in the search for useful chemicals from fungi, working in collaboration with a member of their staff who had been given facilities in our Biochemistry laboratory. He was then given the status of an Honorary Research Associate at Kew which pleased him immensely because he earnestly wished to be identified with the institution. His love and admiration for Kew was well demonstrated by his decision to donate his very large and valuable library to us and in due course a number of very large boxes of books arrived from Boston to greatly enhance our own scientific library. Of course the general congestion in our premises made it impossible initially to shelve and display Tony's collection but it was hoped that a space could be found in due course and that he and I could share some offices and found a new unit at Kew which we were going to call the GRI–The Geriatrics Research Institute. Alas before the date of my retirement and before we could put our plan into effect, the M4 claimed him on a Friday night in late September.

I miss this man–his wit and charm, his ebullience and his sensitiveness, his boyish humour and his generosity. Science and biochemistry in particular will suffer a more grievous loss and it is most fitting that we should be gathered here today in the Jodrell Laboratory with which he so strongly identified, to remember him and his contributions to both our scientific and personal lives.

THE LINK BETWEEN SYSTEMATICS AND ECOLOGY

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While the chemistry of plant phenolics was a prime and abiding interest of Tony Swain's, he always had a lively curiosity concerning the possible systematic and ecological significance of other secondary compounds. It was as Director of the Agricultural Research Council Laboratory for Biochemical Systematics here at the Royal Botanic Gardens, Kew that he carried out experiments to determine whether reptiles are less able than mammals to detect and therefore avoid potentially toxic alkaloids in plant materials. Some of us may not have been totally convinced that the disappearance of the dinosaurs was related to the appearance of alkaloid-synthesizing angiosperms on the evolutionary scene. None of us, however, who took part in the stimulating and invariably amusing discussions with Tony on this and a hundred other theories was less than totally convinced of the impetus that his ideas were giving to biochemical ecology.

It was during this, his first period at Kew, that he and Dr Gillian Cooper-Driver, whom we welcome again today, made their observations on the selection of acyanogenic forms of bracken and the avoidance of cyanogenic forms by deer and sheep grazing in Richmond Park [1]. With accounts of these and other experiments Tony would enliven the lectures which he gave, as Visiting Professor, in my former Department at King's College, London. His entertaining classes, his breadth of knowledge in both chemistry and biology and above all his willingness to give his time and share his ideas with his students made him a much valued teacher. He was greatly missed in King's when he moved to Boston.

When eventually he came back to England and the Royal Botanic Gardens, it was with pleasure that I, now moved to Kew myself, was able to tell him how the seeds that he had planted in the Annex of the Jodrell Laboratory were flourishing.

Of particular interest to him was the discovery in plants of polyhydroxy alkaloids which resemble sugars [2]. Several of these are not only able to inhibit glycosidase enzymes in phytophagous insects but also inhibit enzymes involved in the synthesis of glycoproteins found in the cell walls of viruses. One such compound, castanospermine, which is active against the AIDS virus *in vitro* [3] was first isolated from the monotypic Australian legume *Castanospermum australe*. Subsequently, however, it was possible, using dried herbarium material, to detect it in eight species of *Alexa*, a morphologically related genus from South America and isolate it from *A. leiopetala* [4]. This work provided not only information about alternative sources of castanospermine but independent chemical evidence of a close evolutionary link between the two genera and support for the view that selectionary pressures, possibly exercised by phytophagous insects, have favoured the synthesis and accumulation of castanospermine since it first arose in some early ancestor of our present day *Castanospermum* and *Alexa* species that flourished when Australia and South America were not yet separate continents.

Another investigation which was underway in the Jodrell Laboratory at the time of Tony's return was again one which involved many of those elements that fascinated him most. It concerned the interaction of the rare butterfly *Eumaeus atala floridana* and its host plant, *Zamia floridana*. The conspicuous larvae of this insect which are coloured red and have two parallel lines of yellow spots running down the back, feed on the young leaves of *Z. floridana*. Like other members of the Cycadales *Z. floridana* synthesizes and accumulates glycosides of methylazoxymethanol, a potent toxin and carcinogen. The adult butterfly is also brilliantly coloured even though, as Dr Miriam Rothschild pointed out, warning coloration is virtually unknown in species of other Lycaenid genera. Using a population of insects reared in captivity it was shown that *E. atala* did not avoid the anticipated toxic effects of the plant carcinogen by metabolizing it but rather sequestered it as the β-D-glucoside, cycasin. The young leaves of *Z. floridana* on which the larvae had fed contained 0.2% of cycasin, the adult butterflies between 1.0% and 1.8%. The ability of the insect to sequester cycasin together with its warning coloration suggest a very ancient association between *E. atala* and its host plant, the insect having apparently not only circumvented the plant's chemical defence but turned it to its own advantage [5].

Established as an Honorary Research Associate in his old laboratory, Tony planned a programme of work on physiologically active compounds from higher plants and fungi which would have complimented ongoing work such as that described. This programme was to have involved the staff and interests of both the Royal Botanic Gardens and CAB International Mycological Institute. Both institutions will sadly miss his cheerful self, his ideas and his enthusiasm.

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TANNINS—CHEMICAL ECOLOGY IN ACTION

(A tribute to the contributions of Professor Tony Swain)

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The name of Tony Swain is well known to all scientists, young or old, who have more than a passing interest in either the chemistry of tannins or in their potential to influence the feeding behaviour of herbivores. His contributions to these topics span four decades and many continue to be widely cited. In this tribute it is not my intention to list and discuss all of these but to highlight a few that illustrate the diversity of his interests. These will not include his review papers [i.e. 1–3] but will concentrate on his own original work.

For my first selections I go back to 1959, when Tony was working in Cambridge. In that year he published, in collaboration with W. E. Hillis, two papers on the phenolic constituents of *Prunus domestica.* These were not the first papers Tony had produced on phenolic compounds as he had previously worked closely with E. C. Bate-Smith. However, I feel that it is these papers that mark the real beginning of Tony's contribution to chemical ecology.

The first of these papers [4] dealt solely with methods of analysis of phenolic compounds. It included a whole battery of procedures (Folin–Denis, butanol/HCl or leucoanthocyanin reagent, vanillin reagent) through which the authors tried to assess the phenolic profile of their plant material. Despite the inherent problems involved with all of these assays due to critical operating conditions and non-stoichiometric reactions (which Tony recognised), the strategy adopted in this paper remained, until the 1980's, the 'norm' for most quantitative studies of tannins and other phenolics.

The second paper [5] was particularly revealing of Tony's attitude to his research. His initial remit had been to investigate why Victoria plums sometimes underwent deleterious changes due to excessive lignification of the stone and surrounding flesh. What was finally reported was a far more wide-ranging set of observations including (a) that extensive changes occurred in tannin concentrations and astringency during fruit ripening; (b) changes in tannin levels occurred during leaf development; (c) shaded leaves produced less tannins than sun leaves; (d) healthy leaves produced more tannins than unhealthy leaves. Now, thirty years on, the importance of observations (b–d) are beginning to attract great attention as we recognise that many extrinsic factors (biotic and abiotic) can influence the synthesis of phenolic compounds with consequences for a plant's resistance to pests and pathogens.

The next two papers I have selected mark Tony's collaboration with Judith Goldstein. In the first of these [6] he returned to the problem of changes in astringency during fruit ripening, studying not only the plum but also apple, pear, banana, grape and persimmon. Tannin measurements were based on the same colorimetric measures adopted previously [4] but now they were used not only singly but as ratios in an attempt to gather information on changing tannin structures. The conclusion reached, that decreasing astringency in ripening fruits is due to increasing polymerization, remains plausible although recent work suggests other mechanisms whereby astringency may be reduced during fruit ripening without this happening.

The second paper with Goldstein [7] is, in my view, one of the most significant Tony produced. It deals directly with the ability of tannins to interact with the protein β-glucosidase. The exciting thing about the results were that they showed clearly that the concept of an irreversibly bound tannin-protein complex was not tenable. 'Strong' complexes between tannins and this enzyme were readily disrupted by surfactants, PVP and variation in ionic strength of solutions. Unfortunately this work was never adequately followed up and its implications were either missed or ignored when, later, the role of tannins as non-reversible digestion inhibitors was being woven into the folk-lore of chemical ecology. It is only now, twenty years later, that the importance of high gut pH, natural surfactants (lecithins, bile acids), mucoproteins, variation in the specificity of tannin-protein interactions, and soluble tanning-protein complexes in modifying the activity of tannins are at last being thoroughly explored.

By the 1970's Tony's work on tannins had tended to move out of the laboratory into the field with a number