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Professor R.B. (Bob) Clark (1923 – 2013) – polychaete biologist and environmentalist: a pioneer in comparative endocrinology of reproduction, growth and regeneration.

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Professor R.B. (Bob) Clark, an outstanding scholar and leading polychaete biologist of his generation, died quietly at his home on 28th September 2013, shortly before his 90th birthday. He was born in London in November 1923, the son of Joseph L. Clark and Dorothy (nee Halden). In his later career he was widely acclaimed for his work in Marine Pollution, a field of study that he did much to establish and one that has ever increasing global significance ¹. He was appointed a member of the Royal Commission on Environmental Pollution² which, together with his authorship of the various editions of his text book on Marine Pollution (Clark, 1986-2001) and other major publications (e.g. Clark, 1982) rightly establish his preeminence in this field. He was also invited to give evidence at the Royal Commission Enquiry on oil drilling on the Great Barrier Barrier Reef which was chaired by Prof J.E. Smith FRS, then the Director of the Plymouth Marine Laboratory in the early 1970s. This enquiry was instrumental in defining the boundaries of the GBR Marine Park which was declared in 1975 and ensured that no oil drilling could occur within the park. This Park was later declared a World Heritage Area.

Bob Clark took a first degree in physics and graduated from Chelsea Polytechnic in 1944. After working for a while in this role he entered Exeter University to read Zoology in 1947, graduating in 1950. His first appointment as a zoologist was at the University of Glasgow and, while at the University



Bob Clark during a visit to China in the 1990s (photograph by Prof. Wu Boa Ling).

of Glasgow, he was able to study in the USA at Universities of Washington, Seattle and University of California (Berkeley) where he was Assistant Professor during a Sabbatical awarded to polychaete biologist Ralph Smith. He also worked extensively at the Friday Harbor Marine Laboratory, teaching there till 1978. He was appointed to the University of Bristol as Lecturer in 1956, awarded a DSc by the University of London in 1965 and appointed to the positions of Professor and Head of the Department of Zoology and Director of the Dove Marine Laboratory at Newcastle University, UK in 1965. He was also honoured with election as a Fellow of the Royal Society of Edinburgh in 1970. Bob married Mary Clark, a USA citizen and they had a productive professional collaboration for many years. After his move to Newcastle upon Tyne, Mary returned to the USA to pursue an independent academic career and they divorced. Bob remarried and is survived by Sue, their two children, Juliet and Stephen and grandson Gus.

¹ From mimeos to e-copy – a tribute to Professor RB (Bob) Clark, founding editor of the Marine Pollution Bulletin. Marine Pollution Bulletin 46(9):1051-1054

^{2 8}th report of Royal Commission on Environmental Pollution : Oil Pollution in the Sea 1981 HMSO, London

Bob did much to establish polychaetes as models in experimental and evolutionary zoology and created vibrant, polychaete research schools at Bristol and Newcastle Universities, supervising and mentoring many of the next generation of polychaete scientists. He was also the supervisor in Bristol of Barrie Jamieson, who became a leader in the field of oligochaete biology (see Brinkhurst and Jamieson 1971, Jamieson 1971 supplementary bibliography). The relationship between the polychaetes and oligochaetes (clitellate annelids) was among the issues Bob addressed (Clark, 1969, 1978) that is finally being clarified with the aid of molecular data. As a supervisor, Bob generously encouraged his students to publish independently and did not follow the modern tradition of publishing jointly. His influence therefore extends well beyond his own publications. Athough it is not appropriate here to cite all the publications of his students, a supplementary bibliography listing some of the work arising from studies carried out under his supervision is included.

The polychaete studies begun at Glasgow University resulted in the publication of one of the first keys to Polychaete families in English (Clark, 1960a) and tellingly, a short paper on pelagic swarming in Scalibregmatidae (Clark, 1954), a topic which would re-emerge in various forms during much of his research career. His ecological studies include a survey of the distribution of *Nephtys* species in the British Isles (Clark, Alder and McIntyre, 1962; Clark and Haderlie, 1960) and in California (Clark and Haderlie, 1962) and the food of *Nephtys* (Clark, 1962). The problem of niche partitioning and geographical distribution of *Nephtys* species he addressed, has been reprised by former students (Olive and Morgan, 1991, supplementary bibliography) and remains a topic of importance for the polychaete community.

Bob's early training, and initial career in mathematics and physical sciences, underpinned much of his work on polychaetes, especially his investigations into biomechanics and movement and his work in this field influenced many others. He became an expert histologist and combined studies of polychaete structure, often in collaboration with Mary Clark, with experimental studies (Clark, 1956, 1958, 1962; Clark and Clark, 1960a, b). He re-appraised the nature of undulatory swimming in polychaetes, demonstrating that, in species with prominent parapodia, the wave form propagates from tail to head (direct locomotory wave) and the power stroke of the parapodium, exerted at the crest of the wave, produces the main propulsive force (Clark, 1964; Clark, 1976, Clark and Tritton, 1970). He also investigated swimming in smooth bodied species, such as Opheliidae, in which the parapodia play no significant role in the generation of locomotory forces and the locomotory wave is retrograde as in other smooth bodied worms and fish (Clark and Hermans, 1976). Colin Hermans became a close friend of Bob's and has provided the authors with illuminating reminiscences of his early scientific career and influence in the States. His investigations into the role of the coelom and septa in the shape changes, that enable annelids to work in their environment, was fundamental to his thinking and his studies extended to investigations of non-coelomate invertebrates (Clark and Cowey, 1958). The combination of his histological

and experimental investigations, together with his rigorous scholarship, enabled him to produce a definitive review of the evolution of swimming forms among annelids in relation to reproduction (the phenomenon of epitoky) (Clark, 1961) which remains a classic and is an essential introduction to the subject. As a student of biomechanics in annelids he became greatly interested in the deeper evolutionary implications of the relationship between form, function and phylogeny of metazoans. His interests culminated in a major synthesis, the book "The Dynamics of Metazoan Evolution" (Clark, 1964), which remains a masterpiece of scholarship and is a testament to the depth of his knowledge and thought.

'The Dynamics' subtitled "The origin of the coelom and segments" addressed metazoan phylogeny, a topic which has re-emerged in current biology in the wake of the genomic revolution, and to which the polychaete community is continuing to make important contributions. In it he, addressed theories relating to metazoan relationships in the light of "the principles of comparative morphology", which he argued, "must be taken into account when phylogenies are proposed, but which have hitherto escaped serious discussion in this context". In particular he explained, "as a student of the annelids, he was exercised by two outstanding problems: the nature and origin of the coelom and of metameric segmentation". He proceeded to a detailed analysis of the relationship between structure and movement in various grades of metazoan organisation, adopting what he described as, " ... a purely functional point of view". He then proceeded to a discussion of various theories relating to possible phylogenies of Metazoa in the light of comparative morphology and biomechanics. He recognised that "it is certain that many of the derivations of major groups of organisms that are accepted now will be re-examined, rejected and changed in the future." But, he cogently argued, "stem forms, from which several modern phyla diverge, must be possible animals...they must be conceived as living organisms, obeying the same principles that we have discovered in existing animals, and any new structures... must have conferred some selective advantage upon them". The argument that any putative ancestral, or primitive organism, must have obeyed the same physical laws as living organisms, is as valid now, in the 'molecular age', as it was then. Bob continued to evaluate theories relating to the relationships between worm like phyla (Clark, 1969, 1978). This was, of course, well before molecular and phylogenetic studies of polychaetes which are now providing new insights into these problems and which, a perhaps rather incredulous Bob, discussed with Peter during their morning chats over a coffee and a whisky in his later years.

To return to Bob's development as a polychaete biologist, during his early years at Glasgow, when he held a post as Assistant Professor at the University of California (Berkeley), and worked at the Universities of Washington and Seattle and Friday Harbor Marine Laboratory he formed many deep friendships and developed a deep interest in the emerging fields of neurosecretion and comparative endocrinology of invertebrates. He subsequently made a major impact on the comparative endocrinology of growth, regeneration and reproduction in polychaetes that indirectly led to subsequent endeavous to breed worms commercially and to the establishment of aquaculture businesses in Europe, China and SE Asia (see Olive, 1999, supplementary bibliography).

Invertebrate comparative endocrinology, was at the time dominated by studies of insects and Bob, together with contemporaries, Hauenschild in Germany and Durchon in France, stimulated an interest in the endocrinology of polychaetes. His studies of the histology of the *Nephtys* brain (Clark, 1955, 1958a,b,c), laid the foundations for experimental studies of *Nepthys* endocrinology as subsequently pursued at Newcastle University by Peter Olive and his students and, for the masterful ultrastructural studies of his former student D.W. Golding, which lead for instance to the discovery of 'neurosecretory endfect systems' with ramifications for neurosecretory studies throughout the metazoa.

While at the University of Bristol (UK) his research largely focussed on growth, regeneration and the 'once per lifetime' switch to reproductive maturation, typically observed in Nereididae but he also reviewed the subject in great depth providing the key reviews for anyone seeking an entrée into the subject (see Clark, 1965; Clark and Olive, 1973). His chosen model organism for his own studies was the estuarine Nereis diversicolor (now Hediste diversicolor), a species in which epitoky has been suppressed, but in which sexual maturation and the ability to regenerate lost caudal segments are, nevertheless, negatively linked to the onset of sexual maturation. This complemented the work of the Durchon laboratory at Lille, France, on the epitokous species Perinereis, and that of the Hauenschild laboratory in Germany, using Platynereis dumerili as the experimental model. The nature of the regulatory control by the supracesophageal ganglion proved difficult to establish (e.g Clark and Bonney, 1960, Clark and Ruston, 1963) but Bob's student at Bristol, D.W. Golding, brilliantly established the permissive nature of this control and demonstrated the existence of a caudal growth field, such that the number of segments regenerated is a function of the number lost and not, as previously thought, determined by the level of hormonal output (Golding, 1967e-f, supplementary bibliography). The proof that the ganglion has a permissive role, essential for segment proliferation, but not itself determining the rate nor the number of segments regenerated, is crucial to our understanding of caudal regeneration in nereidids and given the resurgence of interest in segment formation in polychaetes (especially in nereidids) following the discovery of pan-metazoan Hox-gene regulatory system, this work remains highly relevant and will no doubt lead to further investigations of the nature of the influence of the so called juvenile brain hormonal function in nereidid regeneration. His studies of Hediste diversicolor also included aspects of behaviour and learning (Clark, 1960 b, c, d), and his postgraduate student Stuart Evans also took this subject forwards (Evans, 1969, supplementary bibliography).

Following his appointment at Newcastle University, Bob re-established a polychaete based research school, both on the University Campus and at the Dove Marine Laboratory. He attracted a large number of visiting scientists from USA and around the world to work at the Dove Marine Laboratory including Marianne Pettibone, Ralph Smith, Larry Ogglesby, Colin Hermans, Fu Chiang Chia, Arthur Fontaine, Bao Lin Wu and Son Lin Zhang, making the Dove Marine Laboratory, a dynamic research environment for a new generation of polychaete students. These included the authors of this appraisal (PJWO and PAH) but also John Daly, Peter Gibson, Peter Garwood, Ivan Estcourt, Evelyn Jaros and others (see selected publications of their student work in the supplementary bibliography). Students at this time were encouraged to explore the diversity of polychaete life histories, with a particular focus on comparative aspects of reproduction and the timing of reproduction. He encouraged an experimental approach and tellingly distinguished clearly between the so called 'ultimate' and 'proximate factors' controlling the timing of reproductive events (Clark, 1979). He gave his students a free head in the choice of experimental material and this resulted in the study of a remarkable array of polychaetes, drawn from several different clades. The species studied at this time included: Cirratulus cirratus (Cirratulidae, with Peter Olive), Dodecaceria spp. (Cirratulidae, with Peter Gibson - see Gibson and Clark, 1976), Melinna cristata (Ampharetidae, now Melinna elisabethae, with Pat Hutchings), Harmothoe imbricata (Polynoidae, with John Daly, Peter Garwood), Fabricia sabella (Sabellidae, Fabriciinae with Dave Lewis, Evelyn Jaros). This approach continued to be a feature of the Newcastle polychaete school and over the next few years, the array of species studied was expanded to include members of the Nephtyidae, Phyllodocidae, Hesionidae, Spionidae, Capitellidae and Arenicolidae, leading to an appreciation of the diverse patterns of control of reproduction in polychaetes commensurate with their long evolutionary history (Clark, 1979; Clark and Olive, 1973). As a supervisor Bob had a 'hands off' approach, so each student had to solve the problems they encountered in their own way, sometimes made all the more difficult by the choice of experimental material. He insisted that his students followed the highest standards of scholarship, making sure that all citations were based on a detailed study of the original material, and he expected an accurate, succinct style of writing like his own. Pat and Peter both remember that this could be very challenging. We may not have reached his high standards, but the trying did no harm. The research output emanating from this school took polychaete endocrinology and the study of reproduction into new territory and clearly demonstrated that there is no such thing as a 'typical polychaete'. The outcome has had a profound influence on the current agenda in polychaete science.

Away from the laboratory, Bob was always generous in his hospitality - Professor D.I.D. Howie, on learning of the passing of Bob Clark, recalled the excellent hospitality he enjoyed at the home of Bob and Mary Clark during the first neurosecretion conference held at Bristol University and commented on how this experience stimulated his own interests in neurosecretion and endocrinology of the lugworm *Arenicola marina*, which, in this way, also entered into the canon of experimental endocrinology of polychaetes. Bob's hospitality was extended not only to his peers, but also to his research students both at Bristol and at Newcastle where, during 'polychaete discussion groups' held at Bob's house in the evenings, with a glass of wine or beer to aid proceedings, his many research students learned to engage in the cut and thrust of scientific debate, to state clearly, and defend their emerging ideas – a perfect grounding for their later careers.

Bob Clark was a stimulating teacher, expecting students to reach the cutting edge of science and to pursue their own ideas. He held temporary posts at the University of California (Berkeley) and was visiting lecturer at five Western Canadian Universities (Sept. '78 - March '79). Colin Hermans has told us of how Bob's period at Berkeley had a long lasting though largely unseen influence. At Newcastle, as previously at Bristol, he had a strong influence on degree programme development, emphasising the role of University teaching not only in imparting knowledge "but more importantly, to give students the ability to think independently, to form judgements which they can justify and support with tested evidence" (preface to Clark, 1986). Peter and Pat were both student demonstrators to his practical classes, supporting his course on comparative morphology. The labs required a not insignificant understanding of mathematics, and Pat remembers classes, in which nereidids were encouraged to swim, and the students being asked to get a handle on how the worms moved forward - although of course if they try too hard they go backwards - a challenging practical for students and demonstrators alike. Bob also promoted teaching in other areas in which he had an active research interest. He appointed former students S.M. Evans to teach animal behaviour and D.W. Golding to teach endocrinology and neurosecretion and each of them proceeded to create their own research schools in these fields. He appointed Fu Chiang Chia to teach developmental biology taught later by Peter Olive. These appointments ensured that the curriculum for Zoologists and Marine Biologists at Newcastle continued to reflect his influence. He instigated honours student projects, requiring them to carry out investigations of a real problem under the guidance of a member of staff, and to write up their results in the form of a research paper. Peter, who was at Newcastle University as an undergraduate when Bob first burst onto the scene, remembers having to carry out three projects, one comparing the muscular and segmental anatomy of nereidids and glycerids in relation to their mode of life and learning from him trichrome staining techiniques for the histology required.

Bob entered enthusiastically into the scientific life of the North East England. He was an active member of the Natural History Society of Northumbria, taking great interest in the Hancock Natural History Museum, (now Museum of the North), he served for many years as a committee and council member, advising, for instance, on the management of the Farne Islands, as well as being a successful and influential editor of the The Transactions of the Natural History Society of Northumbria (1988-1997). He was honoured by election to a Fellowship of the Royal Society of Edinburgh in 1970. His lay interests in Newcastle included his active participation in local education at all levels, he was a governor of Newcastle Prep School, and a well remembered Church Warden at St Georges Church, Jesmond. The vicar at the time, Canon Michael Middleton, recalled at the service of remembrance held at the Church, that Bob brought the same attributes foresight, clear decision making and a dry wit - to his work for the Parish, just as in his professional life. Peter and Pat have received many emails from friends and former colleagues who recall with warmth his wit and humour as well as his foresight, and excellence as a scientist, scholar and writer.

At Newcastle his interests expanded to include the important field of Marine Pollution. There were at the time a number of serious oil spillages affecting UK coastal waters - most notably the Torrey Canyon in 1968. His response was incisive and practical; he established with John Croxall, an oiled sea bird research unit, to develop a methodology for removing oil from affected sea birds (Clark, 1984; Clark and Croxall, 1972) and, realising the need for a medium for rapid communication of results, he began the series of, at first mimeographed, newsletters, which eventually developed into the leading journal in the field - Marine Pollution Bulletin - that he edited for 25 years (see footnote a). He was appointed to the Royal Commission on Environmental Pollution, working on the 8th RCEP report Oil Pollution in the Sea, the findings of which he published in a hugely influential paper in Transactions of the Royal Society (Clark, 1982). He travelled widely, investigating and advising on the effects of oil spills around the world (Clark, 1985, 1987, 1991; Dicks et al., 1982, Larmine et al., 1987, Mann and Clark, 1978; Wu and Clark, 1983; Sell et al., 1995). His unrivalled knowledge of marine pollution, clear objective analysis and his characteristic direct writing is shown in the text book Marine Pollution (Clark, 1986), which he saw through five editions (the last in 2001). As a text book it is an exemplar of concise, lucid writing which remains the ideal introduction to the subject. Bob continued his work as a marine environment consultant long into retirement. His development from polychaete biologist to world expert in marine pollution, with special expertise in relation to biological impacts of oil spills, presaged by some 30 years, subsequent developments Newcastle University, where marine sciences, at oceanography and marine zoology together with marine technology, naval architecture and offshore engineering now form a unique School of Marine Sciences and Technology (www.NewcastleMarine).

Bob Clark was one of the outstanding scientists of his generation - a great scholar and writer, fondly remembered not only for his scientific work, but for his dry wit, good humour and friendship. In recent years Peter Olive was able to share time with Bob, who would chat over a coffee and a glass of wine or whisky about the old days. He retained a keen interest in the work of his former students, even when increasing infirmity limited his ability to get out and about. Pat remembers being a surprise guest at his 75th Birthday when she again greatly enjoyed his hospitality. Bob's role as a mentor and supporter helped greatly in her move to the Australian Museum, enabling her to take forward polychaete studies and to become involved in the management of the environments Bob had done much to protect. Peter was even able to update Bob on the hosting of the 11th International Polychaete Conference in Sydney (2013). On behalf of the polychaete community, we extend sympathy to the family and friends who survive him, and we hope that our thoughts and remembrance at least recall for others the significance of his scientific life.

Professor R.B. Clark (1923 -2013): polychaete biologist and environmentalist

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