Heredity (2014) 112, 569–570

www.nature.com/hdy

OBITUARY

Bryan Clarke

Heredity (2014) **112,** 569–570; doi:10.1038/hdy.2014.50

Bryan Clarke, who has died at the age of 81, was a pioneer of ecological genetics. He studied under EB Ford and AJ Cain at Oxford and was part of the generation that rescued population and evolutionary biology from its lengthy flirtation with the Scylla of frozen mathematical exactitude untrammelled by facts and the Charybdis of data collection free from ideas.

Looking back to the 1950s, when he began his scientific career, and even to the mid-1960s, when I became the first of his 30 or so PhD students, it is difficult to remember how hard it was to find creatures in which to study inherited diversity, the raw material of evolutionary change. Now, of course, in the molecular era, it is everywhere. Not only are all the men and women who have ever lived, or ever will live, unique, but the same may well be true of all human sperm and eggs ever made, in their unimaginable billions. Back in those perhaps happier days there were no more than a few polymorphic butterflies and ladybirds, *Drosophila* chromosome inversions (which not many had the skills to identify) and human blood groups with which to ask fundamental evolutionary questions. And then, of course, there were the polymorphic snails of the genus *Cepaea*, which carried at least some of their genes on their backs, or their shells, in the form of inherited variation in colour and numbers of bands.

Then, as now, there were two approaches to studying diversity. One was straightforward and rather dull, to count allele frequencies in separate places and to try to work out why they differed. The other was more challenging, to find out why the differences were there in the first place (molecular population genetics is still largely stuck with the first question). Bryan always went for the difficult issues. Early in his career, he found that the two British species, *Cepaea nemoralis* and *Cepaea hortensis*, shared many of the same loci for shell pattern, but differed in the tactics they used to construct the optimal phenotype of camouflage against woodland or grassy backgrounds, as an early hint of the complexity and geographic differentiation of quantitative characters at the DNA level in many species, ourselves and our relatives included (Clarke, 1960).

He went on to show that, in some regions at least, there was a negative relationship between the incidence of shell pattern alleles in each of the two species and speculated that this was due to 'apostatic' selection (a word he invented, based on the 'apostasy' of those who switch religions; Clarke, 1962). The idea was that predators would concentrate on a relatively abundant target form, which they have found to be palatable, so that rarer morphs (perhaps in a related species) would be favoured even if they were less well camouflaged. As they became more common as a result, a predator might then be tempted to try one, find it good and switch to that now abundant form. Such negative frequency-dependent selection is now known to be important in many systems, from mimetic butterflies to (as he was among the first to point out; Clarke and Kirby, 1966) human histocompatibility alleles and plants' self-incompatibility systems. He went on to model this process and began, with his students, a series of experiments, in which wild birds were fed with coloured baits, and showed a strong tendency for just that kind of behaviour (Allen and Clarke, 1968).

At around that time Bryan Clarke began the sorting of practical palaeontology, which is possible with sluggish animals such as snails, for he re-surveyed some of the classic *C. nemoralis* locations first studied by Captain Cyril Diver (who also found time to be Clerk of the House of Commons) in the 1930s. He found consistent changes in allele frequency that had become even more marked in a later survey, as a strong hint that selection was at work (Clarke and Murray, 1962; Murray and Clarke, 1978).

From there he moved on to what became several decades of research on the Polynesian snail *Partula*, most of it on Tahiti's sister island, Moorea (the Bali Ha'i of the film *South Pacific*). He and his wife Ann visited the island on eight occasions, collecting many thousands of snails. These creatures had speciated on a tiny scale, and Bryan set out to investigate the genes involved by making crosses both within and among species, finding that reproductive isolation often broke down in the wild across narrow hybrid zones (Murray and Clarke, 1980). As is the case for *Cepaea,* the loci for *Partula* shell pattern are tightly linked as 'supergenes' of the kind then thought to control polymorphic mimicry in *Papilio* butterflies (Murray and Clarke, 1976).

Some *Partula* species are polymorphic for shell coiling, be it dextral or sinistral. For obvious reasons that interferes with their sex lives and might, Clarke suggested, be an early phase in the origin of species but was unlikely to produce reproductive isolation instantly as some had claimed (in other snails, recent work shows, that seems to be true because a reversal of symmetry gives an instant defence against predators and a strong selective advantage). Its inheritance in *Partula* was a classic example of maternal influence, with the phenotype determined by the mother's genotype (Johnson *et al.*, 1990).

In the 1970s, Bryan Clarke, with almost every other population geneticist, went over to the molecular side. Those already involved were repeating exactly the same arguments that the modest snail community had been having for the past 50 years—selection versus drift, gene flow versus local adaptation, effective population sizes—small or large, and inherited diversity used (and abused) to make evolutionary trees—with, too often, more polemic than evidence. Bryan chose one system, the alcohol dehydrogenase enzyme in *Drosophila*, and—as many years before he had done with *Cepaea*—

began a systematic series of experiments (for example, Day *et al.*, 1974). It soon became clear that some of the alleles involved differed greatly in their response to high levels of ethanol in the laboratory and that, given the alcoholic environment that *D. melanogaster* experience in the wild, this is also likely to be the case in natural populations. Since those early observations at the protein level, the study of *Drosophila* ADH using DNA technology has become a cottage industry of its own, with evidence of pervasive physiological differences associated with sequence changes. The neutral model of molecular evolution is, oddly enough, still more or less pervasive among those who study sequence change in the genome as a whole or those who use such data to construct phylogenetic trees.

In his later years, Clarke himself extended his taxonomic interests to participate in a first attempt at a molecular phylogeny of land gastropod molluscs. It supported much of the traditional taxonomy at the family level. The deeper taxonomy—like that of many other groups—remains uncertain, and new research hints that some of the supposed major divisions are in fact polyphyletic (Wade *et al.*, 2001).

In the early 1980s, his attention was drawn to a looming disaster on the island of Moorea, first made public in his magnificently entitled paper *Lutte biologique et destruction du patrimoine génétique: le cas des Mollusques gastéropodes pulmones dans les territoires français du Pacifique* (Tillier and Clarke, 1980: Bryan was a fluent French speaker). In the late 1960s, the giant African land snail *Achatina* had been introduced as a food source, and (as it did all over the tropics) soon became a major agricultural pest. Imbued by the ecological dogma of those days, the French tried biological control by introducing the carnivorous snail *Euglandina rosea*, a native of Florida, in 1977. It had a voracious appetite for members of its own phylum, but unfortunately it preferred the taste of the local *Partula* to that of the African invader. It soon drove many of them out, and now Moorea (with several other Pacific islands) is almost *Partula*-free.

Bryan continued his research on his laboratory stocks, but his attention also turned to a more or less desperate attempt to rescue the remaining *Partula* with the hope that perhaps, one day, they might be re-introduced to the wild. Stocks were sent to zoos all over the world and, at least in that environment, the various species are more or less safe. Whether they will ever return to Bali Ha'i is a more open question.

In 1996, Bryan Clarke was one of the founders of the Frozen Ark project, an attempt to rescue DNA and, where possible, cell lines from the many species—*Partula* included—now under the threat of extinction across the world. The scheme, which compares itself to the Millennium Seed Bank at Kew, became a consuming interest and has expanded to zoos, museums and universities across the world, with its headquarters still at his native Nottingham University, where, 40 years ago, he founded the Department of Genetics.

Charles Darwin described himself in his autobiography as a 'man of enlarged curiosity' and the same phrase is appropriate to Bryan Clarke. His students, his colleagues and his friends remember him with affection and admiration, and as sometime Editor of this Journal and the joint founder of the flourishing Population Genetics Group, which is coming up to its fiftieth anniversary, so should the larger community of evolutionary genetics.

S Jones
Department of Genetics, Evolution and Environment, University College London, London WV1E 6BT, UK
E-mail: j.s.jones@ucl.ac.uk

Allen JA, Clarke BC (1968). Evidence for apostatic selection by wild Passerines. *Nature* **220**: 501–502.
Clarke BC (1960). Divergent effects of natural selection on two closely-related polymorphic snails. *Heredity* **14**: 423–443.
Clarke BC (1962). Natural selection in mixed populations of two polymorphic snails. *Heredity* **17**: 319–345.
Clarke BC, Kirby DRS (1966). The maintenance of histocompatibility polymorphisms. *Nature* **211**: 999–1000.
Clarke BC, Murray J (1962). Changes of gene-frequency in *Cepaea nemoralis (L). Heredity* **17**: 445–465.
Day TH, Hillier PC, Clarke BC (1974). Properties of genetically polymorphic isozymes of alcohol dehydrogenase in *Drosophila melanogaster. Biochem Genet* **11**: 141–153.
Johnson MS, Clarke BC, Murray J (1990). The coil polymorphism in *Partula suturalis* does not favor sympatric speciation. *Evolution* **44**: 459–464.
Murray J, Clarke BC (1976). Supergenes in polymorphic land snails. I. *Partula taeniata. Heredity* **37**: 253–269.
Murray J, Clarke BC (1978). Changes of gene frequency in *Cepaea nemoralis* over a fifty-year period. *Malacologia* **17**: 317–330.
Murray J, Clarke BC (1980). The genus *Partula* on Moorea: speciation in progress. *ProcRoy Soc B* **211**: 83–117.
Tillier S, Clarke BC (1980). Lutte biologique et destruction du patrimoine génétique: le cas des Mollusques gastéropodes pulmones dans les territoires français du Pacifique. *Genet Sel Evol* **15**: 559–566.
Wade CM, Mordan PB, Clarke BC (2001). A phylogeny of the land snails (Gastropoda: Pulmonata). *Proc Roy Soc Lond B* **268**: 413–422.