TAXONOMY AND BIOLOGY OF AUSTRALASIAN SOLANACEAE WITH ADDITIONAL STUDIES OF ASSOCIATED VEGETATION COMPONENTS

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TABLE OF CONTENTS

The following papers are submitted.

ABSTRACT

Over forty papers dealing with Subterranean clover (*Trifolium subterraneum*), *Cassia* (*Senna*), contributions to the floristics of selected areas of South Australia and the Solanaceae, mainly *Solanum*, are presented.

The topics include the establishment and domestication of Subterranean clover, the diversity and taxonomy of *Cassia* (*Senna*), the floristics of potential nature reserves, and the taxonomy and biology of *Solanum*. The papers on *Solanum* include studies of chromosome number, steroidal alkaloids, fruit diversity, prickliness, sexuality, phytogeography, cladistics and formal taxonomy.

DECLARATION

This work contains no material which has been accepted for the award of any other degree or diploma in any university or other tertiary institution and, to the best of my knowledge and belief, contains no material previously published or written by another person, except where due reference has been made in the text.

I give consent to this copy of my thesis, when deposited in the University Library, being available for loan and photocopying.

July 1995 David E. Symon

PAPERS SUBMITTED FOR A HIGHER DEGREE

by

DAVID E. SYMON

The papers submitted for a higher degree represent work on the taxonomy, biology and floristics of Australian plants. Surprisingly each of the four principal topics, Subterranean clover, *Cassia* (*Senna*), plant floristics and the Solanaceae arose from practical needs. The first was interest in the domestication of an important pasture plant and the need for access to publications on it. The second arose from the difficulty in identifying specimens of *Cassia* sent in by pastoralists. The third was the need for information on the floristics of important areas of the State to enable decisions on conservation to be made. The fourth and major topic, the genus *Solanum*, arose from problems in identifying an important weed of cereal areas. All of them proved to be of interest.

A bibliography of publications is provided at the end of this commentary.

The work submitted is presented in six groups of topics. They are not in chronological order. For ease of reference each paper has been given a number.

Group 1: Subterranean clover

Subterranean clover (*Trifolium subterraneum*) is the most important pasture legume in southern Australia. It is a closely self-fertilised annual but shows a great deal of minor variation which has been profitably exploited for agricultural cultivars. It is one of the relatively few crop plants that has been domesticated in Australia. This history is well documented and the essential details are brought together in the two bibliographies of *T. subterraneum*. Mr Amos Howard of Blakiston played a crucial part in establishing the species as a pasture plant and **Paper 1:** "The early production by A.W. Howard of subterranean clover seed", records his early efforts at selling seed and popularising the plant.

Paper 2: "Heterozygosity in subterranean clover", was the first publication to give some measure of heterozygosity in a natural population. Professor D.G. Catcheside gave me advice on the calculations.

Papers 3 & 4: "Bibliography of subterranean clover" No 1 & No 2. Two substantial bibliographies of subclover have been produced. The first with about 1200 references and the second with about 1900. Bibliographies do not rank highly as research work, but these two comprehensive bibliographies, with their cross indexing of topics have been of use to all subsequent workers.

Group 2: Work on *Cassia* (now *Senna*)

A field trip to Central Australia in 1953 was supported by the University of Adelaide. Many plant collections were made. It was known that the genus *Cassia* was very variable and a taxonomic nightmare. A transect of a natural population on a hill-slope near Alice Springs was made with physical assistance from the late Dr G.M.E. Mayo. The study of this material resulted in **Paper 5:** "A hybrid swarm in *Cassia*". It was the only paper published as a result of the field trip and gave some insight into the problems of *Cassia* variability. In addition, it was one of the early papers published in Australia on hybridity in the flora. Examination of the material brought to light first evidence of the peculiar reproductive biology of *Cassia*. **Paper 6:** "Polyembryony in *Cassia*" revealed abundant multiple embryos, though a single early record of 1890 was later found. This finding led to the extensive work, and the award of Ph.D. degree to B.R. Randell, though this was too late for my **Paper 7:** "Revision of the genus *Cassia* in Australia". This was the first comprehensive account of *Cassia* in Australia since Bentham (1864). The paper has stood up well in the test of time though the later understanding of apomixis and hybridity as revealed by B.R. Randell has resulted in changes in taxonomic concepts and ranks used by me (see also **Paper 33** below). The work on *Cassia* has revealed a reproductive system apparently unique to Australia (for this genus). It has contributed to an understanding of plant diversity and evolution in arid Australia.

Although not closely related to the *Cassia* story **Paper 8:** the book "Acacias of South Australia" is conveniently listed here. The first edition of this popular and successful handbook was prepared by D.J.E. Whibley and published by the Government Printer. When that edition sold out I agreed to prepare a revised edition. The number of species increased from 97 to 122 and comprehensive accounts of biology were added. I had assistance from B. Chandler and G.R.M. Dashorst who drew the illustrations and from M.C. O'Leary for some mapping, frequent discussion and I assisted him on a field trip. Though much of D.J.E. Whibley's first edition was re-used he took no part at all in preparing the second edition.

Group 3: Floristic lists of selected arid areas

Huge parts of Australia are arid and the floras they support are of interest both here and overseas. Plant lists of specified desert regions have not been available for study. The first of these, **Paper 9:** "Flowering plants of the Simpson Desert" was the first up-to-date account of the plants in this area and brought together the scattered records of numerous collectors including Beauglehole, Boyland, Chippendale, Crocker, Forde, Hill, Lothian, Maconochie, Must, Nelson and Winkworth including my own collections from the desert. A partial, now very dated, list had been provided by C.M. Eardley in 1946. I was assisted in a visit to the Simpson Desert by the later R. Sprigg. This paper has been cited in most subsequent publications on the desert.

The mound springs in South Australia form localised oases in a very arid region. **Paper 10:** "Plants of Dalhousie Springs" was the first comprehensive account of their vegetation. This too has been cited in most subsequent papers on the springs. Innes National Park **Paper 11:** represents one of a dozen biological surveys done in South Australia, most, but not all, conducted by the Nature Conservation Society of South Australia. They included Hambidge, Blesing, Hincks, Pearson Island, Koonalda Cave, Oraparinna, Gawler Ranges, Carappee Hill, Innes National Park, Ninety Mile Desert, Mound Springs and bores and the Great Victoria Desert. The information from these surveys has been of significant importance in many of them becoming gazetted reserves. In all these surveys I made plant collections, all are deposited at the State Herbarium of South Australia (AD).

All these reports had multiple authors and **Paper 11** is submitted as a single typical example.

Paper 12: "Pearson Island Vegetation" resulted from a visit to the island by some members of the Royal Society of South Australia. Not only were new records of species added to the list but it was possible to rephotograph sites photographed by Professor T.G.B. Osborne in 1923. Comparisons of these photographs showed substantial vegetation change in the 46 years separating the photographs. As Pearson Island is unoccupied the changes occurred in the absence of man, sheep and rabbits.

Group 4: Paper 13: "Food plants of Australian butterfly genera"

While R. Fisher was preparing his handbook on the "Butterflies of South Australia", I provided him with many plant identifications. When his book was published with a summary of the food plants eaten I recognised botanical patterns of such interest that I followed these up, getting information from Common and Waterhouse "Butterflies of Australia" and in correspondence with Common. Though my paper seems to have been little used (perhaps published in the wrong journal) I still consider it of interest and significance. It showed that food plants of butterfly larvae of Australia belong mainly to plant families of tropical origin. Australian, or characteristically southern, plant families provide food for the larvae of very few species of butterflies. Efforts to repeat the work, on other groups of insects, revealed equally striking patterns but foundered on the inadequacy of biological knowledge of so many insect life cycles.

Group 5: Miscellaneous publications on the Solanaceae

Paper 14: "Solanaceae genera ... naturalised in Australia" was a precursor paper to Volume 29 "Flora of Australia: Solanaceae", (see below). It brought together taxonomic information on 11 genera of Solanaceae, many not dealt with since Bentham 1864. It involved much research particularly for the genus *Physalis* for which there was no recent account in Australia. My assistant R. Pearce drew the maps and grew material.

During my career I have named and described about 60 new species. Many of these are included in publications below and will not be listed separately. Examples of publications on *Nicotiana* (tobacco) are **Papers 15, 16 & 17,** adding several unusual species to those already known.

Paper 18: "*Datura* is a New World genus". *Datura* species (thornapples) are now widespread in the temperate and tropic areas of the world. They are important as weeds and in addition are very toxic. The world distribution of the species was intriguing, with the centre of speciation clearly in Mexico, but with species attributed to China, Europe and Australia. My co-author, L. Haegi, collaborated to provide convincing evidence that the Old World species were of post-Columbian origin and that all species could be found in Mexico and adjacent regions. Some of the older literature had been seriously misinterpreted. Our conclusions have been accepted by other Solanologists and have certainly changed the thinking on the phytogeography of this genus.

Group 6: Research on the genus *Solanum*

Solanum is a very large cosmopolitan genus with at least 1000 species. It contains important food, drug, weedy and horticultural plants such as potato, eggplant, black nightshades, silver leaf nightshades and jasmine nightshade. It has long been considered a "difficult" genus and I became interested in it due to the problems in identifying local and introduced weedy species. No comprehensive account had been published since Bentham 1864 and the various State flora accounts were quite inadequate. I commenced working towards a revision of the species in Australia and supported the more formal aspects of their taxonomy by wide ranging biological investigation. Several collecting trips were done to central and northern Australia and vouchers for chromosomal and chemical work (see below) are all deposited at AD.

Paper 19: "Chromosome numbers in Australian *Solanum* species". This was a joint paper with B. Randell, who did all the cytological work while I provided the plant material and the taxonomy. It was probably the most extensive chromosomal study of any plant genus in Australia up to that time. The results provided basic information on the cytology of the genus but did not lead to any new interpretation of the taxonomy.

Paper 20: "A survey of Australian *Solanum* plants for potentially useful sources of Solasodine".

Several Australian species of *Solanum* (Kangaroo Apples, see **Paper 44**) were being grown extensively in eastern Europe as the source of solasodine a precursor to the important cortico-steroid drugs. Despite this there was virtually no knowledge of the value of most other Australian species. In collaboration with a team of chemists at Monash University an extensive survey of Australian species was made. All the chemical work was done at Monash and I provided plant material and taxonomic expertise and led a plant collecting trip to central and western Australia for research material. Most of the paper was written by the Monash team and the results were

presented to the International Solanaceae Conference at Birmingham, United Kingdom by J. Swan of Monash as **Paper 21**.

Paper 22: "A survey of *Solanum* prickles and marsupial herbivory in Australia" was a wholly original effort to seek some biological basis for the distribution and varied abundance of prickliness in *Solanum*. To my satisfaction at least there is some relationship between prickles and marsupial herbivory. The paper was presented to the International Solanaceae Conference in St Louis, Missouri, United States of America.

Papers 23, 24, 25, 26 & 27: "Fruit diversity and dispersal in *Solanum* in Australia". Fruits are poorly represented on herbarium specimens. The diversity of Australian species was examined and related to dispersal. Two new fruit types were described (one jointly with R. Lester).

Paper 26: "Placentation patterns and seed numbers in *Solanum* fruits". In this the placentation patterns of many species were examined. M. Nee of New York Botanic Gardens also worked on this aspect. We were unknown to each other for some time. In addition to dealing with many more species, my account gave much information on seed numbers per fruit not previously known for *Solanum* or indeed for many other genera.

These various papers have contributed knowledge of *Solanum* fruits and the information has contributed to improvements in the taxonomy of the genus and has helped in better grouping of the Australian (and overseas) species. These papers have certainly heightened the interest of overseas taxonomists in the various qualities of *Solanum* fruits.

Paper 28: "Dioecious Solanums" represents the first of a series of publications on the pollination and sexuality of *Solanum*.

Paper 29: "Sex forms in *Solanum* and the role of pollen collecting insects". Although andromonecy had been known in *Solanum* for many years it had not been studied in recent times. I had earlier drawn attention to dioecious species in Australia, **Paper 28**, and when the first paper was presented at the International Solanaceae Conference in Birmingham it aroused considerable interest and set off a train of interest by other workers in the sexuality of plants – e.g. Whalen, Dulberger, Anderson, Lloyd, Buchman and Lester. Anderson later worked with me on a sabbatical and together we produced **Papers 30, 31 & 32**. All of these added much to the knowledge of *Solanum* reproductive biology. The paper on extrafloral nectaries was the first record of such nectaries in the family Solanaceae. In these last three papers the actual writing was largely Anderson, while I supplied all the material, taxonomy and discussion.

A series of papers on the phytogeography of *Solanum* began with a **Paper 33:** "*Cassia* and *Solanum* in arid Australia" written jointly with B.R. Randell. This showed many relic populations of both genera distributed in lacunae in the sand sheet.

Paper 34: "*Solanum* in arid Australia" was presented to an Australian Systematic Botany Society Symposium held in Adelaide. It looked at characteristics of the genus in arid Australia and demonstrated that the species were derived from border areas, that morphological adaptations to arid conditions could be recognised, and included small leaves, dense pubescence and clonal habit.

Also related to *Solanum* distribution was **Paper 35:** contributed to "Pacific Plant Areas" the volumes on Pacific plant distribution edited by M.M.J. v. Balgoy. Another on species distribution was **Paper 36:** "Phytogeography of New Guinea *Solanum*" developed from the revision of New Guinea Solanum (see below). This showed a suite of species related to the red fruited species of eastern Australia. There was some intrusion of weedy species from both Asia and America and a significant group of Australian species was not represented in New Guinea. Finally on *Solanum* distribution **Paper 37:** "Gondwanan elements of the Solanaceae" was presented to the International Solanaceae Conference at Bogota in which the world distribution of the Solanaceae was surveyed. Distinct geographical patterns were demonstrated for many suites of species, but it did not perhaps clinch a Gondwanan distribution, as distinct from early long distance dispersal.

The phylogeny of *Solanum* on which much more work needs to be done was researched in **Paper 38:** "A study of phylogeny using amino-acid sequencing". The choice of plant material and taxonomy was overwhelmingly mine, all the sequencing and most of the writing was by P. Martin and his team. A surprising result was that diverse Australian species were more closely related to one another than to expected close relatives in Africa. The sequencing by Martin and Dowd showed two unusual amino-acid substitutions common to all but one of the Australian species of subgenus *Leptostemonum* that were analysed. The reasons for this are not known but the results suggest long isolation and speciation in Australia rather than recent long distance dispersal.

The latest contribution to *Solanum* in Australia has been **Paper 39:** "A preliminary cladistic analysis of Australasian *Solanum* and *Lycianthes*". This was done jointly with B. Lepschi. He did all the computation and wrote most of the paper. We consulted closely throughout the work and I did all the scoring and was the principal contributor to the array of characters selected. It is hoped to continue this work which has been interrupted by B. Lepschi changing his job and moving house. We hope to analyse the large distinctive subgenus *Leptostemonum* in greater detail.

This broad array of biological insights has contributed to my major taxonomic "Revision of the genus *Solanum*". The first **Paper 40:** "A revision of *Solanum* in Australia", was the first comprehensive account since Bentham, 1864, and at the time was probably the largest monographic revision published in Australia. The various contributions were acknowledged. A. Szent-Ivany drew the plates though I illustrated the fruits and reproductive parts. R. Pearce drew the maps. This volume was used almost immediately for the first taxonomic volume of the new *Flora of Australia*,

Volume 29 Solanaceae. Although I was frequently consulted, the conversion to flora format was done by R. Purdie. (**Paper 41**.)

This was followed by **Paper 42:** "Solanaceae of New Guinea". The first comprehensive account of the family in New Guinea. Many new species were described and further insights into the subgeneric structure of the genus *Solanum* were revealed. Again M. Szent-Ivany drew the illustrations and R. Pearce the maps.

I was invited to contribute the Solanaceae to the new flora of Hawaii, **Paper 43**, and finally the booklet "Kangaroo Apples" **Paper 44**, a monograph on the Australasian section *Archaesolanum* was prepared for the International Solanaceae Conference held in Adelaide. The fine illustrations were drawn by G.R.M. Dashorst and there were contributions by C. Morris, A. Rowett and W.R. Barker appropriately acknowledged.

I have attended and presented papers at each of the four successive "International Conferences on the Solanaceae" at Birmingham, St Louis, Bogota and Adelaide and was the principal organiser of the last.

Other papers by me are listed in the attached bibliography **Paper 45**.

In addition to knowledge of the botany of South Australia I consider that my work has made a significant contribution to the biology and taxonomy of the Solanaceae.

Of particular interest have been increased awareness by overseas botanists of the varied sexuality of the genus. The work on fruits has increased our knowledge of the diversity of seed dispersal. Many other Australian botanists have been interested in the Gondwanan component of our flora and it is fair to say that there has been a major contribution to world plant geography from Australia. The addition of the Solanaceae to this list is recent and is largely due to studies here. The formal taxonomy of *Solanum* in Australia and New Guinea has certainly contributed to a better understanding of this larger, economically important, cosmopolitan, wonderful genus.

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