a few miles to the North West of the area and a short distance over the north eastern boundary is the town of Felixstowe and a series of largish villages.

In the year 1906–7, the headkeeper of Woolverston Park, a large estate less than a mile from the village of Freston, noticed that rats were dying in large numbers and that the corpses showed no signs of wasting such as one might expect after a prolonged illness. The year was a dry one and this was thought a sufficient explanation.

Three miles east south east of Woolverston Park is the village of Shotley; a cottage here was occupied at the beginning of December 1906 by 8 persons, two children, a man of 56 and five women. They were all alive and well on December 8th 1906, by Jan. 7th, 1907, 6 were dead and all had been attacked by what seemed to be a very contagious pneumonia.

Three years later a similar tragedy occurred within two miles of Shotley, at Trimley just across the Orwell (and therefore beyond the bounds of our triangle, but very near it). It concerned a family of 7 persons and a little girl on a visit. Of these 8 persons 5 died between Decr. 22nd. 1909 and February 4th. 1910. This household was a very poor one; father, mother, and five children occupied a two roomed cottage. It is said that the cottage was infested with fleas.

Of the victims' signs and symptoms there were preserved details which naturally enough attracted little notice at the time, but were afterwards seen to be of significance. The mother of the family, the first to sicken, was said to have had red spots on her hands and face and a swelling the size of a small hen's egg at the angle of the lower jaw. A daughter, taken ill the day after the mother died, complained of a lump at the left angle of the jaw which was very tender—she screamed if it was touched. This girl died on Janr. 5th. A younger sister who died five days later is said to have had a large swelling on the neck. The father of the family, taken ill the day before the younger girl died, had a swelling in the right groin, it yielded no pus on incision, but finally sloughed away. The man recovered. In neither of these tragedies was any suspicion aroused that there was the least connection between the deaths of the cottagers and the deaths of rats in Woolverstone Park which the head keeper attributed to drought in 1906–7. Indeed we have now no conclusive proof of a connection; but the next incident affords some grounds for presumption.

A cottage in the hamlet of Freston, within a mile of Woolverston Park, housed two adults and five children. On September 12th. 1910, a child was taken ill; it died on the 16th. The death was thought to be due to "Gastric Catarrh and Pneumonia." The mother, who nursed her daughter, was taken ill on Septr. 21st. and died on Septr. 23rd. The cause was entered as Septic Pneumonia. The father was taken ill on the day of his wife's funeral, Sept. 26th. and died three days later. Death was certified as due to "Influenza and Pneumonia." On the same day, there died a neighbour who had nursed the mother of the family through the night of Sep. 22–23. Her death was ascribed to "Influenza and Pneumonia."

In this series of cases, suspicion was aroused. The medical attendant supplied a specimen of the sputum from the second case to a trained bacteriologist who detected bacilli morphologically indistinguishable from *B. pestis*. From the third patient blood and from the fourth lung material were obtained; from all these specimens agar cultures yielded a bacillus presenting the ordinary characters of *B. pestis*. It was also reported that hares and rats had been dying in the vicinity of the cottages where this outbreak occurred. Lastly, a field inquiry was made by C. J. Martin and Sidney Rowland who detected 17 plague stricken rats out of 568 examined and mapped out a series of infected points just to the north west of the triangle and one within it.

The epizootic was indeed widely spread for five infected rats were found out of 35 trapped and examined in the Labour Colony of the Woodbridge Union, ten miles north east of the triangle.

This was the state of affairs in the autumn of 1910. It was established that at that date an epizootic was wide spread, it was rendered highly probable that the four deaths at Freston were due to infection by plague, a strong presumption was created that the six deaths in Shotley 4 years before and the five deaths in Trimley 12 months before were likewise due to plague.

In the following year a careful survey of the rat population was made and on 27 farms distributed from Alderton on the north east to East Bergholt on the south west of the triangle, plague stricken animals were found. One human life fell, that of a seaman in Shotley barracks; his symptoms were much the same as those of the earlier victims; he is said to have cut his finger while skinning a rabbit caught in the neighbourhood.

Infected rodents continued to be found in the succeeding years. In 1914 of 500 examined the bacillus of plague was isolated from 8, viz 3 ferrets, one rabbit and 4 rats. No other case occurred amongst the human population until June 1918 when two neighbours resident in Erwarton (1½ miles south of Shotley) died of plague. No other case has yet (1922) occurred and at the last field inquiry no rodents were found diseased.

If we conclude that the epizootic began in 1906–7, when the Woolverston Park keeper first noticed rats to be dying without obvious reason, we have the record of an epizootic continuing for at least 12 years, possibly continuously reinforced and yet responsible for only 18 deaths of human beings over the whole period. I have spoken of the possibility of continuous reinforcement, because Ipswich, within a few miles of the scene of the outbreak, is an important grain centre and had received cargoes of grain from Levantine and other ports where plague was known to exist.

Some features of the story are completely explicable in terms of Bacot and Martin's work, if we merely postulate a reservoir in the form of a steady epizootic, when a small number of the fleas which bite man will become infective[1]. Of these a still smaller number will succeed in reaching a human host. But (*a*) the long survival period of the infective flea, demonstrated by Bacot, and (*b*) the very considerable powers for evil of the plugged fleas, proved by Bacot and Martin, combine to render it probable that some of the few shots will hit a mark. There remain points which are not explained, which, given an opportunity, Bacot might have explained.

Why did this invasion fail or, to speak with more caution, why has it so far failed? There are sufficient reasons why a serious epizootic should not now

[1] Martin and Rowland found that half the fleas on the rats they examined were of a species not known to bite man and, in experiments, definitely averse from doing so; they also noted that the density of the flea population on the rats was very much less than in Indian experience.

lead to consequences for mankind like those of 300 years ago, but none to account for such a modest result as we have witnessed.

It is highly probable that the substitution of the brown for the black rat has been an epidemiological advantage; but the brown rat did not reach England (apparently in or about 1728) until a generation after the extinction of plague as a reigning epidemic.

Bacot's opinion was that success depended upon an adjustment of small details, only to be ascertained by a minute study of natural conditions, by attending to the ways of beasts and insects in the field. It was planned that he should undertake such a study of East Anglia; the late Dr Bruce Low was particularly anxious that he should do this. But more urgent work had to be performed and it is idle to speculate whether he would have discovered anything. Perhaps after all these little outbreaks *were* mere accidents of re-importation, having no deeper significance than the sporadic outbreaks which have been fairly frequent in the great seaports. Still one regrets that he did not in fact have the opportunity to look into the matter at the time of the last human cases.

Bacot published three other memoirs inspired by his association with the work of the Advisory Committee on Plague. One deals with the practical value of vapours as insecticides. He concluded that napthalene was the most generally effective agent for the destruction of fleas in all stages of their life-history. A second, written in collaboration with the late Dr W. G. Ridewood, is an exact morphological study of flea larvae. The third paper deals with the mechanism of infection with plague by bugs.

Bacot, like Verjbitzki, succeeded in infecting rodents by the bite of bugs and he gave a careful account of the mechanism. He found that a meal of septicaemic blood was fatal to newly hatched larvae, but that an adult was capable of re-infecting a mouse after 48 days' starvation. The paper is also, I think, of interest from the biographical point of view in its improvement of form; he never became an attractive writer but his more recent papers are better knit together than his earlier ones.

This work filled Bacot's time from his appointment to the Lister Institute to the summer of 1914. In August 1913 we made our last long cycling trip together, reaching Keswick by way of the Eastern counties and Wensleydale. Bacot was a strenuous rider. The programme he most enjoyed was to start after an early breakfast, ride 25 or 30 miles, stopping to inspect any village church of merit and travelling if possible by roads not infested by motors—the drivers of fast cars, game preservers and party politicians, were the only fellow citizens with whom he was not in charity—to lunch on cakes and chocolates at a village baker's; then to ride another five and twenty miles and eat bread and jam at a wayside inn; after this, twenty miles in the evening and a supper of bread and cheese sent him happy to bed. In his later years, the care of his pets sometimes led to delays. Our very last outing together was in August 1921; we had planned to ride out to the Suffolk border and photograph an old Manor House. We started on a sultry morning and when we were some ten miles from home Bacot remembered that he had left a box of lice on my drawing room table which would surely perish unfed. So we had to turn back and it was *very* hot. When we started off later in the day, we rode, as I thought, very fast for an hour or two; I was about to say as much and to make self congratulatory remarks upon the physical vigour of sedentary researchers over forty, but Bacot anticipated me by calling my attention to the fact that it was getting dark and asking tentatively whether I should much mind pushing on a bit. I thought of my twelve years' juniority and made a determined but wholly unsuccessful attempt to keep ahead.

In the 1913 trip, there was never the least doubt who was the better rider. I recollect our crossing a toll bridge south of Selby late in the evening. The custodian was sitting with his cronies and regarded us with pitying contempt. He eyed Bacot disparagingly and said very audibly to his friends, "Its just madness that's what it is—killing themselves they are, especially the old 'un." Then he turned to me and said "I suppose you two will be riding on to Newcastle?" "No," I said, "to Selby." "Why," he said indignantly, "that's only seven miles." Our experience of the inn led Bacot to regret that we *had* only ridden the seven miles. There was a waiter and a table d'hôte dinner, but no adequate cheese and inferior jam. At the end of our journey we stayed at the Fabian Summer School near Keswick. One evening an impromptu discussion was got up and Bacot was invited to open it. He chose the subject of diplomacy and criticised modern diplomacy in a way which was not relished by those members of the society who had a more extensive acquaintance with the literature of modern history than he had. I recollect that one of them defended our modern diplomatists quite warmly, gave chapter and verse for the wars that had been prevented, and reproved the suggestion Bacot had put forth that we might be drifting towards a war then. That was in August 1913.

In the summer of 1913 and the first six months of 1914 he continued to work on fleas. Early in the summer it was decided that he should take part in the researches of the Yellow Fever Commission and study the bionomics of mosquitoes at Freetown. He sailed a few days before the declaration of war.

IV. SERVICE ABROAD—*STEGOMYIA FASCIATA*.

Bacot spent just over a year in Freetown and the results of investigations there are contained in the Report published by the Yellow Fever (West Africa) Commission. A better idea of its quality will be afforded by a detailed examination of some sections than by a précis of the whole document. I choose for this purpose his investigation of the hatching of eggs.

Bacot began with an experiment upon the eggs of two female mosquitoes (*S. fasciata*) kept with several males. The eggs were collected daily, separated into 30 batches, submerged and watched. Some batches were kept in separate dishes, others—although of course separated one from another—were immersed in one large dish of water. This preliminary experiment at once showed that a *change* in the conditions to which the eggs were exposed acted as a stimulus to hatching. Thus batch No. 20 consisted of 80 eggs laid on 28th Sept. 1914; five hatched on 1st Oct., 24 on 2nd, six on 3rd and then no more for a fortnight. The water had gradually dried and on 18th Oct. the remaining eggs were re-immersed and on the next day eight more hatched; on 21st October more water was added and within a few hours 35 more eggs hatched out.

These preliminary trials led Bacot to formulate the following series of questions.

(1) Does the quantity of water affect the hatching rate?

(2) Are all eggs laid capable of survival after drying; if some only, is resistance evenly distributed through the batches laid?

(3) Is the viability of eggs diminished by storage; if so, do the conditions of storage as regards humidity affect the result?

(4) Is a change of temperature the adequate stimulus causing resistant eggs to hatch when dried and re-immersed, when transferred to fresh water or when fresh water is added to that in which they are already immersed?

(5) How long after impregnation can a female continue to lay fertile eggs?

(6) How many females can a single male impregnate and what percentage of the eggs of any one female will prove sterile after impregnation by a single male?

(7) To what extent can resistance and the tendency to defer hatching be induced by external conditions after incubation?

First Question. This, suggested by variations in the preliminary experiment, was answered by comparing the emergence rate when eggs of the same laying were exposed in large or small pans of water. The answer was not absolutely decisive. The cleanest experiment, No. 7 of the series, showed 94 per cent. hatched out of 94 eggs in the small pan, 86 per cent. of 98 in the large pan; an insignificant difference. Exp. 8 which gave 65 per cent. of successes of 200 eggs in the small pan, 80 per cent. of 200 in the large pan might seem strong evidence in favour of the large pan but a somewhat sudden fall of temperature which occurred during the experiment might have had a greater effect upon the small than upon the large pan. An interesting fact discovered in the course of this series of experiments was the great length of time which may elapse between the submersion of an egg and its hatching. In one series of experiments, the interval exceeded four months.

Second and Third Questions. The first experiment of the series (No. 9 of the Report) concerned batches of eggs laid by a single female; half of each batch were immediately immersed, the remainder stored for at least a month. Some of the batches were spoiled by the depredations of book lice, but in a clean controlled series 82 per cent. of immediately immersed eggs (244) hatched, 72 per cent. of deferred samples (242) eggs. Another experiment on eggs laid by several females gave a practical equality of hatching rates. 38 of 66 immediately exposed hatched; 42 of 78 retained in storage 39 days;

https://doi.org/10.1017/S0022172400008226 Published online by Cambridge University Press

percentages of 57 and 54. A third experiment when the storage time was increased to 82 days gave a much lower proportion: 137 of 197 immediately tested hatched, but only 51 of 196 stored. A fourth experiment where the interval was a month gave a balance of 12 per cent. in favour of the immediately immersed.

In view of the fact that there was no sensible difference between the survival rates of the first sixteen batches in Exp. 9, Bacot inferred that the answer to the first part of his second question was "yes" so that the second part did not arise. The answer to the third question was that long storage did increase mortality but that owing to the reduction of numbers consequent upon ravages of book lice (*Psocidae*) a precise measurement of the depreciation could not be made.

Question 4. Bacot divided a batch of some 1300 eggs into two lots; lot *B* was stored dry for 107 days, lot *A* immediately immersed. Of the latter, about 700—it was impossible to count them quite accurately—138 hatched in a week. The remainder were divided into two portions:

A′, about 420 eggs and shells, placed in a pan containing some of the water in which they had been immersed from the beginning of the experiment, were cooled in an ice chest to 74° F. Within 1½ hours 102 hatched.

A″, about 250 eggs and shells, in a pan of water were warmed in an incubator from 80 to 95° F. Only 2 hatched in the first 1½ hours. In 2½ hours—by when the temperature had again fallen to 80° F.—6 more hatched; in another hour 26 more hatched and a further 6 by the end of the day.

On the next day both *A′* and *A″* were put into the ice chest, 3 more of *A′* hatched and 15 more of *A″*. In other words, 104 of the *A′* set hatched in response to cooling, 25 per cent. of the total. Only 2 of the *A″* set hatched in response to warming but 53, about 21 per cent. responded to a fall in temperature. In both cases a fall of temperature was the effective stimulus; it seemed a matter of indifference from what point on the scale the fall began.

The residue of these batches and the whole set *B* were then treated with the results set out in the following table.

	March						April														
Lot	25	26	27	28	29	30	2	5	6	7	8	9	10*	11	12†	13	14	15	16	18‡	19
A 1 (cooled)	—	10	—	—	1	2	1	—	—	1	—	—	7	3	41	12	3	1	—	6	3
A 2 (heated)	—	1	—	—	—	2	—	—	1	2	—	—	16	4	23	3	—	—	—	1	3
B (stored dry)	109	15	16	17	6	—	—	1	1	1	2	1	32	22	3	5	3	—	2	4	5

* On 10th April, the eggs hatched within one hour of the *commencement* of the cooling.

† The second cooling on 12th April was slight, the fall being only 3 or 4° F., but it was long continued (it lasted five hours).

‡ *The third cooling on the 18th of April was for one hour, the fall was from 85 to 74° F.*

The answer to the fourth question was therefore unequivocal, that cooling was an important stimulus.

Questions 5 *and* 6. The experiments answering these (No. XLVI, p. 122 of the Report) do not illustrate any new point of technique, so it will suffice to note that six females in company with a single male which emerged on 25th Oct.

and died on 1st Nov. laid 1,139 eggs of which 753 hatched. One female which began to lay on 8th Nov. laid 110 eggs of which 55 hatched. The complete record of one of these females from 30th Oct. to 3rd Dec. was 837 eggs, 680 hatched. She laid 32 eggs on 3rd Dec., 28 of which hatched. A male which lived 21 days and kept company with 21 females was responsible for the fertilisation of 584 eggs hatched from 1,264 laid.

Question 7. 385 eggs were incubated in a moist chamber for 50 hours. 192 of these immersed immediately gave 189 hatchings within 30 minutes. From the remainder two dead, and one living larvae were extracted. The balance of the 385, 193, were dried. Upon the following day 168 remained—the others had been devoured by book lice. Of the remaining eggs 86 were immersed and 72 ultimately hatched, 18 within 24 hours. The residue, 82, were immersed seven days later; 35 hatched within 24 hours, 44 hatched in all. As Bacot wrote, the evidence is "so definite and conclusive, with regard to the determining powers of drought or humidity (subsequent to incubation) either to bring the resting habit into action or to allow it to remain latent that the only point remaining to be solved would seem to be whether the effect is invariable and relates to all eggs laid or if it is occasional only, related possibly to a seasonal change in the constitution of the eggs."

In answering this question, Bacot made another discovery of remarkable interest, that the hatching of eggs cannot normally occur in sterile water. Preliminary results are given in the Report (p. 51) but the whole matter is discussed in a subsequent joint paper by Bacot and Atkin from which I abstract the chief findings.

The general nature of the results is illustrated by the first protocol (Bacot and Atkin, p. 502) which I give in full.

First experiment. 100 c.c. of tap water was put into each of two glass pans. The water temperature during the course of this experiment was about 65–67° F. A batch of about 350 eggs laid on filter paper three weeks previously and allowed to dry after incubation, but stored in a moderately humid atmosphere, was divided into two lots, approximately half being immersed in each pan. To the water in one pan (*A*) was added 3 c.c. of sewage water (a fragment of human faeces was placed in water and allowed to incubate for 48 hours at 80° F), to the water in the other pan (*B*) nothing was added. After one hour in *A* 4 eggs had hatched, in *B* no eggs had hatched. After 4 hours in *A* 10 additional eggs had hatched in *B* no eggs had hatched. After 20 hours, in *A* 113 additional eggs had hatched, in *B* 6 eggs had hatched. After 70 hours in *A* 9 additional eggs had hatched. Total 136 eggs, in *B* 36 additional eggs, Total 42 (p. 502).

In a second experiment under like conditions horse dung was added to pan *A* and in 18 hours 148 eggs had hatched, in the control 11. Then pan *B* was contaminated and within 18 hours 159 more eggs had hatched in that pan.

More exact experiments were then performed. The eggs were sterilised externally by repeated washings in lysol and batches immersed in the presence of (1) horse dung, (2) a sterile filtrate of *Bacillus coli*; (3) 1/1000 solution of washing soda; (4) 1/1000 solution of ammonia; (5) a living culture of *B. coli*. All the eggs in (1) and (5) hatched within 68 hours, a majority of (2), few of (3) or (4).

Further experiments proved that living bacteria or living yeast cells were in general far more effective stimuli to hatching than either acidity or alkalinity in sterile media or sterilised bacterial or mycetozoal cultures. But it was found that autolysed cultures could provide an effective stimulus so that the presence of living cells although far the most effective was not an absolutely essential stimulus.

The development of larvae after incubation was studied in similar fashion; it appeared that the presence of living bacteria or yeast cells while not essential was so greatly more favourable than any other arrangement that it was probable that bacteria or yeast cells were in fact the normal food supply of developing insects.

From the merely utilitarian point of view, the results are of some importance, since they show that the ordinary methods of purification of water from bacteria will also be of service in the reduction of the mosquito population. As starting points of further research into the bio-chemistry of growth they are still more valuable and suggestive.

A very good judge, Prof. A. E. Boycott, thinks that it is by this beautiful research Bacot would wish to be remembered.

V. WAR WORK. THE BIONOMICS OF THE LOUSE.

Bacot's war work began immediately after his return from West Africa. He had been busy with lice for some months when he wrote to me (on Feb. 1st, 1916):

> I am still working out the lice, it is a slow *itching* drudgery but quite interesting in its way. I must say that I wonder the troops put up with it. I should scratch on parade but perhaps the men do. I saw an officer walking up by the barracks with his hands in his breeches pockets to-day. He turned in at the gate and only took one out—evidently we are progressing and shall win some small affair shortly. To return to the lice—on the western front, it appears to me a scandal that there should be any trouble; the whole of the people in the trenches ought to have clean underclothing once a week but if the washing of the garments is beyond the powers of the army organisation they should have new ones. I understand that the cost per man per year is about £300. For another £10 one could get a lot of new underclothing.
>
> I fancy it is nervousness of the idea rather than the expense is a difficulty. If it were a change of ammunition it would be done, and the absence of lice would make a lot of difference.

Bacot dealt with lice exactly as he had treated fleas and mosquitoes, he adapted his experimental methods to suit the subjects, he did not confine his experiments to those subjects which happened to survive some technique convenient for the experimenter. His wartime publications were numerous but mostly short practical notes. The fullest account of his work is given in a paper read by him to the Section of Epidemiology and State Medicine of the Royal Society of Medicine in 1918.

Bacot summarised the bionomic characters of lice which are of sanitary

https://doi.org/10.1017/S0022172400008226 Published online by Cambridge University Press

importance in the following propositions the truth of which he established by a long series of experiments.

(1) Eggs take seven to ten days to hatch under normal conditions, in clothing that is constantly worn; if clothing be discarded and allowed to cool for a period each day, the time of hatching may be extended to five weeks.

(2) Active lice can survive without food and apart from a host as long as nine days.

(3) Young lice attain sexual maturity in from 10 to 14 days.

(4) Females begin to lay within two to four days after attaining sexual maturity.

(5) Egg production cannot take place without food or when the temperature falls below 65° F.

(6) Virgin females cannot lay fertile eggs.

(7) A single impregnation is not effective for longer than 20 days.

(8) A female may lay from 10 to 12 eggs daily.

(9) As many as 300 eggs may be laid by one female.

Bacot considered that the most suitable method of lousing clothes was, wherever practicable, by exposure to dry heat; he found that exposure to 55° C. for 30 minutes was ample for the destruction of both nits and adults. He insisted strongly on the economic extravagance of various plans which, he once told me, were apparently inspired by the technic of the witches in *Macbeth*. The same thought is expressed in the following passage which I quote as an example of the improvement in literary expression which is evident in his later writings.

"I am rather labouring this point, because it is one of the peculiarities of the destruction of insects that economy of thought and extravagance in practice should be so general. The spirit which dominates the illustrations of Mr. Heath Robinson seems also to exert considerable control over the inventors of insecticides, whose common practice it is to endeavour to raise the general efficiency level of their preparations by complexity in combination. The following, though possibly somewhat flamboyant, is a not unfair illustration of the process: 'Kummerfeld's wash is useful, and is prepared as follows; Twenty parts precipitated sulphur are incorporated in a mortar with fifty parts glycerine; two parts of camphor are separately ground with fifty of Eau de Cologne, and twenty of borax and 870 parts of distilled water are added; the whole is mixed together, and three drops of an extract of musk are added; shaking in order to prevent the sulphur from settling down; fifty parts of ether are added to the mixture.' This principle pervades a large proportion of the pre-war remedies, and some of the recent ones, and has even crept into the work of scientific importance. For instance, it was remarked by one experimenter that cyllin water when cool was not effective, but became so when heated to 60° C; yet it had already been pointed out in his own paper that dry heat at 60° C killed the nits."

Bacot devised a method of accurately testing the efficiency of insecticides and employed it in a long series of experiments. His apparatus consisted of a body belt upon the body side of which lice were imprisoned in gauze pockets at assigned distances from a pad impregnated or dusted with the insecticide. The prisoners could feed on his body and the percentage mortality when the distance of the prison from the depot of insecticide was varied gave a quantitative scale of efficiency. He concluded that, for all practical purposes, every insecticide only acted by contact. For the impregnation of garments, crude carbolic emulsified in soft soap was the most efficient agent. He found that in the summer a shirt treated with a 5 per cent. solution of the emulsion, *i.e.* containing $2\frac{1}{2}$ per cent. carbolic was efficient for five days. During the winter a like efficiency was attained by impregnation with 10 per cent. of the emulsion, *i.e.* 5 per cent. carbolic. An average sized shirt having an area of some 1600 square inches would take up about 1000 c.c. of fluid and retain 500–600 after wringing. Thorough drying before use was of course essential and flannel so treated could be stored at least 15 days before use without deterioration.

The drawback of the method was its slow development of efficiency. Of quickly acting remedies, napthalene proved the best. Being readily soluble in benzene, paraffin, or, most important of all, oil, it could be used to impregnate garments; at a concentration of 10 milligrammes per square inch—about 16 grammes to a shirt—it killed all lice present within three hours when used as a powder, but lost its efficiency within five hours; thus it should be used in conjunction with an emulsifying agent.

In war time, the authorities received a continuous supply of worthless specifics from both knaves and fools. Bacot, as honorary consulting Entomologist to the Army Medical Department, was able to prevent a good deal of waste of money and more disappointment. Some of these incidents had their comic side. One concerned a preparation which I will call Jericho powder. It seems that the War Department had come into possession—whether by purchase or benevolence—of a large supply of Jericho powder, and a sample was submitted to Bacot for examination in the routine course. He reported that it was inefficient. Then he received a sample of Jericho powder modified by the addition of a small percentage of napthalene; this was rather better but not nearly as good as neat napthalene. Successive samples containing more and more napthalene were forwarded until Bacot—grudging the time involved in the testing process—made the suggestion that, in view of the heavy demands upon the Army Service Corps, the best plan would be to send napthalene and Jericho powder to France in bulk, to retain a dump of Jericho powder at the base and to send on the napthalene to the trenches. I think he had no more samples of modified Jericho powder to assay.

The other case may be given in his own words.

"Two trials were made with the *Kergold anti-vermin body belt* for which the suppliers made the following claims: 'Perfect immunity from all insect pests. The Kergold is the only belt that affords instant and permanent relief from the bane of the soldier on active service. Vermin simply cannot exist when the Kergold anti-vermin body belt is worn; protects the wearer from head to foot. Total immunity from all further attacks. The medical properties of the belt last for approximately six months.' The first trial gave results so greatly at variance with these claims that a second belt was purchased in order to avoid the risk of the first one being a 'bad egg.' In the first series of trials the lice were confined in gauze pockets fastened to the shirt so that the insects could feed during the course of the test.

In all, eight pockets were placed at varying distances above and below the belt, from the neck to the thighs; during the course of a continuous twenty-four hours' trial the only lice which died were a few in one of the pockets on the upper part of the chest, apparently from pressure of the braces. In the second trial much trouble was taken to wear the belt before trial and to induce a perspiration by work in a hot room at 97° F. Four gauze pockets containing lice were suspended within an inch of the belt and most of the insects fed heartily at intervals during a twenty-four hours' test. After this period it was found that out of sixty lice nine were dead, four were feeble, while forty-seven were active. While conceding the possibility that the dead and feeble were due to the action of the belt, I incline to the view that they were overlaid during sleep.

After the belt had been continuously worn for sixty-two hours another test was carried out. After twenty-four hours there were three dead, two feeble and twenty-nine active lice in the pockets. The belt was then worn for a further period, and after five days' continuous wear it was given a last chance. After a twenty-four hours' trial, during which many of the insects fed heartily, one was dead and twenty-nine were active, including one pair 'in copula.'"

Most of Bacot's time between 1916 and 1918 was devoted to the subject of the prevention of lousiness, but before the end of the war he had begun work upon the specific aetiological rôle of the louse, in disease transmission. In the first instance his attention was specially directed to Trench Fever; from 1919 to the end he specialised on Typhus. In the following chapter, Dr Joseph Arkwright describes this stage of Bacot's career.

VI. TRENCH FEVER AND TYPHUS.

By J. A. Arkwright.

By the autumn of 1917 the seriously reduced efficiency of the British Expeditionary Force in France as the result of Trench Fever had become sufficiently recognised to bring about the appointment of a War Office Committee to investigate the cause and prevention of this incapacitating epidemic.

Since MacNee first described Trench Fever and showed it to be an infective disease in the spring of 1915, suspicion had fallen on lice as the transmitting agents. The plague of lice was still on the Armies in France in 1917 and so far no effectual means had been taken to subdue it.

At last then the needful means for dealing with the matter were attained and in addition to a well organised hospital for trench fever cases at Hampstead with a well equipped clinical department, the laboratory side of the subject was attacked more seriously and above all the need was realised of a skilled entomologist able to undertake with knowledge and experience the management of lice in captivity and under experimental conditions.

Bacot as explained in the last chapter had made himself an expert in dealing with these elusive and, in captivity, delicate insects. An immense amount of time, thought and trouble had been given by him to finding out the best methods of handling, keeping, feeding and breeding, and maintaining an adequate stock for experimental purposes of these agelong intimates of mankind, the biology of which very few had attempted to study before the war.

Bacot, undeterred by the disagreeable and irksomely frequent needs of his subjects, devoted himself to the task and, with unfailing regularity provided fresh stocks as required, carefully graded as to age and not open to doubt as to their uniformity of race and freedom from disease. These he had fed and reared on his own blood under definitely known conditions. Not only did he thus provide an absolutely essential element for the W.O. Committee research, but he gave unstintedly help, advice and stocks of lice to workers in other places including the American Committee in France.

To the uninitiated it may seem that the public service of providing a supply of normal lice for research was a matter which could have been easily performed by any unskilled assistant. That was not the case, though later as the technique became surer it was possible to get much help from specially trained careful laboratory assistants. The devotion, knowledge and skill needed to have at hand for experiments a large number of healthy, young lice all of approximately the same age and carefully confined in suitable boxes, were attained to by very few to anything like the degree reached by Bacot. Many have tried and failed. In the care of the untrained in spite of advice the lice invariably died. To the ignorant or selfishly fastidious such personal devotion may not appeal.

Besides his work for the W.O. Committee, Bacot gave much help and advice to sanitary and school authorities who rightly dreaded the extensive introduction of lice into England by soldiers from the trenches. Though he was always ready to do all he could to help schemes for stemming an invasion by vermin and was not by any means blind to the unpleasant or even dangerous possibilities, Bacot expressed the opinion that so long as the economic conditions of the general population were not seriously depressed and the housewife was able to maintain the weekly wash, body lice would not be able to get a hold in the family to any serious extent.

During the investigation Bacot at first spent much time going to the New End Hospital at Hampstead where Major Byam and his staff were working at the clinical side of trench fever. He also put in long hours of work at the Lister Institute, Chelsea, making detailed dissections and examinations of lice as well as continuing his disinfection experiments with chemical substances and methods reputed to destroy lice and de-infest the men in the trenches. At the same time he usually had at least one other entomologist working in his room to whom he gave ungrudging help. Soon after the Trench Fever Committee had been formed, Capt. Peacock, the entomologist who was working at Hampstead, returned to France and Capt. Lloyd took charge of the work at the hospital, while Bacot maintained control and gave much help.

The result of Bacot's skilled entomological work was soon apparent and with his assistance exact experiments of different kinds became possible, which could not have been undertaken before. His careful system of numbered boxes of lice and his knowledge of their needs—how often, and for how long they must be fed, how best they should be applied to the skin, at what temperature and at what degree of moisture they should be kept between feeds in order

https://doi.org/10.1017/S0022172400008226 Published online by Cambridge University Press

that they might be maintained alive and active—these and many other points of detail were most valuable practical contributions to the advance of the investigation. The best methods of rapidly increasing the stock or keeping down the numbers by varying the frequency of the feeds and the temperature at which the insects were kept, without wasting time by unnecessary sorting and manipulation, had only been learnt by continuous care and observation; information as to the extent to which with proper precautions feeds could be omitted for any reason was an important factor in the success of the experiments. The energy and organisation of Major Byam and the generosity of the Lister Institute brought to use the self-sacrifice of a number of volunteers, and, by experiments with lice which had been previously carefully fed on trench fever patients, it was shown that the virus was contained in the bodies and excreta of these insects, and that it could reproduce the disease in man. Simultaneous work by the American Committee in France led to similar results. It was also established that the easiest and probably most frequent manner of transmission from man to man in the trenches was the inoculation of louse excreta into small skin lesions.

The high state of concentration in which the virus was found to exist in the excreta of lice a definite time after they had fed on a trench fever patient opened the way to the investigation of many further problems. Microscopic examination of the excreta and the lice showed that both contained the *Rickettsia* bodies characteristic of the disease and Bacot threw himself with zeal into the study of the conditions needed to ensure the appearance of these bodies in lice, and of their exact location in the insect.

The latter question he elucidated by laborious microscopic dissections and sections of the lice cut with a microtome.

This work went on till in 1919 the end of the war and the establishment of less arduous conditions in the army brought trench fever as a recognisable infective disease to an end. Among other problems tackled was the question of heredity in the louse of the virus and of the *Rickettsia*. This appeared to be settled in the negative sense. Whether larvae and nymphs could become infected and whether the *Rickettsia* appeared in them as in adults were answered by showing that the age of the lice was not a condition controlling the development of either virus or *Rickettsia*.

As may be imagined the labour which all this entailed was considerable. During this period Bacot was working early and late and can only have spent very few hours out of the 24 at Loughton. His eagerness to leave no part of his share of the work undone and indeed to think of more tasks in connection with it were a constant source of surprise and admiration to his colleagues. No amount of work that he could do nor time that he could spend in furthering the investigation seemed too much. His nights must have been short and his meals were often taken when and where he could find time to eat apples, biscuits and chocolate which he carried with him.

In December 1918 fresh problems presented themselves to him. The resemblance of typhus fever to trench fever in the apparently exclusive part taken by lice in the transmission of the two diseases and the reported similarity of the visible accompaniments of the virus in lice led naturally to an attempt to throw light on this disease also. The presence of typhus at that time in the north of Ireland enabled the Lister Institute workers to procure some infected lice. Monkeys and subsequently guinea-pigs were infected and feeding lice on infected animals was undertaken with enthusiasm by Bacot. His aim in these experiments as in those connected with trench fever was to obtain as accurate results as possible.

Lice were therefore used in limited numbers, about 20, in each box, so that each louse came under his supervision. The number of males, females, nymphs or larvae was recorded, and the number dying daily with the results of dissection of those found dead or killed were noted. Difficulties of detail arose for which he was on the watch and which he was often successful in overcoming. One difficulty was the reluctance of human lice to feed on a monkey, and it was soon found that they did not readily suck monkeys' blood through the gauze covering of the boxes but had to be let out to browse free on the skin. This entailed a long and vigilant watch over the feeding flock and much care lest they should stray too far and escape. The risk from escaped lice was thoroughly recognised. In spite of all his care there was always a large mortality among lice fed on monkeys.

Bacot was able to establish several interesting facts during those trying hours of feeding. He had shown before that head and body lice could equally well be infected with *Rickettsia quintana*, the species associated with trench fever, and that both were capable of transmitting this disease. He now found that *Pediculus capitis* was better suited to feeding on the hairy skin of the monkey than *P. corporis* and was therefore a much better stock with which to conduct experiments on monkeys. It was also shown that both the forms of *P. humanus* could be infected from a monkey both with typhus virus and the associated *Rickettsia* (*R. prowazeki*). One louse with these contents was a sufficient dose to infect a guinea-pig or *Macacus rhesus* when inoculated subcutaneously. In the course of the work it was found that macaques when infected and ill with typhus, often became infested with swarms of a small louse peculiar to the monkey, *Pedicinus longiceps*, though few if any of the vermin were to be found when the monkey was in health. Bacot was intensely interested in all the phases of parasitism and these occurrences afforded him much food for thought. He translated his observations on the monkey into terms of probable human experience and infestation. His reflections and deductions from the facts were often original and quaint and were suggestive of equal sympathy with the insect and the host.

The monkey lice taken from a *Macacus* ill or dead of typhus proved to be infective for a fresh monkey and also to contain *Rickettsia* very like and apparently identical with those found in *P. humanus* infected with typhus. This made a new and to Bacot fascinating line of research which was laborious and difficult and moreover limited by time and the supply of monkeys. The *Pedicinus* did not lend itself to culture in boxes like *Pediculus humanus*, but one consolation was afforded by its refusal to bite human beings.

The typhus problem presented many puzzles and Bacot's active mind well stored with insect lore was constantly at work endeavouring to visualise the behaviour of the virus in the insect vector and the reaction of the insect to it, and speculating how far the virus was in true symbiosis with the louse and how far pathogenic to it; whether the cycle of louse to man and man to louse was likely to be continuous or interrupted, and how far the effect of different seasons on the interaction of virus and louse and louse and man was sufficient to account for lacunae in our knowledge of the epidemiology. He searched with great care and diligence for microscopic evidence of the infection of the mouth parts, salivary glands and other organs of infected lice, in order to throw light if possible on the actual method of transmission to man, but no evidence of this was forthcoming to encourage the belief in infection by the bite. The even more important question of the possibility of transmission of the virus from one generation of lice to the next through the egg appealed to him still more strongly. He examined the fluid of the body-cavity, the ovaries, eggs and unhatched embryos with great skill and patience, and he believed that he had found indications that *R. prowazeki* might infect the egg. The evidence was not sufficient to satisfy him completely, though it tended to confirm the scanty evidence of occasional transmission of virus from adults to their offspring brought forward by others.

Bringing his experience and success in rearing and keeping other insects to bear on the work, he endeavoured to infect the bed-bug (*Cimex lectularius*) with typhus and we were at first surprised and interested to observe bodies in many ways very like *R. prowazeki* in bugs fed on typhus animals. This was soon found to be a *post* and not a *propter* sequence for in all specimens of this species of *Cimex* examined the same form could be found if diligently searched for. The bugs after feeding on typhus animals were moreover not infective for guinea-pigs. This refutation by Bacot himself of the suggestion that bed-bugs were perhaps capable of harbouring the typhus virus, founded on the first observations of typhus-fed *Cimex*, brought no reaction in his mind leading to the neglect of this interesting association, as it probably would have done to his colleagues.

He immediately saw that a study of this form in bugs might be a help to the understanding of the relation of other kinds of *Rickettsia* to their insect hosts and eventually to the associated diseases of mammals. The infestation of *Cimex* proved an interesting one, for this *Rickettsia* (*R. lectularii*) was found to occur in both coccus-like and thread forms as was subsequently shown to be the case with *R. prowazeki* in lice, and it also resembled the latter parasite in that it was found in large numbers inside certain cells of the alimentary system. In the case of *R. lectularii* the cells infected are those of the malpighian tubules, whereas *R. prowazeki* inhabits the cells of the gut itself.

Bacot further pursued the subject and found that the body-cavity, organ of Berlese, ovary, eggs and embryos are often infected with the *Rickettsia lectularii* and that this latter is undoubtedly passed on from parent to offspring through the egg.

In the spring of 1920 Bacot was asked to join the United States Red Cross expedition to Poland to investigate typhus, the American entomologist who was to have gone being prevented from accompanying his colleagues. Bacot fully realised that the work and especially the handling of typhus lice would be risky and especially so to a man of his years, but he did not hesitate a moment on this account and enthusiastically began to plan the procedure best calculated from the entomological point of view to advance the knowledge of typhus, and to consider how to obtain the best results with the least danger to his colleagues and himself.

In considering the risks which he readily incurred at this time and subsequently, it must be remembered that he was not a medical man and therefore not accustomed from his youth to look upon association with disease as part of the day's work; nevertheless his contempt for a safe life at the sacrifice of progress in knowledge was complete.

The journey and time spent in Poland were full of novelties in which he took a deep interest from many points of view. The climate, vegetation, manners and customs of the people all fed his imagination and his thirst for new facts.

He found the opportunities for research rather more confined than he had hoped, but was able to do some good work dissecting and examining lice, and was filled with admiration for the work of Prof. Weigl who was at that time working at Warsaw. Though their means of communication were limited owing to the language difficulty they were able to exchange information. Weigl showed Bacot the remarkable technique which he had devised for infecting a louse with typhus virus and subsequently feeding the insect by injecting blood into its gut *per anum* through a very fine pipette. Bacot took up the method with enthusiasm, made his own minor modifications in the technique and by this means was enabled to continue his work on typhus in England. The great obstacle to work at home which this method overcame was the difficulty in finding a host on which to feed typhus-infected lice, since human lice throve badly when fed (with considerable difficulty) on a monkey, and could not be nourished on other laboratory animals, while human immune typhus convalescents were not available in London. Bacot attained great skill at this technique and was able to give an infecting feed to lice, and thereafter give them two feeds daily, all by means of a pipette, and to keep the insects alive in some cases for over 20 days. At the end of a prolonged period of artificial feeding only a few out of the initial number of infected lice had survived; some succumbed to the intense infection with *Rickettsia*, some to bacterial infection, and a few to injuries received during the feeding operation. Even under the most favourable conditions normal lice fed in the natural way did not as a rule live longer in boxes than about 30 days (average 27–34, maximum 46 days).

This amazing and spectacular technique required much skill and patience, but fine manipulations were always attractive to Bacot and in them he excelled.

The work in Poland was unfortunately shortened by an attack of trench fever, which he apparently acquired whilst examining lice from persons believed to be healthy or at any rate not suffering from nor associated with typhus fever, as far as could be ascertained. Some of these lice examined between the 31st March and the 5th April had been found by Bacot to contain *Rickettsia* exactly like those found in England in lice fed on trench fever patients. On the 17th April he had a sharp attack of fever and was removed to hospital on the suspicion of typhus fever, but his temperature fell to normal in two days and then he had two or more characteristic relapses. Normal lice which he was feeding on himself before and during illness excreted no *Rickettsia* till the 27th April, when *Rickettsia* began to appear in the excreta, and thereafter lice which he fed on himself yielded microscopic *Rickettsia* on and off for nearly four months. These observations and the preparations from these lice were made by Bacot himself at the time or from material set aside then and examined as soon as he was able to return to the laboratory. Some of these films are still extant and show typical *R. quintana*. Bacot published an account of his illness in the *British Medical Journal*, 29th Jan., 1921, and the lesson to be drawn therefrom, that a disease like trench fever may exist without being recognised in a louse-infested population is pointed out in his paper. He was very much impressed by the inertia and mental depression induced in himself by this illness and he described with something like awe the disinclination for work which he felt as a sensation which to him was new and strange. This experience elicited from him renewed sympathy for the soldiers who during the war had been deprived of energy and efficiency by what often seemed a trivial illness to onlookers and consequently procured for them little consideration.

After his return to London Bacot was able by means of the new technique learnt from Weigl to enhance enormously the evidence of close association of the typhus virus with *R. prowazeki*. After the virus had been passed through a number of guinea-pigs, a monkey and then another guinea-pig in series, he injected a number of lice *per anum* with minute quantities of blood from the last guinea-pig in the series and was then able to demonstrate the presence in them of virus and *Rickettsia*. After a suitable incubation period the presence of the virus was shown by inoculating one of these lice into a guinea-pig and the *Rickettsia* were demonstrated microscopically.

In 1921 he worked with Dr Ségal on the question of the virus of typhus being especially closely associated with the platelets in the blood of man and other mammals. The attempt to render lice infective by injecting them *per anum* with a thick emulsion of platelets was very successful. Previously Bacot

https://doi.org/10.1017/S0022172400008226 Published online by Cambridge University Press

had tried to infect lice in this way with the blood or brain of typhus guinea-pigs, but the results had been uncertain and only successful in a small proportion of the insects used. By the use of platelets from infective blood a sure infection was obtained and with the experience which Bacot had now acquired failure on account of bacterial infection and consequent death of the lice was a much rarer event.

After many observations he came to the conclusion that bacterial infection of the gut of a louse was usually rapidly followed by its death. Three sets of observations helped towards this conclusion:

(1) The early examinations by means of films of the contents of lice without much attempt at the segregation of the parts had given the impression that bacteria were often present in large numbers inside the normal louse, but careful dissection and examination of the separate organs led Bacot to the conclusion that few if any bacteria were ever to be found in the healthy internal organs including the alimentary canal. This was confirmed by the examination of numerous sections. An explanation of the first observations of numerous bacteria in the films was found in the existence of a constant infection of the sheath of the penis with masses of a large bacterium (*B. pediculi*) which appeared to be constant in its characters in strains derived from different lice.

(2) Lice sometimes died or were found in a very feeble condition a day or two after anal feeding by a pipette and were then almost invariably found to contain many bacteria in the gut. An improved aseptic technique much reduced this cause of death.

(3) It was the view of Friedberger, and an almost identical hypothesis was accepted by Weil and others, that the virus of typhus was identical with the *O* form of *Bacillus proteus* X 19 which had given such remarkable and uniform agglutination results with the blood of typhus patients. The injection of lice *per anum* with this bacterium appeared to be a way of testing this hypothesis, and Bacot made several attempts to produce a lasting infection of lice with this strain of *proteus*. All these experiments led to a massive infection of the gut and the early death of the insects, although very small doses of a weak bacterial emulsion were administered and the effect was tried of keeping the lice at different temperatures after the injection. The results gave no support to the suggestion of identity of *B. proteus* with the virus of typhus or *R. prowazeki*.

Bacot gave much time to the study of the morphology of *R. prowazeki*, and finding that he could obtain a certain and unusually severe and rapid infection of lice with *Rickettsia* by injecting them *per anum* with a minute quantity of an emulsion of the gut of a previously infected louse, he adopted this method of culturing *in vivo* as a source for his microscopic preparations.

The lice infected in this way had subsequently to be fed twice daily by the same fascinating but laborious technique. In the material obtained in this way he found a great variety of forms of *Rickettsia*. Of these he retained an accurate recollection and made many drawings, hoping to be able to throw light on the nature of these parasitic microbes and endeavouring to link them up with certain forms which he had seen in blood films from human patients and typhus guinea-pigs. How far the hints and suggestive appearances which he detected in blood films are really related to phases of *Rickettsia prowazeki* under different conditions, he never obtained sufficient evidence to decide.

All this time he was framing and trying to test hypotheses of the origin and phylogeny of the different kinds of *Rickettsia* and their relations to their hosts, and was tracing analogies with other insect parasites. These speculations led him to obtain and examine other species of *Cimex*, lice from other animals than man and monkeys, and the wingless blood-sucking flies (*Melophagus* and *Stenopteryx*) parasitic on sheep and birds. Much of this work demanded considerable energy and enthusiasm in order to obtain the insects, breed, rear, feed and dissect them, in addition to his other work, and was left in a very imperfect state, but it constantly suggested fresh views of the subject to his eager mind.

In 1920–21 Bacot became especially interested in *Rickettsia melophagi* which infects the intestinal canal of the sheep ked, *Melophagus ovinus*, and is apparently "hereditary" being passed on from the parent insect to the offspring through the egg. The ked is in some respects not quite so satisfactory as a host in which to study *Rickettsia* as the louse, since in the case of the former insect there is no known mammalian condition correlated with the presence of *Rickettsia* and all adult keds appear to be affected; moreover cultures of the *Rickettsia* could not be obtained though Noller had previously reported success in this direction. Observations therefore could only be made by dissecting and examining the parts of the ked at different stages of its life. The results nevertheless were interesting and unexpected. Strong evidence was obtained that in the hind-gut of the adult insect and in the mid-gut of the newly emerged adult before it had sucked blood, forms of the *Rickettsia* occurred which were much larger and more like a wide bipolar staining bacillus than the usual minute forms. These observations interested Bacot very much because he believed that he had seen somewhat similar forms of *R. prowazeki*, but only rarely, and had been unable to identify them with certainty. He hoped that eventually the life-histories of *R. melophagi* and *R. lectularii* would throw much light, from the point of view of ontogeny and phylogeny as well as epidemiology, on *R. prowazeki* in the louse infected with typhus. His ideas on the origin and degree of parasitism of the different kinds of *Rickettsia* were continually being turned over in his mind and modified by fresh evidence. He tentatively regarded the species of *Rickettsia* as parasites originally derived from the mammalian host and adapted in different degrees to the special blood-sucking insect. *R. prowazeki* was probably a relatively recent acquisition by the louse since it damaged the gut of the host and probably often caused its death, but *R. quintana* was better established and did not harm the host since it merely inhabited the lumen of the gut. *R. melophagi* and *R. lectularii* had

https://doi.org/10.1017/S0022172400008226 Published online by Cambridge University Press

become thoroughly adapted as symbionts causing no serious harm and infecting generation after generation through the egg without the need of a mammalian intermediary. These views never reached in his mind sufficient definiteness for him to express them in print, but he was always on the look out for facts for or against these hypotheses, and they serve to show the bent of his mind. The possibility that the resemblance between different kinds of *Rickettsia* was only superficial was not forgotten.

During 1921 experiments by Bacot and Atkin with the excreta of lice feeding on a typhus monkey gave results which were taken as evidence against the infectivity of such excreta. This was perhaps unfortunate since the negative results biassed the experimenters against the likelihood of man being infected by similar material. It may be mentioned however that attempts to infect by the bites of infected lice were also negative and Bacot was sceptical about the direct transmission by the bite as the result of his examinations of the head-parts etc. of infected lice by dissections and sections and also because of the previous experiences of the English workers with trench fever lice.

In November 1921 the invitation came from the Egyptian Government to spend five months in Egypt working at typhus in a well-equipped laboratory in Cairo with the expectation of an abundant source of typhus virus in the fever hospital and the probability of assistance from typhus convalescents in feeding infected lice. It seemed a great opportunity to investigate doubtful points under more normal circumstances and with fewer obstacles, to examine more thoroughly the development of *R. prowazeki* in lice and to gain more exact information about the relations of lice and *Rickettsia* to the epidemic. He accepted with alacrity and the present writer who went with him as a colleague had the advantage of his skill, knowledge and comradeship.

Bacot arrived in Egypt on the 5th of February and started work next day at the laboratories of the Public Health Department full of energy and enthusiasm. Dr Charles Todd the director and all his staff gave every possible assistance, the laboratory was well appointed and all promised well. Dr Sami at the Abbassia Fever Hospital also helped in every possible way. It was strange that in the early part of 1922 the cases of typhus in Cairo were very few and instead of hundreds of cases being admitted to hospital as often happened there were barely ten. However, two cases were admitted in February and from them a supply of virus was obtained at the laboratory and work was soon in full swing.

Whilst waiting for typhus material an attempt was made to sample the pediculi from the poorer inhabitants of Cairo by obtaining lice for dissection from a number of labourers, etc.

This enquiry and the work on typhus-infected lice and laboratory animals was stopped by the illness of both the workers, but such observations and experiments as there was time to make have been recorded elsewhere (Arkwright and Bacot, IV. 1923). Amongst other lines of research the question was again taken up whether the excreta of typhus lice contained the virus in an

https://doi.org/10.1017/S0022172400008226 Published online by Cambridge University Press

active state and as a result there was no doubt that the excreta of lice infected by Bacot *per anum* were highly infective for guinea-pigs. It therefore seemed highly probable that the excreta of lice fed naturally on typhus patients would also prove active. Nicolle had affirmed the infectivity of the recently passed excreta of lice in 1914 and again called attention to his experiments in 1921, though Rocha-Lima and others had failed to infect guinea-pigs by the inoculation of similar material.

There seemed therefore to be need for further experiments with excreta. The handling of a number of boxes containing typhus lice in order to allow the insects to feed on an immune typhus convalescent and the collection of the excreta from them was a necessary part of the work. Moreover Bacot was not satisfied to treat a box of lice as a whole but, as often as time permitted, he removed the gauze covering from each box, counted the survivors, and removed and dissected the dead or sick lice, in order that as much as possible should be learnt of the progress and the extent of the *Rickettsia* infection in the lice. I well remember his distress at the suggestion that some work should be undertaken that he thought would hinder the finer entomological part of his research, *i.e.* careful dissection of all the lice, etc. It seems almost certain that he himself became inoculated with a minute quantity of the excreta of lice through a small scratch or abrasion of the skin or possibly through the conjunctiva or nasal mucous membrane. In spite of continual watchfulness he had been unable to detect any escape of infected lice, but the contamination with excreta of the fingers could not be altogether avoided.

On Sunday 26th March he had a headache with a rise of temperature to 99° F. and felt poorly; on the next day he maintained that he felt very well and insisted on going to the laboratory where his temperature was found to be 101·6° F. The onset of his illness was rather unusually gradual but he was decidedly ill on the 29th and went to the fever hospital on the 30th. He appeared to be quite conscious till the 4th April on which day he made a partially successful effort to read a letter. His enquiries whilst in hospital were almost entirely about the progress of work at the laboratory. His attack of typhus was of a severe type but on the 7th April the temperature fell about 2° F. and remained between 100° and 101° F. and hopes were entertained of his recovery. Nevertheless his temperature never quite reached 99° F., the lung complications became worse and he died on 12th April.

The failure to rally after a definite crisis caused intense disappointment and sorrow to his friends and to Dr Sami, the medical officer in charge of the hospital, who had spared no trouble in his attendance and whose skill and experience in dealing with typhus cases was very great.

Bacot's intensely active life was ended in the midst of work into which he had put his whole heart and mind. Entomology was his hobby; the problems connected with the study of insects and ingenious methods for solving them were his pastime. The harnessing of entomology to the use and advance of human society was to him a great achievement—the realisation of a high ideal and the fruit of the labours of a long line of entomologists past and present. He worked as hard as it was possible to work in order to fulfil, as far as might be, his ideal of human aim.

His interests were by no means confined to entomology. He had definite ideas and convictions as to the course which should be taken for the reform of Society in several directions. He was inclined to be pessimistic in his views of the ways of the world and especially of politicians, but his pessimism was of that amiable sort which, whilst distrustful of many human agencies, almost always saw the best side of and made excuses for those human beings with whom he came into immediate contact.

Though latterly he did not find much time for reading he had a keen appetite for any knowledge of human sociology ancient or modern. For this reason as well as on account of their inherent beauty he was enthusiastic about the art, monuments and tombs of ancient Egypt for which he spared a few hours as recreation. He displayed a surprising amount of information, learnt mostly in past years, about archaeology and ancient and modern human customs and beliefs.

In this subject as in his entomological work he loved to ponder over and try to connect into a consistent whole the fragments which he saw and of which he read.

As a colleague he was always loyal and considerate and anxious to help in any way. The chief difficulty in working with him was that of trying to keep pace with his amazing activity of mind and body.

He had no jealousy in his composition and his chief anxiety in publishing accounts of his work was to give recognition to the right person, and as far as his own contributions were concerned to see that any credit due should be given to him as a member of the staff of the Lister Institute rather than as an individual.

VII. THE LAST JOURNEY.

In the preceding chapter Dr Arkwright has described the scientific work which occupied the last years of Bacot's life, there only remains to add a few words on personal aspects. Bacot suffered not less than the rest of us from the post-war reaction; he had never indeed cherished dreams of a new heaven and earth to follow victory, but his temperament was not that of the prophet who can draw comfort from the fulfilment of his forebodings. I think he suffered much and his comments upon public affairs were bitterer than before. But he was not unhappy, for he never lost the key of fairyland given him in 1911.

His visit to Poland in 1920 was not, for various reasons, including an attack of trench fever, an agreeable one; his last journey began under happier auspices. His letters from shipboard were in his earlier vein, the voyage down the Mediterranean delighted him; the laboratory and colleagues at Cairo were thoroughly congenial and the last letter I was to have from him the most cheerful of all. It was written with the knowledge that a serious cause of anxiety had been lightened. That letter was written on 24th March, 1922;

within a few days he was taken ill; an oblivion soon followed—in his delirium he spoke only of the research; on 12th April he died. His body was carried to the grave, in the British Cemetery of Old Cairo, by his friends and colleagues from the laboratories, both British and Egyptian.

In this memoir two friends have attempted to describe some of his positive contributions to knowledge; the reader will agree that they were important contributions. We have failed to paint a worthy picture of a man who was greater than his work. He cannot live for future generations as John Ray and Gilbert White live; he has left behind no book which will charm by its literary quality after the discoveries it records have become incorporate in the general stock of knowledge. But his personal influence will not die with him. Those who worked beside him and loved him will often be restrained in moments of petulance by a memory of some act of kindness, by a recollection that a great researcher could be as selfless as a child. Any scientific man tempted to measure his own services against their rewards in income or fame, may pause to think how little made this man happy. From Bacot's small circle of intimate friends, the same influence will pass, diluted and weakened, but not destroyed, to others.

...Though much
Will have been lost—the help in strife,
The thousand sweet, still joys of such
As hand in hand face earthly life—
Though these be lost, there will be yet
A sympathy august and pure
Ennobled by a vast regret,
And by contrition sealed thrice sure.

VIII. BIBLIOGRAPHY.

A. W. Bacot's Scientific Contributions[1].

1893–1910.

General Entomology.

Series A. Titles extracted from The Entomologist's Record.

(1893). Variation of the Larvae of *Saturnia carpini*, IV.
(1895). Perils of Egg Life, VI.
„ The Genus *Smerinthus* (a paper read before the City of London Entomological and Nat. Hist. Society), VI.
(1896). The Relationship of *Endromis versicolor* to the Sphingides, VII.
„ Notes on the Breeding of *Psilura monacha*, VII.
„ Notes bearing on Heredity, VII.
„ Notes on the Genus *Smerinthus*, VIII.
„ Notes on the Life-history of *Papilio machaon*, VIII.
„ Notes on the Early Stages of *Enodia hyperanthus*, VIII.
(1897). Notes on the Early Stages of *Epinephele ianira*, IX.
„ Notes on the Cocoon and Pupa of *Saturnia pyri*, IX.

[1] We are indebted to Professors Martin and Ledingham for permission to use the bibliography compiled for them and printed in the *Brit. Journ. of Exp. Path.* III. 121.

https://doi.org/10.1017/S0022172400008226 Published online by Cambridge University Press

ARTHUR WILLIAM BACOT

1866—1922

https://doi.org/10.1017/S0022172400008226 Published online by Cambridge University Press

(1897). On the Trapezoidal Tubercles of *Saturnia*, IX.
„ Note on the newly-emerged Larva of *Polygonia egea*, IX.
„ On the Development and probable Origin of certain Ocellated Spots in the Larva of *Lasiocampa quercus* and *Odonestis potatoria*, IX.
„ On the Caudal Horn of *Agdistis*, IX.
(1897–8). Notes on the Hybrid *Smerinthus populi-ocellatus*, IX, 1897, continuation in X.
„ The Larvae of certain Geometrides, X.
„ The British Liparid Moths, X.
„ The Origin of the Stemapoda of *Cerura*, X.
„ Notes on the Larvae of *Tephrosia bistortata* and *T. crepuscularia*, X.
„ Notes on Hybrids obtained by crossing *Tephrosia bistortata* and *T. crepuscularia*, X.
„ Collecting on the Broads, X.
„ Position of Egg laid by *Sphinx ligustri*, X.
(1899). Contribution to the Life-history of *Tinea vinculella* var. *leopoldella*, XI.
„ On the Relationship of the Lepidopterous Pupa to its Larva, XI.
„ Contribution to the Life-history of *Psyche zermattensis*, XI.
(1900). Newly hatched Larvae of *Erebia ceto*, XII.
„ Vitality of *Smerinthus ocellatus* bred in Confinement, XII.
„ Eggs of Lepidoptera, XII.
(1901). Weismannism and Entomology, XIII.
„ Larvae of *Lasiocampa quercus* and its vars. *callunae* Palm., *viburni* Gn., *meridionalis* Tutt, and *sicula* Staud., and of Cross-pairings between these races, XIII.
„ Eggs of *Lasiocampa fasciatella* var. *excellens*, XIII.
(1902). Larvae of *Hyperchiria io*, XIV.
„ Notes on the Life-history of *Aglia tau*, XIV.
(1903). Notes on the Life-history of *Coenonympha corrina*, XV.
„ Notes on the Life-history of *Melitaea didyma*, XV.
„ Eggs of Lepidoptera, XV.
(1904). Egg of *Spilosoma mendica* compared with that of *Phragmatobia fuliginosa*, XVI.
„ Eggs of Lepidoptera, XVI.
„ Egg of *Polyommatus escheri*, XVI.
„ Comparison of the Ova of *Noctua triangulum* and *N. ditrapezium*, XVI.
„ The Preference of Butterflies for Sunlight, XVI.
„ Notes on the Egg, Larva, Pupa and Cocoon of *Phragmatobia fuliginosa*, XVI.
„ General Notes on the Larval and Imaginal Habits of *Phragmatobia fuliginosa*, XVI.
(1905). Proportion of Sexes in Lepidoptera reared from the Egg, XVII.
(1906). Notes on the Pupae of *Smerinthus ocellatus* × *populi* Hybrids, XVIII.
„ Scents of Insects and their Meanings, XVIII.
„ Structural Details of the Pupa of *Heliothis peltigera*, XVIII.
„ A critical Point in the Structure of the Larva of *Daphnis nerii*, XVIII.

Series B. Titles from Various Journals.

(1902). Exhibition of Hybrid Larvae resulting from a Pairing between a Male *Malacosoma neustria* and a Female *M. castrensis*, also Larvae of *M. neustria* and a reputed Larva of *M. franconica* for comparison. *Proc. Entom. Soc.* p. 25.
(1903). Exhibition of a Number of Specimens of *Malacosoma neustria* × *castrensis*. *Proc. Entom. Soc.* p. 8.
(1906). Exhibition of a Specimen of *Catocala nupta*, and three female Specimens of *Lasiocampa quercus* L., *Proc. Entom. Soc.* p. 102.
(1909). On the Cross-breeding of the Moth *Acidalia virgularia*. *Proc. Roy. Soc.* ser. B, 81, 133 (with L. B. Prout).

BIONOMICS OF FLEAS AND BED-BUGS IN RELATION TO PLAGUE.

1910–1922 (classified).

BACOT, A. (1914). A Study of the Bionomics of the Common Rat Fleas and other Species associated with human Habitations, with Special Reference to the Influence of Temperature and Humidity at Various Periods of the Life-History of the Insect. *J. Hyg. Plague Suppl.* III. 447.

BACOT, A. W. and MARTIN, C. J. (1914). On the Mechanism of the Transmission of Plague by Fleas. *J. Hyg. Plague Suppl.* III. 423.

BACOT, A. W. and RIDEWOOD, W. G. (1914). Observations on the Larvae of Fleas. *Parasitol.* VII. 157.

BACOT, A. W. (1914). On the Survival of Bacteria in the Alimentary Canal of Fleas during Metamorphosis from Larvae to Adult. *J. Hyg. Plague Suppl.* III. 655.

BACOT, A., PETRIE, G. F. and TODD, R. E. (1914). The Fleas Found on Rats and other Rodents living in Association with Man, and Trapped in the Towns, Villages, and Nile Boats of Upper Egypt. *J. Hyg.* XIV. 498.

BACOT, A. W. (1915). Notes on the Development of *Bacillus pestis* in Bugs (*Cimex lectularius*) and their Power to convey Infection. *J. Hyg. Plague Suppl.* IV. 777.

—— (1915). Further Notes on the Mechanism of the Transmission of Plague by Fleas. *J. Hyg. Plague Suppl.* IV. 774.

—— (1915). Observations on the Length of Time that Fleas (*Ceratophyllus fasciatus*) carrying *Bacillus pestis* in their Alimentary Canals are able to survive in the Absence of a host, and retain the Power to re-infect with Plague. *J. Hyg. Plague Suppl.* IV. 770.

—— (1919). The Fleas Found on Rats, and their Relation to Plague. *J. Roy. San. Inst.* XL. 53.

BIONOMICS ON *STEGOMYIA FASCIATA*.

BACOT, A. W. (1916). *Yellow Fever (West Africa) Commission. Entomological Report,* p. 191 (J. and A. Churchill, London).

ATKIN, E. E. and BACOT, A. (1917). The Relation Between the Hatching of the Eggs and the Development of the Larvae of *Stegomyia fasciata* (*Aëdes calopus*) and the Presence of Bacteria and Yeasts. *Parasitol.* IX. 482.

BACOT, A. (1918). A Note on the Period during which the Eggs of *Stegomyia fasciata* (*Aëdes calopus*) from Sierra Leone Stock retain their Vitality in a humid Temperature. *Parasitol.* X. 280.

ON INSECTICIDES GENERALLY.

BACOT, A. W. (1914). The Effect of the Vapours of Various Insecticides upon Fleas (*Ceratophyllus fasciatus* and *Xenopsylla cheopsis*) at each stage in their Life-history and upon the Bed-Bug (*Cimex lectularius*) in its Larval Stage. *J. Hyg. Plague Suppl.* III. 665.

—— (1916). The Temperature necessary for the Destruction of Lice and their Eggs. *Brit. Med. J.* I. 167.

—— (1916). The Improvement of Fly-spraying Fluids and the Control of Experimental Trials. *Brit. Med. J.* II. 807.

BACOT, A. (1916). The Use of Insecticides against Lice. *Brit. Med. J.* II. 447.

—— (1917). A simple Means of ascertaining if a Sterilising Hut is hot enough to destroy Lice and Nits in Clothing and Blankets. *Brit. Med. J.* II. 151.

BACOT, A. W. and LLOYD, L. (1918). Destruction of Nits of the Clothes Louse by Solutions of Cresol Soap Emulsion and Lysol. *Brit. Med. J.* I. 479.

BACOT, A. (1918). The Unreliability of Sulphur for the Destruction of Lice in Clothing. *Brit. Med. J.* II. 464.

BACOT, A. and LLOYD, L. (1919). Experiments concerning the Destruction of active Lice (*Pediculus humanus*) by Solutions of Cresol Soap Emulsion and Lysol, and of Lice and Nits with Kerosene, with a View to the Use of these Remedies for the Treatment of Verminous Heads. *Brit. Med. J.* II. 704.

BACOT, A. and TALBOT, G. (1919). Experiments on the Destruction of Lice and Nits. The Survival Period of Lice and Nits (*Pediculus humanus*) when submerged in Tap Water and Water containing 1 per cent. of Salt at various Temperatures. *Brit. Med. J.* II. 703.

BACOT, A. and TALBOT, G. (1919). The comparative Effectiveness of certain Culicifuges under laboratory Conditions. *Parasitol.* XI. 221.

BACOT, A. (1921). Wood-tar Oils for the Destruction of Lice (*Pediculus humanus*) on Hair-clad Areas. *Brit. Med. J.* II. 853.

BIONOMICS OF LICE IN RELATION TO TRENCH FEVER, TYPHUS FEVER AND THE *RICKETTSIA* QUESTION GENERALLY.

BACOT, A. W. (1917). A Contribution to the Bionomics of *Pediculus humanus* (*vestimenti*) and *Pediculus capitis*. *Parasitol.* IX. 228.

—— (1917). The Louse Problem. *Proc. R. Soc. Med. Epidem. Sect.* X. 61.

ARKWRIGHT, J. A., BACOT, A. W. and DUNCAN, F. MARTIN (1918). Preliminary Note on the Association of *Rickettsia* Bodies in Lice with Trench Fever. *Brit. Med. J.* II. 307.

BACOT, A. W. (1919). Lice; The Diseases caused by them and the Measures available for the Protection of Children and Civilians. *School Hygiene*, March.

ARKWRIGHT, J. A., BACOT, A. W. and DUNCAN, F. MARTIN (1919). The Association of *Rickettsia* with Trench Fever. *J. Hyg.* XVIII. 76.

—— —— —— (1919). The Minute Bodies found in Association with Trench Fever, Typhus Fever, and Rocky Mountain Spotted Fever. *Trans. R. Soc. Trop. Med. and Hyg.* XII. 61.

BACOT, A. and LINZELL, L. (1919). The Incubation Period of the Eggs of *Haematopinus asini*. *Parasitol.* XI. 388.

ARKWRIGHT, J. A., ATKIN, E. E. and BACOT, A. (1921). An Hereditary *Rickettsia*-like Parasite of the Bed-Bug (*Cimex lectularius*). *Parasitol.* XIII. 27.

ARKWRIGHT, J. A. and BACOT, A. (1921). A Bacillary Infection of the Copulatory Apparatus of *Pediculus humanus*. *Parasitol.* XIII. 25.

BACOT, A. W. (1921). On the Probable Identity of *Rickettsia pediculi* with *Rickettsia quintana*. *Brit. Med. J.* I. 156.

ARKWRIGHT, J. A. and BACOT, A. (1921). The Stages of *Rickettsia* in the Sheep Ked, *Melophagus ovinus*. *Trans. R. Soc. Trop. Med. and Hyg.* XV. 146.

BACOT, A. and SÉGAL, J. (1922). The Infection of Lice (*Pediculus humanus*) with *Rickettsia prowazeki* by the Injection *per rectum* of the Blood Platelets of Typhus-Infected Guinea-pigs and the Re-infection of other Guinea-pigs from these Lice. *Brit. J. Exper. Pathol.* III. 125.

BACOT, A. (1922). Details of the Technique adopted in following Weigl's Plan of feeding Lice infected with the Virus of Typhus Fever by Rectal Injection. *Brit. J. Exper. Pathol.* III. 72.

ATKIN, E. E. and BACOT, A. (1922). Experiments on the Infectivity of Typhus Virus contained in Lice (*Pediculus humanus* and *Pedicinus longiceps*). *Brit. J. Exper. Pathol.* III. 196.

ARKWRIGHT, J. A. and the late BACOT, A. (III. 1923). Observations on the Morphology of *Rickettsia prowazeki* occurring in Lice (*Pediculus humanus*) infected with the Virus of Typhus Fever. *Parasitology*, XV. 43.

ARKWRIGHT, J. A. and the late BACOT, A. W. (IV. 1923). Investigation of the Aetiology of Typhus Fever, especially undertaken by the Egyptian Government in the Public Health Laboratories, Cairo. *Brit. J. Exper. Pathol.* IV. 70.

Miscellaneous Papers on Entomology.

1910–1922.

Bacot, A. (1911). On the Persistence of Bacilli in the Gut of an Insect during Metamorphosis. *Trans. Entom. Soc. Lond.* 497.

—— (1911). The Persistence of *Bacillus pyocyaneus* in Pupae and Imagines of *Musca domestica* raised from Larvae experimentally infected with the Bacillus. *Parasitol.* iv. 68.

Bacot, A. W. (1914). The Influence of Temperature, Submersion and Burial on the Survival of Eggs and Larvae of *Cimex lectularius*. *Bull. Entom. Res.* v. 111.

—— (1914). Notes respecting the Common Bed-Bug (*Cimex lectularius*). *J. R. San. Inst.* xxxv. 495.

—— (1914). Diseases carried by Insects. *J. R. San. Inst.* xxxv. 26.

Bacot, A. (1914). Attack on *Triphaena pronuba* by a Sparrow. *Entomologist's Record,* xxvi.

—— (1916). Second Generation of Hybrid *Pediculus humanus* and *P. capitis*. *Proc. Entom. Soc.* p. 14.

—— (1916). A Question concerning the Hatching of Eggs of *Stegomyia fasciata*. *Proc. Entom. Soc.* p. 51.

—— (1917). Temperature at which insect Life is destroyed. *Proc. Entom. Soc.* p. 14.

—— (1917). Further Note dealing with the Question of the Specific Identity of *Pediculus capitis* and *P. humanus* (*vestimenti*). *Proc. Entom. Soc.* p. 4.

—— (1918). Lice and Trench Fever. *Proc. Entom. Soc.* p. 56.

—— (1918). Experiments in Colour-Inheritance in *Pediculus humanus*. *Proc. Entom. Soc.* p. 157.

—— (1918). Mosquitoes and the Danger of Malaria in England. *The Essex Naturalist,* xviii. 241.

Bacot, A. and Harden, A. (1922). Vitamin Requirements of *Drosophila*. 1. Vitamins B. and C. *Biochem. J.* xvi. 148.

(*MS. received for publication* 23. vi. 1923.—Ed.)

THE SEGREGATION OF BIOLOGICAL FACTORS IN *B. ENTERITIDIS* (*AERTRYCKE*).

By W. W. C. TOPLEY and JOYCE AYRTON.

ADDENDUM

To the paper published in *Journal of Hygiene*, XXII, pp. 305—313.

The results of experiments, carried out since this report was submitted for publication and the proof corrected, have led us to alter our views with regard to the nature of those cultures of *B. aertrycke*, which are agglutinated by both type and group antisera.

The conclusions set out in the body of the report cannot, therefore, be accepted in their present form, so far as they deal with the correlation between serological varieties and the degree of faecal excretion.

The questions at issue are being re-investigated in the light of the fresh evidence obtained.