BIOGRAPHICAL MEMOIRS

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Linda Maddock

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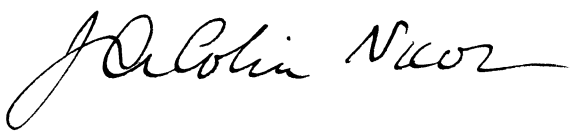

JOSEPH ARTHUR COLIN NICOL

5 December 1915 — 20 December 2004

Elected FRS 1967

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Colin Nicol was a Canadian citizen but spent most of his working life based in the UK, at the Marine Biological Association in Plymouth, and in the USA, at the University of Texas Marine Science Institute at Port Aransas. His most important work was on the physiology of marine organisms, in particular their relationship to light, both natural and biologically produced. He was the first to show that bioluminescence is under nervous control and he made an extensive study of the tapetum lucidum, the reflective layer at the back of the eye of a wide range of animals, particularly those living in dim light. Many other subjects caught his interest and resulted in some 145 publications spanning 50 years.

Early years

Colin was born in Toronto on 5 December 1915. The family soon started on the frequent moves that characterized Colin's life right up until his retirement to Cornwall in 1981. He was the firstborn of the family, having a brother and three sisters.

Colin's father, George Nicol, was born in Edinburgh in 1886. Although earning his living as a corporate accountant, he was a classical scholar and retained a lifelong enthusiasm for literature. He was particularly interested in authors of the Augustan period and wrote a pamphlet on Robert Fergusson (an eighteenth-century poet, much admired by Robert Burns). In his youth he made several trips to Canada, on the last of which he met Colin's mother, Josephine Noele Petrie, in Sherbrook, Quebec. She was born on a small farm in a French-speaking area of Quebec, of an English father and French-Canadian mother. Colin relates that his mother was not educated above primary level and wrote both French and English with 'a somewhat uncertain hand', but that she was 'a very good mother'.

The Nicol family left Canada soon after Colin's birth and moved around Connecticut, Massachusetts and New Jersey, leading to a somewhat patchy early education. He and his

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brother Donald suffered bullying at the American schools as provincial Canadians with a French accent. Colin thought that 'my brother and I ran rather wild, and we paid inadequate attention to our lessons'. He remembered that while living in Jersey City the children were taken several times to the Zoological Gardens of the New York Zoological Society and to the Aquarium at the Battery in New York, which helped to spark his lifelong interest in natural history. This was further reinforced when he was sent to a summer camp after the family moved back to Toronto when Colin was about 10 years old.

Another move, this time to Montreal, meant that Colin had to relearn French and make a big effort to catch up on missed schooling. He succeeded well enough to win a scholarship to high school, where chemistry was the only science taught. However, he pursued his enthusiasm for natural history out of school. 'I spent a great deal of time roaming the fields and woods about Montreal and further afield: I observed birds, photographed nests, ran a little trap line for small mammals.' He also went to lectures at the thriving local bird society and at the local museum, where he made contact with older naturalists. He published a few short notes on the habits of local birds (1)*. Colin was fortunate to meet V. C. Wynne-Edwards (FRS 1970), then an assistant professor at McGill University (later Professor of Zoology at Aberdeen), and to attend some of his public lectures on ornithology. The two remained friends and corresponded until Wynne-Edwards's death in 1997.

Colin's brother, Donald, remembers that

> Colin was a quiet, reserved, studious individual, never sociable in the sense of engaging in sporting activities or of going along with the crowd, but he always had a few close friends with related scientific interests. As long as I can remember he had a study with a desk, at which he spent long hours both day and night. Colin collected things, stamps, butterflies, animals, birds, reptiles and, of course, books. Once I remember walking into the kitchen where my mother was preparing a dish of mushrooms from a bushel or so that Colin had brought in. They were colourful: reds, yellows, browns, whites with flecks of black. Not as trusting as my mother, I asked Colin if he knew what he was doing. His disdainful answer was that of course he knew what he was doing! The Nicols survived this and other eating experiences so one would have to conclude that he was right.

Higher education

Colin wrote that 'my eccentric hobby led inexorably to consideration of a career, to zoology, and to the necessity of university'. His father had hoped that Colin would follow in his own footsteps in commerce or industry, and was puzzled by his elder son's interests. He arranged with a friend for Colin to have some psychological tests, and, the results confirming that Colin would be ill-suited to the commercial world, consented to his enrolling in honours zoology at McGill University in 1934. Colin speaks highly of the courses taught by Wynne-Edwards, N. J. Berrill (FRS 1952) and Mrs Kathleen Terroux, who had been introduced to comparative physiology at Cambridge. This relatively new topic made a welcome change from the main part of the course, based on classical comparative anatomy. Zoology was supplemented by organic chemistry, genetics, botany, physiology (for medical students), statistics, French, German, trigonometry and physical chemistry. In the final year, courses on animal behaviour, distribution and ecology were being introduced, but Colin found the four-year course too long and became very restless by the end.

* Numbers in this form refer to the bibliography at the end of the text.

Again, it was away from the lecture-room that Colin gained experience that was to prove invaluable in his later research career. Wynne-Edwards was at this time studying the Gaspé Peninsula, being interested in glacial relicts and sea birds. In the summer of 1938, Colin helped him with a survey of the freshwater fishes of this wild and beautiful area, for the Quebec Department of Fisheries. They collected fish from all the rivers and streams and did a chemical analysis of the waters. It was a puzzle as to how the stenohaline fishes were able to colonize the rivers flowing north–south into the Bay of Chaleur. The northern part of the peninsula was glaciated, but not the south; they concluded that the Bay of Chaleur must have been heavily flooded with glacial run-off, allowing the freshwater fishes to move along the coast in dilute surface water.

In 1938 Colin moved to the University of Western Ontario, working as a demonstrator in zoology and obtaining an MA degree in 1940 (2). His research project was a study of the development of the air bladder of the bowfin, *Amia calva*, an air-breathing lungfish of Canadian rivers. He was influenced by Professor E. J. Goodrich's ideas concerning the evolution of the lung. He traced the outgrowth of the air bladder from the gut, and found that the arterial supply began as a pair of arteries, only one of which continued development to become the main arterial supply. During the course of this research he gained experience of embryology and histology.

It was at this time that Colin met his wife, Helen Wilhelmina Cameron, who was at art college in London, Ontario. They married in 1941, shortly before Colin joined the armed forces and left for Europe. Helen came from Newfoundland; her father, Duncan Henry Cameron, and mother, Mildred Clarice Gould, were both from old Newfoundland families, the Camerons originating from the Isle of Mull, Scotland. D. H. Cameron was an electrical engineer at the Western Union cable station in Bay Roberts, made several valuable inventions, and wrote a book on cable communication.

During the summers of 1939 and 1940 Colin was employed as a student investigator by the Fisheries Research Board of Canada at Moser River, Nova Scotia. He worked for A. G. Huntsman and his field worker, Harley White. His duties involved measuring and monitoring river flow, helping with tagging salmon and trout, counting fish ascending and descending the river, and mapping and studying a trout stream.

For his PhD Colin decided that he would be better to move back to the USA. At that time the zoology departments at Canadian universities were small, had few doctoral students, and offered few job opportunities. He thought that a degree from a large American university would carry more prestige. He accepted a laboratory assistantship at the University of Minnesota and spent nine months there in 1940–41. He was assigned the task of determining the effect of vitamin C deficiency on the longevity of rats and began a study of bone development with the use of alizarin red. He soon discovered that this approach was unsound, having been used previously only in birds. His stipend was low because he was British, and he found that could not afford to eat properly and was losing weight. On the advice of a fellow student he got a job serving at table in the city hospital. Payment was in meals and he says, 'I ate voraciously, the food was good', and the weight problem was overcome.

In the summer of 1941 Colin worked for the State Fisheries of Minnesota, as leader of a group making a survey of the fish of the St Louis River in northern Minnesota. On his return to Minneapolis he found a letter from the Superior Court of the United States, informing him that he had been deprived of US citizenship. Although born in Canada Colin held a British

passport, Canadian citizenship not being instituted until after the war, and he had also become a US citizen as a child when his family was living in the USA. The next day he received a demand from the British Consul in Chicago to send in his British passport. He was thus stateless and had to move fast to avoid being drafted into the American army as an alien. Canada was already at war and it was well-nigh impossible to cross an international frontier without documents. He took the first train to London, Ontario, before surrendering his British passport. Then, academic life suspended and without work, he walked into the Canadian Army recruiting office and volunteered for overseas service. In 1945 Colin was granted a Canadian passport. He was clearly upset by this stateless period, mentioning it several times in his written memoir.

War service

The recruiting officer, learning that Colin was a science graduate, enlisted him in the Royal Canadian Corps of Signals. After a year's training, he was put in command of a draft of soldiers to take overseas to England.

At holding camp in Farnham he volunteered for a unit using homing pigeons, thinking there would be some biology involved. He spent several interesting months managing a pigeon troop, watching keen pigeon fanciers training birds for mobile warfare and employment at night (3). His experiences led him to conclude that vision was the main factor in homing ability. The birds learnt the appearance of the countryside around their home loft, or anywhere they were fed and watered. Attempts to get the pigeons to fly at night showed that they took much longer to learn and longer to return. Illuminating the loft helped, but this would not have been advisable in wartime.

His brother Donald remarked that 'from Colin's professed low opinion of homing pigeons I would surmise that relatively few of the pigeons came home to roost'. Possibly the powers that be agreed, as in the spring of 1944, 'when the countryside of Kent was looking particularly beautiful', Colin took a cipher detachment to Dover Castle. This was to simulate a heavy flow of wireless traffic to deceive the enemy into thinking that the major invasion effort was to come from Dover.

He was then sent to France, landing at Courcelles and moving on daily after the retreating Germans. Crossing into The Netherlands they spent the winter near Nijmegen, came under infantry attack at Otterloo while moving to relieve Rotterdam, ending up at Groningen. Here, through a Dutch intermediary, he visited the Professor of Zoology at the university. He was working on physiology of lower animals, which rekindled Nicol's enthusiasm for scientific research.

After the surrender of the Germans, the Canadian authorities instituted a programme of adult education. Appointed officer in charge of this programme for the regiment, he was sent on a training course in England. He visited Oxford and was urged by Professor J. Z. Young (FRS 1945) to obtain discharge, for which he would receive benefits. On returning to his regiment, discharge was granted and he entered Magdalen College to complete his doctorate.

Oxford

As a retired soldier, Colin received a grant from the Canadian Government and was also awarded a British Council Scholarship. He spent two years at Oxford, 'savouring University life'. Helen joined him from Canada and worked at the Sir William Dunn School of Pathology as a typist, witnessing the exciting period of research on penicillin by Sir Howard Florey (later Lord Florey) FRS and his staff.

J. Z. Young was interested in research on the anatomy and functioning of the brain, and Colin followed up on his wartime experiences with homing pigeons, studying the effect of ablation of the cortex on training in domestic pigeons. Injuries to the higher cortex did not affect training ability, but those to the lower cortex made the birds lethargic and prevented learning. The experiments gave results similar to those of Lashley on the effect of cortical lesions on learning in rats, and were therefore not of great interest and were never published.

When at the University of Western Ontario, Nicol had taught himself histology and histological techniques. This was before electron microscopy, when biologists still had to reconstruct microstructure and histological organization from stained sections. On returning to research after the war, he learnt how careful visual inspection and dissection of fresh material were invaluable before undertaking more detailed histology.

Looking through some of Young's microscopic slides, Colin came upon the giant axon of *Myxicola*. This seemed to be worth investigation. It is exceptional among sabellids (which usually have two giant axons) and in its size (at least 1 mm in diameter).

He thus switched to a study of the giant axons of polychaetes for his doctoral thesis, concentrating on *Myxicola*. Giant axons were known to occur in crustaceans, annelids and cephalopods, being nerve fibres that are larger than normal. They conduct nerve impulses very rapidly, causing synchronous, or nearly synchronous, muscular contractions for quick escape or withdrawal. Nicol found that the giant axons of the Sabellidae were multicellular throughout and were the final common pathway to the longitudinal muscles for the withdrawal reflex.

He was awarded a DPhil in 1947 (4).

University of British Columbia

In the spring of 1947 J. Z. Young asked Nicol whether he wanted to apply for the position of research assistant at Naples, involving study of behaviour and brain function of the octopus. This might have been tempting if he had not already been 32 years of age with a wife to support. He felt that 'after nine years on the academic ladder it was time to settle in permanent employment'. He wrote to W. S. Hoar, then a professor at the University of British Columbia (Vancouver), and was offered an assistant professorship. He and Helen thus returned to Canada.

He taught histology and embryology to some 200 students, mostly discharged war veterans who were going into medicine. Despite a heavy teaching load of four lectures and many laboratory classes each week, he found time to follow up his doctoral research and examine the double giant axon system of a sabellid, *Eudistylia*, found in Vancouver Harbour. He also wrote a review of current knowledge of the giant axons of annelids, including his own recent work as well as the historical background (5), the first of several review papers on a variety of topics.

Nicol also began to take an interest in a chimaerid, *Hydrolagus*, found in the coastal waters of British Columbia. He studied the innervation of the alimentary tract of chimaerids, which are unusual in lacking a stomach (9). This involved the use of novel histological techniques (6, 7) that proved invaluable in obtaining his next job, in Plymouth.

Colin and Helen's daughter, Josephine Marie Nicol, was born in 1949 in Vancouver, but by then Colin had decided it was time to move on again. The salary at the University of British Columbia was low; there seemed to be no opportunity of widening his academic horizons. Having visited the Plymouth Laboratory of the Marine Biological Association (MBA) on several occasions during his postgraduate studies at Oxford, he wrote to the director, F. S. (later Sir Frederic) Russell FRS. Colin was offered a post as Experimental Zoologist, on the strength of his previous experience in histology. Colin left for England, Helen following with Josephine.

Marine Biological Association

Over the 17 years that Nicol spent in Plymouth he studied various aspects of luminescence and vision in marine animals, producing a solid body of meticulous work that resulted in the award in 1958 of a DSc by Oxford University, and his election to the Fellowship of the Royal Society in 1967. The citation for the latter mentions his work on giant nerve fibres of polychaetes, the autonomic nervous system of fishes and the bioluminescence of marine organisms, and in particular that he was the first to show that light production is under direct nervous control. He also wrote a successful textbook, dedicated to his father, which was first published in 1960 (18), with a second edition in 1967 (22). This described marine animals and their physiological adaptations to the sea. In 1950 and 1951 he organized the first MBA courses in experimental biology. These were the first of a wide range of courses and workshops on experimental techniques that continue to this day.

Life was rather spartan for the Nicol family for several years; Colin's salary was low and there was still postwar rationing. Looking for a suitable research project, he continued his earlier studies on sabellids, investigating the startle reflex of *Branchiomma*. This worm has a crown of tentacles, each of which is provided with a compound eye, a light receptor in the brain and statocysts. It is very sensitive to sound and change of light intensity, each of which provokes the startle reflex (8).

He had been influenced by Pantin's research on neuromuscular mechanisms and wondered whether the production of light in luminescent animals could be under neural control. Some luminescent species use symbiotic bacteria to produce light, whereas others use their own biochemical processes. Some have light organs that glow within the body, whereas others secrete a glowing material into the seawater as a means of confusing predators. More species were being found to produce luminescence but little was known about the processes involved, or the nature of the light. Nicol investigated bioluminescence in a range of species, describing the anatomy and histology of the organs involved, as well as the production of light in response to a number of mechanical, electrical and chemical stimuli.

His first study was of a tube-dwelling polychaete, *Chaetopterus*, specimens being readily obtained by dredging in Plymouth Sound. When stimulated, parts of its body glow, and it also discharges a copious luminescent secretion. As a sensor he used a photoelectric cell, which he coupled to a galvanometer, and employed the technique of A. V. Hill FRS of projecting a beam

of light from a mirror on the galvanometer, across a room for registering on moving photographic paper. The response was found to be under nervous control, and transmission took place through longitudinal pathways (10–12).

Nicol turned his attention to polynoid worms; these have two rows of scales on the upper surface of the body. Light is produced by granular eosinophilic photocytes, which form a unicellular layer on the lower surface of the scale, and this is indeed under nervous control (13, 14). Excitation is transmitted through longitudinal nerve tracts to the scales. These can flash repetitively. They are also readily autotomized, whereupon they continue flashing. He recorded luminescent responses and examined the scales microscopically, discovering a ganglion in the centre of the scale, responsible for the repetitive nervous discharge.

In contrast, unicellular organisms, such as *Noctiluca*, and eggs and larvae of metazoans before the development of the nervous system, will also light up in response to mechanical or electrical stimulation (16, 17).

Nicol also considered the physiology and biochemistry of luminescence in a variety of other species, particularly those from the deep sea. This necessitated some fairly extended scientific cruises, on the MBA's RV *Sarsia* and on RRS *Discovery II* of the National Institute of Oceanography. As he was not a very good sailor he found various distractions to take his mind off the *mal de mer*, including learning ancient Greek. He also visited the laboratories at Millport and Aberdeen in Scotland to study fish physiology. He never liked to waste time in socializing on such occasions, but did find time to visit an aged aunt in Edinburgh.

Acquiring a photomultiplier with calibrated spectrum sensitivity, he determined the spectra of luminescent animals in the laboratory and at sea. He used coloured filters, finding the calculations tedious in the days before electronic computers, but had little confidence in the measurements of light intensity because the conversion into physical units ($W\,cm^{-2}$) involved some uncertainties.

In 1953 Nicol visited the Friday Harbor Laboratories, University of Washington, funded by a John Simon Guggenheim Memorial Foundation Fellowship, where he collaborated with D. Davenport (Santa Barbara College, University of California) to look at luminescence in hydromedusae. Luminescence was found to be intracellular, and while nervous or mechanical stimulation of the photogenic tissue produced light, this was a localized response, each photogenic mass having an independent nerve supply (15).

He then moved on to study the neural control of another kind of effector, melanophores, whose changes and responses could be followed by photoelectric recording. In most selachians there is a tapetum lucidum, a shiny layer behind the retina. This has the function of reflecting light back into the retina and thus increasing visual sensitivity in dim light. To avoid dazzling under bright light the tapetum is occlusible; Nicol determined that the mechanism involves the migration of melanin pigment through cell processes and is independent of central control. During this investigation Nicol found a method of studying the isolated eye as a normally responsive organ, an invaluable technique for much of his later work.

M. F. Land (FRS 1982) had already dealt with the biophysics of such a reflector in scallops, and Nicol and E. J. (later Sir Eric) Denton (FRS 1964) worked on the optical properties of ocular reflectors of dogfish and sturgeon (19). They found that the tapetum allowed a fish to achieve the same absorption of light with only about half as much photosensitive pigment. Denton was a biophysicist with especial interest in photobiology and at the time was measuring retinal transmission to obtain spectra of retinal pigments. This led to a fruitful, if not always harmonious, collaboration on specular reflectivity from the skin of fishes. They

investigated the orientation of reflecting platelets in fish skin, by optical and microscopic methods, and used histological preparations, but did not study ultrastructure because of the hardness of the scales. The reflecting platelets in the skin are preferentially oriented so that they reflect light in the same direction as background illumination, and cause the fish to melt into its background (20, 21).

From 1966 to 1968 Nicol was Visiting Professor at the University of Texas, moving to Port Aransas in September 1966. During this period he left the MBA, worked at the Friday Harbor Laboratories and spent a few months in Oregon before returning to Texas in a permanent post until his retirement in 1980.

Technical skills

Nicol was always eager to acquire new practical skills. During a study of the green pigment of *Chaetopterus* he learnt a great deal about modern techniques of chemical and microchemical analyses from G. Y. Kennedy, a visitor to Plymouth; later, at the Marine Science Institute, Port Aransas, Texas, he learnt chromatography from Chase Van Baalen, a microbiologist, and lipid analyses from personnel in P. L. Parker's laboratory. He gained access to electron microscopy by collaboration with H. Arnott, a botanist at Austin, Texas, who had been studying crystals in plants, and they collaborated in research on specular and diffuse reflectors. To increase his knowledge of electron microscopy, he took a course in the subject at Texas A&M University one summer, under E. L. Thurston, and they then collaborated in research on fish eyes. He also worked with A. C. G. Best of the MBA, using electron microscopy in studies of fish eyes over many years.

Oregon

After leaving Plymouth, Nicol spent a few months in 1967 as Visiting Professor at Friday Harbor (University of Washington) and in 1968 was appointed Professor of Zoology and Director of the Marine Institute at Coos Bay, University of Oregon. However, he found the administrative duties problematic and spent only a few months there before resigning and moving to Texas.

In this brief period in the Pacific northwest he became interested in two unusual local fishes. He studied the tapetum of the sturgeon (24) and the ratfish *Hydrolagus*. The soft skin of *Hydrolagus* afforded an opportunity to study the ultrastructure of reflecting cells by transmission electron microscopy, which filled in a gap in the earlier work with Denton. The reflecting platelets in the skin were oriented like those of teleosts, to provide camouflage of the fish's outline; students at Friday Harbor photographed *Hydrolagus* under water to illustrate this feature. Nicol worked with H. Arnott, of the University of Texas, and found specialized cells that contained a well-organized series of platelets. Each cell contained a stack of 10 or so regularly arranged flat crystals of guanine of quarter-wavelength thickness, each crystal having its own membrane-enclosed compartment (25). Subsequently the same organization of well-ordered crystals was discovered in tapetal reflecting cells of the glasseye *Priacanthus* (27).

Texas

After leaving Oregon, Nicol was appointed Professor of Zoology in the University of Texas at Austin, a post he held from 1968 until his retirement in 1980. During most of this period he was based at the University of Texas Marine Science Institute in Port Aransas.

The inshore waters of Texas have a very rich fish fauna (in terms of numbers of individuals and species). Obtaining a specimen of the ladyfish *Elops*, Nicol was struck by the abundance of reflecting material in the eye; it issued from a dissected eye in white streams, and he decided to look for reflectors or tapeta lucida in other species. This soon revealed that tapeta lucida are common and widespread among bony fishes (they are present in all, or nearly all, cartilaginous fishes).

For this study most fishes that possessed tapeta lucida had to be dark-adapted for at least an hour. This is because the tapetum is usually covered or occluded in the light. When the fish is dark-adapted, the presence of a tapetum is revealed by eyeshine; this can be confirmed by dissection, for which Nicol invested in a set of surgeon's eye instruments. This was a new approach; hitherto the usual method of investigation had been to preserve eyes for histological observation. Careful observation of fresh material revealed much about tapetal structure and function, and dissection was a preliminary to preparing material for physical measurements and chemical analysis. This was accompanied by studies of the histology of the eyes by light microscopy and ultrastructure by electron microscopy. He studied the tapetum in the eyes of not only a wide range of fish species but also invertebrates and crepuscular birds.

At that time it was believed that the reflecting material of fish eyes was guanine, located in the choroid on the pigment epithelium. Nicol soon discovered that many tapeta contained other substances. One, very common, was a lipid, a triglyceride (tridecasahexaenoate) that contained only one kind of fatty acid, with a high refractive index. The material was obtained from finely dissected tapeta and was characterized by saponification, methylation, column chromatography, thin-layer chromatography and gas chromatography. Other substances found were uric acid, a pteridine, 7,8-dihydroxanthopterin, and two melanoid pigments.

There was a strong tradition of paper chromatography at the University of Texas at Austin, on which he was able to draw; H. S. Forrest of the Department of Zoology, an expert on pteridines, afforded invaluable assistance by providing reference compounds. Edward Zyznar, a graduate student, participated in this research (26). As there was a great deal of research going on at Port Aransas with naturally occurring lipids, the methods employed there were a great help in studying lipid tapeta. In collaboration with Chase Van Baalen, chromatographic and enzymatic methods were devised for characterizing and quantifying purines in samples of eyes and skin (23, 32).

The difficulties in dealing with melanoid pigments of tapeta lucida were far more formidable, and Nicol collaborated with Shosuke Ito, a postgraduate student from Japan. He isolated and characterized catfish reflecting pigment as a tetramer of 5,6-dihydroxyindole-2-carboxylic acid coupled with decarboxylated *S*-adenosylmethionine (29).

On several occasions, while examining eyes of fishes for tapeta lucida, Nicol encountered red retinae, first in the light-adapted pike (*Esox*), then in characins and wrasse. He was awarded a Percival Fellowship by the University of Canterbury, Christchurch, New Zealand, and spent March to June 1972 there investigating the red pigment epithelium of the eyes of the local parrot fishes. The retina was dark red, non-fluorescent and intractable and the colour was due to retinal, not visual, pigment. It was found to replace the melanin usually occurring

in the pigment epithelium, occurring in tiny cylinders or rodlets in the processes of the epithelial cells, and in granules in the bases of the cells. The red cylinders undergo radial migrations, as melanin particles do, during the transition from light to darkness and vice versa, in characins and pike but not in wrasse, where they are static and continuously shield the visual cells. The diameters of these red cylinders were found to be very small, some 0.2–0.3 μm, yet easily resolvable by light microscopy, which was puzzling; the cylinders also transmitted circularly polarized light. There was no fluorescence, so a phorphyropsin was unlikely, and the pigment was found to be a polymer of oxidized adrenalin (28).

Brian A. Fineran, a botanist, helped with electron microscopy in the New Zealand parrot fish study, and this led to a very fruitful collaboration when he was able to spend a sabbatical leave with Nicol at the University of Texas. They worked together on anchovies, resolving the complicated and very unusual microstructure of the retina. Nicol already had an intimation that lamellae in outer segments of some visual cells were longitudinally aligned, through observations on eyes of juvenile fish. They found that the lamellae in the outer segments of the cones are longitudinally (vertically) aligned, and the outer segments are precisely aligned with reference to a specular reflector (30, 31). This peculiar orientation of cone lamellae was also observed in some anchovy fry, collected during the spring rush of young fish from the Gulf of Mexico into the bays through the Pass at Port Aransas, when Arnott examined the eyes by electron microscopy. George Best from the MBA in Plymouth also helped Nicol with light and electron microscopy in further study of the red retinae of various species of fish.

Nicol joined two expeditions of the RV *Alpha Helix* from the Scripps Institution of Oceanography. The first (April to June 1975) was to Indonesia to study bioluminescence. The second expedition (1977) was to the Amazon River in Brazil. Nicol was the leader of an international group that joined the *Alpha Helix* for the month of February. The overall objective was to study vision in fishes, with special reference to riverine waters of different optical qualities. Two fishes with especially interesting eyes were collected, namely pirarucu, *Arapaima gigas*, and freshwater herring, *Pillona* (two species). They had tapeta lucida. Adam Locket collected eyes of the former; Nicol examined the latter and found a tapetum formed of guanine crystals. Under light microscopy it showed a well-organized structure resembling the tapetum of the ladyfish *Elops*.

In 1979 Nicol visited the Marine Laboratory of the Johnson Foundation at Harbor Branch near Fort Pierce, Florida, to investigate the eye of the snook, *Centropomus undecimalis*. He had been led to believe that it might contain a new kind of ocular reflector, but in the event the tapetum basically was like that of sciaenids and contained the lipid glyceryl tridecasahexaenoate (33). While at Harbor Branch he noticed a toadfish *Opsanus* in an aquarium showing eyeshine during the day. On investigation the eyeshine was found to originate in the stratum argenteum, which is a shiny layer in the outer choroid. This layer does not normally act as a reflector, because light is prevented from reaching it by the intervening black pigment epithelium and black choroid. In the toadfish, however, all the pigment migrates down the cell processes in the light, leaving the cell bases free of pigment. Consequently there are gaps in the cell bases and light is able to pass the choroid of the photic eye and reach the argenteum, from which it is reflected. The argenteum was a duplex layer consisting of yellow crystals lying over a layer of silvery crystals. The latter were guanine; the former were probably riboflavin. This kind of argenteum was also found in other fishes, scorpion fishes, toadfishes, hairy blennies and lion fishes. Nicol retired before he could follow up this work.

Nicol retired officially at the end of 1980 but received an invitation to lecture in the Department of Zoology at the University of Texas in Austin and spent the first part of the spring semester 1981 giving a series of lectures on sensory mechanisms of marine animals. He was still taking advantage of new techniques right up to his retirement. He returned to the Marine Science Institute at Port Aransas from Austin and carried out an investigation that he had been postponing for years. This was to measure reflectance from diffuse tapeta of a range of species, compared against a standard. This was accomplished with the aid of fibre optics, and the Computer Center of the University at Austin used a simulation program to show that reflectance obeyed Lambert's law. This simulation program, using parameters similar to those found in diffuse tapeta, and making extensions therefrom, provided useful models of tapetal photic function. Apart from published results, the computerized data were sent to Ottawa for storage and future reference.

During his time at Texas, Nicol could hardly avoid the local industry, and he became involved in a number of studies on the effects of fuel oil and other pollutants on marine life (34).

Retirement

Nicol was still reluctant to leave scientific endeavour behind and accepted a fellowship in the Department of Zoology at the Academica Sinica, Taipei, Taiwan, and went there in September 1981. He writes:

> A Chinese student, Hong-Young Yan, was given the task of looking after me. I was almost totally submerged in a Chinese milieu for six months. Hong-Young (I think this means Big Ocean) was very helpful and attentive to my needs. He and some others took me about Taiwan from north to south. I saw a great amount of country and visited various research laboratories and commercial establishments. A great deal of attention was paid to rearing penaeid shrimp which were a popular source of food in Taiwan.

Nicol's final work, in collaboration with Hirokai Somiya, was completed after his retirement and resulted in the publication of *The eyes of fishes* (36). He explains that the paucity of references to his work in the book was because he had to scale down the list of references, which are given in full in his earlier review (35).

Personal

I first got to know Colin Nicol shortly before he retired. His wife, Helen, had returned to England to look after their house in Cornwall. This had been let while they were in the USA and was in need of some care and attention. My husband Robert had been Colin's scientific assistant at the MBA in Plymouth in the 1950s and 1960s and had become a family friend, and Helen called him in for some practical help with the house. We were then both still working at the MBA laboratory. We became very friendly with Colin and Helen, and with their daughter Jo and her family. We lived not far away in southeast Cornwall and sometimes dropped in for tea on a Sunday afternoon. Colin would be in the thick of some energetic project outside, to which he gave his all, as he did to everything he undertook. After retirement he worked in the garden in a city suit, complete with waistcoat, until all were worn out, whereupon he went to the opposite sartorial extreme, sporting a floppy red hat and unravelling cardigan.

He had formal and somewhat old-fashioned manners and was inclined to be brusque. This could be alarming for students and for those who did not know him well. Underneath was a kind heart, a dry sense of humour and a great enthusiasm for discussing a wide range of subjects. He had no time for bureaucracy and was impatient with those who were incompetent or did not take science seriously. If the conversation drifted to a topic about which he had inadequate knowledge, he would immediately leap to his feet and scour the house until he had found a relevant book or article.

One of Colin's Texas colleagues between 1975 and 1980, Wen Yuh Lee, wrote warmly of his professor:

> To his colleagues and students, Dr Nicol was a respected scholar and professor. But to me he was much more, he was a friend, a mentor and an elder with warmth of affection. He taught me what real science is and showed me how to paint an automobile! During the morning coffee and afternoon tea time, we discussed experimental progress; we also talked democracy, religion, economy, history, astronomy, and even about plants along the Texas highway.

Colin was never very patient with mechanical devices and his driving was somewhat erratic. He was just about able to cope in the wide open spaces of Texas, but the narrow Cornish lanes entirely defeated him. This did not deter him from living outside Plymouth for most of the time he was working at the MBA and commuting to Plymouth by motor scooter or train.

In 1961 Helen decided she had had enough of moving around and they settled deep in the Cornish countryside near Lostwithiel, in a small farmhouse complete with outbuildings and some land. They rented the property out while Colin was working in Texas, but returned to spend their retirement there. They created a large garden, which kept Colin busy; while he was fit enough, he always had some big project under way: tree-felling, wall-building or a new planting scheme. In the last few years of his life he cared for Helen as she became increasingly disabled through Parkinson's disease, until her death in 2002. He ran the house with great efficiency and cooked excellent meals.

Colin and Helen are both buried in the grounds, and Jo, their daughter, now lives in the house. Colin is survived by Jo and two grandchildren, Katherine and Richard.

The mark that Colin left on many areas of marine science, and many marine science institutions, is summed up by Patrick Parker, a colleague from Texas: 'I feel that knowing him was as good a thing as can happen to one' and 'we are all diminished by the loss of Colin Nicol'.

Awards and societies

Nicol received a Scholarship in Biology at McGill University, and a British Council Scholarship at Oxford University from 1945 to 1947. During his years at the Plymouth laboratory he held a Guggenheim Memorial Fellowship (1953) and was Visiting Professor at the Scripps Institution of Oceanography. In 1953–54 and again in 1967 he was Visiting Professor at Friday Harbor Laboratories (University of Washington) and in 1961 at Woods Hole Oceanographic Institution. From 1966 to 1968 he was Visiting Professor at the University of Texas. In 1972 he was Erskine Fellow at the University of Canterbury, Christchurch, New Zealand.

He was on the Council of the Society for Experimental Biology and also a member of the Challenger Society, the New York Academy of Sciences, The American Society of Zoologists,

the Marine Biological Association of the United Kingdom, and the American Association for the Advancement of Science.

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In writing this memoir my task has been made much less onerous by Colin's having left a full account of his life and parts of his scientific career. He also persuaded colleagues, friends and relatives to write memories. For this I am very grateful, both to him and to all those who contributed.

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