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The history of plant and soil nematology in Australia and New Zealand, with particular reference to the contributions of six pioneering nematologists

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Abstract. In an era of rapid technological advancement, it is easy to overlook those who established the knowledge base that underpins today's research programs. This paper traces the history of plant and soil nematology in Australia and New Zealand and recognises six pioneers who contributed significantly to its development, namely N. A. Cobb, R. C. Colbran, H. R. Wallace, A. F. Bird, J. M. Fisher and W. C. Clark. Collectively, these scientists described many unique and economically important nematodes, advanced our understanding of the biology and ecology of both plant-parasitic and free-living species, laid the foundation for many of the nematode control measures that are in use today and also contributed to the development of the discipline of nematology at an international level.

Additional keywords: *Heterodera*, *Meloidogyne*, plant pathology, *Radopholus.*

Introduction

In both Australia and New Zealand, nematodes have been recognised as plant pests and as contributors to soil processes for more than 100 years. However, for much of this time, nematodes were studied by naturalists, soil biologists, helminthologists, entomologists and plant pathologists, and nematology was, therefore, not recognised as a separate discipline. This situation changed during the period from 1950 to 1970 when nematology came of age. Increasing numbers of scientists were employed to work specifically on nematodes, and national and international networks were established to help them communicate with each other.

Other than a few brief comments on some of the early work on nematode diseases in Australia (Fish 1970) and New Zealand (Clark 1963), there are no historical accounts of the development of nematology in the two countries. Therefore, this paper reflects on the major advances in Australasian plant and soil nematology before about 1975 and recognises six pioneering nematologists who made significant contributions to the development of the discipline.

Australia

The early years: before 1920

The first person to recognise that nematodes were important pests of crops in Australia was probably Joseph Bancroft, a medical practitioner and naturalist who arrived in Queensland from England in 1864. Apart from his role as a surgeon, his advice was sought on the many medical problems of the young colony, including leprosy and typhoid fever. Bancroft was one of the first to suggest that mosquitoes could transmit disease and his microscopic investigations led to the discovery of the worm that causes filariasis. His contribution was recognised when the worm was later described and named *Filaria bancrofti* (now *Wuchereria bancrofti*).

Bancroft also showed a keen interest in problems affecting stock and agriculture, experimenting with wheat, rice and grapes in an attempt to find suitable crops for the subtropical climate. He also prepared reports on diseases of sugarcane and banana. In one of those reports, Bancroft noted that root-knot nematodes, which he referred to as 'flask worms', were responsible for colonists abandoning farmlands in south-east Queensland (Bancroft 1879). He mentioned that most culinary vegetables, grape, banana and many weeds, including *Solanum nigrum* and *Sida rhombifolia*, were hosts of the nematode and that infection could occur on plants growing in virgin ground. Bancroft's paper also included a description and illustration of root-knot nematode on banana (Fig. 1). This figure of 'Banana disease as observed in Queensland, Australia, March 2, 1879', has handwritten notations indicating various stages in the worm's life cycle: (1) Section of diseased root showing sect (sic) of the parent flask-worm, natural size, (2) Parent flask-worm measures 1/30th of an inch across, (3) Eggs, (4) Newly hatched, 1/50th of an inch long, (5) Supposed male, and (6) Young females assuming the flask-like form.

The only other contributor to Australian plant and soil nematology during the 19th century was Dr Nathan A. Cobb (Box 1). Considered the 'father of nematology in the United States' (Huettel and Golden 1991), Cobb was an American who

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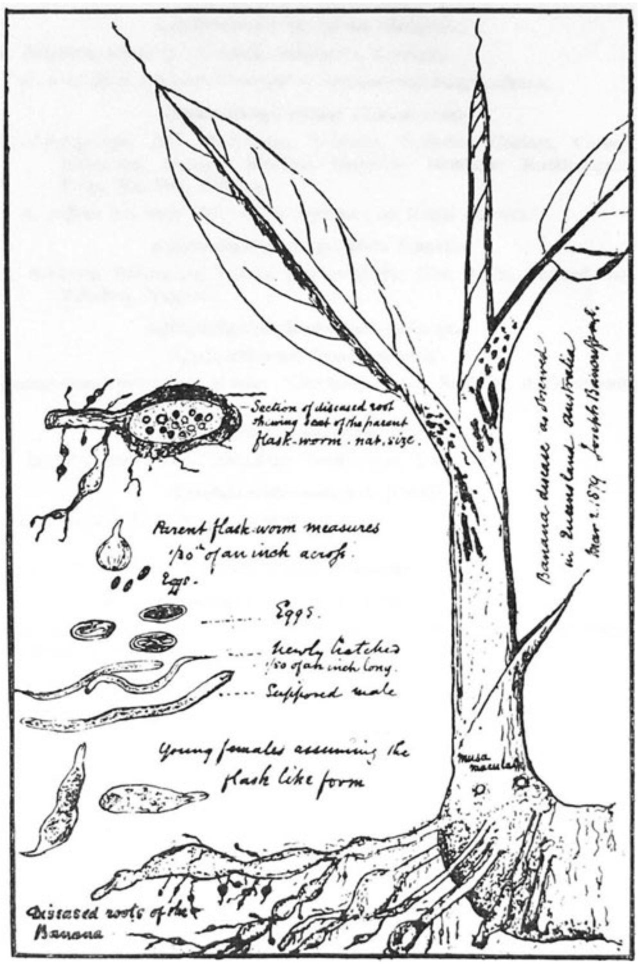


Fig. 1. Root-knot nematode in banana, the first known record of a plant-parasitic nematode in Australia (reproduced from Bancroft 1879).

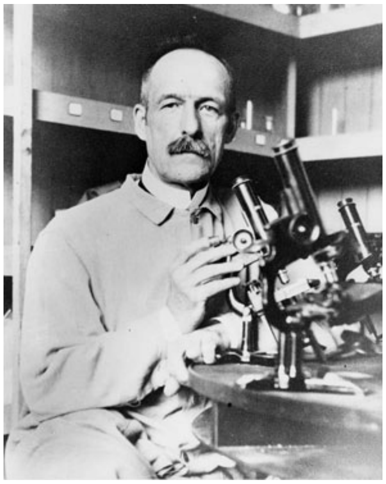
undertook postgraduate studies in Germany before moving to Australia with his young family in 1889. At the time of his arrival, the Australian continent consisted of six separate British colonies and had a population of a little over 3 million. The economy was dominated by agriculture, with new industries such as wheat, meat, dairy products and fruit beginning to supplant wool, which had been the major income earner for most of the century.

Cobb arrived in Australia in early 1889 and initially worked as a salesman in Sydney, but in 1890 he took a position as a stand-in professor at the University of Sydney. Soon after, he was appointed Vegetable Pathologist with the New South Wales (NSW) Department of Agriculture, and this position provided him with an opportunity to continue his work on nematodes. This work had commenced with a PhD study of nematodes associated with whales (Huettel and Golden 1991) and continued with a study of marine nematodes collected while on the ship to Australia (Cobb 1890*a*). Cobb's appointment made an immediate impact, as he soon found nematode problems in agriculture. Thus, the first volume of the *Agricultural Gazette of New South Wales* (published in the same year that Cobb was employed by the Department of Agriculture) contained three articles on nematodes. The first paper (Anon. 1890) described how Cobb had diagnosed a root gall problem on crops such as potatoes, parsnips, carrots and peach. Later in the same volume was a 31-page paper on the nematode worm that caused the problem (Cobb 1890*b*). That paper contains a plate showing galling symptoms on nine different plants and also has neat line drawings of all stages of the nematode. Although Cobb used the combination *Tylenchus arenarius* (Neal), this nematode is now known as *Meloidogyne arenaria*. He also provided a comprehensive discussion of the life cycle of the nematode and included a taxonomic description of the 24 nematode species included in the genus at that time. Finally, he presented a detailed discussion of several possible remedies for the problem, including resistant varieties, fallowing and chemical control. Cobb also commented on trap cropping (repeatedly planting host plants and removing them after the nematode had invaded the roots but before reproduction had occurred). By extrapolating from German observations with the sugar beet gall-worm, he suggested that the time from planting to ploughing up the roots of the trap crop should be reduced from 4 to 3 weeks when managing *T. arenarius*.

The third paper in the first issue of the *Agricultural Gazette of New South Wales* (Cobb 1890*c*) proposed a simple formula for summarising the dimensions of a nematode in taxonomic studies. Cobb argued that his formula was concise, it clearly indicated the position of important taxonomic characters such as the nerve ring and it provided an immediate indication of the general form of a nematode's body. Cobb used the formula in his numerous descriptions of nematodes, and it was also used by many others until about 1940, when most workers switched to the de Man formula.

Cobb was employed as a plant pathologist in NSW, so diseases caused by nematodes were only a part of his responsibilities. Nevertheless, he was constantly on the lookout for new nematode problems and in 1891 he was sent specimens of nematodes obtained from diseased onions in Victoria (Cobb 1891*a*). The nematodes were examined microscopically and found to be *Tylenchus devastatrix* (now *Ditylenchus dipsaci*), which had previously been shown to cause bloating and distortion of onions. Cobb was keenly aware of the nematological work being done elsewhere in the world because 2 years after Ritzema Bos described a new disease of strawberry caused by *Aphelenchus fragariae* (now *Aphelenchoides fragariae*), Cobb was pointing out to local strawberry growers that they should be on the lookout for the problem (Cobb 1891*b*). In the same paper, he took the opportunity to describe a new species of *Aphelenchus* that was common on grass around Sydney and also included a key to the 13 known species in the genus. At about that time, Cobb obtained soil and roots from banana in Fiji, and he later described a nematode from these samples that was named *Tylenchus similis* (now *Radopholus similis*) (Cobb 1893*a*). This nematode was eventually spread around the world and is now the most economically important nematode pest of banana.

Cobb's experience in Australia was a stepping stone to his next position in Hawaii and his eventual return to the USA. Soon after arriving in Australia, he studied sugarcane in the area around the Clarence River and later made numerous excursions into the sugarcane growing areas of northern NSW and also Fiji. These visits resulted in a comprehensive account of the diseases of



Box 1. Nathan Cobb

Nathan A. Cobb was born in Massachusetts, USA, on 30 June 1859 and, because of work responsibilities during his childhood, had little formal education. However, his self-taught knowledge enabled him to pass a local teacher's examination and become a school teacher during his teenage years. Cobb graduated in chemistry from Worcester Polytechnic Institute at the age of 21, and after teaching science for several years he moved to the University of Jena in Germany. His keen interest in microscopy and talent for mathematics, optics and art enabled him to cope well with microscopic organisms and, in just 10 months, he completed his PhD on nematodes associated with whales. After a brief sojourn in Italy, Cobb moved to Sydney in 1889. Although he had no formal training in agriculture, he was soon appointed to Australia's first full time position in plant pathology.

Cobb undertook a significant amount of pioneering work on nematodes in the 15 years he spent in Australia. He created awareness among farmers of common pests such as root-knot nematode and suggested a range of possible control measures. He also described many new species of plant-parasitic and free-living nematodes and published papers on animal-parasitic and marine nematodes. However, Cobb's contribution to Australia was much wider than the field of nematology. He wrote many articles on plant diseases and how to prevent them and spent a considerable amount of time handling diagnostic enquiries from farmers.

In 1895, Cobb took a position as manager of the Wagga Experimental Farms at Wagga Wagga (470 km south-west of Sydney), where tents, a seed shed and a weatherboard building provided his only accommodation until a research laboratory was erected in 1897. Nevertheless, despite the relatively primitive facilities available to him, Cobb did a lot to help the rapidly expanding wheat industry. Epidemics of wheat rust were causing major losses in all the Australian colonies at the time and Cobb represented NSW at several inter-colonial conferences that were held to tackle the problem. He also provided farmers with detailed information on the major wheat diseases in Australia, developed methods of treating wheat seed for stinking smut and provided support for wheat breeding programs by developing methods to identify and classify wheat varieties. Cobb was concerned that much agricultural research lacked a proper scientific basis and, through his own rigorous and labour-intensive experiments, he was able to show others the type of methodology that was required to make progress. With a background in teaching from his early years in the USA, he encouraged researchers to contribute to agricultural bulletins, prepare extension leaflets and participate in field days for farmers. Cobb also promoted the development of farm schools and colleges to educate young people in the technical and practical skills required for work in agriculture.

Cobb was a gifted and hard-working person with broad interests, a rigorous approach to research, a holistic outlook on agricultural development and a flair for explaining scientific matters to others. Cobb's wife and children were his greatest supporters, but they had to fend for themselves for prolonged periods when he was absent due to work commitments. His home was once classed as an official NSW Government Laboratory and, when Cobb was at home, his family provided additional help!

In 1905, Cobb left Australia for Hawaii, where he studied fungal maladies and nematodes on sugarcane. He then accepted a position in the United States Department of Agriculture in Washington DC where he had a profound and permanent influence on the development of nematology in the USA. Cobb died on 4 June 1932 at the age of 72 and is generally recognised as 'the father of nematology in the United States'. More complete accounts of Dr Nathan Cobb's career and his qualities as a person and scientist are given by Blanchard (1957), Huettel and Golden (1991) and Spennemann (2003).

sugarcane (Cobb 1893*b*), which covered diseases caused by bacteria, fungi and nematodes. The section on nematode worms associated with sugarcane contains descriptions of 30 new species of plant-parasitic and free-living nematodes, some of which were included in the new genera *Brachynema*, *Neonchus*, *Chaolaimus* and *Cephalonema*. Cobb clearly gained a good understanding of all aspects of sugarcane production while in Australia, and this was undoubtedly the reason he was offered a position at the Hawaiian Sugar Planters Association Experiment Station in Honolulu in 1905.

In the period after Cobb left Australia, most reports of nematode problems were from entomologists, who were aware that nematodes were pests of plants but rarely studied them. Henry Tryon, the government entomologist and vegetable pathologist in Queensland, for example, often mentioned nematodes in his annual reports from 1902 to 1919. In one of his first reports, Tryon (1903) reported the presence of *Tylenchus* on banana. This was the first record from Queensland of the nematode (now known as burrowing nematode) that Cobb had found 10 years previously in Fiji. However, the nematode pest mentioned most frequently by Tryon was root-knot nematode, largely because it was readily identifiable by the symptoms it produced. Tryon referred to the pest as nematode root gall caused by *Heterodera radicola* (possibly a misspelling of the species name *radicicola*). This species is currently classified in the genus *Subanguina* but was previously placed in many genera, including *Anguina*, *Ditylenchus* and *Anguillulina*. It is almost certainly a misidentification of a species of *Meloidogyne* (Siddiqi 2000). The crops commonly listed as hosts included tomato, potato, banana and tobacco (Tryon 1902, 1907, 1917, 1919) and the nematode's common occurrence prompted Tryon to prepare an educational article (Tryon 1909) that was probably based on material written by Cobb while he was in NSW. Although brief details of the nematode's life history were given, the most interesting comments were on how the nematode was disseminated: (1) 'to introduce the nematode into cultivations previously free of its presence, the farmer has only to bring a few 'pimply potatoes' to his holding, use these for culinary purposes, cast the skins onto the rubbish heap, and then distribute the resulting compost on to his land', (2) 'if horse implements are worked from nematode-infested soil towards soil not in this condition, the parasite may be transported to the latter by their instrumentality, or even so by the soil which the horse's foot may convey', and (3) 'the parasite may pass spontaneously down slopes borne along by water traversing them, as after rainfall'. In situations where the disease was limited in its distribution, Tryon (1909) suggested lifting 'tubercle-affected roots' from soil, burning them and then dosing the site with quicklime or watering it with strong limewater. If the disease was more widely distributed, it was considered better to 'abandon the soil to some other purposes than that of raising the affected crop'.

In 1908, Tryon made perhaps the first comment on interstate quarantine as it pertains to nematodes. He was concerned that introduction of nematode-infested potato tubers 'might occasion root disease in the majority of plants forming Queensland's staple crops' and recommended that 'all potatoes, as a condition of entry into the state, should on their arrival be accompanied by an official declaration issued by the exporting state, that they are free of all readily recognisable diseases' (Tryon 1908). Tryon also documented instances of nematode-infested tubers being sent from southern states, a complaint that is still heard 100 years later!

Prior to World War I, most other reports of nematode problems were from vegetable crops in NSW and Victoria, where eelworms were causing damage to crops such as potato and onion. Examples of papers on vegetable nematodes include Tidswell and Johnson (1909), Laidlaw (1910), Laidlaw and Price (1910) and Laidlaw (1914). There was also one interesting paper on root rot of banana that described the damage caused by burrowing nematode. It was published at the end of the war (Illingworth 1920) and contained some excellent illustrations of the nematode and the lesions it produced on roots, and included a diagrammatic cross section of a root showing nematodes embedded in the rotting cortical tissue. The following statement indicates that at that time, fungi were commonly perceived as the main cause of root rotting: 'examination of these (root) sections under the compound microscope revealed myriads of nematode worms, especially at the point of contact of diseased and healthy tissue. Strange to relate, there was little indication of fungus present. Hence, I do not consider the disease in any way due to fungus'.

The period between 1921 and 1945

There were spasmodic reports of nematode problems on various crops in the 1920s, '30s and '40s, but they mainly widened the known distribution of common nematode species (particularly root-knot nematode) and provided growers with suggestions on nematode control. One disease that had been known since the turn of the century and was still often mentioned was ear cockle of wheat caused by *Tylenchus tritici* (now *Anguina tritici*).

The cereal industry was the backbone of the rural economy during the 1920s and 1930s, and one problem that received increasing attention during that period was cereal cyst nematode (CCN). One early report was by Samuel (1928), who commented on the large number of samples received by plant pathologists from stunted or diseased wheat and oat crops in South Australia and indicated that the most likely cause was either nematodes or a fungus known as *Rhizoctonia*. To help develop an understanding of these diseases, Samuel asked farmers to forward samples from diseased crops to a plant pathologist at the Waite Agricultural Research Institute in Adelaide, and also requested that they include information on the history, distribution and severity of the disease with their specimens.

Dr J. Davidson examined the samples requested by Samuel and clearly established that *Heterodera schachtii* (now known as *H. avenae*) was one of the causes of stunting. He also confirmed that the nematode had been known in South Australia since 1922 and suggested that it had probably been affecting crops for many years previously (Davidson 1930). Davidson discussed work that had been conducted on the nematode in Europe and considered that resistant varieties were the most promising control option. In the same year, Hickinbotham (1930) made detailed observations of affected cereal crops at Roseworthy Agricultural College (just north of Adelaide) and noted that nearly every wheat, barley and oat crop on the farm and in surrounding areas was affected by CCN. He indicated that the nematode could damage plants in four different ways: (1) by delaying the production of crown roots, (2) by reducing rooting depth so that the plant was more prone to drought stress, (3) by reducing the capacity of the crop to compete with weeds, and (4) by weakening or damaging root tissue so that it was more susceptible to fungal attack.

Garrett (1934) provided the first clear evidence that rotation sequence had a major impact on infection levels. Observations on a long-term rotation trial at the Waite Institute showed that wheat following wheat, barley or oats was severely affected by CCN, whereas levels of infection were relatively low after peas or fallow. Manure treatments had little effect on the level of nematode infestation. Garrett (1934) concluded that the beneficial effects of bare fallow and a non-susceptible pea crop were due to the 'starving-out' effect of a year without a susceptible host plant. He also noted that leaving land to pasture was unlikely to be an effective control measure because, as Johnston (1934) had shown, two common weeds in pastures (barley grass and sterile Brome grass) were capable of hosting the nematode.

C. R. Millikan in Victoria was the first person in Australia to tackle the CCN problem in a comprehensive manner and his report on several years of research (Millikan 1938*a*, 1938*b*) contains 45 references and provides an excellent summary of the state of knowledge of CCN at the time. Millikan's papers were wide ranging, his conclusions were based on experimental evidence, and his contribution to CCN research deserves more recognition than it has received in the past. In his initial experiments, Millikan grew wheat in pots, inoculated the plants with *H. avenae* and was able to reproduce the symptoms observed in the field. The nematode reduced plant height from 24.1 to 13.3 cm and the root systems of inoculated plants were much shallower and more branched than the non-inoculated controls (Millikan 1938*a*).

Millikan's experiments on resistance were the forerunner of much more work in this area over the following 50 years. In 1936 and 1937, his resistance screening experiments included ~200 varieties of wheat, barley and oats, with a susceptible variety included in every tenth plot to check that the nematode infestation was relatively even across the site. The number of white cysts on roots was assessed in October (and sometimes also in December) and varieties were then rated as resistant, moderately resistant, susceptible or very susceptible. Millikan classified all wheat varieties as susceptible or very susceptible, but oat varieties (and to a lesser extent barley varieties) exhibited varying degrees of resistance. Results of a further experiment showed that the nematode-resistant oat varieties Mulga and Guyra markedly reduced nematode populations relative to susceptible varieties of wheat, barley and oats (Millikan 1938*a*).

In studies on the pathology of nematode infestation in a range of cereal varieties, Millikan showed that second-stage larvae penetrated roots of resistant and susceptible varieties equally, but further development occurred only in susceptible varieties. In wheat and barley, giant cells and syncytia (required to maintain nematode feeding and reproduction) were observed in vascular tissue at the head of the developing worm but were not observed in a resistant variety of oats (Millikan 1938*a*). This phase of the work was illustrated with some excellent photographs showing the symptoms induced by the nematode in roots. There were also photographs of partially developed nematodes in transverse sections of roots of resistant and susceptible varieties.

Millikan (1938*b*) confirmed Garrett's observations in 1934 on the benefits of fallowing and a rotation crop of peas. He also reported on the effects of soil properties on nematode populations, the role of fertilisers (particularly zinc) on root development and the yield of nematode-infested crops, and on relationships between the time and depth of sowing and nematode infestation levels.

The post-war years: 1945–75

Employment of scientists with specific responsibility for nematodes

The 20 years after the end of World War II was a period of rapid expansion in nematology in Australia, with many research organisations appointing the first specialists to work on nematodes. The various state government agencies responsible for applied agricultural research and extension had become aware of the importance of nematodes as crop pests and one of those agencies (the Western Australian Department of Agriculture) appointed Olga Goss to a nematology and plant pathology position in 1945. Robert (Bob) Colbran joined the Commonwealth Scientific and Industrial Research Organisation (CSIRO) in 1948 but transferred to the Queensland Department of Agriculture and Stock in 1954, while J. W. (Jack) Meagher and C. D. (Cliff) Blake were later appointed to the Victoria and NSW Departments of Agriculture, respectively. CSIRO appointed Max Sauer and Alan Bird to nematology positions in the mid 1950s, and H. R. (Harry) Wallace joined them in 1963. Within the university system, John Fisher was appointed by the University of Adelaide in 1956, while Warwick Nicholas began his career at the Australian National University in 1960.

Cataloguing Australia's nematode fauna

One attribute that stood out in many of Australia's pioneering nematologists was their remarkable versatility. Although their main roles included applied research, basic research, diagnostics, extension work and teaching, nematologists such as Colbran, Meagher, Sauer and Fisher were also excellent taxonomists and were the main source of taxonomic expertise in Australia during the 1950s and 1960s. Together with Cobb, they described or identified most of the plant parasites and some of the free-living nematodes associated with crops and native vegetation in Australia. Today, nematode taxonomy is seen as a specialist discipline, but 50 years ago it was one of the many skills expected of those working with nematodes.

Some of the nematodes Cobb described during his time in Australia have already been mentioned (e.g. Cobb 1893*a*), and after he returned to the USA, he continued to describe nematodes that he had collected in Australia (Huettel and Golden 1991). It was another 40 years before the next generation of taxonomists began describing other Australian nematodes. Colbran (Box 2) was the most prolific of this group, publishing 13 taxonomic papers and describing 36 new nematode species in numerous genera over a period of 16 years from 1956 to 1971. Interestingly, the first nematode described by Colbran (*Trichodorus minor* Colbran 1956) was of interest to nematode taxonomists for many years because of its similarity to a nematode known as *T. christiei* (Allen 1957) in the USA. Both names were retained for many years because some taxonomists believed there were minor differences between the two species. Finally, in 1975, after both the nematodes had been transferred to the genus *Paratrichodorus*, *P. christiei* was declared a junior synonym of *P. minor*.

One of Colbran's most important contributions was to carefully document all the plant-parasitic nematodes that he had found in Queensland. His records were the most comprehensive nematode host lists available in Australia at the time, with the first paper (Colbran 1958) listing 269 plant species in 62 botanical families as hosts of *Meloidogyne* spp. in Queensland. A second paper listed the hosts and localities where 105 nematode species had been recorded (Colbran 1964*a*). Goss (1958*b*) produced similar records from Western Australia (WA) and these publications encouraged others to produce nematode host lists for their own states.

Another nematologist with an interest in taxonomy was Max Sauer who published eight taxonomic papers between 1958 and 1969. In his early papers, Sauer described several new species of plant parasites and in 1965 established the genus *Morulaimus* to accommodate a group of nematodes that are found only in Australia and New Zealand (Sauer 1965). He described three new species of *Morulaimus* and transferred species previously described by Colbran (1961) and Fisher (1964*a*) as *Belonolaimus hastulatus* and *Telotylenchus whitei*, respectively, to that genus. Later in his career, he described a range of free-living nematodes, including *Basirotyleptus*, *Carcharolaimus*, *Bullaenema*, *Tylolaimophorus*, *Leptonchus*, *Tylencholaimus* and *Chitwoodius*.

Other taxonomic contributions during the 1960s included descriptions of *Dolichodorus* and *Paralongidorus* from South Australia (Fisher 1964*b*) and a description of *Xiphinema monohysterum* from NSW (Brown 1967). Jack Meagher also contributed by erecting the genera *Tylodorus* and *Aconotylus* (Meagher 1963, 1968*a*) to accommodate nematodes from *Eucalyptus* forest that appear to be unique to Australia.

When Sher (1968) revised the genus *Radopholus*, he considered the genus was indigenous to Australia, New Zealand and neighbouring countries and also mentioned that the large number of species present in native habitats in Australia was remarkable considering the relatively small number of samples collected. Therefore, it is not surprising that taxonomists working in Australia have made a major contribution to the taxonomy of this genus. Cobb (1893*a*) described *R. similis*, the most widespread and economically important species, from banana in Fiji, while two of the species (*R. inaequalis* and *R. neosimilis*) included by Sher

Box 2. Bob Colbran

Robert C. Colbran (known by his family and colleagues as Bob) was born on 3 August 1926 and grew up in the Brisbane suburb of St Lucia, only a few hundred metres from the campus of the University of Queensland. In 1948, he graduated with a BAgSc degree from that university and then accepted a position with CSIRO at Stanthorpe, an apple-growing area about 220 km south-west of Brisbane. Colbran was asked to 'find out why growers were having trouble replanting apple trees', and so he started his research by sectioning stained roots with a microtome. In a recent interview, he commented that 'I noticed many red, worm-like organisms in the tissue that I thought may have been nematodes'. His supervisors and colleagues knew nothing about them, so he was forced to undertake research on his own. By 1953 he had published his first paper showing that lesion nematode (*Pratylenchus*) was present in the roots of most apple trees in the district; that the nematode stunted apple trees grown in pots; that treatment with dichloropropene–dichloropropane or formalin killed the nematodes and improved plant growth; and that all available apple rootstocks were susceptible to the nematode (Colbran 1953).

In 1954, CSIRO asked Colbran to move to Canberra but because he wanted to stay in Queensland, he joined the Queensland Department of Agriculture and Stock (later the Queensland Department of Primary Industries). He was placed in the Entomology Branch because the Department 'didn't know where else to put me' and was told by his supervisor that 'I don't care what you do as long as you publish the results'. His paper on plant nematodes in Queensland (Colbran 1955) and his description of *Trichodorus minor* and *Hemicycliophora truncata* (Colbran 1956) were the start of a long and productive career with the Department.

In 1958, Colbran was awarded a fellowship from the Rockefeller Foundation in New York and spent 12 months at the University of California, Berkeley in the laboratory of Dr Merlin Allen. It was an opportunity to learn more about nematodes and refine his taxonomic skills. On his return to Australia, Colbran continued his taxonomic studies and also tackled the practical issues faced by growers trying to overcome problems caused by nematodes on a wide range of crops, including pineapple, banana, citrus, grapevine, tobacco, strawberry, ginger and numerous vegetable crops. In 1962, Colbran received his PhD from the University of Queensland for studies on some of those crops.

Colbran was an excellent nematode taxonomist and in the 16 years from 1956 to 1971 he sampled many of the natural and agricultural habitats in Queensland, describing 36 new nematode species in numerous genera. He also published comprehensive records of the nematodes present in Queensland and, with the help of colleagues in other states, his host lists were later expanded to cover the whole of Australia.

Colbran's other major contribution was his work on nematode control. He began his career at the start of the nematicide era and his experiments with soil fumigants and non-volatile nematicides in the 1950s and 1960s formed the basis of the chemical control programs that were used in many industries for the next 30–40 years. However, Colbran gained more satisfaction from his work on non-chemical controls: his recommendations on hot water treatment of banana and ginger planting material, on the use of sawdust mulch as a control measure for root-knot nematode in ginger, and on the value of cover crops for managing nematodes in pineapple have stood the test of time and are still used by growers today.

In 1976, Bob Colbran was awarded the Agricultural Science Medal by the Australian Institute of Agricultural Science for his services to agriculture. He finished his career as Director of the Plant Pathology Branch of the Queensland Department of Primary Industries, retiring in 1986. When asked in 2007 what aspects of his work gave him the most satisfaction, he replied without hesitation: 'finding and describing new nematode species and developing nematode control measures that were useful to farmers'.

(1968) in his revision of the genus were described by Sauer (1958). Two years after Sher's publication, Colbran (1970) added another 11 new species and included keys to both males and females of the 22 species in the genus at that time.

Nematodes in cereals and other field crops

Although losses caused by CCN had been observed in both South Australia and Victoria since the late 1920s, most of the early work on root disease problems in cereals was done by mycologists (Fish 1970). Thus, it is not surprising that the prevailing view among plant pathologists in the mid 1960s was that poor growth and patchiness in wheat was primarily caused by *Gaeumannomyces graminis* var. *tritici* (the take-all fungus) and *Rhizoctonia solani* (the cause of *Rhizoctonia* root rot).

This state of affairs changed considerably over the next 10–15 years because for the first time, there were enough nematologists in Australia to seriously address the CCN problem. A review paper by Wallace (1965) was important in crystallising ideas about the direction to be taken because it set out the issues that had to be researched before growers could be provided with 'recommendations based on scientific facts relevant to Australian conditions'. The 10 key research topics listed by Wallace were: (1) the distribution of the nematode in Australia, especially in areas outside South Australia and Victoria, (2) an estimate of losses in yields, (3) the influence of environmental conditions on survival, dormancy, hatching, infection and population increase in relation to the Australian climate, (4) the factors in different soil types affecting distribution and abundance, (5) the taxonomic status of Australian populations of *H. avenae* and whether different races exist, (6) host preferences of different populations and races, (7) changes in population density with season, soil type and crop locality, (8) the relationship between crop damage and nematode population density under different environmental conditions, (9) the testing of wheat varieties for resistance to the nematode, and (10) the use of nematicides in badly infested areas. It is a tribute to Wallace's insight that, within 2 years of arriving in Australia and having no experience with CCN, he was able to present such an astute plan of action. Twenty years after Wallace's paper was published, all his suggestions had been acted upon and CCN was being managed through a combination of resistant and tolerant varieties, crop rotation and nematicides (Brown 1987).

The period from 1965 to 1980 was a high point in plant nematology in Australia. CCN was the primary focus of all this activity, with five organisations (the Departments of Agriculture from NSW, South Australia and Victoria, the University of Adelaide and the CSIRO) contributing resources for work on the nematode. John Fisher (Box 3), Jack Meagher, Rob Brown and Albert Rovira played leading roles during this period, but the fact

Box 3. John Fisher

John M. Fisher was born on 14 March 1932. He graduated in Agricultural Science from the University of Sydney in 1953, and then worked as a plant pathologist in the NSW Department of Agriculture for a few years. Fisher joined the Waite Agricultural Research Institute (part of the University of Adelaide) in 1956, at a time when it was becoming apparent that plant-parasitic nematodes were having a major impact on agricultural crops. His appointment was the first lectureship in plant and soil nematology at an Australian university, but Fisher admitted that he knew little about nematodes at that time. He taught himself the basics of nematode biology and identification and in 1961 he studied nematology with Merlin Allen and Dewey Raski at the University of California, Davis.

Fisher soon turned himself into a well-rounded nematologist who was able to contribute to the discipline of nematology in many ways. Early in his career he surveyed agricultural and natural habitats, described several new nematode species and identified many of the common plant-parasitic nematodes in South Australia. Fisher also collected insect-parasitic and fungal-feeding nematodes and those specimens are still held in the Waite Nematode Collection. Another early contribution was to clarify the life cycle of *Fergusobia*, the only nematode known to have a generation in a plant (gall) followed by one in an insect (fly).

Since the fungal-feeding nematode *Aphelenchus avenae* was readily cultured in the laboratory, Fisher used it in many of his studies on the biology and physiology of nematodes. In collaboration with others, he found that cell divisions in the gonad of the nematode were restricted to periods of lethargus in the second and third moults. He also showed that a minimal amount of feeding was essential before a moult would occur, and he used ligatured nematodes to explore the role of ecdysteroid hormones in the moulting process.

Fisher made a significant and lasting contribution to Australian agriculture through his work on *Heterodera avenae* (cereal cyst nematode, CCN). He supervised many postgraduate students and over a period of more than 30 years they collectively investigated the egg hatching process, assessed the infectivity of second-stage juveniles under different temperature and moisture regimes, studied the impact of environmental factors on nematode development, examined the effects of nutrients such as manganese on nematode damage and determined economic thresholds by relating nematode population densities to yield loss and by understanding the relationship between initial densities and nematode multiplication rates. John also played a key role in identifying useful sources of resistance to *H. avenae*, determining mechanisms of resistance and tolerance and developing laboratory assays to assess resistance. He was also involved in work with ethylene dibromide, which alerted the cereal industry to the extent of problems caused by CCN.

Fisher's other significant contribution to agriculture was through his involvement in Annual Ryegrass Toxicity. When he first saw galled ryegrass with bacterial slime, he wondered whether the anguinid nematode and the bacterium in the galls were involved in toxicity to stock. Later, with the help of several students, the relationship between *Anguina* and *Corynebacterium* (now *Rathayibacter*) was confirmed, the role of the nematode vector was elucidated and studies of nematode population dynamics and control were carried out in the field.

Fisher was always enthusiastic about nematodes and he encouraged and motivated his students, many of whom went on to become well-respected nematologists. These students included Adrian Evans, Bob Banyer, Graham Stirling, Chris O'Brien, Alan McKay, Julie Stanton, Vivien Vanstone, Tony Pattison, Julie Nicol and Sharyn Taylor (the latter two were co-supervised by Kerrie Davies who worked with Fisher as a postdoctoral fellow). When asked what he was most proud of, John Fisher cited his CCN work, his students, his work on chemical stimuli for feeding and his studies on moulting. In 1987, he was awarded the Urrbrae Medal by the Urrbrae Memorial Board of Management for the work that led to the control of CCN.

that 11 scientists contributed to the 50 or so papers on CCN published in peer-reviewed journals between 1965 and 1980 indicates the level and breadth of activity involved. Inter-organisational and interstate rivalries were a feature of this period, but fortunately they did not stifle innovation. In fact, the competitive forces that were unleashed probably hastened progress.

The first research papers on CCN during this period covered a wide range of issues related to the biology and ecology of the nematode, including its distribution in Victoria and NSW (McLeod 1968; Meagher 1968*b*), seasonal population dynamics (Meagher 1970), hatching mechanisms (Banyer and Fisher 1971*a*, 1971*b*) and interactions between *H. avenae* and *R. solani* (Meagher and Chambers 1971). Papers on various control measures also began to appear and they covered topics such as rotation crops (Meagher and Rooney 1966), variability within the nematode and potential sources of resistance (Mathison 1966; Brown 1969; Brown and Meagher 1970; O'Brien and Fisher 1974) and chemical controls (Brown *et al*. 1970). This level of activity continued into the 1980s, but the more recent work on CCN is not covered in this manuscript because it appears in a companion paper in this volume (Vanstone *et al*. 2008).

The first Australian work on lesion nematode (*Pratylenchus thornei*) on cereals was also undertaken in the 1960s. Colbran and McCulloch (1965) found high populations of the nematode in wheat fields in Queensland and suggested that it could be economically important. Baxter and Blake (1968) then studied *P. thornei* in NSW and concluded that it was likely to reduce crop yields in relatively dry seasons if wheat was planted in fields with relatively high nematode population densities. These studies were the precursor of more recent work in north-eastern Australia that is discussed elsewhere in this volume (Thompson *et al*. 2008).

Nematodes in horticultural and vegetable crops

Prior to ~1950, there were numerous records of nematodes attacking horticultural and vegetable crops in Australia, but they largely documented observations of damage. However, this situation changed rapidly in the next decade or so, as the first specialist nematologists began using experimental approaches to investigate nematode problems in horticulture.

Tree crops. When Colbran was first appointed in Queensland, he was based in an apple-growing area and began his career by studying the role of nematodes in apple replant disease. He found that a nematode identified as *Pratylenchus coffeae* was widespread in orchards around Stanthorpe (Colbran 1953), although later studies (Colbran 1979; Dullahide *et al*. 1994) showed that the species involved were actually *P. penetrans* and *P. zeae* (syn. *P. jordanensis*). Colbran (1953) showed that stunting in apple seedlings could be induced by inoculating them with roots infested with *Pratylenchus*, and that growth improved markedly when infested soil was fumigated. Since all apple rootstocks available at the time were susceptible to the nematode (Colbran 1953), a follow-on study investigated the potential of fallowing as a control measure. These results showed that suppressing weeds with sawdust mulch markedly reduced lesion nematode populations in soil (Colbran 1954).

Work in South Australia on nematodes in tree crops commenced with a study that confirmed previous observations on the resistance of two peach varieties to *Meloidogyne javanica* and *M. incognita* (Burdett *et al*. 1963). Fisher then went on to study the population dynamics of *Paratylenchus nanus* on apples and apricots (Fisher 1967*a*) and also showed that its morphometric variability was partly due to environmental factors (Fisher 1965). Although *P. nanus* was relatively common in orchards in South Australia, work on the nematode was terminated when Fisher (1967*b*) found that it did not damage the host plant.

Pineapple. Soil fumigants became available in Australia in the early 1950s and some of the initial studies on soil fumigation were done on pineapple. The first experiments (established by Colbran in 1955) compared the efficacy of ethylene dibromide, dichloropropene plus dichloropropane and dibromochloropropane, and the recommendations arising from those experiments (Colbran 1960*a*, 1960*b*) formed the basis of control procedures that were used in the pineapple industry for another 40 years. Later, Colbran (1969*a*) demonstrated that a combination of green panic (*Panicum maximum* var. *trichoglume*) and Rhodes grass (*Chloris gayana*) or legume siratro (*Phaseolus atropurpureus*) were useful as rotation crops for pineapple, with the yield response from fumigation being much smaller (~10%) following these crops than following pineapple.

Banana. Australia's banana plantations are located in tropical and subtropical regions of NSW and Queensland, and some of the world's first detailed studies of nematode problems on banana were undertaken by Cliff Blake in northern NSW. Root-knot nematode was not considered economically important, so Blake's studies concentrated on the burrowing nematode (*Radopholus similis*), a major pathogen of banana wherever it is grown (Blake 1961). His keynote paper in 1961 described the histopathology of root lesions, showed that *R. similis* was the primary cause of banana root rot and demonstrated that 11 months after soil was fumigated, nematode populations had returned to relatively high levels. Blake (1961) also showed that burrowing nematode was being spread to new areas in infested planting material (sets) and that nematicide treatment was ineffective because the chemicals failed to adequately penetrate the set. Therefore, Blake carried out a series of experiments on the effect of hot water on *R. similis* in various types of banana planting material and concluded that a temperature of 55°C for 20 min gave effective control with minimal losses. He showed how a hot-water tank suitable for treating banana planting material should be constructed and indicated that in northern NSW, ~45 000 sets were treated commercially with hot water in the 1960 planting season. Colbran and Saunders (1961) and Colbran (1964*b*) showed that similar treatments were effective in Queensland.

In his pathogenicity studies with *R. similis*, Blake (1961) co-inoculated bananas with *Fusarium oxysporum* and *R. solani* and observed rotted roots only on plants inoculated with *R. similis*. Later, he extended this work on interactions between *R. similis* and fungi and found that lesions were more extensively necrotic and increased more rapidly in size when *F. oxysporum* was inoculated with the nematode (Blake 1966). The endodermis was strongly suberised and prevented *R. similis* from invading the stele whereas *F. oxysporum* was able grow through the endodermis, colonise stellar cells and cause necrosis of vascular cells. Since necrosis of the stele is a significant component of the disease syndrome in the field, Blake concluded that nematodes and fungi both play a role in destroying roots and reducing the economic life of banana plantations. Blake later prepared two reviews (Blake 1969, 1972) that summarised worldwide knowledge of banana nematodes at that time.

Grape. Grapevine nematodes received considerable attention during the 1950s and 1960s from Max Sauer, who was based in the grape-growing area around Mildura, Victoria, where nematodes were a major factor limiting grape production. Sauer was assisted in his initial survey work by J. W. Seinhorst, who was visiting Australia from the Netherlands at the time, and their results indicated that root-knot nematode, citrus nematode (*Tylenchulus semipenetrans*) and lesion nematode (*Pratylenchus* spp.) were widespread in Sunraysia vineyards (Seinhorst and Sauer 1956). A follow-up survey by Sauer (1962) showed that root-knot nematode infestations were more common in coarse-textured soils, whereas citrus nematode tended to occur in soils that were slightly finer in texture. The finding that citrus nematode could parasitise grapevine was the first record of this association anywhere in the world, and later work showed that the nematode could markedly reduce the yield of grapevine (Sauer 1966, 1969).

In 1957, Sauer embarked on a rootstock research program that was to have a major impact on viticulture throughout Australia. Initially, five phylloxera-resistant rootstocks were tested in the field and two rootstocks with some tolerance to *M. javanica* (101–14 and du Lot) were found to increase the yield of sultana (Sauer 1967). The responses of vines in the first few years of this experiment prompted Sauer to import several other rootstocks that had performed well in nematode-infested soils in California. Numerous rootstock trials with sultana as the scion variety were established between 1962 and 1966, and the results (Sauer 1972, 1974, 1977) clearly showed the benefits of some of these rootstocks in light-textured, nematode-infested soils. When yields were averaged over 5 years and 10 experiments, vines on the resistant rootstock varieties Ramsey and Dogridge, for example, yielded 2.5 and 2 times more fruit, respectively, than own-rooted vines (Sauer 1974). Sauer's work was extended by others to wine grapes with similar results, and rootstocks are now recommended wherever grapevines are grown in situations where nematode problems are expected (i.e. warm climates and coarse-textured soils).

Vegetables and other annual crops. From the time Bancroft made the comment in 1879 that root-knot nematodes were responsible for vegetable growers abandoning land in south-east Queensland, nematodes were recognised as an intractable problem on vegetables and other annual crops. However, the options available for managing nematodes were limited until Colbran in Queensland, Goss in WA and Sauer in Victoria began working on controls for root-knot nematodes in a wide range of annual crops, including tomato, potato, pumpkin, tobacco, strawberry and ginger. Much of their early work was on soil fumigants and by the early 1960s, experimental evidence of their effectiveness was available on several crops (Colbran and Saunders 1957; Goss 1958*a*, 1965*a*; Sauer and Giles 1959; Colbran and Green 1961). Other nematode pests of vegetables were also recognised, with Goss (1961, 1965*b*) reporting on the management of *Pratylenchus* and *Heterodera* in vegetable crops.

Soil fumigation was not the only control measure in annual crops investigated by Australia's pioneering nematologists. Sauer and Giles (1957) evaluated the performance of tomato hybrids with resistance to root-knot nematode and also made observations on the value of fallowing, the effectiveness of barley as a rotation crop and the potential for resistance-breaking biotypes to develop when nematode-resistant plants were grown repeatedly. In Queensland, Colbran (1969*b*, 1974) showed that hot-water treatment and sawdust mulch were vital components of an integrated management program for root-knot nematode on ginger. In crops that were planted as seedlings rather than seed, the importance of clean planting material was recognised, with Colbran and Saunders (1957) demonstrating the efficacy of soil fumigants in tobacco seedbeds. Goss was also an enthusiastic promoter of pathogen-free planting material, and her booklet on nursery production and hygiene techniques (Goss and Harrison 1979) outlined the procedures for keeping planting material free of nematode and plant disease problems.

Nematodes, the soil environment and plant disease

As interest in plant and soil nematology grew during the post-war period, one research topic that received considerable attention was the role of soil environmental factors in influencing nematode behaviour. One of the key contributors in this area was Harry Wallace (Box 4), whose initial studies on cyst nematodes in England during the 1950s showed that factors such as soil structure, soil moisture, temperature and aeration had major effects on egg hatch and nematode motility. Those studies formed the basis of his book on the biology of nematodes (Wallace 1963), which was published in the same year that Wallace moved to Australia. Wallace then switched his attention to root-knot nematode and in the next few years he

Box 4. Harry Wallace

H. R. (Harry) Wallace was born on 12 September 1924 in Lancashire, England. He trained as a zoologist and then studied wood-boring beetles for his PhD, which he received from the University of Liverpool. In 1952, he joined the School of Agriculture at the University of Cambridge and began working on nematodes, studying seasonal emergence and the effects of soil structure, particularly aeration, on hatching in *Heterodera schachtii*. While at Cambridge, Wallace's discussions with Sir James Gray, Professor of Zoology, led to his work on locomotion in nematodes, which commenced soon after he moved to Rothamsted Experimental Station in 1955. However, Wallace also continued to investigate the effects of environmental factors on hatching of nematode eggs and infectivity of larvae, including attraction to roots, particularly in *Heterodera* spp. and *Ditylenchus dipsaci*. For some of these studies, he worked collaboratively with Audrey Shepherd and J. J. Hesling. In 1960, he was awarded a DSc from the University of Liverpool.

In 1962, Professor W. R. (Buddy) Rogers visited Rothamsted and encouraged Wallace to move to Australia. Wallace arrived at the then new CSIRO Division of Horticulture in Adelaide in 1963, where Alan Bird was already employed. There he concentrated his efforts on *Meloidogyne javanica*, arguably the most serious pest nematode in Australian horticulture. He continued his work on environmental factors affecting movement of infective juveniles, studied the development, hatching and survival of eggs, and also became interested in factors affecting reproduction of *M. javanica*, and the effects of the nematode on its hosts. Seymour Van Gundy (University of California, Riverside) spent a sabbatical with Wallace and Bird in 1966, and collaborated with them on a study of aging and starvation in larvae of *M. javanica* and *Tylenchulus semipenetrans*.

In 1971, Wallace was appointed to the Chair of Plant Pathology at the Waite Institute, The University of Adelaide. While this meant contributions to undergraduate teaching and an increased administrative load (and hence less personal time for research), it also meant that he had PhD students and that he could broaden his research interests. He continued his work on root-knot nematode and its effects on photosynthesis and nutrient demand in host plants. One major study with Brian Stynes involved the use of a synoptic approach to assess the relative importance of various environmental factors on the growth and yield of plants. With Frances Reay, he investigated the susceptibility to and effects of *M. javanica* on various native plants; with Greg Walker and Joe Kimpinski he examined interactions between nematodes, environmental factors and host plants; and with Gordon Grandison and Anthony Smith he investigated the distribution and abundance of *Pratylenchus* and *Helicotylenchus*.

One of Wallace's great strengths was his ability to write with clarity and enthusiasm. He was able to integrate, effectively summarise, critically examine and review large amounts of information. His first book, *The Biology of Plant Parasitic Nematodes* was published in 1963 (Wallace 1963). In 1965, he published an influential review paper on cereal cyst nematode (CCN) and directions for future research (Wallace 1965). Later, with Alan Bird, he wrote a chapter on the chemical ecology of the Acanthocephala and the Nematoda (Bird and Wallace 1969). His ideas on etiology and the nature of disease were expressed in his book *Nematode Ecology and Disease*, published in 1973.

Wallace was a particularly able administrator. On most days, his desk was cleared by lunch time, and the door to his office was then opened – a signal to everyone that he was available for advice and discussions. In this way, he helped and influenced countless people, including undergraduate and postgraduate students and academics (and even an ex-Premier of South Australia, who often dropped in to discuss disease problems in his cherry orchard!). Wallace's students included Sariah Meon, Joe Kimpinski, Greg Walker, Jackie Nobbs and Brian Stynes, and with John Fisher he co-supervised a number of students working on CCN. In 1975, Professor Harry Wallace was made a Fellow of the Australian Academy of Science.

investigated the effects of temperature, aeration, moisture stress and detergents on the hatch, development and survival of *M. javanica* (Wallace 1966, 1968, 1969*a*; Bird and Wallace 1965).

As Wallace mentioned in the preface to his second book (Wallace 1973), his ideas on many aspects of plant nematology gradually evolved as he came to recognise the ecological complexity of cropping systems. Since nematodes were only one of many factors contributing to plant disease, his later papers considered the effects of nematode × environment interactions on the reproduction of *M. javanica* and on the growth of the host plant (Wallace 1969*b*, 1970, 1971). The conclusion from these studies was that, in a given ecological situation, nematode numbers and environmental factors affected nematode reproduction but host tolerance and numerous environmental stresses influenced the response of the plant to nematode attack. This theme was expanded in *Nematode Ecology and Disease* (Wallace 1973), which should remain required reading for any student of plant nematology. Wallace outlined the various ways that nematodes caused damage to plants, considered the way plants responded to nematode infection and discussed the environmental factors that influence both nematodes and their hosts. He pointed out that disease problems in the field were complex, that nematodes were only one of many factors (both biotic and abiotic) contributing to the problem and suggested that a multidisciplinary approach was needed when diagnosing diseases and developing strategies to reduce losses caused by a disease. Later papers with one of his students provide a detailed example of the use of such an approach to determine the relative importance of various environmental factors on the growth and yield of wheat in South Australia (Stynes *et al*. 1979, 1981).

The structure, physiology and biochemistry of nematodes

After World War II, new technologies such as the electron microscope became available to nematologists and they were used to build on knowledge of the fine structure of nematodes that had been accumulated with the light microscope. Alan Bird (Box 5) was fortunate to have access to an electron microscope and he soon became a leader in ultrastructural research on nematodes, both in Australia and internationally. Bird worked for many years on *M. javanica* and made a major contribution to our knowledge of one of world's most important nematode pests. In a series of papers that are too numerous to cite here (e.g. Bird 1967, 1968; Bird and Rogers 1965), Bird studied ultrastructural changes in the egg shell during development and hatching, documented the changes in cuticular structure that took place with the onset of parasitism and observed

Box 5. Alan Bird

Alan F. Bird was born in Seremban, Malaysia on 11 February 1937 and went to school in Northern Ireland. Later, he moved to Perth, where he was awarded a BSc in Zoology from the University of Western Australia in 1952. Bird's lifelong passion for nematodes was ignited during his Master's degree studies at the University of Adelaide on the cuticle of strongyle larvae (vertebrate-parasitic nematodes). His next move was to the University of Edinburgh in Scotland to undertake PhD studies. Although his work at Edinburgh was biochemical in nature (use of the newly developed technique of electrophoresis to examine proteins in the cuticle of nematodes), his introduction to electron microscopy was a pivotal experience. This new tool enabled him to look at the ultrastructure of nematodes at a level of detail that had never previously been possible.

After receiving his PhD in 1956, Bird returned to Australia to take up a nematology position with CSIRO at Merbein, Victoria, in the centre of one of Australia's largest citrus, grape and vegetable-growing regions. Root-knot nematode (particularly *Meloidogyne javanica*) was an important pest in this region and Bird began a lifelong journey to understand all aspects of its biology, physiology, ultrastructure and mechanisms of parasitism. Initially, Bird worked mainly with the light microscope, but after transferring to Adelaide in 1958, he had access to an electron microscope and was also able to adapt many new techniques (e.g. serology, radioautography and time-lapse cinematography) to the study of nematodes. A chapter on techniques in the 1971 edition of his book *The Structure of Nematodes* provides a clear and concise account of many of the methods that served Bird well over the years and is still a good starting point for anyone interested in undertaking detailed studies of nematodes.

Bird made an enormous contribution to our knowledge of root-knot nematode, publishing more than 100 papers during his career, many of them on *M. javanica*. His studies on the cuticle, the egg shell, embryogenesis, hatching and moulting formed the basis of the first edition of his book, while his early work on host-parasite relationships (feeding, nematode growth and development, and plant responses to nematode attack) were summarised in a review in the *Annual Review of Phytopathology* in 1974 (Bird 1974). His 1978 publication *Root-knot Nematodes in Australia* provided a comprehensive account of the taxonomy, biology and economic significance of this important pest (Bird 1978). In the latter stages of his career, he also made important contributions in the area of nematode-microbe interactions, firstly with *Rathayibacter* (the bacterium associated with *Anguina* in Annual Ryegrass Toxicity) and secondly with *Pasteuria penetrans* (a bacterial parasite of root-knot nematode).

Although Bird made an important contribution to plant nematology, he never accepted the artificial disciplinary distinctions that separated those working on plant- and animal-parasitic nematodes. In 1982, he launched *Australian Nematologists Newsletter* to encourage communication between nematologists, regardless of their disciplinary interests. It was a broad-ranging and informative newsletter, but unfortunately it met its demise for financial reasons. Its successor (*Australasian Nematology Newsletter*) is the poorer for its narrower focus on plant and soil nematodes. The breadth of Bird's scientific contribution to science is demonstrated by the societies that presented him with awards at the end of his career: the Society of Nematologists, the Helminthological Society of Washington, the Royal Society of South Australia and the Australian Society of Parasitology.

Despite his stature within the nematology community, Alan Bird remained a modest and unassuming man who was liked and respected by all who knew him. He retired from CSIRO in 1993 and died on 13 December 1999. A personal account of his life and work (written by his son David, also an eminent nematologist) can be found in Bird (2000).

morphological and chemical changes in oesophageal glands soon after the nematode entered a host plant. However, Bird's contributions were not restricted to a single nematode species. He was interested in nematodes of all shapes and sizes, whether they were parasitic in animals or plants, or free-living in soil, fresh water or the sea. Bird's holistic view of nematodes was reflected in his comments about the conformity of structure and the remarkable similarity of developmental mechanisms within the Nematoda (Bird 1971). Those comments appeared in his book entitled *The Structure of Nematodes*, which provided the first modern and comprehensive account of what was known about the structure and function of nematodes. It remains today a standard reference on this topic.

Bird studied not only *M. javanica* but also its interactions with the host plant at a cellular level. He investigated the attractiveness of roots to the nematode (Bird 1959) and then moved on to study the development of nematode-induced syncytia (e.g. Bird 1961, 1962, 1972*a*, 1972*b*) and the nature of the chemical forces responsible for syncytial formation and maintenance (e.g. Bird 1964, 1966, 1968, 1969). Since syncytial induction and growth in the host is dependent on stimuli from the nematode, research of this nature was fundamental to understanding how damage from root-knot nematode might be reduced by blocking the metabolic pathways involved in establishing and maintaining the parasitic relationship. Therefore, Bird's (1974) review of plant responses to root-knot nematode was important in stimulating further research in this area.

Other Australian contributions in the physiological and biochemical area came from John Fisher, who used ligatured nematodes to show that the receptors for the stimulus that induced moulting were in the anterior part of *P. nanus* (Fisher 1966). His later work on the fecundity of *Aphelenchus avenae* showed that eggs were laid over a period of ~20 days, with the nematode responding to adverse conditions (e.g. suboptimal temperatures, lack of food or an unsuitable host) by slowing the rate of egg production (Fisher 1968, 1969). Observations on the nematode's feeding behaviour in liquid media indicated that stylet thrusting (required for the nematode to penetrate a cell wall) occurred as a response to glucose and/or amino acids, whereas pumping of the metacorpus (required for a nematode to ingest cell contents) was a response to amino acids alone (Fisher 1975). A minimal amount of feeding was found to be an essential precursor to moulting, even though the feeding could have occurred in a previous stage (Fisher 1970). When the development of the gonad in *A. avenae* was studied in relation to feeding, Fisher and Triantaphyllou (1976) found that cell divisions in the gonad were restricted to the periods of lethargus in the second and third moults.

Warwick Nicholas commenced work at the Australian National University in Canberra in 1960 and his early work on nematode nutrition and culturing had far-reaching consequences for physiological and molecular studies of nematodes, including plant parasites. Before he came to Australia he was involved in some of the initial studies on axenic culture of *Caenorhabditis* (Dougherty *et al*. 1959), a nematode that has since become a widely used model for biological studies. Nicholas brought cultures of the nematode with him when he moved to Australia but he then went on to work mainly with nematode parasites of vertebrates. However, he also had an interest in plant and soil nematodes and studied them in a wide range of habitats, including marine muds, mangrove ecosystems, sandy beaches, deserts and natural vegetation. His paper with student Richard Marchant on energy budgets of nematodes is frequently cited in studies of nematode growth and metabolic needs (Marchant and Nicholas 1974).

Training in plant and soil nematology

Tertiary education expanded rapidly during the post-war period but plant and soil nematology was never a formal part of the curriculum of most Australian universities. External specialists (e.g. Bob Colbran and Cliff Blake at the universities of Queensland and Sydney, respectively), presented occasional lectures on nematodes as plant parasites within courses on plant pathology, and nematodes were introduced as a phylum to zoology students studying invertebrates. Opportunities to obtain specialist training in plant and soil nematology first became available when John Fisher was appointed to the then Waite Institute in Adelaide in 1956. During the 1960s and 1970s he was one of eight lecturers in a relatively large Plant Pathology Department at the University of Adelaide. The collective expertise of the department covered most aspects of plant pathology (e.g. mycology, bacteriology, virology, nematology, disease epidemiology, fungal ecology and the physiology and biochemistry of pathogens) and enabled the department to offer a comprehensive course in plant pathology. Thus, undergraduates who wished to specialise in plant pathology were able to attend ~80 lectures and 40 practical sessions, with ~10% of that time spent on nematodes. Postgraduate training in nematology was also available for the first time in Australia. The key role of the Waite Agricultural Research Institute in fostering plant nematology was further consolidated by the appointment of Harry Wallace to the Chair of Plant Pathology in 1971.

Other nematologists in the Australian university system were Buddy Rogers and Slim Sommerville (the University of Adelaide) and Warwick Nicholas (the Australian National University). All taught nematology within zoology and parasitology courses and trained many postgraduate students during their careers. However, Mike Hodda (a student of Nicholas) was the only one of them to specialise in plant and soil nematodes.

Nematodes and insects

Australia has a long history of research on insect-parasitic nematodes and, although this group of nematodes is largely outside the scope of this review, two species warrant mentioning because of their association with insects known to attack plants. The first, which was noticed for the first time by Morgan (1933), is associated with flies in galls on *Eucalyptus* leaves and flower buds. In an excellent paper published a few years later, Currie (1937) described *Fergusobia tumifaciens* and provided a comprehensive account of its mutualistic association with *Fergusonina* flies. The second nematode was *Deladenus siricidicola*, which was found by Bedding (1968) to have alternative fungal-feeding and insect-parasitic life cycles. This nematode has now been mass produced and is used to control the European wood wasp (*Sirex noctilio*) throughout the world (Bedding 1984).

New Zealand

The early years: before World War II

Migrants undoubtedly brought nematodes to New Zealand with the plant material they hoped to establish. On the basis of accounts of European settlement, the crops planted by settlers, the agricultural produce traded and records of damage, Yeates (2004) considered that most of the 52 alien species of the plant-parasitic nematodes known from New Zealand were probably introduced before about 1920.

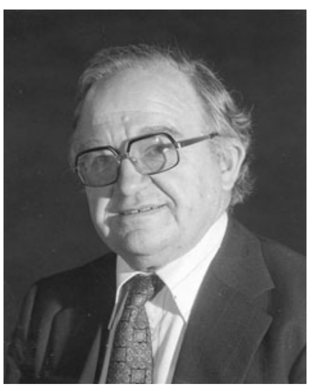
The first record of a plant-parasitic nematode from New Zealand, indeed of any nematode not associated with a vertebrate host, is that of *A. tritici* from Waimate (South Canterbury) by Kirk (1899). Thomas W. Kirk (1856–1936) was a biologist in the Department of Agriculture from its establishment in 1892 until he retired in 1921. He had broad interests and presumably identified the species on the basis of galled seeds. In his 1899 *Leaflet for Farmers*, Kirk noted that the disease had been known in the colony for the previous six years. The Annual Report of the Department of Agriculture for 1908 contains an account of eelworms known in New Zealand up to that time. Taxa are poorly defined by modern standards but records can be taken to include *Anguina*, *Meloidogyne*, *Heterodera* and *Ditylenchus*.

Mermis novaezealandiae, *Mononchus* (*Iotonchus*) *rex*, *Dorylaimus novaezealandiae* and *Dorylaimus profundis* were the first free-living nematodes to be described from New Zealand material (Cobb 1904). The samples were collected in 1902 by English biologists K. Lucas and G. L. Hodgkin and came from lakes at depths of 60 m or more. Molluscs and oligochaetes were also described from the same collections (Lucas 1904; Suter 1905).

A further overseas worker reporting on New Zealand nematodes was the German Benedictine monk and zoologist Gilbert Rahm (1885–1954). He collected nematodes from thermal areas in Rotorua in 1936 and reported the water temperature to have been 61.3°C (Rahm 1937). While the material from the hot springs was not identified, he recorded *Dorylaimus* and *Plectus* from associated algal mats. Plant-feeding nematodes were rarely recorded during this period but *Aphelenchoides ritzemabosi* was recorded on chrysanthemums in 1935.

The post-war period

In the period just before and after World War II, there were several articles mentioning nematodes as pests of agricultural and horticultural crops. In many cases the nematodes could be identified from plant symptoms but, according to Clark (1963), material was probably also sent to the Institute of Agricultural Parasitology in England (where Tom Goodey led a plant nematode group from 1921 to 1946), and later to the CAB



Box 6. Wallie Clark

'Father of nematology in New Zealand'

Walter C. (Wallie) Clark was born on 22 October 1927. His family lived at Jacks Bay, South Westland and Clark grew up wandering the bush glades and the seashore, eating kiekie and pipis. He did not go to secondary school but obtained his School Certificate by correspondence. In the 1940s he worked for the Post and Telegraph Department before going to Christchurch Teachers' College. At 21, he was entitled to 'provisional entrance' and attended Canterbury University College, earning a BSc in zoology. His first appointment was as assistant lecturer in biology at Christchurch Teachers' College (1954–55). He then became an assistant lecturer (1956–57) in the Zoology Department, Canterbury University College, completing his Master's degree on an intertidal gastropod.

After appointment to the Department of Scientific and Industrial Research Entomology Division in 1958, Clark made collections of nematodes from many soils throughout New Zealand before embarking for England. His PhD studies in nematology were conducted at the Imperial College of Science and Technology and Rothamsted Experimental Station from 1958 to 1961 under the guidance of B. G. Peters, J. B. Goodey and F. G. W. Jones. His work centred on the Mononchoidea and is now commemorated in the genus *Clarkus*. Why did he study mononchids? 'Because they were relatively large and easy to see', he said in 1966. However, his systematic work included a benchmark revision of the classification of Enoplida and descriptions of plant-parasitic species of *Dolichodorus*, *Trichodorus* and *Longidorus*. Like most overseas students of his day, Clark had to undertake a 'minor' project for a Diploma of Imperial College and his study concerned fumigation with methyl bromide and chloropicrin to control seedborne infestations of *Ditylenchus dipsaci* on lucerne. This further broadened his nematological background.

Returning to the Entomology Division at Nelson in 1961, Clark was very active in nematology, describing species in various orders. He compiled a list of plant-parasitic nematodes recorded from New Zealand and raised awareness among horticulturalists of their importance. Some 20 papers on plant and soil nematodes can be attributed to his PhD and his time with the Entomology Division. A 1964 paper in the *New Zealand Journal of Agricultural Research* was probably the first to consider the possible role of fungal-feeding nematodes as plant pathogens (Clark 1964). He was also involved in the first identification of *Deladenus* from *Sirex* wood wasps.

In 1964, Clark was appointed Professor of Zoology at Massey University and shouldered a heavy teaching load so younger staff could advance their scientific careers. At Massey, he supervised three nematology students (Pat Dale, Olefunke Egunjobi and Gregor Yeates) before returning to the University of Canterbury, Christchurch in 1967. Initially free of administration, but still with a significant teaching load, there was a resurgence of personal scientific output, with at least 10 papers describing new nematodes from New Zealand arthropods and wildlife. As a teacher, Clark conveyed to many students an extreme enthusiasm for coming to grips with animals, their environments and their parasites. Frank Wood and John Marshall were among his PhD students at Canterbury. Inevitably, administrative duties and tensions returned, but Clark regarded himself primarily as a teacher. Like many dedicated teachers, Clark declined to have his name on his students' publications and, like himself, he expected students to stand on their own two feet. He formally retired from the university in 1988.

Through research, teaching, supervision and raising grower awareness, the efforts of Wallie Clark were pivotal in establishing plant and soil nematology in New Zealand. As zoologists seek a greater understanding of nematodes as animals, they turn to his well-founded publications and his students.

Institute of Helminthology. From Clark (1963) it appears that, in 1957, J. B. Goodey was associated with the identification of a species similar to but distinct from *Anguina agrostis* from the grass *Agropyron scabrum*.

Romanian-born H. (Harry) Jacks (1908–1994) returned to the Plant Research Bureau of the Department of Scientific and Industrial Research (DSIR) after war service and was appointed to the permanent staff of Plant Diseases Division in March 1945. He worked on soil disinfestation and published at least five papers on ‘eelworm control’ (e.g. Jacks 1944), focusing on *Meloidogyne* [*Heterodera marioni* (Cornu) Goodey] on tomatoes. He spent 1947–50 at Imperial College, London and worked on the control of soil and seedborne disease in fruit and vegetable crops before moving to Massey Agricultural College where he lectured in soil science (1956–69).

Rather than continue to rely on overseas experts and collectors, Australasian biologists were keen to develop nematology and build links with overseas centres of expertise. Tom Goodey had made preparations to visit Australia when he died suddenly in 1953 (Bawden 1954) and J. B. Goodey died in 1965 *en route* to New Zealand (Jones 1965).

W. Cottier, an entomologist, collated the most comprehensive account of plant parasitic nematodes in New Zealand, drawing on available records in the DSIR and the Department of Agriculture (Cottier 1956). However, the only new record was that of *Aphelenchoides fragariae* from begonias and several ferns.

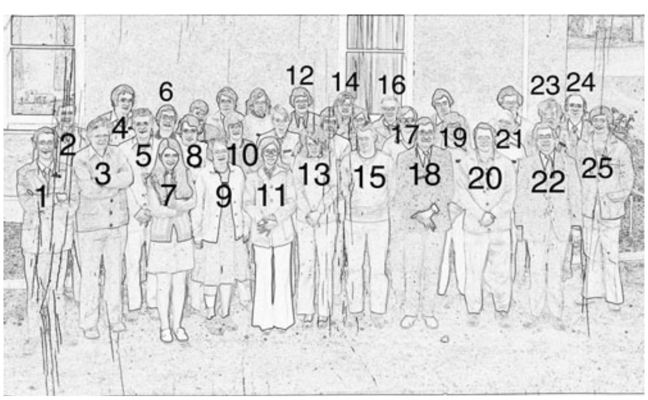


Fig. 2. This photograph was taken at a nematology workshop held at Mildura, Victoria, in 1975. Participants included some of the major contributors to plant and soil nematology in Australia [Max Sauer (3), Bob Colbran (5), Jack Meagher (6), Olga Goss (9), Harry Wallace (21), Alan Bird (22) and John Fisher (23)] together with some of the next generation of Australasian nematologists [Adrian Harris (1), Rob Brown (2), Chris O’Brien (4), Frances Reay (7), Frank Wood (8), Graham Stirling (10), Ray Akhurst (12), Janet McCulloch (13), Robin Bedding (14), Barry Thistlethwaite (15), Rod McLeod (16), Alan Dube (17), George Khair (18), Brian Stynes (19), Bob Banyer (20) and Roger Broadley (25)]. Also included are Sariah Meon (11), a student from Malaysia and Mike McClure (24), a visitor from the USA. Some technical staff and representatives of chemical companies were also present.

The Wallie Clark era

In 1958, the zoologist W. C. (Wallie) Clark (Box 6) was appointed to the DSIR Entomology Division, but he soon left for England to undertake his PhD studies. For the next few years, Clark focussed on predatory nematodes, but he also worked with other groups, including plant parasites. On returning home, he continued his taxonomic work and published a list of plant-parasitic nematodes recorded from New Zealand (Clark 1963).

In 1964, Clark began a teaching career, first at Massey University and later at the University of Canterbury, and it was in this capacity that he played a leading role in the development of plant and soil nematology in New Zealand. Clark was an enthusiastic and dedicated teacher and, through his role in mentoring students, he built up the level of nematological expertise within the country and gave New Zealand the capacity to deal with its nematode problems. The effectiveness of the national response to identification of potato cyst nematode in August 1972 (Dale 1972) was largely due to the robust foundations he built.

Concluding remarks

It is clear from the preceding discussion that plant and soil nematology has a long and proud history in both Australia and New Zealand. That history dates back to the very start of the discipline of nematology; it embraces nematodes that are unique to a relatively isolated region of the world and it involves people who made contributions that were recognised nationally and internationally. Although Australia and New Zealand have a distinctive nematode fauna, the main nematode problems confronting the pioneers in nematology proved to be similar to those causing problems elsewhere in the world, presumably because both countries were settled by immigrants and they brought their crops and nematode pests with them.

In preparing this review, one decision we had to make was whose careers should be highlighted. Although we feel comfortable with those we have chosen, we recognise that others such as Max Sauer, Jack Meagher, Cliff Blake, Warwick Nicholas and Olga Goss also made significant early contributions and we hope that this is apparent from the text. We also had to make a judgement on when the transition to the modern era took place and in the end decided to cover the period up until the early 1970s. Therefore, an informal nematology meeting held at Mildura in 1975 is relevant, because most of the pioneers highlighted in this review were present at that meeting, together with many of the next generation of nematologists (Fig. 2).

A series of review articles, which accompany this paper (in the June 2008 issue of *Australasian Plant Pathology*), demonstrate that plant and soil nematology remains in a healthy state in Australia and New Zealand. The breadth and depth of recent work is testimony to the strong foundations laid by those mentioned in this paper.

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