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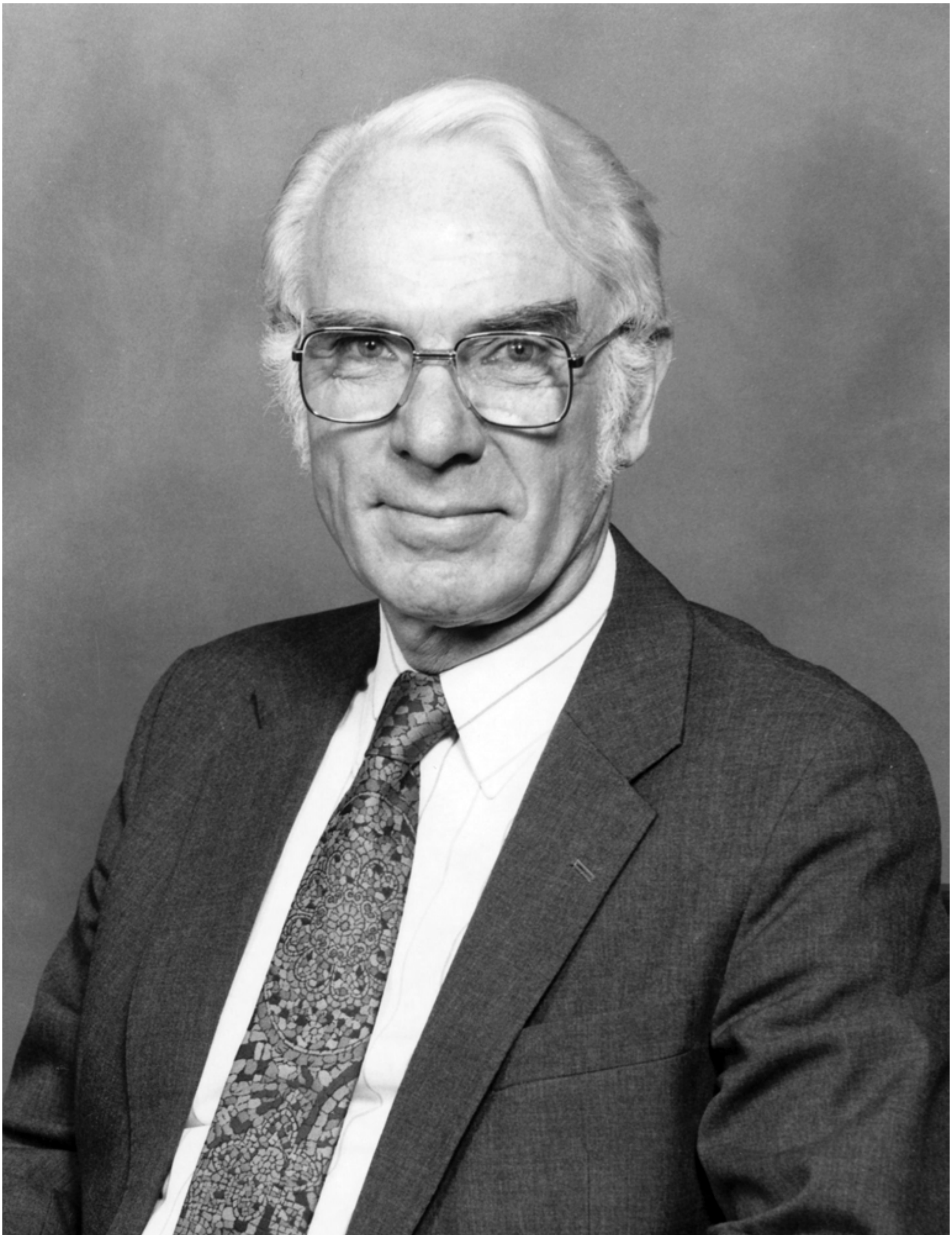

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Elected FRS 1967

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Sir Alwyn Williams was distinguished as a geologist and palaeontologist and as a university administrator. His PhD investigation of a classic area of his native Wales led to a lifetime of research on the rocks of the Ordovician System, and on fossil and living brachiopods. He became an international authority in both fields, with his original contributions and his organization of multiauthored syntheses. He pioneered the application of electron microscopy to palaeontology using observations on living representatives to inform his interpretation of the fossils. He maintained an active research programme during a remarkable career as a university leader, guiding the University of Glasgow through government restructuring of university finances in the late 1970s and early 1980s. He was determined, decisive and eloquent in his promotion of the ideals of university education.

EARLY YEARS

Alwyn Williams, the eldest of three children of D. Daniel (Danny) and E. May Williams (*née* Rogers), was born in Aberdare, South Wales, in 1921. His early years coincided with the Great Depression. Although his father had abandoned the hardship of the coal face to become a bus driver and eventually an inspector, even in this secure, relatively comfortably-off family, financial sacrifices were essential to secure secondary and further education—the means of escape from those valley communities dominated culturally by the chapel and socially by the consequences of heavy industries. Many years later, in an interview coinciding with his retirement from the University of Glasgow, Alwyn stated that he fervently believed, to the point of fanaticism, that education is the main source of uplift for mankind. As a child, he was particularly influenced by an uncle who, when a miner, had studied to qualify as a teacher and became a playwright and expert on the Welsh language, the only language that Alwyn knew until he was five years old. Under his uncle's guidance Alwyn won a coveted scholarship to the much respected Aberdare Boys Grammar School, where his academic performance led to a scholarship to the University College of Wales, Aberystwyth. However, his sporting and particularly athletic prowess at school was curtailed by tuberculosis with a long convalescence in 1939, a misfortune that also denied him a hoped-for enlistment in the Fleet Air Arm.

Alwyn's illness led to the suggestion that an open-air life would benefit his health, and an undergraduate degree in agriculture was advised. In the event, agriculture was deemed inappropriate to a science scholarship and Alwyn transferred to geology. He graduated with first-class honours in 1943 and likewise in geography in 1944. During his undergraduate years he became involved in student politics. As President of the Students Representative Council and Vice President of the National Union of Students, he began honing his debating skills and the art of persuasion and managing people. Alwyn himself was apolitical, and it is hard to imagine this extremely shrewd but overtly kind manipulator of men as a subversive student activist. After graduating, he remained in Aberystwyth to research the classic Lower Palaeozoic rocks in the Llandeilo area and so began his lifelong involvement with brachiopods. Having gained his PhD in 1946, he won a postdoctoral position as a Fellow of the University of Wales. His stay at Aberystwyth was equally significant to his private life, for there he met Joan Bevan and thus began a formidable partnership. They married in 1949 during a brief visit to Toronto through the ingenuity of a registrar who invoked regulations applying to vagrants and itinerant musicians!

Alwyn won a highly competitive Harkness Fellowship to visit the US National Museum in Washington just after he had been appointed to his first lecturing post in the University of Glasgow. He returned in 1950 after two years in the USA to join the Department of Geology, where Professor T. N. George (FRS 1963) was assembling some of the brightest hopes in British geology. Within four years in Glasgow Alwyn had so enhanced his reputation that he was invited by the Vice Chancellor of Queen's University Belfast, Sir Eric (later Lord) Ashby FRS, to apply for the Chair and Head of the Department of Geology—an enormous challenge for a young man of 33 at a time of turmoil in Northern Ireland. He might have gone to Princeton instead had not, some have surmised, his involvement with the student union as an undergraduate led, in those McCarthyite days, to considerable delay in processing his visa application. More likely it stemmed from overreaction to his earlier health problems. Whatever the case, Princeton's loss was certainly Belfast's gain!

Queen's University Belfast, 1954–74

Alwyn's approach at Queen's was not that of the remote professor. He immediately established a culture of personal involvement at all levels with both his staff and students—not only entertaining them in his home, but encouraging senior students to join staff for daily coffee and discussion. Such was their enthusiasm for this activity that they clubbed together to buy newspapers so that they could be better versed in the topics of the day. Alwyn taught a wide range of geological subjects and was nowhere happier than leading an enthusiastic group of students in the field. These arduous days were followed by very civilized dinners and evening discussion—the most momentous was probably at the end of a day spent on Dalradian metamorphic rocks in northwest Donegal in 1967, when Alwyn's election to Fellowship of the Royal Society was announced. His students spontaneously purchased a gift from a local chemist. The Waterford Crystal sherry glasses were always produced at student functions at the Williams home and have survived, miraculously, to this day. Under Alywn's leadership the Geology Department at Queen's greatly increased its numbers of honours students and became a centre for the study of biomineralization with the development of a scanning electron microscope (SEM) laboratory.

Alwyn's involvement in university administration began at Queen's, where he was successively Dean of Science, Secretary to the Academic Council (the last person to hold that post part-time), Pro Vice Chancellor (1967–70) and acting Vice Chancellor during a lengthy illness of the incumbent. In all of these roles Alwyn tried to introduce student participation and to anticipate major changes and issues facing university administrators. This was more than adequate training for the dominant role in national University politics that he was to play later in his career. His relationships with the wider community of Queen's students were mixed, ranging from champion, when he denied a belligerent Ian Paisley access to student residences with what was described as 'the cold-contained anger of an outraged smouldering Welsh dragon' (according to Sir Robert Smith, University of Glasgow), to critic, when he observed that the students at Queen's had employed 'the propaganda techniques of Goebbels'. By then Alwyn was a passionate humanist, and while he doubtless despaired at the aversion to ecumenism in Ulster, he remained an optimist with enduring faith in his fellow human beings. After 20 years in Ulster, Alwyn took up the Lapworth Chair in Birmingham in 1974, only to be lured back into university administration by an invitation to become Principal of the University of Glasgow in 1976.

University of Glasgow, 1976–88

Alwyn was the first Regius Principal of Glasgow who was not a graduate of the university, the first non-Scot, and indeed the first distinguished scientist in a post more usually occupied by able administrators. But his appointment by the Scottish Office was seen as a stroke of genius. Here was a pan-Celtic nationalist who was born in Wales and had learned his trade in Ulster—a combination that certainly silenced those who felt that Scotland was the place for Scots. Alwyn's was also an incredibly suitable appointment for a university in need of change and one that, like all universities in the 1970s and early 1980s, would be subjected to stringent cuts and government interference. This was at a time when there were major increases in student numbers, with no commensurate increases in funding. As Sir Robert Smith observed at Alwyn's Memorial Meeting, here was a man who defied the image of a remote or ineffectual don. He gave 'no cause to see in him the prevalent caricature of an academic as financially naïve and, as far as public money was concerned, totally irresponsible'. True, when Alwyn first arrived in Glasgow he was optimistic that North Sea oil revenues would be used to the advantage of the nation. However, within the year there was a 4% cut in central funding by a Labour government, increased to 8% by the Conservatives when Margaret Thatcher came into power in 1979.

Alwyn immediately set in motion some very tough and unpalatable proposals for rationalization and retrenchment, stealing a march on other universities. Glasgow was the only university to practise such economies in those early days, to the extent that some perceived it to be struggling. Alwyn's task was facilitated by his eloquence (with the rhythm and lilt of his Welsh delivery), his clarity of delivery and purpose, his mastery of argument, and his deep understanding of the academic ethos and the challenges faced by academics in adapting to a rapidly changing world. Although Alwyn was receptive to the opinions of others, those who proffered advice soon learnt the futility of debate when his mind was made up. He familiarized himself with the activities and finances of all 131 departments in the university, and chaired and steered the committee responsible for prioritizing capital grants. His restructuring led to rationalization of arts departments (ensuring the survival of classics and divinity), and the rebuilding of computer sciences.

At a time when salary increases for public employees were prohibited by government, Alwyn was particularly concerned over the plight of poorly paid technicians. With the assistance of the ASTMS General Secretary, Clive Jenkins, he hoped to persuade Mrs Shirley Williams (later Baroness Williams of Crosby), Education Minister in the Callaghan government, to relax the wage restraint and to make the technicians a special case. He failed: even Alwyn feared the financial penalty that would be inflicted on his university if this pay freeze were broken. Morale was maintained by the very active involvement of the Principal in both ecumenical and social activities. Within 18 months of their arrival, he and Joan had entertained large numbers of staff and students and forged strong links with the wider Glasgow public, reflecting his understanding of the value of a metropolitan university. Their hospitality and friendliness to individual staff were legendary. Despite his own loss of Christian beliefs, Alwyn tried to unite all religious groups within the university, and particularly to integrate Catholics with the wider community.

Thanks to Alwyn's preparations, Glasgow had plans in place that reduced the impact of new Conservative legislation in 1979. Indeed, by 1981 the university had identified two-thirds of the cuts expected and exploited areas such as overseas student recruitment for additional income. Not so the Committee of Vice Chancellors and Principals, who seethed with anger, and whom Alwyn described as a 'hotbed of cold feet' (his collective noun for VCs was a *lack* of principals!). Alwyn's eloquence was also directed at the Conservative government. As late as 1988, on his retirement from the university, he described its education plans as 'a recipe for bland bumbledom and half-baked political expediencies'.

Despite Alwyn's foresight, large-scale redundancies and economies became necessary in 1982 to ensure the survival of the university, and Sir Alwyn eventually offered his own, rejected, resignation. Yet throughout this period he retained an absolute commitment to wider access to higher education, as well as the protection and increased rigour of research. Here, too, Alwyn led by example. He continued his own research programme publishing papers and earning grants. He had a laboratory constructed beneath the Principal's lodgings. His working day started early and he even remained occasionally involved with undergraduate teaching. Financial pressure of another sort led to a funding shortfall for the completion of the new Hunterian Art Gallery. Alwyn's threat to sell some minor Whistlers in the museum's collection generated outrage. A rescue fund saved the paintings—and as an added bonus the museum acquired several works by contemporary painters who were persuaded to contribute them if the Principal succeeded in saving the Whistlers.

Despite his quarrels with a succession of unsympathetic governments hostile on funding, Alwyn gained the respect of politicians (and a knighthood in 1983) through his plain speaking and his conviction that universities should not be viewed as untouchable. He considered that universities should be financially accountable and was the first university head to present a business plan to the University Grants Committee (UGC). Alwyn knew only too well the importance of political nous and had the ability to anticipate various directives and to react to them with cunning. As Principal he felt it his duty to steer the politicians to develop an education system that would underpin the civilized world and function as a major driver of its social machinery.

Leadership of other bodies

Alwyn promoted his ideals as chairman or member of a number of influential committees, including the UGC, the Natural Environment Research Council and various medical and educational trusts. He advice was much sought after. A period (1974–79) as chair of the Trustees of the British Museum (Natural History), now the Natural History Museum, was followed by a far more challenging task in 1979 when he was invited to chair a committee to inquire into the scope and functions of the National Museum of Scotland. This committee visited all museums and related institutions in Scotland and some south of the border. After 14 meetings Alwyn produced a list of recommendations in 1981, described as a model of common sense. In summarizing the prevailing condition of Scottish museums he identified their potential for rationalization and exploitation for education. Although this report placed museums on the political agenda, Alwyn was frustrated when most of the recommendations were rejected by the Secretary of State. The only major success was the development of the Museum of Scotland, based on a merger of the National Museum of Antiquities and the Royal Scottish Museum.

Alwyn chaired a working party in the early 1980s to explore the potential for rationalizing geological activities within the University of London. It recommended, somewhat controversially, the strengthening of three centres at University College, Imperial College and Royal Holloway, and was hugely influential in establishing criteria later followed by the Oxburgh Report on the rationalization of Earth science departments on a national scale.

Another Scottish national institution that benefited from Alwyn's astute leadership was the Royal Society of Edinburgh (1985–88). During his presidency the rooms rented in George Street were purchased with assistance from the Scottish Office, the Society's library was taken over as part of the Scottish Science Library, and finance was obtained for several research fellowships. Alwyn fostered links with the two other UK academies to which he belonged—the Royal Society and the Royal Irish Academy. He introduced meetings between the three, and with similar overseas institutions, such as the Polish Academy of Sciences. This modernization of Scotland's Academy of Sciences and Letters raised its profile not only overseas but also in Scotland, where it is now a leading source of advice to the Scottish Executive.

Scientific work

Brachiopod taxonomy and phylogeny

The brachiopods (so-called lamp shells) are invertebrates characterized by two, usually unequal, valves that enclose the soft parts, apart from a fleshy stalk (the pedicle), which attaches the animal to the substrate. Some brachiopods lack a pedicle and are cemented to a hard substrate or lie free in or on sediment. Brachiopods are bottom-dwelling animals, normally sessile. They use the shell as a filter chamber, capturing food with the lophophore. The phylum is uncommon in the living fauna, where it is represented by about 350 species; fossil species outnumber living ones by a factor of at least 35. Thus it is not surprising that most of the research on the living forms was done by palaeontologists. The mineralized shell of brachiopods accounts for their abundant fossil record, which ranges from the earliest Cambrian, and for their importance in stratigraphy and in the history of biomineralization.

Alwyn Williams was the prime mover in developing our understanding of brachiopod taxonomy. In his first major contribution on shell structure and classification, published in 1956 (2)*, Alwyn pointed out that only about 50 papers on living brachiopods had been published since 1900. 'It has been left to palaeontologists to provide the bulk of the information available today and to organize the group into a satisfactory taxonomic hierarchy' ((2), p. 243). Indeed, because of his work on brachiopods, he became a pioneer in integrating a knowledge of living organisms with that on their fossil counterparts (Budd 2001). Alwyn bemoaned the fact that classifications of the Brachiopoda have tended to rely on 'one particular character at the expense of others, and since there is no agreement on which feature has the greatest taxonomic importance the more influential classifications are in a state of uncompromising conflict' ((2), p. 243). He recognized the need to build the classification upwards from genera on the basis of morphological comparison, and with no preconceived idea about the taxonomic value of particular characters. His 1956 paper was a landmark in using shell structure in living articulates, particularly the presence or absence of punctae, to underpin the classification of the group. He considered the superfamily as 'the taxonomic limit to the use of the brachiopod skeleton in determining affinity by detailed morphological comparison' ((2), p. 283). He segregated 22 superfamilies into six 'groups' typified by familiar genera, namely *Orthis*, *Strophomena*, *Pentamerus*, *Rhynchonella*, *Spirifer* and *Terebratula*, noting that a few superfamilies were difficult to place. Alwyn did not assign a rank to these groups.

Alwyn made fundamental contributions to the systematics of the brachiopods with a series of major monographs on Ordovician taxa, most notably from Girvan (3), Bala (4), the Shelve District in Shropshire (23) and Tourmakeady in the west of Ireland (24). The Tourmakeady Limestone is a beautiful red colour and yields a remarkable silicified fauna but, unfortunately, it is rarely exposed in the field. Alwyn spent many years scouring the countryside of County Mayo in search of it. One day he came across a drystone wall with several big blocks of Tourmakeady Limestone distributed through it. As he was examining it someone on a bicycle stopped, and in the ensuing conversation Alwyn negotiated a price for the wall and proceeded to dismantle it as the cyclist disappeared into the distance with his money. Later he overheard people in the local pub complaining that someone had demolished one of their walls; the opportunist on the bicycle was not the owner! Alwyn pioneered the use of statistical data in defining species and genera (using a handheld calculator even in the 1950s—a black cylinder with a rotating handle on the top!), mindful of the need for precise definitions of taxa used in stratigraphic correlation. He recognized the requirement for objectivity as opposed to authority in determining identifications: 'the only opportunity for an objective approach arises during the morphological comparison of faunal constituents. Everything else, even the naming of a completely analysed sample, is tinged with personal opinion and experience' ((3), p. 79). It

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

was these descriptions of entire and diverse faunas of brachiopods that gave Alwyn the background and authority to direct international projects on the group.

Alwyn and A. J. (Bert) Rowell, two British authorities, were asked by R. C. Moore of the University of Kansas to organize the preparation of the volumes of the *Treatise on invertebrate paleontology* (the definitive compilation of invertebrate fossil taxa and an essential tool for systematic palaeontology) on brachiopods, focusing on the articulates and inarticulates, respectively (Carlson 2001). This first edition of the brachiopod volumes of the *Treatise* took over 10 years and was published in 1965. It catalogued the 1700 genera of fossil brachiopods then known. In addition to authoring the chapters on some taxonomic groups (see (9)), Alwyn wrote sections on stratigraphic distribution (10) and on techniques (11), and together with Bert Rowell, those on anatomy (6), morphology (7), evolution and phylogeny (8) and, of course, classification (9). Apart from rejecting earlier criteria, the major advance in this *Treatise* classification was in using shell structure to group the superfamilies into higher taxa—much of it based on Alwyn's own observations on biomineralization in living brachiopods. Information on living brachiopods was applied to fossils. Characters, both macroscopic and microstructural, were interpreted in terms of their evolution, and this led to more secure homologies and a classification that was widely accepted until the end of the twentieth century (Carlson 2001).

A revision of the brachiopod *Treatise* volumes was initiated 25 years on, in the late 1980s, and the project was again coordinated by Alwyn, this time in 'retirement'. Once again he contributed substantially, on anatomy (30), shell structure (31), morphology (32) and several taxonomic groups (see (35)). The number of genera known had increased from 1700 to 4500, in significant measure because of Alwyn's stimulation of interest in the group. By this time phylogenetic methods had advanced significantly and cladistics were widely applied in palaeontology. The challenge was to generate a phylogeny-based classification of the brachiopods based on the range of morphological characters (in the absence of significant molecular data) that would resolve different views among the protagonists and would provide an essential framework for the revised *Treatise*. The difficulty, of course, lay in integrating the data from living and fossil taxa given that most of the morphological characters available for living forms are not preserved in the fossils. Alwyn's solution to this difficulty was to persuade his collaborators to analyse the living and extinct (Cambrian–Ordovician) taxa separately, the living brachiopods based on the full range of characters, the fossils, of necessity, solely on the morphology of the shell. The results of these analyses were combined and translated into a classification. The division into classes Inarticulata and Articulata was abandoned in favour of three subphyla: Craniiformea, Linguliformea and Rhynchonelliformea. This arrangement was something of a contrivance, reflecting the difficulty of determining the relationships of the Craniiformea without a definitive outgroup as a basis for polarizing the characters. The classification was published in 1996 (29) and ultimately in Part 2 of the revised brachiopod *Treatise* (35). The classification of the Brachiopoda will benefit from more molecular data (recent results indicate that the affinities of Craniiformea are closer to the other inarticulated brachiopods (Cohen & Weydmann 2005)) and an understanding of evolutionary development as a key to homologies within the group.

Brachiopod shell structure

Alwyn's interest in the shell structure of brachiopods was kindled very early in his scientific career, during the two years that he spent as a Harkness Fellow at the Smithsonian Institute after completing his PhD at Aberystwyth. There he worked with G. Arthur Cooper, the foremost brachiopod worker in the world at the time, who had made extensive studies of Ordovician brachiopods from North America. Cooper focused on material from settings where the original calcium carbonate of the shell had been replaced by silica during diagenesis, allowing the brachiopods to be isolated from the rock with the use of acid. These are the exception, however. The only way to determine the nature of internal structures, such as the lophophore supports, in most brachiopods was by sectioning, with the sequences preserved on cellulose acetate peels. The use of serial sections to reconstruct the internal structures of the shell in three dimensions was commonplace among brachiopod workers; it was a short step to examine the microscopic structure of the calcareous shell itself. But Alwyn extended his enquiry from the fossils to the living forms, from the calcareous shell to the soft tissues that secreted it (2).

In his 1956 review of the shell of the Brachiopoda (2) Alwyn noted that the shells of living terebratuloids and rhynchonelloids share an outer organic layer, the periostracum, and two layers of calcium carbonate. The thickness of the primary layer is relatively uniform, being formed by relatively few cells at the mantle edge, whereas the secondary layer, which gives rise to many of the internal features of the shell, varies in thickness. Alwyn showed how the caecal outgrowths of the mantle in terebratuloids pass through pores in the shell to connect with the outer periostracum ((2), Fig. 2). Alwyn traced the occurrence of these pores or punctae in well-preserved fossil material and confirmed that they extend back throughout the history of terebratuloids. However, other features of the shell occur only in extinct forms. Rods of calcite, which Alwyn termed taleolae, are found in the core of pseudopunctae in the shells of strophomenoid brachiopods. Alwyn showed that they are not homologous with punctae but provide attachment points for muscle fibres that connect to the mantle. This pioneering paper (2) showed that the structure of the brachiopod shell, information commonly available even in fossils, had the potential to contribute significantly to our understanding of relationships in the group.

With the purchase of an NERC-funded electron microscope at Queen's University in the mid-1960s, one of the first from Cambridge Instruments, Alwyn's research on shell structure moved up a level. He focused on brachiopods but applied the same principles to a major investigation of bryozoan ultrastructure with Tavener Smith. He pioneered the application of transmission electron microscopy to structure in fossils, documenting the ultrastructure and growth pattern of the shell in the range of articulated brachiopods (14). He applied the transmission electron microscope to unravelling the process of shell secretion in the living rhynchonellide brachiopod *Notosaria nigricans*, and documented the structure of the organic periostracum. He compared the periostracum of *Notosaria* with that in *Calloria* (then referred to *Waltonia*), an example of the other major group of living brachiopods, the terebratulides; the terebratulids turned out to be less complex, with one less membrane (15). Alwyn argued that the terebratulide condition was probably primitive, with three essential elements, the mucopolysaccharide layer and fibrillar triple-layered membrane of the periostracum, and the calcareous shell. With a clear understanding of shell formation in the living groups, Alwyn was able to infer the secretory regime in extinct groups based on the evidence of shell structure (13, 15). Most of the important distinctions occur in the calcareous shell itself. The shell of strophomenides, for example, a remarkable group of largely concavo-convex Palaeozoic forms, differs fundamentally from the rest—not just in the presence of taleolae, but in having a laminar secondary layer. Alwyn originally thought that members of this group had just one shell layer, but with the evidence revealed by the scanning electron microscope (18) he became convinced that both primary and secondary layers were present in this group also.

Having researched shell structure in the articulate brachiopods Alwyn turned his attention to the inarticulates. Working with Tony Wright (19) he investigated secretion and structure in the calcareous shell of living *Crania*, which cements itself to hard substrates. The cemented ventral valve differs from the dorsal valve in lacking a secondary laminar layer; it consists of a primary layer and subsequent thickenings, both of acicular crystallites. Both valves are penetrated by caeca (that is, they are punctate), in contact with the periostracum. Williams and Wright included fossils in their study and showed that the structure of the ventral valve of Craniacea varies, whereas that of the dorsal valve is constant. They investigated representatives of other inarticulate brachiopods with calcareous shells, the craniopsids and obolellids, and demonstrated that these inarticulates also had a crystalline primary layer and laminar secondary layer. They regarded this similarity as more likely to be the result of convergence than indicative of relationship. This SEM study showed the growth of laminar shell by screw dislocations ((19), pl. 6, fig. 3). In his contribution to a volume on scanning electron microscopy published in 1971 Alwyn posited that 'electron microscopy promises to revolutionize palaeontological research' ((20), p. 37). He added the new data on shell structure in inarticulate brachiopods to his model of skeletal evolution in the group as a whole, noting that the laminar layer in different inarticulates and in strophomenids evolved independently ((25), Fig. 8).

Alwyn continued to use the SEM to document brachiopod shell structure throughout the rest of his life, and this investigation, together with the coordination of the second edition of the brachiopod *Treatise*, became his 'retirement' projects. He saw four of the six volumes of the new *Treatise* published before his death, a remarkable legacy in itself. At the same time he worked on the SEM two mornings a week, operating it himself in spite of his failing eyesight. This later research focused on the last major gap in his investigation of the brachiopod shell, the organophosphatic shells of inarticulates, including the classic *Lingula*. The approach was systematic, taxon by taxon, but Alwyn was always ready to depart from this program to pursue the unexpected. One such example was the discovery of tablets of silica, 1–2 μm in dimension, in the larval shells of discinids (figure 1), which he published in *Science* at the age of 76 (33). This remarkable observation revealed a biomineralizing regime otherwise confined to sponges among metazoans. But not only living discinids secrete silica: Alwyn and his colleagues were able to infer the same phenomenon in Cambrian inarticulate brachiopods based on impressions in fossil shells.

Alwyn's first target among organophosphatic shells was living *Lingula* (27). He and his colleagues showed that *Lingula* and *Discina* share an arrangement of periostracum, primary layer and stratified laminar secondary layer that is probably ancestral for the organophosphatic brachiopods (26, 27). They noted that the combination of collagen, glycosaminoglycans, chitin and apatite was similar to that in the cuticle of priapulids (although recent molecular phylogenies place these worms among the ecdysozoans, not with the brachiopods in the lophotrochozoans). Having described the living forms, Alwyn and his colleagues turned their attention (28) to the Carboniferous *Lingula squamiformis* from several localities in Scotland, to determine the effects of degradation. These fossil shells preserved much of their structure, clearly showing an arrangement similar to that in the living species, although the organic components were significantly degraded (as demonstrated by the distribution of amino acids). Finally Alwyn and colleagues (34) applied the techniques of electron microscopy to a diversity of linguloid brachiopods from the Cambrian to the present day (35 genera) and analysed their relationships on the basis of the characters of the shells. This led ultimately to a new hypothesis of the sequence of events in the evolution of brachiopod shell structure (figure 2).

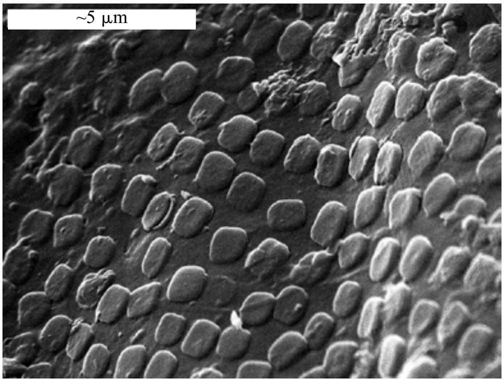

Figure 1. Siliceous tablets on the larval shell of the brachiopod *Discinisca tenuis*. (Courtesy of Maggie Cusack.)

Alwyn Williams's contributions to palaeontology in the second half of the twentieth century were pioneering, not just on his beloved brachiopods but also in the subject as a whole. He introduced the routine application of statistics to the description and identification of taxa. He recognized that fossils were crucial to understanding the evolutionary history and relationships of living forms. He investigated the anatomy and physiology of the living representatives of his group in detail as a key to interpreting the fossils. He was one of the first to make extensive use of electron microscopy to document the ultrastructure of biomineralized fossils. He recognized the potential of molecular palaeontology to yield data on the organic components preserved in association with fossil shells.

Ordovician stratigraphy and palaeogeography

Although Alwyn Williams is justly celebrated for his work on brachiopods, he also made profound contributions on the stratigraphy and palaeogeography of the Ordovician. His PhD thesis at Aberystwyth, directed by Professor H. P. Lewis, involved an investigation of the Ordovician and Silurian rocks of the classic Llandeilo district of central Wales. Alwyn mapped about 40 square miles of the Towy Valley, demonstrated the importance of volcanics in the sequence, and established the first detailed succession of faunas. He was to remark later on the irony that his first paper (1) should be on cryptolithid trilobites from the Llandeilo district while his friend and collaborator, Harry Whittington (FRS 1971), who was to become the international authority on trilobites, published his first papers on brachiopods (see, for example, Whittington 1938). Alwyn, in collaboration with Whittington and Douglas Bassett, extended his research on the Lower Palaeozoic rocks of Wales, investigating the Ordovician and Silurian rocks around Bala and documenting their brachiopod–trilobite faunas (12). Harry Whittington recalls that one summer in the late 1950s he and his wife Dorothy were in the Bala area collecting while Douglas Bassett was mapping. Alwyn joined the party by train, a one-carriage steam engine from Bala junction. Harry and party laid out a strip of red carpet, he and Doug Bassett held geological hammers aloft in a ceremonial arch and Harry's mother presented Alwyn with a bunch of Welsh leeks. This most articulate of Welsh men was for once apparently lost for words!

Before going to Washington in 1948 Alwyn had already begun to consider the Ordovician rocks of the Girvan district. He used his exceptional field mapping skills to unravel the very

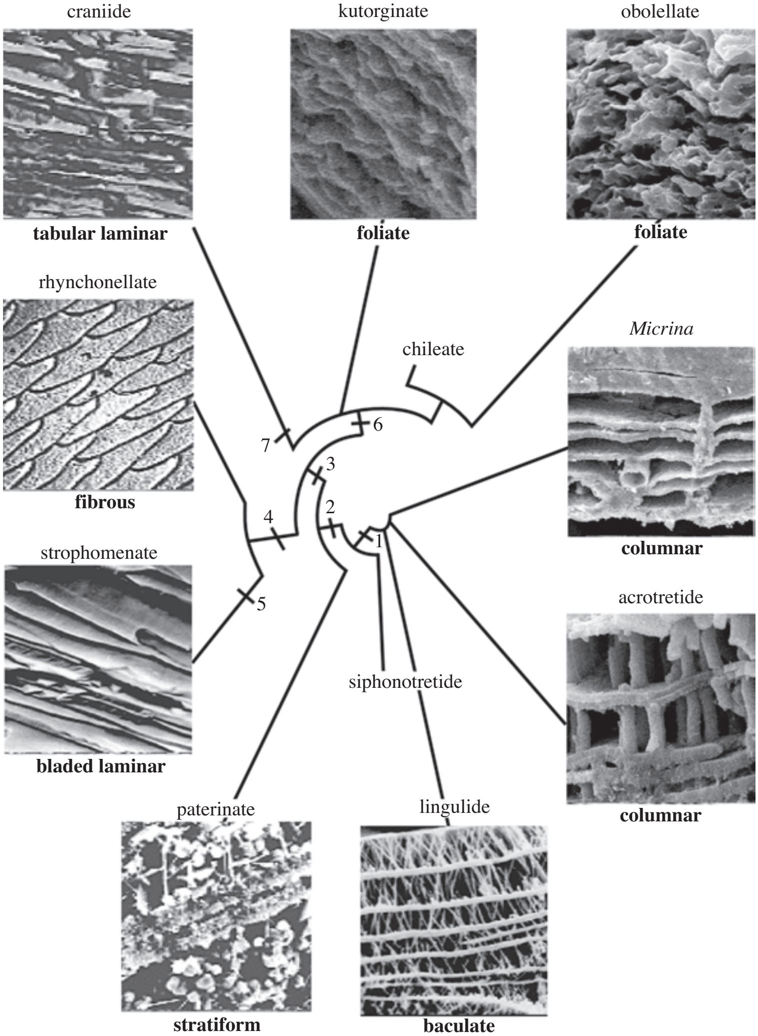

Figure 2. Cladogram illustrating the derivation of the seven main fabrics (in transverse section) of the secondary shell of brachiopods: the halkieriide *Micrina* (columnar, with a column and setigerous tubes to left, ×85), the acrotretide *Prototreta* (columnar sets, ×550), the lingulide *Schizotreta* (baculate sets, ×520), the paterinate *Cryptotreta* (stratiform with poorly developed glycosaminoglycan (GAG) chambers, ×520), the strophomenate *Strophomena* (cross-bladed laminar, ×975), the rhynchonellate terebratulide *Macandrevia* (fibrous, ×2470), the craniide *Novocrania* (tabular laminar, ×4550), the kutorginate *Narynella* (foliate, ×230) and the obolellate *Obolella* (foliate, ×65). The most important transformations (numbered) that affected the brachiopod shell structure and body plan were the following: (i) loss of organic canaliculate framework and well-developed GAGs chambers with columns or baculi, (ii) development of the rhynchonelliform body plan, (iii) replacement of organophosphatic, stratiform shell with GAGs and chitin by organocarbonate shell with foliate secondary layer, (iv) development of fibrous secondary shell, (v) development of composite (cross-bladed) laminar secondary shell, (vi) development of holdfast, and (vii) development of tabular laminar secondary shell. The circle cladogram represents a 50% majority-rule consensus of eight trees generated by a PAUP heuristic search. (From (36), courtesy of Maggie Cusack.)

complex stratigraphy with the aid of the faunas. This project culminated in his 1962 Geological Society Memoir, which included a map of some 60 square miles of southwest Ayrshire and his remarkable interpretation of the palaeogeography of the late Ordovician transgression based on the Girvan successions (3). The suggestion that the Geological Society should publish nearly 200 pages and 25 plates on fossils, in addition to his account of the stratigraphy and his fold-out maps and correlations, raised some eyebrows (the palaeontologists had formed their own association and started to publish *Palaeontology* in 1957) but Alwyn's demonstration of the importance of fossils in working out the stratigraphy and structure prevailed.

Alwyn was an early proponent of continental drift. The brachiopods that he described from the Girvan area revealed remarkable similarities to the faunas from the Appalachians that G. Arthur Cooper was describing at the Smithsonian. Alwyn later recorded ((22), p. 241) that when he 'first attempted to present evidence for continuity of Ordovician faunal boundaries between Europe and North America' (in 1957 at the InterUniversity Congress at Birmingham and the British Association meeting in Dublin), 'the most consistent criticism brooking no compromise was that fifteen million sq. miles of North Atlantic made nonsense of the paper'! Alwyn's cluster analyses of the Ordovician shelly faunas of the British Isles (16, 17) identified three provinces—American, Baltic and Anglo-Welsh. He emphasized that the rigour of his approach relied on comprehensive faunal lists and precise correlation, both dependent on careful fieldwork. Alwyn used the distribution of the faunas to reconstruct the pattern of ocean currents on the late Ordovician palaeogeography of the British Isles, and extrapolated it to the Ordovician world. He provided a more comprehensive account of the distribution of Ordovician brachiopods at the 1971 meeting 'Organisms and Continents through Time' in Cambridge (22). On the basis of his analyses of the brachiopods of the world at five time horizons through the Ordovician, he identified five major provinces. These provinces persisted through most of the period (until the mid-Caradocian), but after that the faunas became much more cosmopolitan, heralding the plate collisions that caused the Caledonian Orogeny and the reduction of provinciality that characterized the Silurian.

Alwyn emerged as an authority on the Ordovician and chaired the Geological Society group that produced the 1972 correlation of the Ordovician rocks in the British Isles (21). This report unravelled the complex history of stratigraphic nomenclature and zonal schemes, a legacy of the establishment of the Ordovician System in the previous century through the work of Charles Lapworth FRS and his predecessors. The Geological Society group followed Lapworth's original concept of the Ordovician System, defining the base as that of the Arenig Series (as advocated by Whittington and Williams in 1964 (5)); the underlying Tremadoc Series was not formally incorporated into the System until ratification of the Cambrian–Ordovician boundary in 1988 (Norford 1988). The report was the first comprehensive account of correlations within the Ordovician of Britain and Ireland, and of correlations between the British succession with those of Bohemia, Estonia, Kazakhstan, North America and Australia. It provided a standard reference for the system that was widely used before it was superseded by the revised correlation of 2000 (Fortey *et al.* 2000).

Coda

Alwyn Williams was remarkable in maintaining a major scientific programme as a university administrator at the highest level. While Principal of the University of Glasgow he published some 20 refereed papers and held three NERC grants. The Palaeobiology Unit at the university was set up on his retirement in 1988 and, as outlined above, he continued his innovative research on brachiopods supported by a further three NERC grants as well as funding from the Leverhulme Trust, the Royal Society, the *Treatise* project and the University of Glasgow. But Alwyn was no single-minded scientist. He was a great admirer of Trollope and aspired to a complete collection of his first editions. He is said to have remarked that he had 'pursued every Trollope in the Kingdom'! He accumulated a significant personal art collection, and encouraged his family to participate in music—his son, Gareth, now Dean of Medicine at Bristol University, provided a musical tribute on the flute at Alwyn's Memorial Meeting. His daughter, Siân, also went into medicine, and is a haematologist at Perth Royal Infirmary. In retirement Alwyn enjoyed his garden and his grandchildren.

For a man of steely determination, confident in his own judgement, decisive and even intolerant of dissent, it may seem surprising that Alwyn commanded, in addition to respect, such enormous affection. This was undoubtedly generated by his fairness and sense of humour. In a delightful 'quirky' address at Alwyn's Memorial Meeting, hosted by the University of Glasgow on Saturday, 2 October 2004, Emeritus Professor P. Walsh suggested that, for the atheist Sir Alwyn Williams, the Christian phrase *requiescat in pace* should be replaced by the more classical pre-Christian Roman tombstone inscription STTL (*sit tibi terra levis*)—'may the earth rest lightly on you'. For a Welshman, indeed the most eminent Welsh geologist of the second half of the twentieth century, and one who so thoroughly embraced Scotland and shaped the University of Glasgow during an extremely difficult period, it would seem appropriate that the earth in question should derive from the Lower Palaeozoic rocks of the Llandeilo region, where he originally established his scientific reputation.

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The frontispiece photograph was taken in 1983 and is reproduced by courtesy of the University of Glasgow Media Services.

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