



Obituary—Donald Henry Colless 1922–2012

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Abstract

Donald Henry Colless (24 August 1922–16 February 2012) was a taxonomist at the Australian National Insect Collection (ANIC) from 1960 until his retirement in 1987. He continued working in ANIC as an Honorary Fellow until his death in 2012. Don's main scientific interests were in the taxonomy and biology of true flies, and in the theory of phylogenetic reconstruction and classification. Don was trained in entomology at the University of Sydney, and spent nearly two decades of his early career in Asia studying mosquitoes and disease transmission, first in the Army during the Second World War in New Guinea and Borneo (1942–45), then after the war in North Borneo (1947–1952) and as a lecturer in the Department of Parasitology at the University of Malaya (1952–1960) in Singapore. We list the 127 scientific papers and book chapters that Don published during his scientific career that spanned 64 years. Six of these papers were published in the prestigious international journal *Nature*, and he was Chief Curator of the ANIC from 1971–1977. Don had extremely broad taxonomic interests, publishing on the taxonomy of 18 families of Diptera that spanned the phylogenetic breadth of the order. He described as new to science the fly families Perissommatidae and Axiniidae, thirteen new genera and over 120 species and, with David McAlpine, authored the Diptera chapters in both editions of *The Insects of Australia* (Melbourne University Press, 1970 and 1991). He published a number of influential critiques of cladistic theory in the 1960's and 1970's, and advocated a phenetic approach to the discovery of taxonomic groups, and phylogenetic reconstruction.

"I see classifications as providing "a precise lingua franca that will be as independent as possible of conflicting theories"...Moreover it seems true that our classifications are used mainly in everyday biology not (as some authors seem to believe) biogeography, and this is where they are most rigorously tested—not for their truth, but their utility." Colless (1982: 102).

School and University

Donald Henry Colless was born on the 22nd August 1922 in the small township of Uralla, just south of Armidale in northern N.S.W. Don's parents, Clifton and Danetta Colless, were farmers at the nearby Returned Soldiers Settlement of Kentucky South. His early childhood must have been Spartan -Kentucky South (30°48'12.40"S, 151°27'11.58"E, 1079m elevation) had no electricity, running water, telephone, motor cars, radio or sealed roads in those days.

Don began his schooling at the one-teacher Kentucky South Public School and obviously was a bright student because after his 6th year of school was awarded a Bursary to Armidale High. This was a welcome benefit as the great depression was beginning to influence the economic prospects of the region by this time. Don did well at high school, being Dux of the class in 1st and 2nd years. In 1937 he moved with his sister Peg to attend school in Sydney, living with a relative and with Don attending North Sydney High School. He sat for the Leaving Certificate in 1938, doing well enough to earn a small bursary and scholarship to pay University fees.

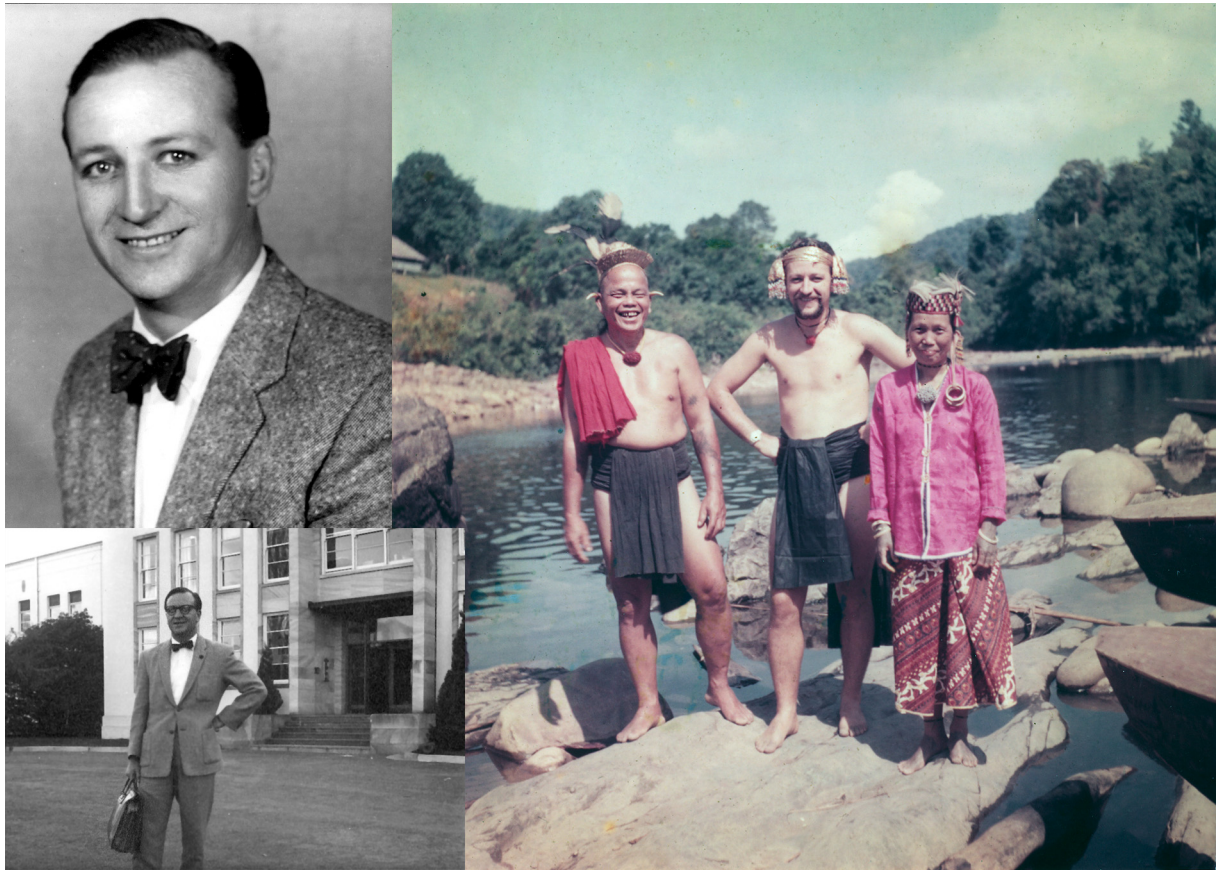


FIGURE 1. Clockwise from top left. Don in his 20's; in native dress with a local headman and wife, Sarawak, 1954; on arrival in Canberra to take up a full-time position, 1960.

Donald's tertiary education was at the University of Sydney studying for a degree in Agricultural Science in 1939. In those days the course was remarkably broad, with physics, chemistry, surveying, geology, genetics, pathology, bacteriology and entomology in the curriculum. By 1942 Don had finished the agricultural science course with High Distinction in entomology, and he was free to join the army. Before enlisting he had made arrangements to return after the war and continue his studies through an Honours year. After the war Don returned to his academic studies in 1946 and submitted his honours thesis on the anopheline mosquitoes of North Borneo, supervised by Dr Tony Woodhill. He was paid a small stipend by the Commonwealth Reconstruction Welfare Scheme. His honours thesis earned him a First Class result and a University Medal.

The Second World War

Like nearly all of his cohort of entomologists, Don's first practical experience was with disease vectors in wartime. In Don's case it was with the 12th Australian Malaria Control Unit (AMCU), into which he was accepted as a corporal by Colonel Ian Mackerras, in 1942. Although stationed initially at Victoria Barracks, Sydney, after a few weeks Don was sent to the 13th AMCU based in Cairns. The 13th AMCU was posted to New Guinea in mid-1943 and stationed in Buna, which had been recaptured by the allies only a few months earlier in the Battle of Buna-Gona. Buna, the trailhead for the Kokoda track, was surrounded by swamp, and the Japanese and allied soldiers fighting in the area had been affected badly by malaria, dengue fever, bush typhus and tropical dysentery. In fact, throughout the Pacific these diseases caused far more casualties than the effects of battle. Here Don had his first taste of war, with scattered wrecks of planes, Bren Gun carriers, Japanese bodies and the terror of enemy air raids. The unit's role in Buna was to reduce the extensive breeding of the local malaria transmitter, *Anopheles farauti*. This was achieved by spraying oil on larval habitats like wheel ruts, bomb craters and trenches.



FIGURE 2. Pinning the night's catch, west Kimberley 1979; inset staff portrait taken in the 2000's.

Soon after his 21st birthday Don and 3 others were sent to Finschhafen to follow a beachhead landing by the Australian 9th Division in the Huon Peninsula campaign. Their role was similar to the one in Buna, namely to reduce the mosquito populations in the area. They travelled to Lae in an American Landing Ship Tank where the invasion convoy was forming. Here Don had further experience of air raids from Japanese Zeros and bombers. Their ship returned fire with Bofors Light Antiaircraft guns. The AMCU landed on the beach at night, a few hours behind the infantry invasion force and made camp beside the 2/2nd Casualty Clearing Station.

For about a month the group endured many Japanese air raids both day and night, but also went about their job of spraying mosquito breeding sites with oil, and at night acting as stretcher bearers, carrying wounded to waiting ships. The Bofors guns couldn't operate at night because the infantry were blinded by the flash of the gun, and Don recalled that the Japanese bombers flew in to their targets at tree top level with their headlights on. During this time their small AMCU group of 4 suffered only one fatality, the result of walking into a booby trap. On the day that the AMCU was to leave a daisy-cutter bomb landed nearby and shrapnel ripped Don's belt and pack as it lay on the ground. Don's unit eventually joined the 9th AMCU, and Don was called from oil spraying duty one day because Major Frank Fenner wanted to see him. Don was filled with gratitude when Fenner sent Don back to a Mobile Entomological Section in Cairns.

Don began work in Cairns as Technical Assistant to the 6th Australian Mobile Entomological Section (AMES) as a Staff Sergeant. In Cairns the AMES mostly helped the Australian Medical Research Team testing antimalarial drugs. His unit was supervised by Major Josephine Mackerras, wife of Ian. The unit collected and reared *Anopheles* mosquitos which were then fed on malaria patients. The mosquitoes were later dissected to see how many had become infected. This information was used to calibrate the number of mosquitoes to feed on a patient to transmit a reasonable dose of malaria. All the patients were volunteers from the army, and they were fed various drugs to test their effectiveness. Eventually Atebrin was discovered to provide the best protection. The unit was the first in Australia to test the effectiveness of DDT, but the insecticidal dust got into their clothing and hair, and killed the laboratory colonies of mosquitos.

In late 1944 the AMES moved from Cairns to the Atherton Tableland, to join up with the Australian 9th Division, which was reforming for the allied invasion of Borneo. They set off from Townsville for Asia with 3 other AMES on Friday the 13th April 1945. In Borneo Don met a completely new mosquito fauna from the northern Australian and Papuan one he knew well, and he collected and dissected many mosquitoes in the area. Eventually Don found that *Anopheles umbrosus* and *A. leucosphyrus* were the transmitters of malaria in northern Borneo. The Pacific war ended with Don in Kuala Belait (now Brunei) and subsequently he collected around Kota Kinabalu until late January 1946. These specimens were to make up material for his Honours thesis at the University of Sydney that year. By the end of 1946 Don was 24 years old, a father to his first daughter Viviane, with a degree with first class honours from the University of Sydney, and a wealth of scientific training and experience from his years in the army during World War II.

A Few Months in Canberra

Don had met Major Francis Ratcliffe (ex-CSIR as CSIRO was known then) during the war and he advised Don to apply to join CSIR with 12 months leave without pay prior to beginning Honours. Don followed this advice, was appointed to the Division, and thus could begin work with 12 months seniority. However, before completing his Honours year he was offered a post as an entomologist with a malaria research unit in North Borneo (now Sabah, East Malaysia). The chief of the Division of Entomology at the time, Dr. Nicholson, was sympathetic and suggested that Don come to Canberra for a few months until a firm offer from Borneo arrived. Don duly arrived in Canberra and worked for 3 months in early 1947 on the mite pests of fruit trees with Frank Wilson, John Calaby and Ted Woolcock until the firm offer came from Borneo. Don resigned from CSIR, and coincidentally Francis Ratcliffe accompanied him on the train to Sydney. Ratcliffe was on his way to meet a new member of staff: the dipterist Dr S.J. Paramonov, who had been hired as the Division's first full-time taxonomist. Of course, one day Don would replace Paramonov in Canberra.

North Borneo and Singapore

Don worked for 5 years in North Borneo (1947–1952) with the Borneo Malaria Research, a small British sponsored unit, and 8 years subsequently in Singapore (1952–1960), as a Lecturer in Parasitology at the University of Malaya (now University of Singapore), studying the taxonomy and biology of mosquitos and their transmission of malaria. Don's PhD, conferred by the University of Malaya in 1956, entitled *Studies in the Systematics and Biology of the Culicine Mosquitos of Singapore*, was supervised by Professor A.A. Sandosham. From Don's base in Singapore he was seconded for periods to the World Health Organisation (WHO) for projects in "longhouses in Sarawak, atolls in the Pacific and other less interesting places". Don visited Europe for 3 months in 1955 examining mosquito collections, assisted by a fellowship from the Nuffield Foundation of the Royal Society. Don's light teaching duties in Singapore allowed him to rack up 31 publications, four of them in the prestigious journal *Nature*, by the time he left for a position in CSIR, Canberra in 1960. At the age of 37, Don who at the time was acting Head of the Department of Parasitology at the University of Malaya, Singapore, left for Australia.

The Division of Entomology

Back in the Division by May 1960, Don settled down to work in a room on the ground floor, in the Australian National Insect Collection (ANIC) squeezed in among the insect cabinets with Zenta Liepa, who had been Paramonov's assistant. Paramonov, retained working space in the adjoining room as an Honorary Fellow. Paramonov was a great help to Don and assisted him in getting acquainted with Diptera at large - hitherto he had been a specialist on mosquitos. Zenta also was a great help to Don, as he acknowledged when he published her obituary in 1988. On arrival in the Division, Don was enthusiastic to get started and experimented with some winter collecting in local exotic pine plantations, a venture with little prospect of success. However, it turned out to be very profitable: he discovered the new family Perissommatidae, larvae of which feed on fungal fruiting bodies

in the pine plantations with winter-active adults. Don's career in ANIC was book-ended by the discovery of new families - he published on the Perissomatidae in 1962 and the Axiniidae in 1994, just after he retired. Don also described the odd genus *Valseguya* (Colless, 1990), known from a single individual collected by Edgar Riek in the Otway Ranges, Victoria. This was later placed in the new family Valseguyidae, which is otherwise only known from Cretaceous Burmese and Miocene Dominican Republic amber.

During the 1960's and 1970's Don conducted many very productive field trips to northern Queensland. He would set up a lab in a motel for a few days and collect as complete a sample as possible of Diptera from the surrounding localities. As much of the material as possible would be pinned on the spot that night. As a result of Don's exhaustive collecting and meticulous pinning, three genera (*Collessia* Bock, Drosophilidae; *Collessimyia* Spencer, Chloropidae and *Collessohelea* Debenham, Ceratopogonidae), and almost 50 species have been named after him. The tens of thousands of pinned Diptera in ANIC now stand as a legacy of Don's extensive collecting efforts. During his career he himself described over 120 species and 13 genera of flies. In the 1970's field trips evolved into combined, group expeditions to distant parts of Australia, such as Millstream in the Pilbara and Alligator River in Arnhem Land. Don was a member of the famous 1977 *Nothomyrmecia* trip when Bob Taylor collected the 'living fossil' ant near Poochera, east of the Nullarbor en route to their destination of Balladonia on the western side of the treeless plain. Bob Taylor recalls that it was Don who exhorted the group to collect on that cool evening near Poochera, as their last opportunity to test their equipment before they reached Ceduna on route to Balladonia.

Don was Chief Curator of ANIC from 1971–1977, between the terms of Ken Key and Ian Common, and had a very long, unbroken association with CSIRO spanning 52 years from 1960 until his death. He also had an extremely long and productive publication career spanning 64 years from 1948 until 2012. During that time he published 127 papers and book chapters listed below. Don was a very broad-ranging Dipterist with taxonomic interest and expertise that spanned the order. His taxonomic work began with Culicidae, but extended to the other nematoceran families Chironomidae, Chaoboridae, Corethrellidae, Perissomatidae, Mycetophilidae, Anisopodidae, Sciaridae, Cecidomyiidae, Tanyderidae, and the brachyceran families Empididae, Chloropidae, Sepsidae, Muscidae, Anthomyiidae, Axiniidae, Calliphoridae and Tachinidae. Don and David McAlpine (The Australian Museum) authored the Diptera chapters in both editions of *The Insects of Australia* (Melbourne University Press, 1970 and 1991). In later life (1982–2001) he collaborated with Ken Key, David Rentz and Lou Koch to produce phenetic analyses of Orthoptera and centipedes.

Taxonomic Theory

Don was always very interested in the theory and philosophy of taxonomy and classification. He was a very early user of computers in CSIRO, firstly using punched cards on a CDC3600, and he used his computer time to experiment in numerical taxonomy - conceptualising and quantifying the taxonomic process. As a result of this interest, Don published 30 influential articles on the philosophical underpinnings and theory of taxonomy from 1966–1996. Most of these papers were published in *Systematic Zoology*, the highest impact journal of systematic theory and practice both then and now. This series of articles began with a critique of E.O. Wilson's consistency test for phylogenetic hypotheses (1966), and his 1967b "*An examination of certain concepts in phenetic taxonomy*" provided a philosophical framework for Sokal and Sneath's *Numerical Taxonomy* published a few years earlier (1963). In this paper he introduced the term operational taxonomic unit (OTU), and distinguished clearly between "character" and "attribute" (= character state) for the first time. He pointed out that there were so many different methods of clustering numerical data to form classifications for taxonomy that the most acceptable single approach "seems attainable only by a consensus of personal preference". The plethora of approaches for measuring similarity among characters, and clustering those measurements, remained a challenge for the phenetic approach because there is no way of deciding which of these methods is the most appropriate for revealing "natural" or phylogenetic classifications.

In his paper titled "*The phylogenetic fallacy*" (1967c) Don wrote that a competent phenetic classification by overall similarity on all available data is the best approximation of a phylogenetic classification, and took aim at three other authors who had set out different phylogenetic methodologies. He criticised E.O. Wilson's consistency test (1965), Willi Hennig's phylogenetic systematics (1965), and Camin and Sokal's caminacule experiment (1965)

because of the difficulties associated with homoplasy between different characters, the difficulty of understanding how character states were related in phylogenetic terms, and the problem of determining the polarity of characters in Hennig's system. He was concerned also about the apparent subjectivity of only including a subset of possible characters in these classification schemes. Don extended his argument that a phenogram was an estimate of phylogeny a few years later (1970).

Don (1967c) characterised Hennig's approach as "an intuitive, prototypical form of statistic-phenetic taxonomy" (p. 292), and not so different from the procedures he advocated in his 1967b paper. It was different only in that Hennig's system clustered by synapomorphies alone, not all available characters. In reality, both homoplasy and issues associated with character polarity and outgroup comparison remained major challenges for cladistic theory as it developed in the 1960's and 70's. In this 1967c work he expressed a very modern view of the place and importance of fossils in phylogeny estimation – they should be treated in the same way as extant taxa, and have no special authority to reveal the correct phylogeny (p. 294), and he realised the promise of molecular data, seeing codons as an approximation of the unit attribute (p. 295).

Extending his critique of Hennig's system in 1969, Don argued that it was inefficient in comparison to phenetic methods, and lacked the statistical rigour demanded of empirical science. By selecting characters to use in a cladistic classification, it took a biased, and perhaps prejudiced sample, and that outgroup comparison relied on appeal to a higher-level phylogeny, invoking an infinite regress. Don also criticised the cladists' lack of an approach to the question of weighting characters (1982), and the apparent asymmetry of cladograms (1982, and again in 1995 and 1996). He was critical of the purported evidence that cladograms were more congruent and therefore more stable than phenograms and thus the best basis for classification (1980, 1981, 1983a, 1983b).

It now seems apparent that the development of quantitative cladistic theory through the 1970's and 1980's; that amalgam of Hennig's phylogenetic systematics and Wagner trees, all justified by appeal to Popper's hypothetico-deductivism; was a response in large part to the criticisms that Colless and others directed towards it.

Philosophy of Science

Don was a deep and original thinker, and he had a long interest in the philosophy of science. Because of his desire to get to the roots of his science he was one of the belligerents in the disputes between the pheneticists, cladists and evolutionary systematists in the 1960's and 1970's. This battle began as a disagreement between the evolutionary systematists of the Simpson - Mayr school and the numerical taxonomists of the Sneath - Sokal school, but soon the numerical taxonomists camp split into the pheneticists and the cladists. Don found himself clearly in the pheneticists camp. This period of intense and often acrimonious debate was treated by philosopher of science David Hull in *Science As a Process* (University of Chicago Press, 1988) as an example of scientific revolution. Don was an important player in these debates and there are 18 references to Colless in the index of *Science as a Process*. On re-reading *Science As a Process*, it is easy to conclude that Don's manuscripts were treated unfairly by the American editors of *Systematic Zoology* in the late 1970's and early 1980's.

Given his background in the philosophy of science, Don was always critical of the use of Popperian logic to defend phylogenetic approaches. Very early on in the debate, Colless was concerned that authors defending phylogenetic systems in terms of Poppers hypothetico-deductive model may actually be reconstructing their logic *post hoc*, and he distinguished between "logic in use", and "reconstructed logic" (Colless 1969a). He extended these philosophical arguments in his 1982 review of E.O. Wiley's book *Phylogenetics: The theory and Practice of Phylogenetic Systematics* (1981).

Don was also interested in the process by which taxonomists cluster individual specimens into species. He argued that the philosophical description of the taxonomic process should take some account of "mundane practice". He provided the philosophical justification for a concept that basic taxa (candidate species) are clusters of individuals that are significantly taxonomically similar to each other (Colless 2006), and different from other such groups. He observed that no particular level of difference is critical, there must just be a "significant gap" or moat in character space between one basic taxon and another. He argued that a phenogram or minimum-spanning tree was a useful metric to discover such discontinuities. These basic taxa are epistemologically prior to species - they must be recognised before they can be explained by evolutionary theory.

We finish with some words from Don himself written barely 12 months before he died, writing in response to a manuscript on taxonomic methods that one of us had sent to him for comments (Yeates *et al.* 2011). Although this was simply a private note and not intended for publication, Don sets out a potted history of the search for a description of the scientific method, along the way giving us insights into his rather agnostic, inductive philosophical outlook.

“David:

Your paper on integrative vs. iterative taxonomy set me to musing on the history of the search for a “formal description of scientific method’ (henceforth FDSM). Just for fun, I’m writing out the results. You may find them interesting, since your paper was essentially about the same topic.

Aristotle and Co. got off on the wrong foot. They were so impressed by their profound results in maths and logic that they thought empirical knowledge advanced by that route. The absence of basic, irrefutable premises didn’t worry them much, and for centuries the Church was happy to supply some. However, by the 16th century Francis Bacon was leading a revolution of empiricist thought. His FDSM was simple: just accumulate as much evidence as possible and the truth will stick out like dogs’ balls. This philosophy persisted explicitly in a few dogged souls into the present (e.g., the late K.H.L. Key of our Division!). As I’ll show, it’s still around in a less obvious guise.

This developed into the more-or-less equivalent, inductive process: that repeated instances of the same causal phenomenon induce increasing probability that it is a fact of nature. Unfortunately, Hume, in the 18th century, destroyed this as a FDSM. As he pointed out, there is no LOGICAL reason for believing that the sun will rise tomorrow morning. Induction can generate strong belief, but not certainty. And science was supposed to do just that.

Enter the 20th century, and the hypothetico-deductive FDSM. At first there was the strictly inductive notion that we generate an hypothesis (by whatever means!). Then seek to confirm it by testing its logical consequences. However, as Hempel pointed out, confirmation of an hypothesis gets us nowhere logically. The hypothesis that “All ravens are black” is logically equivalent to “All non-black things are non-ravens”, which is confirmed by a white shoe.

Here Karl Popper produced his famous maxim: we don’t confirm hypotheses, we falsify them, by rejecting their logical consequences. The corollary, that unfalsifiable hypotheses are not science was pretty well received. But folk soon realised that (as first pointed out by Duhem in the 19th century!), our principal hypothesis is backed up by numerous auxiliary hypotheses, which all need to be tested as well. Also, Popper had not provided a status for the confirmed hypotheses. He tried hard to develop a probability argument; but it failed, like those of e.g. Carnap (and Leibnitz in the 17th century!).

We end up then with the process that you have described as “iterative”. Pierce called it abduction (as have many on his coat tails). More recently it is “inference to the best explanation”: my own preferred term, but some abductionists would die defending their own. Basically, this is your H_0 , successively modified *ad hoc* through H_1 ... H_n . Then, if necessary, through H_2 , H_3 , etc., until you feel satisfied that you have the “best” available. There are two philosophical problems here: (a) what do you mean by “best”?; (b) are you justified in accepting the best hypothesis?. Lipton happily sees “best” as the most “beautiful”; we might perhaps say “credible”. And the latter term applies in (b). By and large I think this is a genuine FDSM, although philosophically arguable. But this will always be the case, because philosophers have no intention of going out of business!

The amusing result of these musings is that “integrative” means just “Baconian”! You have all the available data and infer a result by means that unfortunately do not imply a FDSM. E.G., simplicity is an often-quoted criterion, but the term carries no definite operational baggage. Methods such as Bayesian analysis simply try to lift themselves by their own bootstraps (the problem of “priors”). Likelihood analysis provides just that – likelihood, which is the probability of the data given the hypothesis, not vice-versa! So, in the end Francis Bacon rules!

Happy musings!

Don.”

After a short illness suffering pulmonary oedema from a weakened heart valve, Don passed away on the 16th of February 2012. He is survived by two children from his first marriage, Viviane and Susan, and two children from his second marriage, Gamini and Vimala.

Acknowledgments

Although this was written after Don passed away, he helped us with it in a number of ways. Early biographical sections are based on documents Don wrote entitled “Life And Times of Donald Henry Colless”, and another entitled “A Personal Reminiscence of the Division of Entomology”. The former was probably written over the last decade of his life, the latter was written in the mid 1990’s. We are very grateful to Don’s children for providing access to these documents and to photographs used in this paper. Bob Taylor provided us with some personal reminiscences of fieldwork with Don. Stephanie Oberprieler produced the list of papers from a card file maintained by Don, supplemented by database searches.

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