Evolution of a Naturalist

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For the purpose of this discussion I use the term naturalist for trained biologists who have had ample field experience, at least in the early parts of their careers. Darwin and Wallace were the most important early exemplars of the discipline. Gerald Durrell calls himself an amateur naturalist; but he received substantial professional training in his youth and is really a professional, although he addresses himself to amateurs. The training is usually received, at least in part, in universities; but the committed naturalist pursues knowledge throughout his career. Darwin was trained in university by a reverend gentleman; but what could he have been taught beyond outlines of classification? He took many books with him on the *Beagle* and studied continuously after the voyage was completed. Beatrix Potter was brought up to be a "lady", Victorian style, by parents who abhorred anything smacking of professionalism. She became a competent naturalist by her own endeavours. Among the outstanding biologists, of my acquaintance, Ernst Mayr and Nikolas Tinbergen are proud to be known as naturalists; and I am glad to follow humbly in their footsteps. There are laboratory workers who believe that they alone are biologists. They have my sympathy for their mental myopia.

I suppose that all biologists recall one or more teachers who stimulated their interests and guided them into a career. I met with little such stimulus until I went to university, and consequently was slow in developing serious biological interests.

1. Childhood and school

Spending most of my first six years at Maseno, then a small, isolated settlement on the equator at 1500 m in western Kenya (in those far off days still British East Africa), I had a promising start, as my mother was mildly interested in natural history. I never saw much of the larger animals, except zebras, giraffes, and ostriches, which we saw from the train. (In those days the train ran from Mombasa on the coast only to Kisumu on an arm of Lake Victoria).

When my father went to Maseno, as a missionary and manager of a sisal plantation, the land was largely covered in tall grass, which had to be cut before he could run a survey of the land allotted for development. I suppose the later extensive plantings of maize and sisal may have discouraged a lot of herbivores. Certainly there were carnivores, which we seldom saw; but pet dogs and escaped tame rabbits had a brief existence. My father had to dispose of leopards occasionally, if they turned man-eater. I do remember the hyena. I trotted off one day to meet a visiting relative coming by the trail from Kisumu. Unfortunately, I picked the wrong fork where the trail divided. The guest had arrived before they missed me; and when an adult caught up with me I was standing still, face to face with a hyena. I recall that I was staring solemnly at it, and can only suppose that my steady gaze discomposed it. If I had known enough to be frightened things might have been different. But perhaps I just looked too skinny for it to bother with.

We used to catch chameleons occasionally, trying to make them change colour to match any background. They were also popular as flycatchers. Many of our observations were of insects. I recall mother showing us mantises that closely mimicked a curled up leaf. Very small children can focus down to a few centimeters. When I was perhaps four and my sister close to six, we spent an improving half hour or so watching termites repairing damage to their mud dwelling. Each animal placed its mud pellet in position and then rapped it quite hard with its mandibles. Mother was interested in the story, but, with her adult eyes, naturally could not confirm it. Whether this behaviour was already known I have no idea.

Our attempt at similarly studying safari ants on the march was less successful. We knew enough not to touch the actual column, but thought we could watch from a step or so away. Naturally a scout brought in a company of soldiers to deal with us. My impression was that they bit simultaneously all over me; but perhaps one started and the victim's reaction set all the others biting. We ran screaming to the house,

†Deceased. This personal account of his life was among D. B. O. Savile's papers and well reflects the development of his contributions against the background of people and time he was influenced by. It is complementary to the text and bibliography presented by Ginns and Darbyshire as part of their tribute. It is (except for expanding some abbreviations for clarity) unedited. If Dr. Savile was still living we would have been tempted to negotiate and perhaps soften some of his personal judgements of contemporaries, and eliminate some of the repetition toward the end. Readers should realize that many comments here may be more reflection of a particularly dry sense of humour than purely intemperate judgements. – F. R. Cook

and the household quickly peeled off our clothes. Removing the soldiers is not easy, as the mandibles lock into one's flesh. Pulling often left the head behind and scissors were then used to separate the mandibles, which were pulled out individually. The lesson is that if you must watch the march, stand back about 2 meters — and still watch out for soldiers climbing soft-footedly up you. Today, of course, I would use a pair of field glasses modified to focus down to under two meters (feasible with some center-focusing models).

Returning to England to go to school I received absolutely no stimulus from any teacher in any field of natural history. In high school I did have science teachers, who dealt crudely with the merest fringes of physics and chemistry. One was a motor-cycle enthusiast, from whom I acquired some knowledge of internal combustion engines, to accompany what I learned of steam engines from a model engineering magazine. Throughout my years in England my elder brother and I tried to learn bird identification in summer holidays spent in rural Devon; but, without even a pair of opera glasses between us, we did not achieve very much.

2. Introduction to Agriculture

I moved to Canada in March 1928, to take a two-year course in agriculture at Macdonald College, with summers spent on farms. I travelled, courtesy of the Canadian Pacific Railway Company, who, with the Canadian government, offered assisted passages to potential farmers. The idea was that we would finally buy some of the land held by C.P.R. in Western Canada. It was clear from one summer on a farm that without capital that one could work a life time on farms without getting a down payment on one. However, off I went to a farm at Mystic in extreme southern Quebec, assigned to me by the faculty member at Macdonald who coped with the diploma course students. The farmer, his wife, the hired girl and a permanent hired hand were all supremely ignorant of the world around them. The hired girl did warn me not to touch what she called "poison ivory", but did not even explain that it was a plant. I got a few practical pieces of information from an Irish boy who had been working on a neighbouring farm for a year or two; he at least was vocal.

As the weather warmed up I naturally saw a few animals: woodchucks, the more conspicuous birds and a few snakes. After I had seen my first garter snake, I casually asked if there were any poisonous snakes in Canada — a reasonable question from one reared in the tropics. The response was a mixture of hilarity and indignation. Of course, there were no poisonous snakes in Canada! How could I be so ignorant? Poisonous snakes were tropical!

One day later in the summer the dog and I went along the lane to the back of the farm to fetch the cows. As we crossed the rocky, wooded ridge that divided the cultivated fields a coiled snake raised its head and buzzed at us. Not a very impressive sound, but I could see that the buzz was produced by the tip of the tail. Clearly a rattler! In the days of silent films I could have no idea what a rattler sounded like, but I had imagined something more startling. I grabbed the dog by his collar as he lunged at the snake; then I crippled the snake with a well-directed stone, finished it off with a stick, and hung the corpse on the fence. The rattle was perhaps a centimeter long but with several distinct segments. I was distinctly relieved to have held back the dog, because I would have been held responsible had he been bitten. As junior hired man I was responsible for everything that went wrong on the farm. I did not even mention the incident. In my week or so at Macdonald I had met no biologists, and had not even heard of the National Museum. Consequently I left the snake on the fence and finally forgot about the episode. Many years later, after seeing an article on rattlesnakes, I recalled it and told the story to Clyde Patch. He confirmed that it had to be the Massasauga Rattlesnake, *Sistrurus catenatus*, recorded sparingly in northern New York but not in Quebec*. I realize now that in preagricultural days it must have been more widespread, but clearing the land exterminated it except on rocky ridges.

Returning to Mac, I entered the diploma course and, among others, I took a course on fungal diseases, put on by J. E. Machacek, who was then completing his Ph.D. He was the first teacher who brought a botanical topic to life for me. Already considering transferring to the B.S.A. course, I was persuaded by his lectures to specialize in plant pathology and mycology.

3. Training in Biology

Transferring to the B.S.A. course was not very simple. Like other British students I had entered the diploma course with the understanding that I could take a transition year, followed by the standard third and fourth years. When the schedule was changed, making the first two years standard B.Sc. courses with no agriculture, the transition year had to be abandoned. Four of us protested vehemently and we ended up taking all the courses of the first two years that we could not talk our professors out of agreeing to. I had to skip first year chemistry and math. The chemistry did not matter, but the math showed me

*More likely he meant a Timber Rattlesnake, *Crotalus horridus*, which has occasionally been reported although never verified in Quebec, along the Quebec-New York border (see Claude Melanson 1961. Innconus et Mccones: amphibians and reptiles of Quebec. La Provancher Société, Quebec, Second edition). The Massassauga has never been reported from Québec – F.R. Cook how shamefully I had been ignored in my last year in school: I did not have the coordinate geometry that leads to the calculus. I survived but it was a gruelling undertaking. Dorothy Newton (later Swales) put on the freshman botany course. She was such a spirited lecturer that I would probably have majored in phanerogamic botany had there been such an option.

In the summer of 1931 I worked for J. G. Coulson in the Plant Pathology Department, and this included the planting and care of field plots. When not needed by him, I helped Dorothy Newton in the then primitive herbarium, mounting specimens that had been 15 years or more in newsprint, and also finding my way about *Gray's Manual*, edition 7, in hopefully identifying many specimens.

In the third year I took elementary genetics, a technique course that covered cytological methods, and a comparative morphology course that included substantial cytology of the major plant groups. Thus I had a foundation for a field that I then had no idea of entering. I also had a half year of mycology and a full year of plant pathology.

4. Fire Blight and the Division of Botany

In the spring of 1932 I applied for a position in the fire blight investigation at Abbotsford, Quebec, having heard that a second appointment was planned. As it happened they were considering appointing an entomology student, but no appointment was made that year. However, the Division of Botany at Ottawa now had my name. Thus, when the incumbent was killed in a car accident, I was phoned by H. N. Racicot to get ready to leave, and he picked me up later in the day (a Saturday). So I was hastily indoctrinated into the experimental work and the operation of a weather station. We had to go to church next morning, to a memorial service for my predecessor. The plate came round, so all I could do was to put in the only money that I possessed, a 50-cent piece, which I had earned by inking diagrams for a graduate student's thesis. So before Racicot returned to Ottawa I had to touch him for an advance. We were then in the depression and living on credit was normal.

There was little spare time that summer, as the copying of the weather records was far behind schedule; and, because bacterial diseases were covered in the final year, I had to read up all that I could find on fire blight. Fortunately the pollination of the trees in insect-proof cages had already been done. I was able to buy an ancient bicycle, which I christened the Death Rattle: no bell was needed, for everyone could hear it coming. The chain kept coming off, owing to having been bent. It was not a standard chain, but luckily I found its mate in Eaton's catalogue and replaced it. I could then travel at 10 m.p.h. without mishap. Our plots were mainly in orchards 2 miles in one direction and 3 miles in the other from the home base. On a state visit next year, Dr. Güssow disapproved of my bicycle (a much better one and fitted with a box for carrying Petri dishes, etc.) and said I should buy a car to save the government's time. I replied that I should be glad to do so if given a salary that permitted it. I remained a cyclist. My pay worked out at about $90/mo., based on a 60-hour week. Fortunately, I paid no rent and did my own cooking; and thus I saved substantially toward the next winter's costs.

Being alone that first summer I put in a full 6-day week, well over 10 hours per day, and still had to tend the weather station on Sunday. However, browsing around on Sunday I used to collect a few plants, which I hopefully identified with an acquired copy of *Gray's Manual* or *Bailey's Manual of Cultivated Plants*. Thus I gradually learned many plants of what I later realized to be an attenuated Appalachian flora. (Some plants I did not see again until attending meetings in Massachusetts about 30 years later). What provoked my interest in learning to recognize plants? Surely Dorothy Newton-Swales' stimulus was important; but I recall insisting that if I was to collect and study parasitic fungi I had to learn their host plants. Accordingly, I collected very few fungi during my first two or three summers at Abbotsford. As soon as Arthur's *Manual of the Rusts* appeared in 1934 I bought a copy, and from then on the rusts were my main concern; but I continued to collect other foliicolous fungi as time permitted.

In the summer of 1933 I must have identified a good many plants, although, like most beginners, I was still avoiding the grasses and sedges. My final undergraduate year (1932–33) included systematic botany, under Dorothy Swales, in which I was ahead of the class, partly because I was familiar with the use of keys and partly because I could recognize many genera. I vaguely recollect that in the two exams I received the highest marks ever given for the course. In 1935 Fr. Marie-Victorin commended me for disentangling the dwarf *Euphorbia* spp., including *E. glyptosperma*, which was not in *Flore Laurentienne*.

In the fall of 1933 I registered for my M.Sc. under Prof. J. G. Coulson. Because of my experience with fire blight, Coulson suggested that I study the limiting factors in some bacterial leaf spots, paralleling a recent study on some fungal leaf spots. Some of the observations seemed interesting, and Coulson suggested that I present them at the spring meeting of the Quebec Society for the Protection of Plants. I gave the talk and, at his request, turned the final manuscript over to Coulson who was to deliver it to the editor. In due course the proceedings appeared and my paper was not included. Surprise, surprise! Coulson had failed to transmit the manuscript. This was my first experience with a non-publisher and, coupled with later experiences in Ottawa, it could have been disastrous. I wonder if supervisors (well, *nominal* supervisors anyway) appreciate how much their dilatoriness (or worse) may damage a student's career. How can a student expect a fellowship if he has nothing to show that he can do research?

I barely got my thesis turned in by the deadline for fall convocation. Each edition was pronounced perfect by J.G.C.; then, after it was typed, he would want it all changed. I think there were five editions. Once I got the phone call on Friday even after my fellow-student had gone off for the weekend; and I could not move until Monday as someone had to maintain the weather station. I was to have gone to Ottawa for the winter but was fired by telegram at the last moment (H. T. Güssow having evidently cleaned out the money for one of his royal tours). After convocation I accordingly caught a boat to England for a family visit. Thus the winter was essentially wasted.

The fire blight work continued in the spring of 1935 fairly satisfactorily, except that when I wrote up a report on any aspect of the work it quietly disappeared. I continued with all of the work as originally planned and new aspects as they occurred to me, most of which I cannot now recall. (Yes, despite statements to the contrary, ants were up the apple trees throughout the day and night in fine weather, dodging clearly exuding cankers, but surely carrying some bacteria. I checked one tree group hourly for 72 hours until I crossed the tent to turn off the alarm without waking!) Of course all the notes and drafts went home with Homer Racicot and were never heard of again.

The fall of 1935 was an echo of 1934. I was packed and ready to go to Ottawa in the lab car when I was again fired by telegram (N.S.F.; perhaps another royal tour). Stopping at Macdonald I found that Harold Brodie had come on staff. I had already met him and was impressed especially by his productivity — he had already published several papers. I found a small grant available to add to my $300 summer savings, and registered again in graduate school. I took advanced mycology from him and made a good start in rust cytology, using several differential staining techniques, some of my own devising. Brodie and I were soon firm friends. On the first weekend I walked back to the college woods to look for rusts and to botanize generally; and promptly met the Brodies (Helen wearing a shocking old hat of Harold's to keep the flies off) collecting agarics for class use. As naturalists we spoke the same language. Before winter's end he realized that my interest in the rusts was serious and encouraged me to try to get to Ann Arbor and take my doctorate under E. B. Mains.

In the spring of 1936 I returned to Abbotsford for the last season; really a waste, when I look back on it, as all my writeups kept disappearing, "taken home to read over the weekend." A couple of years later when I read Don Marquis' *Archie and Mehitabel*, I recognized Homer's prototype: Freddie the Rat, another inhabitant of Don Marquis' office, was a literary critic. He would read one of Archie's poems, sniff, and then eat it. Homer Racicot to the life!

Soon after I reached Ottawa, Dr. Güssow, sick of the lack of results from the La Pocatière Lab on what was then known as bacterial wilt and rot of potatoes, dumped the problem on Racicot and me, which in effect meant me. The "bacterial" in the common name was a lucky guess, for all that previous investigation had isolated were yellow saprophytic bacteria and soil yeasts. During the preceding year at Macdonald I had told J. C. Perrault that, if he would fix infected tissue, I would embed, section and stain it. That would have given the answer, for one of my stock methods for showing pathogens in plant tissue was Gram staining with a counterstain; but he declined the offer. When I received material for study I at once started pouring dilution plates, but simultaneously fixed and embedded stem and tuber tissue material. As it happened I first got the pathogen from plates, slightly speeded up by colonies appearing near an actinomycete colony. Obviously it was a slow grower and everyone had thrown out plates after 5 days as sterile. Adding yeast extract to the medium shortened the incubation period. Critics belittled the finding as sheer luck; but a few days after the initial isolation I had stained sections showing the typical Gram positive short rods of what is now recognized as *Corynebacterium sepedonicum*. With Gram positive plant pathogens so rare, its identification took a matter of minutes: bacterial ring rot, known for years in Europe, where small whole potatoes are planted, but causing little damage. In North America, where cut sets are planted (to reduce virus infection), it became extremely serious, for the cutting knife proved to be a more reliable means of inoculation than any that I could devise. I had to take a week's leave and go to Macdonald, at my own expense, to confirm the identification, using differential media in the Bacteriology Department and controlled temperature chambers in the Plant Pathology Department. (I never understood why such facilities were not available in the Bacteriology Division at the C.E.F. How can one study bacteria without them?). I asked Racicot to check symptom development on my inoculated plants in the greenhouse, but he never did so.

Getting priority on this identification was critical, as pathologists in Maine were known to be working on the disease. Accordingly, I wrote up a short paper describing the disease, the pathogen, the main methods of spread, and a Gram smear technique that I had devised for rapid confirmation of the disease. The paper was reviewed by I. L. Conners and F. L. Drayton and was ready for submission to *Scientific*

Agriculture (long since defunct) when Homer roused from his winter dream world long enough to see what was happening. He immediately insisted that he had to be senior author. As he had done nothing all winter except for hindering my work, I said that he had no claim even to be junior author, all my work being done in spite of him. He whiffled off downstairs to Dr. Güssow, who must have had a pretty good notion of the truth, which had been a main topic of conversation in the building for many weeks. He finally came back and said I could be senior author, which I had to agree. After I went to Ann Arbor he, with some additions by I. L. Conners, paraphrased the original paper for *American Potato Journal*, with me as second author. This may have been what persuaded him in later years that all the work had been his.

6. Ann Arbor Days

This key paper fortunately appeared promptly and persuaded the Botany faculty at University of Michigan that I *could* do research. Consequently they yielded to Harold Brodie's urging and offered me a small fellowship. I thus was able to spend two winters at Ann Arbor and secured my Ph.D. in the spring of 1939 under E. B. Mains. My thesis on nuclear structure and behaviour in rusts, successfully disentangled several gross misinterpretations that resulted largely from complete reliance on iron alum hematoxylin staining, which is seriously non-selective. For example, strange figures in mycelium, purporting to be the telophase of one nucleus with a large nucleolus at each end, were shown by Feulgen staining to be four nuclei following simultaneous division of a dikaryon. The "nucleoli" are strongly DNA positive; and the "telophase" is two recently regenerated nuclei squeezing past each other to restore compatible pairing. World War II started just before my paper appeared in *American Journal of Botany* for October 1939. Such esoteric pursuits as rust cytology had to be set aside; J. H. Craigie seems to have forgotten these and other findings when he optimistically turned to rust cytology after his retirement in 1952. He failed to use modern methods and in 1959 published many of the same fictional interpretations commonly made prior to 1939.

I must emphasize that rust cytology is not a topic that can be studied at odd times, especially late in life. I made good progress in the winter of 1935–36, and again in my time at Ann Arbor (1937–38 and 1938–39). Although I used a microscope at Ottawa in 1938 for many hours, mainly checking smears for ring rot bacteria, I received a shock on returning to Ann Arbor after four months absence from cytological study: All the objects in my rust sections seemed extremely small and I could not distinguish fine details. Checking with a stage micrometer assured me that the microscope was undamaged. The trouble had to be in my eyes. To have your eyes fail you half way through a cytological thesis problem is a horrifying thought. I dared not tell anyone but persevered. Sometimes resolution of details was slightly improved and I began to suspect that the problem was physiological or psychological. After a week there was a definite improvement; but it was nearly three weeks before resolution was fully back to normal. This experience should warn anyone against trying to do anything as visually demanding as rust cytology at odd times.

Only recently, when I read Evelyn Fox Keller's *A Feeling for the Organism* (W. H. Freeman, New York and San Francisco, 1983), did I realize that I was not alone in this grim experience. In 1944 Barbara McClintock was invited to visit Stanford to help with the cytological aspects of George Beadle's work on *Neurospora*. She was delayed in completing arrangements before she could pack her microscope and go by train across the continent; so I judge that she must have been away from microscopic work for several weeks. As the story is told, she was also worried that she might not be able to contribute to the project. She set up her microscope and for three days she could see nothing. Realizing (very wisely, I think) that she had to do something positive, she set out for a walk and finally rested on a shaded bench on the Stanford campus. Then suddenly she was sure that everything was going to be all right, and, indeed, everything *was* all right; and the project was very successful. Her recovery was rapid, perhaps partly reflecting a relatively short absence from her studies. It must also be noted that Dr. McClintock was 42 at the time of her experience, solidly established in cytogenetics and probably well prepared to cope with a psychological problem; whereas I, aged 29 and not established in research, was poorly prepared. Whatever the fundamental cause of such a problem, the experience further emphasizes that fungal cytology is *not* something to be taken up at odd moments, and especially late in life when sustained microscopic study is a severe strain.

In 1949, I had a happier experience of visual adaptation. Various people had insisted that the Chimney Swift, *Chaetura pelagica*, beats its wings alternately, despite this being a palpable impossibility because the body would simply oscillate about its long axis with the wings producing little lift or thrust. However, I rigged up a shutter stroboscope in front of one objective of my binoculars and could often briefly stop the wings of a bird flying toward or away from me. The wings were, of course, always both up or both down. The interesting point is that, after doing these observations daily for some two weeks, I could fully resolve the wing motion without the stroboscope (Auk 67: 499–504, 1950). Visual acuity obviously is not wholly explained by geometric optics.

Ann Arbor was a stimulating place to work at in those days. The Botany Department was large and the staff had very varied interests and experience. Unfortunately I could take few courses in the time available. I did take a cytology course (with unfortunately nothing new in it); and I took Professor Ehlers' course in agrostology, finally reducing my ignorance of grasses and sedges (but unfortunately this was 20 years before modern concepts of the grass subfamilies began to appear). I should have profited from another year, with time to learn more about bryophytes, marine algae and geology. However, my contacts were many and stimulating. I retain a mental picture of Carl Larue (experimental morphologist) and myself staring in at some shrub with leaf galls that looked like spinulose gooseberries. We speculated as to whether the resemblance was merely random. In those days, before the acceptance of transposable genes and DNA transfer, the idea naturally did not get off the ground.

7. War-time Turmoil

Returning to Ottawa after commencement Connie and I were married in late July, which was some compensation for having to work nominally under Homer Racicot. That fall I helped inspectors in their field inspection of potatoes. Usually ring rot, our main problem other than viruses, was clearly distinct; but in one area abnormal weather caused it and black leg to look nearly identical, and Gram smears had to be used freely. The outbreak of war put pure science out of the picture. I have a blurred recollection of committees for boosting food production and of posters that presumably appeared in village post offices where they may or may not have been read.

All the junior staff had to help in the famous national registration. The one memorable question was "Can you milk a cow?" Farm boys looking for a lucrative job in a munitions plant said "No". City boys hoping for a safe rural job often said "Yes". Presumably some beneficial outbreeding in the population resulted. The enormous mass of forms, which could never have been indexed by available means, was stored in an Ottawa building that collapsed under the weight. There are less tedious ways of destroying a building.

I recall two technical surveys by which people with assorted talents could be reached. The military people, in search of tropic-proofing talent later in the war, could have found me by looking under meteorology, fungi and optical instruments. But they did not know of the registers, and found our Division by blind luck (good luck as it turned out).

During the early part of the war I examined countless decaying fruits and vegetables; but my only research paper was a short one on malformation of potato starch grains due to viral infection reducing the elasticity of the leucoplasts. That one seems to have slipped through while Homer nodded (American Journal of Botany 29: 286–287, 1942). H. H. Bartlett enthusiastically proclaimed that this would become known as the Savile phenomenon; but the war was on and nobody even noticed it!

Foolishly I joined the R.C.A.F., trying to make some use of my appreciable and varied technical knowledge. Too late I appreciated a warning to the effect that as a civilian scientist you can talk to people of any rank, and are often listened to, (as indeed I found much later as a tropic-proofing adviser); but as a junior officer you cannot advise or help anyone of a rank above you. The next 18 months were continuous frustration to anyone with a conscience, leavened only by an improved understanding of machine-shop operations and of low-speed aerodynamics; not that I expected to make use of the latter, but I was still interested in learning. I did also develop a simple device to stop static charge from bunching up paper in the met. office teletype. This delighted the C.N. teletype technician, who presumably got credit for introducing it at other stations in his area. My commanding officer, Elmer F. (no, not Elmer Fudd, who was funnier and probably smarter) took a rabid dislike of me, mainly because when he asked my opinion on some problem involving several variables, I remarked that an intelligent answer required considerable thought. He blew right up with "That's the trouble with you civilians; you always want to stop and think. In military action a snap decision is all you want." This was accompanied by a snap of his fingers, one thing that he was good at. Because I was still hoping for a transfer to Operational Research I had to clamp on my tongue, instead of replying that that seemed to explain why we lose the first three years of a war, until some intelligent amateurs get into the higher ranks. Much later I found that I had been asked for by Operational Research but Elmer had turned down my transfer. Too late he found out that it was I (the brainless thinker) who had solved the teletype problem. (There being one in the main office he had heard about.) Suddenly, with my minor gadget that any schoolboy with an inventive turn of mind might have dreamt up, I was an engineering genius to his simple mind. He was plainly embarrassed because he had pressed for my discharge. Even the most honorable discharge is distressing during war, and the fact that Elmer had guessed wrongly about me was not particularly heartening. Most guessers expect about a fifty percent score; but Elmer's score was surely under ten percent; he was an uncanny wrong guesser. However, I may have been more use back in Agriculture than in Operational Research as it turned out.

I returned to the Division as assistant to Ibra Conners, who, as curator of the mycological herbarium, compiler of the plant disease survey reports, and registrar of commercial fungicides, certainly needed some help. Things as once went more smoothly.

Lyle Drayton, having had to deal considerably with Racicot in my absence, had found that my complaints about his obstructionism were more than justified.

As the odd jobs section, Conners and I received not only fungal disorders, but mite or insect injuries, physiological disorders, algae, cyanobacteria, etc. Thus when an army officer, worried about fungal damage to optical glass, came to the Division he was brought up to us. This really *was* an odd job, as I soon found out. I took over the project as I had some familiarity with optical instruments and their servicing, and knew a good deal about meteorology. (I used to coach the met. observers at Centralia on cloud recognition and even cloud transformation.) Thus instrument damage and its prevention became my problem for the last two years of W.W.II, during which time I devoted ca. 15 hours per 60-hour week to it. (This included time spent at home making tools for stripping or adjusting instruments.) Salaries were frozen during the war; however, people with extra work loads could receive a $300 p.a. war duties supplement; but no-one in our Division did. (After taking such an emotional beating in W.W.I, Dr. Güssow probably did not dare to apply for any.) Thus I ended the war at a salary designated for a new graduate with no graduate training or experience. It soon became clear that identification of the fungi in instruments was academic: Many common and widespread species were involved. (The situation was probably somewhat different for fabrics and insulating materials, handled by G. A. Ledingham in N.R.C.) My approach was to improve sealing and thus keep molds, mites and moisture out of the instruments. As Mole said to Ratty, after he cut his shin, my attitude was "Never mind what done it."

Two models of binoculars being built by Research Enterprises Ltd. (R.E.L.), a crown company, were substantially improved by minor modifications, aimed at preventing moisture penetration through pressure changes induced by fluctuating temperature. A more significant change, which would have cured the problem by matched contour milling of the cover plates and mating ends of the body castings, was violently rejected by the plant superintendent. He was quite content to go on filling the gaps with luting compound, which cracks on shrinking just as it does when you caulk your window frames. Yet even in 1943 contour milling equipment and techniques were available. A rifle scope was a trickier problem. A computer (They were human in those far-off days) decided to recompute the optics, to eliminate most of the residual aberrations; so I had time for action before the instrument went back into production. I completely redesigned the sighting head, to guarantee a positive seal. Six instruments were hand made for trials. The one that I saw was certainly a beauty. However, the war was coming to an end and C. D. Howe, who had organized the company, cancelled all contracts and the company instantly disintegrated. The army group with which I had worked also disappeared through transfers and demobilization. I eventually turned my notes and drawings for the sighting head over to the newly founded Defence Research Board as the logical safe depository. All my tropic-proofing reports had security ratings; and so I had no acknowledgeable publications for the work.

Although my time in W.W. II was not entirely unproductive, most of it did not promote my development as a naturalist. My varied activities did at least deter me from becoming an extreme specialist. A working knowledge of low-speed aerodynamics, acquired during the war, led eventually to a detailed understanding of the adaptive characteristics of bird wings (Evolution 12: 212–224, 1957). But even by 1948 I was thinking increasingly in terms of evolutionary adaptations in birds and, certainly soon afterward, of those of plants and fungi.

8. Biological Exploration of Canada

After the war I was able to spend slightly more time on mycological studies; but, with Lyle Drayton serving full time as Associate Dominion Botanist, I was still stuck with all the work on diseases of ornamentals and plant quarantine interceptions until a position in this field was filled.

At this point, credit must be given to K. W. Neatby, who, as Director of Science Services, strongly encouraged his staff to explore the country. Tragically he died just when the results of his stimulus were starting to show. With the onset of the Northern Insect Survey, with which I served three seasons as a botanist, describing biting fly habitats, I inevitably learned something of the ecology of the plants and their parasites. For example, in 1949, my first full season in the field, I found that at a tree-line site (Great Whale River or Poste de la Baleine) obligately heteroecious rusts occurred only if the alternate hosts were virtually in contact. Thus my studies of rusts and other parasites were increasingly in terms of hosts and host environment. I think that, by the time I joined J. A. Calder for the start of the British Columbia floristic survey in 1953, I qualified as a professional naturalist although I obviously had a lot to learn — especially as neither of us had set foot in the Cordillera.

Working with Jim Calder was an education in itself. Not only was he a meticulous collector, whose specimens were clean, well-folded and well-dried; but he put more ecological data on his labels than was usual at that time. I like to think that I contributed my bit in 1953 when we invaded completely new country without an appropriate flora for reference. I took along an aircraft altimeter, which allowed us to record altitudes accurately. Equally important in mountain country, as we soon came to realize, is the direction of slope: the difference between north and south exposure may be equivalent to several degrees of latitude. During the previous winter I found that our British Columbia. collections of many plants were devoid of fruit. In case we should not be able to collect fruiting specimens later, we accordingly included old fruiting stems of flowering perennials. Calder's primary training was in geology; and from him I learnt more of physiography and glacial geology than I had worked out for myself in the Hudson Bay region and northernmost Newfoundland. In British Columbia we thought from the start in terms of biogeography and late glacial history. This approach also influenced my mycological work; one example being studies in the co-evolution of Saxifragaceae and their rusts, which developed over many years, terminating in a summary in *Annals of the Missouri Botanical Garden* 62(2): 354–361, 1975.

I worked with Calder in 1953, 1954 and 1957, the last season being spent in the Queen Charlotte Islands. Botanically the Q.C.I. were exciting, demonstrating the occurrence of a low-level refugium on the west coast contiguous to the deep water of the Pacific Ocean. Unhappily I caught a cold on the ship from Vancouver and, in the dank hotel at Queen Charlotte City, never completely threw it off. I was a drag on the party climbing the small, but steep and slippery mountains; and decided that I was too old for such work.

I accordingly was glad to volunteer, on Harold Senn's behalf, to join a party from McGill in 1958 on Somerset Island. I also had a brief arctic field trip before the 1959 Montreal Botanical Congress. In 1960 I worked out of Isachsen on Ellef Ringnes Island, with the Polar Continental Shelf Project. My experience in British Columbia partly prepared me for interpreting what I saw on Somerset and Ellef Ringnes islands. The latter is in the heart of the supposedly ice-free northwestern Queen Elizabeth Islands, pronounced, by those who had never studied them, to be the centre for all Canadian arctic endemic plants. What struck me, as the season developed, was that the flora round Isachsen is very small, the individual plants are very small and sparsely distributed, and, except for *Puccinellia angustata*, which is widespread across the northern islands and Greenland, the endemics are absent. I was able to work out during the summer, from local observations and the known distribution of all the arctic vascular plants, that, although the northwestern islands had intermittently been covered by snow and ice, even since the end of the Hypsithermal Interval, the ice had not been heavy enough to flow appreciably under its own weight. Thus it had wiped out the plants but had preserved rather than erasing small relief features. The fully documented story was presented in *Canadian Journal of Botany* 39: 909–942, 1961. I had clear priority in this crucial discovery, as was fully recognized by arctic workers at Ottawa at that time. (The story was plagiarized a few years later, independently by two other investigators, both of whom had my paper!) It was certainly a breakthrough in our understanding of arctic biology and late glacial to post-glacial history, completely reorganizing several concepts.

The extensive collecting by our botanical and mycological staff saw the introduction of various new techniques, including the evolution of the field press, and caused me to write *Collection and Care of Botanical Specimens* Canada Department of Agriculture, 1962, 1973, which went through two English and one French edition, not to mention a pirated Russian edition.

9. Some Fruits of Field Work

In 1962 I spent the summer at Hazen Camp in northern Ellesmere Island, collecting plants and fungi and supplying the ecological background for studies by the entomologists. Fortunately, I was once more in good condition, for in that dry Shangri-la I had to do a good deal of mountain climbing to reach some species. For a high-arctic site Hazen Camp was very rewarding botanically, mycologically and ornithologically — and indeed entomologically as my colleagues demonstrated. With complementary studies by J. A. Parmelee on Axel Heiberg Island in 1961, and at various DEW Line sites in 1963 and 1967, our picture of geographic patterns of vascular plants and parasitic fungi in the Canadian Arctic was reasonably complete. Thus, I had ample data for biogeographic and evolutionary studies of both plants and rusts. For example, I was able to demonstrate clinal variation in *Puccinia cruciferarum*, a microcyclic rust without pycnia (Mycologia 56: 240–248, 1964) exploding the dogma that without pycnia there could be no genetic recombination. The conspicuous distinctions of *Puccinia poae-nemoralis* ssp. *hyparctica*, in spore size, pigmentation, wall thickness, wall sculpturing and host specialization, have all accumulated since the onset of the Wisconsin glaciation, supplying the strongest support for parasexual recombination in the rusts (*Arctic Adaptations in Plants*, page 61, 1972). The incomplete segregation of *Poa hartzii* from *Poa glauca* evidently occurred in the same period.

My booklet *Arctic Adaptations in Plants* (Canada Department of Agriculture Monograph 6, 1972) brought together most of my own and other peoples' observations on plants and fungi. The first printing of 2000 was exhausted in two years. A second printing of 3000 was exhausted by 1974; and a third printing of 3000 is still in occasionally demand. Clearly it filled a need. About half the content was either original or from my own publications. It certainly represented a large return on a few seasons of field study.

Successful evolutionary studies must usually have an interdisciplinary aspect. When H. J. Brodie (Canadian Journal of Botany 29: 224–234, 1951) clarified the splash-cup dispersal mechanism he spoke of raindrops as the active agents; and probably no-one seriously questioned his terminology. However, even then, through my work on fire blight and my reading in meteorology, I knew that rain rarely falls vertically and that the drops are small; but I did not pursue the question. In the summer of 1958 I found *Chrysosplenium rosendahlii* Packer (misnamed by me in Canadian Journal of Botany 37: 999, 1959, as *C. iowense*) growing freely in moist grass and sedge meadows in southern Somerset Island Although rain is not rare in that region, it is usually fine and slanted by wind. Could the large drops falling scarcely half a metre from grass or sedge panicles possibly operate the splash-cups? It seemed unlikely; but I was uneasily aware that drops from a canopy are large, for their sound on an umbrella is much louder than that of raindrops in the open. I searched the meteorological literature for help in vain. (Meteorologists are more concerned with terminal velocities of drops than with their initial acceleration). In 1972, as the publisher's reader of the first draft of *The Bird's Nest Fungi*, I came on Brodie's report of the dry plain around Lima, Peru, where only fog, and no true rain occurs. The fog supports low tussocks of woody vegetation. There, to his astonishment, he found well-developed specimens of the bird's nest fungus *Cyathus olla* on debris under many of the larger and denser tussocks. I was not astonished, but I was exasperated: This was my Somerset Island puzzle in repetition. Again I failed to get any answers to my questions. Years later, when I was again searching in the Agrometeorology library, the director, Dr. W. Baier, asked what my problem was. When I explained he turned me over to Dr. Henry Hayhoe, a mathematician. With published information on terminal velocities of falling drops in a vertical wind tunnel, Dr. Hayhoe was able to derive an equation to give the velocity of a drop of given size at a given distance of fall (Savile and Hayhoe, *Canadian Journal of Botany* 56: 127–128, 1978). Later calculations showed that a 4.5 mm drop (probably close to the minimum size shed from the canopy) after 0.25 m of fall has a much higher relative momentum than a 2.5 mm drop at terminal velocity (Savile, *Davidsonia* 10(4): 65–69, 1979). It must be noted that natural raindrops rarely exceed 2.2 mm diameter, for larger drops break up in a long fall. Had I had mathematical expertise available, this problem might have been solved in 1958.

Not surprisingly, recognition of the mechanism of the splash-cup quickly led to further observations. Brodie demonstrated the springboard dispersal system in *Salvia*, *Ocimum* and *Kalanchoe* (*Canadian Journal of Botany* 33: 156–167, 1955). Independently I recognized it in *Tiarella trifoliata* in the spring of 1953, simply because Calder and I took our first look at the coastal rain forest of British Columbia on a drizzly day. I recorded it casually in a preliminary study of the rusts of Saxifragaceae (*Canadian Journal of Botany* 32: 400–425, 1954) without christening the mechanism.

The misconception by Brodie, following Buller's lead, that these devices are being powered by raindrops became general and even resulted in a comic strip sequence showing *Cyathus* cups (quite well drawn) with peridioles being dispersed, quite impossibly, by strongly slanted raindrops. Until the derivation of Dr. Hayhoe's equation no-one could be convinced that drops from a low canopy could function adequately. Even Brodie, who had a very receptive mind, could not be convinced until he saw the figures in *Canadian Journal of Botany* (1978) and *Davidsonia* (1979). At last he saw how *Cyathus olla* survived in the Peruvian desert (where, I am sure, some rodent emerges in the cool dusk and effects more distant transfer).

Would I have stumbled on the springboard action of the *Tiarella* capsule if I had seen it only on a fine day? Probably not as promptly, but plainly I was thinking about Saxifragaceae in terms of dispersal and was puzzled by the strange capsule of *Tiarella*. I could scarcely have missed it next year in the humid forest east of Prince Rupert where both *T. trifoliata* and *T. unifoliata* flourish.

Looking back after some 35 years, my activities in British Columbia indicate that I was thinking as a naturalist, considering plants and fungi in terms of Pleistocene glaciation, biogeography, means of dispersal, etc., although I had a lot to learn. Well, the active naturalist never stops learning. For example, I was trying to shake off the appallingly artificial lumping of the rusts of Saxifragaceae. But I was still treating at varietal level rusts that, with more abundant material, later proved to be good species that do not intergrade on contact. Thus it is was not until 1973 (*Canadian Journal of Botany* 51: 2347–2370) that I could present a treatment of all these rusts that still seems essentially satisfactory. My revision was still fully morphological but recognized small, but consistent, differences that most authors had ignored. From work on bacterial diseases and rust cytology I was used to oil-immersion microscopy, which was generally avoided by mycologists because cedar oil had to be wiped off the immersion lens promptly. I pioneered using tri-immersion in examining rusts, and other fungi about the end of World War II, using medicinal paraffin until non-drying immersion oils were available. I found I could measure spores more accurately and faster than with the 4 mm objective. With these characters the rusts of *Mitella diphylla* and *Tiarella cordifolia* (*Puccinia heucherae* var. *minor* and var. *heucherae* respectively) were usually separable; but there were a few misfits. Having a suspicious nature, I checked the foliage of all material in DAO, and found that the petiole hairs were reliably distinct, although a few non-fruiting specimens had been misnamed (*Canadian Field-Naturalist* 87: 460–462, 1973). Returning to the mycological specimens all the misfits vanished. These two plants often grow together in the eastern hardwoods, and occasionally the helpful collector had included an inflorescence — but of the wrong plant. Thus recognition of the small but reliable differences between these two plants led to a reliable way to distinguish vegetative material of *Mitella* and *Tiarella*.

10. Coevolution

Although the term coevolution apparently did not come into use until 1964 (Ehrlich and Raven, *Evolution* 18: 586–608), the phenomenon had been considered for more than a decade previously. But its early history is obscure, for it is often uncertain whether there have been reciprocal genetic changes that are the sign of true coevolution or only a more or less random coexistence. However, when one can trace parallel advancing lineages in both partners I think the occurrence of coevolution must be accepted. (See K. A. Pirozynski and D. L. Hawksworth, Chapter 1 in Pirozynski and Hawksworth, editors, *Coevolution of Fungi with Plants and Animals*. Academic Press, London, 1988). Because I have been cited as a pioneer in coevolutionary studies, I must try to review my role in this field. My early observations were mainly aimed at using rust or smut data pragmatically to improve our understanding of plant relationships. In the first summary of my ideas (*Science* 120: 583–585, 1954), I presented the rather miscellaneous conclusions of a few earlier studies. It was shown that the same rust (not merely a morphologically similar one) attacks *Acorus calamus* and *Sparganium eurycarpum*; and that the two plants, despite superficial distinctions, have several anatomical similarities. Following the mycological conclusions (Parmelee and Savile, *Mycologia* 46: 823–836, 1954) *Acorus* has been variously disposed. According to Cronquist (*Evolution and Classification of Flowering Plants*, 2nd Edition, New York Botanical Garden, Bronx, New York, 1988) it differs from Araceae in so many ways that it has been put into a separate family Acoraceae. However, it will probably prove to be very close to *Sparganium eurycarpum*. In this example the rust is useful to the systematist, but there is no very clear sign of coevolution. On the other hand, it was shown that the rusts of Poaceae, Cyperaceae and Juncaceae are, on average, much more primitive than the rusts of Liliales. Some rust clans can be traced through a group of grass or sedge rusts into greatly advanced autoecious liliicolous species. Here there is evidence of abundant coevolution, not all evident in 1954 but increasingly so as time went by.

By about 1960, although most of my papers dealt with detailed taxonomy of various groups of fungi, I was increasingly concerned with that of the host plants; and minor emendations of the latter were occasionally indicated, including: disposition of *Allium* (Mycologia 53: 31–52, 1961; Nature 196: 792, 1962); *Eriogonium* (*Canadian Journal of Botany* 44: 1151–1170, 1966); *Filipendula* (*Brittonia* 20: 230–231); Veroniceae (*Canadian Journal of Botany* 47: 1085–1100, 1969); *Ledum* (*Canadian Journal of Botany* 47: 1085–1100, 1969); *Scirpus* etc. (*Canadian Journal of Botany* 50: 2579–2596, 1972); Saxifragaceae (*Canadian Journal of Botany* 51: 2347–2370, 1973; *Annals of the Missouri Botanical Garden*. 62: 354–361, 1975); Brassicaceae (*Canadian Journal of Botany* 52: 1501–1507, 1974); *Pedicularis* (*Proceedings of the Indian Natural Sciences Academy* 438(6): 223–227, 1977). Several families, including Poaceae and Cyperaceae-Juncaceae, were discussed in *Botanical Review* 45(4): 377–503, 1979. Poaceae was further discussed in Chapter 16 of *Grass Systematics and Evolution*, edited by T. R. Soderstrom et al., Smithsonian Inst. Press, Washington, 1987. Interrelationships of Poaceae, Cyperaceae and Juncaceae, with confirmatory evidence of Juncaceae evolving from Cyperaceae, are discussed in *Canadian Journal of Botany* (68: 731–734).

11. Why are Scientific Advances so Slow?

Fully professional biologists seem to have appeared ca. 1870 in Germany, where the universities were supported by local princes and not controlled by religious sects; and science consequently flourished. In England, on the contrary, Oxford and Cambridge were rigidly controlled by the anglican church until 1871; until then admission was only to anglicans, and all senior staff positions were held by anglican divines. A vow of celibacy for students and teachers was abandoned only in 1878. Even after 1871 individual colleges could, and most did, refuse admission to jews, catholics and protestant dissenters. Thus presbyterians stayed in Scotland where science and engineering flourished; but science stagnated in England, where only brilliant individuals such as Darwin could advance without aid from the universities. According to C. D. Darlington (*The Evolution of Man and Society*, London, George Allen and Unwin, 1969) the same attitude was still common well into the twentieth century; but new universities, and new colleges, free from the religious system, finally allowed great advances.

Independent achievements were ill-received by self-satisfied members of the establishment. When Beatrix Potter, a remarkable self-trained naturalist, discovered the lichen symbiosis she was ridiculed by the learned men of Kew: Not only was she a woman but she was not a university graduate; ergo she could not discover anything. Luckily for generations of children, she went on to fame and fortune with her animal stories; and the lichen symbiosis was soon rediscovered in Germany.

Professional biology in the United States seems to have developed gradually, perhaps from 1870 to 1890. In Canada, with its small and scattered population, professional training seems to have developed mainly between 1900 and 1910, with delays certainly due in large part to the stagnation of science in England. But in most countries the numbers of professional biologists seem to have been few until about 1920; and progress was understandably slow.

However, even in recent years we do not see one breakthrough leading directly to the next. Why is this so? Are biologists as a whole too slow in their thinking to take faster steps? I do not think so. Consider Stephen Hawking, the theoretical physicist believed by many of his colleagues to have perhaps the finest intellect of the twentieth century. In discussing Hawking's work, John Boslough (1985. *Stephen Hawking's Universe*. Win. Morris, New York) shows that, despite his many contributions, his ideas do not come in a steady stream. After a long period a new idea is born (it may be in the middle of the night) for no obvious reason; then he and his colleagues again pursue the origin of the universe a stage further. Boslough quotes Hawking as saying: "I think we'll come to the unifying theory within the next two decades, probably in a series of small steps. But you know, once we find it, it will rather taken the fun out of theoretical physics." Fortunately biology is so much more complex that we shall surely not lose the fun of it for a long time; but still work hopefully toward that end.

Perhaps we lesser mortals, such as botanists and mycologists, need not be too ashamed of our halting progress; but surely we should try to understand its causes, and then perhaps we may find some remedies. When a theoretical physicist gets a new idea it presumably is born from a particular association of prior ideas. It is like rotating a kaleidoscope to get a new pattern. When a field biologist (i.e. a true naturalist) gets a new idea, or a new understanding, it is often derived from a newly observed structure or mechanism associated with an old idea, or a familiar structure associated with a new idea. When I saw *Tiarella* capsules hit by drops from the canopy I knew at once what was happening because the action of falling drops on splash cups was already in my mind. Would I have understood what was happening if I had seen the plants without having been involved with splash-cups? Well, certainly not immediately; but obviously the mechanism had to be seen in the field to be understood. No one, including myself, who had studied herbarium specimens of *Tiarella* seems to have suspected a function for those "ridiculous" capsules. A character can be "ridiculous" only when we do not understand it. The poet disparages the ragged fingers of a crow; but the crow is large enough to need the extra lift from its wing-tip slots for economical travel even in level flight.

Recognizing the value of field study to clarify a function, let us look at the lamentably slow growth in our understanding of the rust fungi, which was certainly not entirely due to a paucity of students. The history, up to 1928, is told in some detail by J. C. Arthur et al. (*The Plant Rusts*, Uredinales, John Wiley, New York, 1929), with pertinent references. Anton de Bary, an intellectual giant, understood the morphology and parasitism of the rusts as early as 1853; but, despite insistence by farmers of the abundance of wheat stem rust near barberries, he did not countenance the identity of the aecia on barberry with the uredinia and telia on wheat for ten years: The concept of heteroecism was simply too preposterous for an educated man to accept. (Here is a parallel of Beatrix Potter and the lichens: We must have open eyes *and* minds). He finally proved the connection by reciprocal cultures in 1864 and 1865. He then also connected up some other heteroecious species. De Bary's unwillingness to recognize heteroecism in the rusts is curious, for he already knew of the phenomenon in some animal parasites. Although the pycnia were suspected of being spermogonia by Tulasne as early as 1851, there seems to have been little or no progress in understanding them for many years, despite various cytological studies. They are, in fact, a combination of spermogonia, receptive hyphae and a nectary, and are a unique structure whose significance is overlooked by a few workers who call the whole organ a spermogonium. Because the spores did not germinate by germ tube, they were held to be functionless. Surely by 1900 or thereabouts someone should have suspected that a functionless organ would not persist for millions of years in genus after genus. Finally J.H. Craigie (*Nature* 120: 116–117, and 765–767, 1927) demonstrated that insects feeding on the pycnial nectar transferred pycniospores to pycnia of the opposite mating strain, resulting in the formation of dikaryotic aecia. Why did this step have to take three-quarters of a century? Pycnia are prominent in many rusts. I recall in my student days, a few years after Craigie's work, watching assorted insects feeding on the conspicuous pycnia of a *Gymnosporangium* on *Crataegus* leaves. Had no naturalists seen insects feeding on pycnial nectar during all that time?

How was the understanding finally achieved? Craigie's work was done at the then newly founded Rust Research Laboratory at Winnipeg. Craigie must certainly have been influenced by A. H. R. Buller, professor of botany at the University of Manitoba, who, with his intense sense of curiosity, was always interested in the work of other investigators. Staff at the Rust Lab were inclined to give full credit to Craigie, with the inference that Buller was merely in the way. However, Harold Brodie, who was Buller's student at the time, told me many years later that Buller saw flies visiting the nectar on the inoculated barberry plants in the greenhouse, guessed what was happening, and told Craigie to grow seedlings in insect-proof cages and do controlled nectar transfers. After the successful experiments had been completed he urged Craigie to write it up for *Nature*. According to Brodie, who was working in Buller's office at the moment, the first draft of the note was so unsatisfactory that Buller practically dictated the final version. They have all gone now, Brodie being the last, and we shall never know the truth in every detail. As one who several times saw Buller in action and who later worked under Craigie, I can well believe that in his enthusiasm Buller may have told Craigie what to do (even if Craigie was already doing it). Harold Brodie was meticulous in giving credit, and I therefore believe his interpretation of the scene in Buller's office. However, Craigie was a canny Scot, not to be rushed in any action. He was not a ready writer (or speaker), but would keep polishing a statement and changing adjectives until he was finally satisfied. I recall a memorandum that went between him and me for a week before he released it (little changed from my original, but certainly no worse). Therefore, I would not expect the draft that Buller saw to have been wholly satisfactory: It may have been only a first draft, which Craigie would have polished without help (eventually). Buller, in contrast, seems to have been a very ready writer who never had to revise extensively. Buller had tremendous enthusiasm and considerable imagination; but he seems to have been inclined to dictate experiments to others in preference to doing them himself. (Years later he visualized the splash dispersal in *Cyathus* and conned Brodie into finding specimens and running the tests that provided the splash-cup mechanism).

Next A. M. Brown (*Nature* 130: 177, 1932) demonstrated that uredinial cultures of the autoecious *Puccinia helianthi* could dikaryotize isolated pycnial infections by nuclear transfer following hyphal fusion. In 1939 (*American Journal of Botany*. 26: 585–609). I demonstrated cytologically the fusion of pycniospores to receptive hyphae, including a nucleus in transit and the clear circles left on the wall of the receptive hyphae after the pycniospores fell away. Using advanced staining procedures, including the Feulgen method, I was able to interpret realistically some of the improbable figures that had added mystery to rust cytology (see section 6). Incidentally, I showed that the so-called Blackman and Christman fusions in the aecial fundament have no taxonomic distinction; both types and intermediates may occur in a single aecium, and they represent the shortest available route for an introduced nucleus initiating a dikaryon.

In the meantime, it was widely assumed that rusts without pycnia were evolutionary dead ends, incapable of recombination. One of the conspicuous results of our extensive post-war field program, with its good geographic coverage, was the finding that such rusts are usually morphologically uniform over a widely occupied area; but that geographically isolated populations tended to differ from one another although each was homogeneous. It was clear that genetic recombination was operating in such populations: they were not fragmenting like a fully apomictic dandelion. Then I demonstrated a morphological cline between two subspecies of *Puccinia cruciferarum*, and it became clear that any two adjacent dikaryotic hyphae that are genetically distinct must trade nuclei when they meet (*Mycologia* 56: 240–248, 1964). Finally, the high-arctic *Puccinia poae-nemoralis* ssp. *hyparctica*, isolated by the onset of the Wisconsin glaciation, was seen to differ very uniformly from the parental subspecies in the size, pigmentation, wall thickness and sculpturing of its urediniospores and in its host range (*Arctic Adaptations in Plants*. Canada Department of Agriculture Monograph number 6, Ottawa, 1972). Because *P. poae-nemoralis* never produces telia in the arctic, meiosis cannot be involved; and the accumulation of all the mutations adapting ssp. *hyparctica* to an extremely arid climate can only be accounted for by parasexual recombination, following nuclear transfer.

The jumping of rusts to new hosts also involves their genetic make-up. In 1954, collecting in the mossy coastal forest of southwestern British Columbia, Calder and I repeatedly found *Pyrola* spp. and *Goodyera* spp. growing in close association. *Pyrola* often bore uredinia of *Pucciniastrum pyrolae*; and *Goodyera* occasionally bore pustules of *Uredo goodyerae*, which is excluded from *Pucciniastrum* because it lacks telia, but which has urediniospores only slightly distinct from those of *P. pyrolae*. Except for the scarcely separable *U. ishikariensis* in Japan this is the only such rust on a monocotyledon. Clearly it arose by a jump from contiguous *Pucciniastrum pyrolae*. Although I saw, in the humid coast forest, what had happened, I did not see its full significance and thought it a rare freak. Twelve years later, when revising some rusts of Scrophulariaceae, I recognized another unmistakable jump, by *Puccinia palmeri* on *Penstemon* to *Pedicularis*, with the evolution of *Puccinia rufescens*. Both rusts have the relatively uncommon O, I, III life cycle with repeating aecia, and several conspicuous morphological resemblances; but *P. rufescens* has clearly rugose teliospores, in contrast to the smooth or faintly roughened spores of *P. palmeri*, and is certainly the derived species. With field experience in the Cordillera I saw what had happened. *Penstemon* and the cordilleran *Pedicularis* have strong geographic and ecological overlap; and, although *Penstemon* is clearly a modern genus, the cordilleran *Pedicularis* are even more modern, having evidently originated from a late Tertiary asiatic immigrant and radiated mainly in the Pleistocene when climatic fluctuations tended to fragment populations and stimulate speciation. The conditions that promote a successful jump evidently include strong ecogeographic overlap, a young and genetically diverse parental rust (with a large gene pool), and a young and genetically diverse potential host (younger than the parental host). With these conditions the chance of compatible genomes meeting is maximized. I now realize that jumps have occurred abundantly in the evolution of the rusts. At last it was seen why Dietel's early observation that rusts and hosts reflect each other's ages of origin is valid. Why was it not generally understood for 67 years? Well, it should have been understood after a mere 63 years, but ignorance intervened. A fully documented account of the mechanism and supporting taxonomy was submitted in 1966 to *Canadian Journal of Botany*. Both editor and reviewer accepted the taxonomy but insisted that the discussion be purged (editing by axe!). Eventually it was enthusiastically accepted for *Nova Hedwigia* (24: 369–392, 1968 [1969]). This journal deals with all cryptogams but not spermatophytes, so the paper was not seen by many phanerogamists. The jump mechanism was re-explained in a symposium paper in *Quarterly Review of Biology* (46: 211–218, 1971) where everyone saw it. (I stopped counting reprint requests at about 800). When the mechanism was finally explained it was through my field observations combined with detailed microscopic work. This major step in understanding rust evolution was possible because I was an experienced field naturalist, which is surely how most evolutionary advances are achieved.

12. Progress can be speeded

The answers to problems relating to rust biology, and many similar topics, lie in the need for copious field work, but field work with the eyes and mind wide open. Also the collector should either be involved with the laboratory studies or be in close contact with that person. In this way cause and effect are most easily related.

In my nine full seasons of field work between 1949 and 1962, I doubled as botanist and mycologist both by inclination and by necessity; and the value of this broad approach was soon very clear. At three arctic sites where my stay covered the nesting period (Chesterfield, Isachsen and Hazen Camp), I was able to run a breeding bird census, which gives an approximate measure of biomass productivity. A botanist patrolling an area devoid of tall plants can locate nearly all nests; but such counts are impossible in wooded country. If we go into the field with the responsibility to collect and study ecologically all plants and fungi, *and develop an intense interest in them*, we can scarcely avoid discovering new information about many of them. Apart from the personal satisfaction that our observations give us, this maximum yield of information justifies the substantial cost of keeping a party in the field. Once we have fair coverage of an area, specialized collecting, to complete information in a particular field of study, is justified; but to go into an inadequately studied region with the blinkers on, neglecting all but one small group of organisms, may be worse than useless, making it difficult to promote an adequate attack on that region later.

The wealth of new biological information secured in the years 1949 to 1962 (after which funding for biological exploration was drastically reduced) must greatly exceed that of any previous period in Canada.

Personal field and microscopic study explained how a rust jumped from *Penstemon* to *Pedicularis* (see section 11). Because he had described so many rusts J. C. Arthur received many specimens for study from other collectors; and his field observations became increasingly limited to the vicinity of Purdue University. Studies by others at arctic or alpine treeline have shown the limitations of heteroecious rusts. When Holway sent Arthur the type collection of *Puccinia praegracilis* on *Agrostis thurberiana*, collected near treeline, he sent with it a note stating that it "grew adjacent to the *Habenaria* aecidium, and no where else." Arthur named the rust but later buried it in *P. coronata* because he did not appreciate Holway's warning; but Holway was absolutely right, as I have shown repeatedly. Near treeline these exclusive associations are more reliable than artificial rust cultures in which contaminations do occur. If puzzles are to be solved promptly the collector must include full information and the identifier must not ignore it.

Most of my discoveries in various organisms resulted from field observations made with an open mind conditioned by previous experiences. Field work and microscopic study demonstrated gene flow and geographic races in *Puccinia cruciferarum*, which lacks pycnia. I discovered *P. poeae-sudeticae* ssp. *hyparctica* in arid Hazen Valley because, from experience in arid southern British Columbia, I knew enough to look in the axils of the grass leaves where dew lingers; and its distinctness confirmed the occurrence of parasexual recombination in a rust lacking teliospores (see section 9).

Inspired by H. J. Brodie's seminal paper on splash-caps (*Canadian Journal of Botany* 29: 224–234, 1951), I demonstrated splash-cups in *Chrysosplenium* and *Mitella* (*Science* 117: 250–251, 1953), but was puzzled by the strange capsules of *Tiarella*. Soon after my note appeared, as I stood in the coast forest of southwest British Columbia in a drizzle, I saw capsules of *Tiarella trifoliata* flicker as drops from the canopy hit them, and the operation of this elegant springboard was revealed (see section 9: Fruits of Field Work). Five years later, seeing *Chrysosplenium rosendahlii* spreading freely in marshes on Somerset Island, with only nodding grasses and sedges as a canopy, I was puzzled at the thought of drops falling only half a meter being effective dispersal agents. Many years later H. N. Hayhoe derived an equation demonstrating the effectiveness of large drops falling very short distances (information important to plant pathologists) and our understanding of splash-cups and springboards was finally nearly complete (section 9).

Among observations on plants apparently originating with me: *Alopecurus alpinus* and *Papaver radicatum* (s. lat.) have such low temperature tolerances that even in the high arctic their growth is limited mainly by aridity. Field observations disproved claims that *Poa glauca* is fully apomictic, when it was found freely crossing and backcrossing with *Poa hartzii* at Hazen Camp, and also hybridizing elsewhere with a member of the *Poa arctica* complex. Other strongly self-fertile plants were shown to outcross on occasion; e.g. hybrids between *Stellaria edwardsii* and *S. laeta* were found at Hazen Camp. I showed that *Saxifraga oppositifolia* was fully self-fertile at Isachsen, two distinct biotypes being present but no intermediates; sustained observations showed that, about two days after the stigmas became receptive, elongation and curvature of the filaments brought the anthers approximately into contact with the stigmas. (The only abundant potential pollinators were chironomid midges, which prefer white flowers and seemed to feed mostly at *Stellaria* and *Cerastium*.) In contrast, at Hazen Camp, which is much warmer in summer than Isachsen, two bumble-bees (*Bombus polaris* and *B. hyperboreus*) were present, and it was difficult to find any two plants of *Saxifraga oppositifolia* that were convincingly identical. At least three biotypes seem to have been present originally and the bees had mixed them freely. Later P. G. Kevan (Insect pollination of high-arctic flowers. *Journal of Ecology* 60: 831–847, 1972) showed that *S. oppositifolia* at Hazen Camp is about 90% self-sterile.

Detailed observations of plant growth at Isachsen, physical conditions, and the total ranges of plants allowed me to interpret the late glacial and postglacial history of the northwestern Queen Elizabeth Islands. The Islands were lightly snow- and ice-covered; in the postglacial hypsithermal interval they were well vegetated; but with increasing cold many plants were eliminated, leaving broken distribution patterns. The islands were not, as once suggested, a glacial refugium (see section 8). Thus the glacial history of the region was completely reinterpreted.

My observations of the Peary Caribou (*Rangifer tarandus pearyi* on Ellef Ringnes Island explained why, in defiance of Bergmann's rule, this is the smallest, rather than the largest, race. Two distantly separated family groups (buck, doe and one fawn) each seemed, from their tracks, to patrol some 700–800 km^2, clipping off plant tops as they moved. As these regions usually have less than 1% of the ground covered by very small plants, continuous movement of the animals is necessary for their survival; and survival is best assured by small body size, which allows reproduction with minimal food intake. The Red-throated Loon (*Gavia stellata*) is the smallest member of its genus and also has the most northerly limits. Here small body size functions by allowing take-off and landing in relatively small ponds that become ice-free promptly. Large lakes, such as Lake Hazen, are used for fishing, but ice-shove keeps the shores bare of vegetation and impossible for nesting (Savile. A naturalist looks at arctic adaptations. *In* Evolution Today, pages 47–53, G. G. E. Scudder and J. L. Reveal *Editors. Procedings of the 2nd International Congress of Systematic and Evolutionary Biology*, Hunt Institute, Pittsburgh).

I spent nine more or less full seasons (1$^1/_2$-4 months) in the field between 1949 and 1962, with shorter periods in two other years. This abundant exposure to the living world obviously contributed substantially to most of my success in interpreting biological (and occasionally physical) phenomena. It should be equally obvious that exposure to the biota cannot guarantee success. One must keep the eyes and the mind wide open. The unperceptive collector can bale botanical year after year and discover nothing — in fact not even see that unsolved problems exist. To break new ground the field biologist must either have an innate sense of curiosity or have been stimulated by associates (I was twice blest), preferably both, for it generally pays to look at several aspects of a problem. The six blind men could not adequately describe the elephant because none would walk round it.

Unusual characters do not evolve randomly; nor do they exist simply to aid taxonomists. If we can recognize their functions we may get clues to the evolution and paleoecology of the organisms. Sometimes the function is obscure except under particular conditions. The team approach may then speed up recognition; but all team members must obviously be alert to the problem. Seed dispersal is a critical problem in most flowering plants. Years of observation in Saxifragaceae (*senso stricto*), a clearly natural group, revealed a surprising variety of dispersal methods, both local and long-range (D. B. O. Savile. Evolution and biogeography of Saxifragaceae with guidance from their rust parasites. *Annals of the Missouri Botanical Garden* 62: 354–361, 1975). It is worth noting that all these mechanisms have also evolved in other plant groups, reminding us that in important problems there may be repetition of one solution as well as multiple solutions. In the large and ecologically diverse genus *Carex* the fruits may be scattered by wind, lodge in the fur or feathers of passing animals, float across water by virtue of bladdery perigynia, or even be ingested by birds as in *C. aurea* with fleshy, sweet and bright yellow perigynia (Savile, *Botanical Review* 45: 488, 1979). The Asiatic *C. baccans* Hara similarly has fleshy but red-purple perigynia.

As in flowering plants, dispersal in fungi is critically important, involving many modifications. A long-cycled rust initially has two dispersing spore states, aeciospores and urediniospores, which might seem ample; yet in the three advanced rust families, with pedicellate teliospores, diasporic teliospores have evolved in at least 17 genera by at least 9 methods. Spore release is usually accompanied by newly adaptive changes: nearly uniform rather than apical wall thickening, broadened and shortened spores, sculpturing of spore walls, and a tendency for germ pores to drift from the apical or septal position. In the big genus *Puccinia* (and the related *Uromyces*) I was able to recognize the attainment of deciduous teliospores in more than 30 lineages by six methods of release (Savile. Evolution of the rust fungi (Uredinales) as reflected by their ecological problems. *Evolutionary Biology* 9: 137–207, 1976). Diasporic teliospores must be particularly important in short-cycled rusts; but they have also evolved in 47 long-cycled *Puccinia* or *Uromyces* in North America, and they must therefore be strongly adaptive even when aecia and uredinia are present. J. C. Arthur (*Manual of the Rusts in United States and Canada*. Purdue Research Foundation, Lafayette, Indiana, 1934) divided *Puccinia* into two sections: *Eupuccinia* with firm and *Bullaria* with fragile pedicels. Even in 1954 (D. B. O. Savile. Cellular mechanics, taxonomy and evolution in the Uredinales and Ustilaginales. *Mycologia* 46: 736–761) the functions of the correlated changes in diasporic teliospores were clear and I identified several lineages of *Puccinia* and *Uromyces* that occur in both of Arthur's sections. His sections are thus completely unnatural and taxonomically misleading. Indeed some species have incipiently diasporic teliospores and defy disposition to section. Arthur apparently thought more in terms of a convenient pigeon-holing system, comparable to that of Engler and Prantl for the flowering plants, than of a classification reflecting active evolution in the rusts.

13. Truth and Beauty in Biological Research

What drives the research biologist? Scientists expect to make an adequate living from their work; but if money were their main objective they would be in other professions. Recognition by one's peers, or rarely by the general public, may be satisfactory, but is a result of rather than an impulse to research. Surely we are driven largely by the excitement of discovery and the ultimate delight of establishing a truth built up from a series of observations. Basically we seek to establish facts and, from them, to establish the truth of a system. But truth, for a scientist, goes beyond the bald statement of truth vs. falsity sought in a court of law. Establishing a scientific truth is a matter of great satisfaction, the true picture becoming a thing of beauty. The search for, and demonstration of, truth must surely be the driving force behind all dedicated scientists, whether or not they equate truth with beauty; but the imaginative worker must generally recognize beauty.

Although Keats' statement — "Beauty is truth, truth beauty" — is surely the most famous equation of truth and beauty in English, Chandresekar's essay (S. Chandresekhar. Ph. 4, Beauty and the quest for beauty in science, in *Truth and Beauty: Aesthetics and Motivations in Science*. University of Chicago Press, Chicago and London, 1987) shows us that many people down the centuries have discussed the same theme.

The concept of beauty in truth is surely an important stimulus to the research biologist. Much of his time in the field or back in the lab is taken up by routine collecting, processing or identification of specimens, leavened by unexpected observations or the finding of unexpected species. But once in a while he discovers the function of a character or finds the specimen that explains earlier observations. How wonderful life suddenly is! Such revelations of beauty do not occur very often (just as well, for they can be pretty intoxicating), but they break the routine. The discoveries need not be major, but they clarify a problem, as two examples show. (1) On a drizzly day in southwestern British Columbia. I saw a *Tiarella* capsule flicker under a falling drop; and suddenly its strange form was revealed as a functional and beautifully engineered springboard (Section 9); and it was clear that *Mitella* and *Tiarella* diverged in humid forests from a heucheroid ancestor, each evolving an effective but separate splash dispersal mechanism. (2) When Calder and I were revising the subspecies of *Saxifraga punctata*, we found plants near Prince Rupert that possessed characters of two mainland subspecies but also some of an unknown plant. Suspecting these characters to be from a Queen Charlotte Islands race, we advanced our visit to these Islands. I can think of few more rewarding moments than when, after struggling up Tan Mountain, we first saw *S. punctata* ssp. *carlottae* looking exactly as we anticipated.

It has been suggested that its aesthetic value may justify a theory that is shown to disregard facts; but surely an honest scientist cannot support such an idea. If a theory is false it is so defaced that, to me, it immediately loses any beauty. However, it is sadly true that some workers find it difficult or impossible to discard an old belief despite accumulating evidence against it. Although it was plain even in 1954, partly from parasite data, that Liliales are younger than Poaceae and Cyperaceae, a few authors have even recently indicated them to be older (e.g. A. L. Takhtajan. Outline of the classification of flowering plants, oragnoliophyta. *Botanical Review* 46: 225–359, 1980; R. M. T. Dahlgren and H. T. Clifford. *The Monocotyledons: A Comparative Study*. Academic Press, London, 1982).

Biology differs from the physical sciences in several respects. In physical sciences simple laws are applicable because the systems are simple. In biology, as Ernst Mayr has shown more than once, the systems are infinitely complex: All the molecules of a chemical compound in the universe are identical; but in sexually reproducing organisms no two individuals, except identical twins, are ever the same.

The physical scientist, often after years of labour, produces laws or principles that are applicable because the systems are simple. Chandresekhar indicates that most physical scientists make their major contributions early in life; and he contrasts them with great poets, writers and musicians, who often produce very fine works late in life. It is notable that many biologists show a pattern similar to that of workers in the arts. Charles Darwin published *The Origin of Species* (his first major work) at age 50; and his other volumes appeared during the next 24 years. Ernst Mayr, born in 1904 and arguably the greatest evolutionary biologist of this century, has been publishing on evolutionary topics continuously since 1940, with important books appearing in 1942, 1963, 1970, 1976, 1982 and 1988. Many other biologists of my acquaintance have continued in productive research to formal retirement and beyond, as long as their health permitted.

A biologist's main contributions may all be made relatively late in life, as was true of Darwin, simply because accumulating countless small observations and fitting them into a useful and informative structure inevitably takes a long time. This tendency reflects the complexity of biological systems. The young field biologist collects specimens for taxonomic study, and records their geographic range, general ecology, habitat (with orientation and altitude where pertinent), and associations. Eventually all these bits of information will lead to a broader understanding of the biology of the organisms. Thus we may often pass most of our careers before we are prepared to present a complete picture of a topic. But, because we are dealing with living and genetically variable organisms, the picture is seldom really complete, and in later years we, or others, will add to and modify it. There can be no mathematical proof that the picture is correct, for the pieces of the puzzle may change in shape and numbers at any time. What we aim at is the simplest explanation that conforms with all the data. If the data are abundant the most parsimonious solution is nearly always correct; but we are dealing with probability rather than mathematical proof. As time passes we generally discover additional pieces to fit into the puzzle; and the probability of a correct solution finally becomes enormous and can be accepted.

About 1973 I started to assemble observations, which I had been accumulating for about 30 years, into a paper on evolution and ecology of the rusts (D. B.O. Savile. Evolution of the rust fungi, Uredinales, as reflected by their ecological problems. *Evolutionary Biology* 9: 137–207, 1976). When I finished it late in 1975, I hoped that the story was reasonably complete. Scanning my annotated copy I see considerable additional information from more recent publications, but nothing to change the main conclusions. Thus the timing was evidently appropriate. If I had attempted it many years earlier it would have been very inadequate; and if I had delayed it for more than 10 years I probably could not have achieved it, because of other involvements.

When Arthur Cronquist suggested, in 1977, that I write an article for the *Botanical Review* on fungi as aids in plant classification, I had no illusions about a complete treatment, for much information is buried in papers whose titles and abstracts contain no appropriate key words. However, by postponing the attempt until after a related symposium at Uppsala in 1978, I was able to present considerable information in this field. I also made a few discoveries; one that surprised and excited me was that three rust lineages that arose in lower Cyperaceae reached their greatest morphological advancement not only in *Carex* (as expected) but also in *Juncus* or *Luzula*. As the lineages are based on several correlated characters, and the trends in morphological advancement are widely recognized in other rusts, the age and relationship of Juncaceae, as an offshoot of Cyperaceae, seemed incontrovertible. As Juncaceae have been classically accepted as ancestral to Cyperaceae, the indication of their advanced position is understandably unpopular, and was disparaged by two recent authors who, however, attempted no other explanation of the data. The multiple morphological characters of each rust lineage make it extremely unlikely that random similarity would occur even once, the probability being surely at least 100:1 against duplication. That it should occur three times is really unthinkable. Elementary probability tells us that in repeated similarities the odds are multiplied. Thus the odds against random duplication in all the lineages are at least 1 000 000:1. However, in a recent restudy of these families (D. B.O. Savile. Relationships of Poaceae, Cyperaceae and Juncaceae reflected by their fungal parasites. *Canadian Journal of Botany* 68: 731–734.) I found that a smut, *Entorrhiza caricicola*, occurs on *Eleocharis gracilis*, *Carex* spp. and *Juncus* spp., further indicating and advanced position for *Juncus* and relationship with *Carex*. The paper dealing with this and related smuts (J. M. Fineran. A taxonomic revision of the genus *Entorrhiza* C. Weber. *Nova Hedwigia* 30: 1–68, 1978, received in Ottawa 9 April 1979) appeared too late to be incorporated in my *Botanical Review* paper. However, the host range of *E. caricicola* causes the odds against random similarity in the parasites Juncaceae and *Carex* to be perhaps 100 000 000:1. It would probably be hard to find a biological conclusion closer to mathematical proof than that!

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