

THE PHYTOGEOGRAPHY OF NEW GUINEA SOLANUM (SOLANACEAE)

D. E. SYMON

Agronomy Department, Waite Agricultural Research Institute, Glen Osmond, South Australia,
Australia, 5074

SUMMARY

The Solanaceae, of which *Solanum* is the type species, comprise a southern hemisphere family. A general biogeographical introduction is given, with an account of plate tectonics and a discussion of Wallace's Line and the geographic history of New Guinea. The widely accepted sections of *Solanum* are discussed as are the sections that may be redefined in the future.

THE SOLANACEAE COMPRISE A SOUTHERN FAMILY

The Solanaceae comprise one of the southern hemisphere families though it is rarely listed or considered as one (Hawkes & Smith, 1965). Failure to recognise its southern origin is probably due to the now cosmopolitan distribution of its principal genus *Solanum*. The family also lacks a modern conspectus of its principal stronghold in South America. The recent thesis by Haegi (1983) revising the previously neglected Australian genera in the tribe Anthocercideae has significantly strengthened the southern family concept. The main contra-indication to the southern origin of the family is the cluster of small closely related genera in the tribe Hyoscyameae centred in the northern Himalaya–southwest China region (Kuang & Lu, 1978). Their origin is obscure and they are not clearly related to any of the main southern genera except perhaps *Physalis*.

The seven Australian endemic genera, *Anthocercis*, *Anthotroche*, *Crenidium*, *Cyphanthera*, *Duboisia*, *Grammosolen*, and *Symonanthus* recently monographed by Haegi (1983) are basically southern in their distribution in Australia. With one exception (*Duboisia*) which extends along the eastern coastline and then to New Caledonia, none occur in our tropics. Either New Guinea did not receive the ancient Australian Solanaceous genera or they have not persisted there during the drift north of the Australian tectonic plate. The only other genus and species of the Solanaceae possibly native to New Guinea is *Physalis minima* L. It is as anomalous in New Guinea as it is in Australia and it is probably an historically recent introduction to both places. It is closely related to the weedy, widespread and variable *P. angulata* L. of the Americas and could have been introduced by early Portuguese-Spanish voyagers to the region (Symon, 1981a).

The following analysis is based on my recent account of *Solanum* in New Guinea (Symon, 1985), which includes the genus *Lycianthes* Hassl. Maps of some of the taxa involved are to be found in Van Balgooy (1984).

No fossil (or pollen) record for *Solanum* has been detected and a recent compilation of records of fossils does not even list the family (Muller, 1981).

The species of *Solanum* appear to be dispersed mainly by vertebrates, small mammals and birds (Symon, 1979). Many species are short-lived perennials of disturbed sites and they are less common in climax communities and are rarely if ever dominants. The genus has the faculty for speciation as it is one of the worlds numerically large genera. According to Schuster (1972) this weakens its value for phytogeographic analysis. This opinion may be due in part to the fact that it is difficult to get up to date, comprehensive accounts of very large genera from which to draw conclusions. The taxonomy of *Solanum* is still very uneven. Some groups like the tuber-bearing species are reasonably documented and some sectional units of the genus have been revised. Some geographical areas have recent accounts but there are still huge gaps in knowledge especially in Central and South America.

GENERAL BIOGEOGRAPHICAL INTRODUCTION

New Guinea has long been considered an interesting area by biologists, lying as it does between the Asian and Australian landmasses, between the tropical rainforests of Southeast Asia and the sclerophyllous flora of Australia, between the placental mammals of Asia and the marsupials of Australia. The key position occupied by New Guinea was first recognised by Wallace from a study of vertebrates in the Malayan region and what became known as 'Wallace's Line' has become a famous biogeographical marker dating from about 1869.

"... we can draw a line among the islands which shall so divide them that one-half shall truly belong to Asia while the other shall no less certainly be allied to Australia." (Wallace, 1890, early editions not seen).

This was well before plate tectonics became acceptable. Since then there has been an abundance of papers, books and symposia concentrated on the many problems of the area (Van Balgooy, 1971; Raven & Axelrod, 1972; Schuster, 1972; Walker, 1972; Whitmore, 1981; Gressitt, 1982). A general account of the vegetation of New Guinea will be found in Pajmans (1976).

The biological influences on New Guinea have come from three directions: Asia, Australia, and the Pacific Islands.

1. Asia

The Australian tectonic plate probably first collided with the Asian plate 15 to 5 million years ago, i.e., middle Miocene to Pliocene, a relatively recent event (Whitmore, 1981). This meeting may have been first at the SE. Peninsula of Sulawesi (Celebes) island. The details of the degree of contact, the amount of dry land, how

much was above or below water is difficult to decide, but there does not appear to have been continuous land between Asia and New Guinea at any time. As the Australian plate swept northward it gathered up some island arcs on its northern margin and it is probable that these now constitute the Torricelli, Adelbert, Finisterre and Saruwaged Ranges. The Kubor Range, part of the mountainous spine of New Guinea, has been exposed since the Mesozoic. Some of the Laurasian plate has overridden the Gondwanic plate in the region of Flores and Timor. Buckling and deformation have undoubtedly both created and drowned islands, in addition to which there have been worldwide changes in sea level. Wallace himself makes frequent references to raised coral reefs and exposed coral terraces. Ahead of the tectonic plates are several subduction zones with waters of profound depth, as well as the volcanoes associated with such zones, part of the Pacific 'rim of fire'. The general picture is further complicated by islands such as Borneo, apparently broken off from the Laurasian block. At best it can be said that there has been broken contact between many islands and island groups. Audley-Charles (in Whitmore, 1981) states that geologically the region is one of the most complex zones known in the world. It is unlikely that any precise general biogeographical line can be drawn through the area. In one sense the true 'Wallace's Line' can only be the junction of the two tectonic plates. All other lines reflect the chaotic environmental history of the islands and the ability of the varied biota to disperse. One kilometre of permanent sea is a very different barrier to a Javan rhinoceros compared to a flying fox, and in the same way a kilometre of sea is a different barrier to a large-seeded *Araucaria* compared to a windblown composite. The fruits of *Solanum* are frequently dispersed by birds and fruit bats and it does not seem unreasonable to expect narrow water barriers to be crossed (Symon, 1979). It is simplistic to expect a precise borderline for all biota but rather a sieve-like effect might be created depending upon the ability of a species to disperse.

The extent to which India carried elements of the southern flora north until it collided with Asia is debatable. In its passage almost due north at a relatively rapid rate the original flora must have been subject to both rapid and substantial climatic changes and extinctions may have been extensive. Well-known southern families are either poorly represented or are totally absent, e.g. Proteaceae, Cunoniaceae, Philesiaceae or Restionaceae. In addition secondary invasion with plants of southern origin via Africa or from Australian stock after tectonic junction is conceivable, and the Pittosporaceae is a possible example.

2. Australia

New Guinea is part of the Australian tectonic plate, but is now separated by water at Torres Strait. A relatively recent symposium 'Bridge and Barrier: the natural and cultural history of Torres Strait' (Walker, 1972) has been published. From this it will be seen that Torres Strait was land from the Carboniferous to the Pleistocene. The block was stable until the early Tertiary when deformation began to intensify. This increased in the Miocene and by the end of the Pleiocene the present island was created. Therefore Torres Strait and the New Guinea landscape are geologically recent phenomena. The landscapes of New Guinea are dominated by young folded and

faulted mountains, with shallow, stony and immature soils; in contrast the soils of Australia are largely derived from Tertiary erosion surfaces with deeply weathered profiles. Other papers show a steep environmental gradient between New Guinea and Australia which coincides with Torres Strait. Webb & Tracey (in Walker, 1972) made ecological comparisons of vegetation between the two areas and, using 15 structural types of rainforest, showed a common derivation and evolution in similar environs of the forests on both sides of the Strait. The low proportion of species in common and the few endemic families and genera, mainly on the Queensland side, suggested independent evolution almost entirely uninfluenced by recent migration. Any disjunction as a result of the relatively recent appearance of the Strait seemed to be largely irrelevant. They comment that genera in common were often readily dispersed. Wace (in Walker, 1972) when summarising the symposium considered the floristic boundaries of the region to be substantially ecological rather than physical. Van Steenis (1979) in an analysis of the Lesser Sunda Island's flora comes to a similar conclusion.

3. The Pacific Islands

I have seen no suggestion that the north side of New Guinea contains continental remnants other than the island arcs already referred to. A substantial distance away are New Caledonia and New Zealand, both very old continental fragments and of similar age to the Owen Stanley Ranges of southeastern New Guinea. Closer islands are the Solomons, New Hebrides and Fiji which had a volcanic origin in the Oligocene and Eocene well before the tectonic plate collision. The influence of these islands on the New Guinea vegetation is almost proportional to their distance.

BIOGEOGRAPHY OF SOLANUM

The infra-generic taxa of *Solanum* are not yet well defined. In the following account significant references are cited where available. The sections *Solanum*, *Asio-melanesia*, *Cypellocalyx*, *Archaeosolanum* and *Lasiocarpa* appear widely accepted or have had recent accounts published. The sections *Gracilliflora*, *Dunaliana*, *Micracantha* and *Torva* may be redefined when further work has been done.

1. Section *Solanum* (Black Nightshades)

This section is almost cosmopolitan and the ubiquitous black nightshades *Solanum nigrum* L. and *S. americanum* Mill. are amongst the best known and most widely spread weedy plants. The species have been treated in detail in Australia (Henderson, 1974) and a conspectus of the section in South America is available (Edmonds, 1972). The principal species in New Guinea, *S. americanum* is a subcultivar. It is grown and eaten as a green vegetable and is available in local markets and such use extends to the Pacific Islands. It has a wide ecological range and its distribution is now pan-tropical, probably aided by man. It is known that the fruits of the morphologically similar *S. nigrum* L. are dispersed by birds and there is every reason to expect those of *S. americanum* to have similar agents. A second species, *S. opacum*

A. Br. & Bouché is shared with Australia where it occurs along the east coast from Cape York to Tasmania. In New Guinea it occurs at moderate to higher altitudes. It has not been recorded from either Southeast Asia nor the Pacific. This species is a hexaploid; the diploid *S. americanum* is not an obvious parent and the origin of *S. opacum* is obscure. The fruits of *S. opacum* are drab green, highly aromatic and are readily shed when ripe. A different dispersal agent could be expected and this is likely to be a small ground ranging vertebrate. This may possibly explain why it has not been distributed from the Australian plate.

2. Section *Asiomelanesia* Bitter

The early comprehensive account by Bitter (1920) lists 12 species and 27 infraspecific taxa. The large number of infraspecific taxa reflects the taxonomic problems he found. The more recent accounts, of Deb (1980) and Kuang & Lu (1978), only consider species within Indian and Chinese regional political boundaries and contribute little to an understanding of the whole complex. No American species have ever been attributed to this section. The succulent bright red or black berries suggest bird dispersal though I have found no records. The bulk of the species are undoubtedly restricted to Asia where they are widespread and some are subweedy. Two species occur in New Guinea. One is the widespread subweedy *S. biflorum* Lour., and the other is the endemic *S. bitterianum* Symon, located only in the vicinity of Bulolo. Neither species extends further east to the Pacific nor to Australia. This group seems to represent a definite Asia–New Guinea link. The origin of the section in Asia remains a problem. The members of section *Asiomelanesia* do not seem as closely related to American species as do the members of section *Cypellocalyx* (see below). The likelihood of long distance dispersal from American stocks is extremely unlikely. The section *Asiomelanesia* could have been rafted north on India and so reached Asia. Such an occurrence could also account for the presence of the tribe Hyoscyameae in the northern Himalaya–Southwest China, both derived from ancient stocks of the Solanaceae. This would represent a very old pathway indeed, not yet acceptable to many botanists.

3. Section *Cypellocalyx* Bitter

This is a group of about 20 species unquestionably centred on New Guinea where the majority of species and greatest diversity occurs (Bitter, 1920; Symon, 1985). One species, *S. vitiense* Seem. extends to Fiji but no further east. One or two species extend to the Philippines and Sumatra, e.g. *S. parasiticum* Blume, and this just enters the Asian mainland near Malacca close to Sumatra. One species, *S. shanesii* F. Muell. has recently been recognised in North Queensland (Symon & Clarkson, 1984), but is not recorded in New Guinea.

The species of this section are certainly adapted to high rainfall tropical forests and extend to relatively high altitudes (2500 m). One could expect to find at least relics in the rainforest of Queensland. The one Australian species, *S. shanesii* occurs in disjunct sites on the margins of isolated monsoon vine thickets. In New Guinea the species do not occur to any extent in the lower drier portion of the island.

The taxonomic affinities of the entire group of species in New Guinea (but particularly *S. shanesii*) appear to be with section *Synantheroides* Bitter from Central America (South Mexico to Panama). There are only about 6 species in this section in America and if they are in fact closely related to the New Guinea species, it presents us with all the problems of trans-Pacific movement. Although long-distance dispersal is not impossible, there is no convincing evidence for it. The relatively large number of species in New Guinea indicates that the section must have arrived long ago. An alternative explanation is that they are a very old group, now extinct in Australia except for *S. shanesii*. They may represent the most northerly distribution of a group once widespread in both Australia and South America.

4. Section *Archaeosolanum* (Marzell) Danert (Kangaroo Apple)

This group of eight species is centred on southeastern Australia and forms a distinctive section. Its base chromosome number of $n=23$ is not known to occur elsewhere in the genus. This number implies two chromosome changes, i.e. $n=12 \rightarrow 24 \rightarrow 23$; it is the only group with distinctive cytology amongst those being discussed, and close relatives with $n=12$ or $n=24$ have not been recognised.

Two species, *S. aviculare* Forst. f. and *S. laciniatum* Ait., which occur in Australia, have reached Tasmania and New Zealand. In New Zealand some subspeciation is recognised which could be quite recent. *Solanum aviculare* also reaches New Guinea where it occurs at high altitudes. A new species, *S. multivenosum* Symon, is also found at high altitudes in New Guinea and it has not been recognised elsewhere. The spread of *Solanum* from Australia to New Zealand is possibly by birds as the fruit, which is succulent and finally pulpy, is known to be eaten (Symon, 1979). The nearest possible relative to *S. multivenosum* is *S. vescum* F. Muell., which occurs in southern Queensland and south along the east coast of Australia. The New Guinea species is distinctive and is certainly not a recent descendant of an Australian species. It may therefore represent an early Australian element in the New Guinea flora. The second species, *S. aviculare* appears identical with Australian material and may be of more recent origin there.

5. Section *Lasiocarpa* (Dunal) D'Arcy

This is a small section of about 12 species recently monographed by Whalen et al. (1981). Section *Lasiocarpa* has its maximum diversity in northern South America. Two species found in New Guinea, *S. lasiocarpum* Dunal and *S. repandum* Forst. f., both of which have close relatives in America, extend through the Pacific and South-east Asia. A third species based on a single collection, *S. atheniae* Symon, has recently been named from New Guinea. The collection lacks mature fruits so that critical comparison is difficult, but *S. felinum* Bitter ex Whalen, from Venezuela may be related to it. The relationships and distribution of the species are intriguing and suggest recent trans-Pacific movement perhaps linked with human migration across the Pacific in the last 1000 years.

6. Section *Gracilliflora* sensu Symon (1981b) non (Dunal) Seithe; Group *S. ferocissimum* of Whalen (1984)

The application of the sectional name *Gracilliflora* to the Australian species by Symon (1981b) is probably in error. Whalen (1984) considers it to apply to a group of American species. He separates the Australian species in his informal *S. ferocissimum* group and restricts the species to Australia. Unquestionably a number of the New Guinea species belong here. It is also probable that five New Caledonian species, *S. actephilum* Guillaumin, *S. hugonis* Heine, *S. pancheri* Guillaumin, *S. pseuderanthe-moides* Schlechter, and *S. vaccinioides* Schlechter belong here rather than with section *Dunaliana* as indicated by Whalen.

There are 10 species of this group in subtropical eastern Australia, 17 species occur in New Guinea and 5 in New Caledonia with no species in common. The group is closely allied to Whalen's *S. bahamense* group (*S. bahamense* L.) from the Caribbean which consist of five species.

The widespread occurrence and speciation of this group in Australia, New Guinea and New Caledonia suggests a long establishment in this area and any connections with the Caribbean species must be ancient. The disjunct distribution of two species in arid Australia apparently disrupted by climatic change supports this claim (Randell & Symon, 1977; Symon, 1982). All the species have red (or finally black) succulent fruit and some Australian species are known to be dispersed by birds.

7. Section *Dunaliana* (Bitter) Symon

This small section contains about a dozen species and has not yet been monographed. Seven species occur in New Guinea which appears to be the centre of diversity. Of these species, *S. dunalianum* Gaud. is most common in New Guinea; it extends to nearby islands to the east and west and reaches Cape York in Australia. *Solanum torricellense* Bitter, *S. incanoalabastrum* Symon and *S. mankiense* Symon are confined to New Guinea, and *S. peekelii* Bitter occurs on the nearby Normanby Islands. *Solanum tetrandrum* R. Br. and *S. viridifolium* Dunal occur in northern Australia and adjacent areas of New Guinea. The status of this section in the Pacific has not yet been clearly defined but it is possible that *S. viride* Forst. f. ex Sprengel (syn. *S. uporo* Dun., *S. anthropophagorum* Seem.) (Pacific Islands) and three species in New Caledonia, *S. camptostylum* Bitter, *S. insulae-pinorum* Heine and *S. styraciflorum* Schlechter also belong to this section.

The fruits of all species are yellow, orange or red to black and one species, *S. viridifolium* is known to be eaten by pigeons.

Apart from these occurrences in the Pacific the evidence suggests that this section has diversified in New Guinea and has spread to adjacent areas. There is some evidence also, that this group has affinities with series *Giganteiformia* Bitter, in eastern Africa.

8. Section *Micracantha* Dunal

A small section of about 15 species widespread in the tropical lowlands of Central and South America. A single species, *S. schefferi* F. Muell. has been recognised in

New Guinea. It is unlike any other species in Southeast Asia or Australia but may be related to *S. lianoides* Elmer from the Philippines which Whalen (1984) includes in his *S. macoorai* group. The section needs revision before definite opinions can be expressed on relationships. Nevertheless like sect. *Lasiocarpa* and sect. *Torva* this appears to be another small section with its main affinities in South America.

9. Section *Torva* Nees

This section contains about 50 species (Whalen, 1984), which are concentrated in the northern half of South America and extend through Central America to Mexico. One species, *S. torvum* Sw. is now widespread as a weed in tropical areas. Species of this section are known to be dispersed by fruit bats and frugivorous pigeons. In addition to the alien *S. torvum* two native species occur in New Guinea, *S. dammerianum* Lauterb. & K. Schum. and *S. torvoideum* Merrill & Perry. Neither occur in Australia nor to any extent in westward regions. *Solanum inaequilaterale* Merrill, present in the Philippines, may also be related. Their relationships are clearly with the species in America, especially *S. chrysotrichum* Schldl. (*S. hispidum* auct. non Pers.) and *S. asperolanatum* Ruiz & Pavon.

DISCUSSION

Two large groups in Australia have not been found in New Guinea. Section *Oliganthes* sensu Symon (1981b) is widespread and successful in arid Australia where about 40 species occur. It may well be one of the oldest and most widespread groups with considerable diversity in Australia. In Australia it is rare in the rainforest areas.

Whalen (1984) has redefined section *Oliganthes* and divides it into several, mainly African, groups. He retains the Australian species in three informal groups, *S. hystrix* group confined to Australia; *S. macoorai* group, tentatively including *S. lianoides* Elmer from the Philippines; and *S. ellipticum* group including *S. elaeagnifolium* Cav. from both North and South America. However, none of the species have been collected in New Guinea or New Caledonia.

Section *Melongena* sensu Symon (1981b) with seventeen dioecious and monoecious species mainly in Northwest Australia has also been further divided by Whalen (l.c.). His divisions consist of the *S. dioicum* group confined to Australia and the *S. incanum* group in Africa, Middle East and southern Asia. None of these have been collected in New Guinea. While not agreeing with all Whalen's placements of the species in these groups the new alignments strengthen an autochthonous Australian element and reduce close connections with other continents.

It is possible that both groups are ecologically unsuited to New Guinea rainforest but could be expected to tolerate the drier monsoonal climate of southeastern New Guinea, as they occur in the arid and monsoonal areas of Australia.

Links with the Pacific are somewhat tenuous and need more taxonomic study to clarify, but they are not strong, and appear to involve the continental fragment New Caledonia more closely than the Pacific volcanic sea mounts.

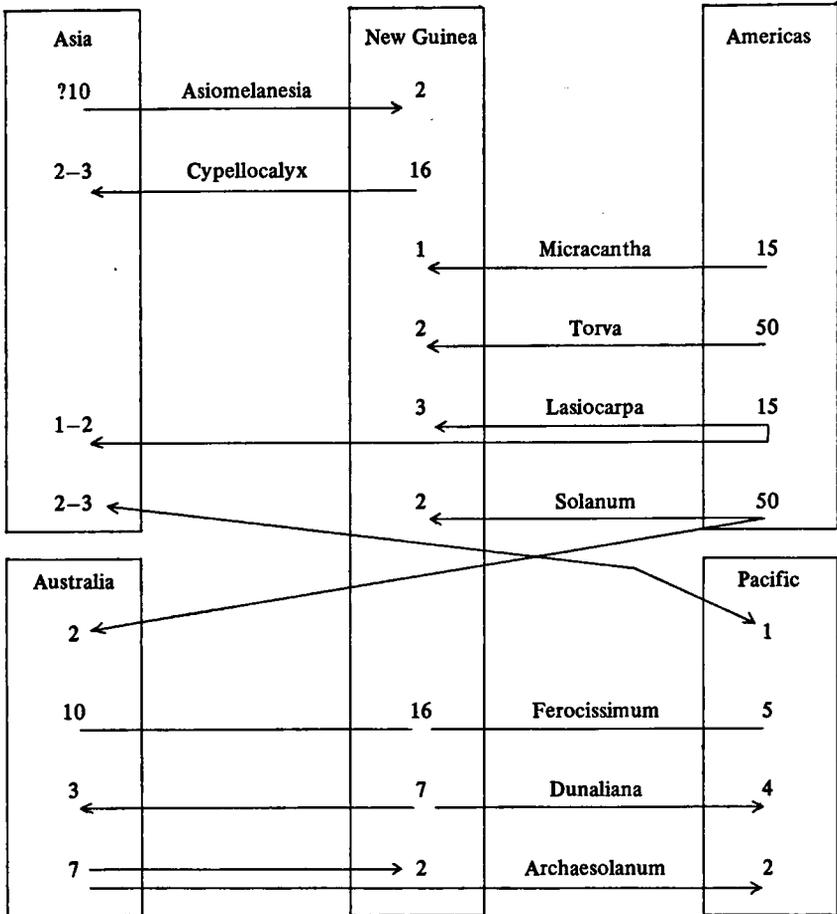


Fig. 1. Distribution of *Solanum* sections and groups about New Guinea.

Possible links with Central America are intriguing and occur with species from both New Guinea, e.g. sections *Cypellocalyx*, *Lasiocarpa*, *Micracantha* and *Torva*, and Australia with *S. shanesii* F. Muell., *S. callium* White ex Henderson, *S. elaeagnifolia* Cav.

Figure 1 summarises the relationships of the genus in New Guinea.

ACKNOWLEDGEMENTS

I am grateful to L. A. R. Haegi, B. R. Randell and K. W. Shepherd for helpful criticism.

REFERENCES

- BALGOOY, M.M.J. 1971. Plant geography of the Pacific. *Blumea Suppl.* 6: 1–222.
- (ed.) 1984. *Pacific Plant Areas 4*: maps 313–314, 316. Rijksherbarium, Leiden.
- BITTER, G. 1920. Die Gattung *Lycianthes*. *Abh. Naturwiss. Ver. Bremen* 24: 292–520.
- DEB, D.B. 1980. Enumeration, synonymy and distribution of the Solanaceae in India. *J. Econ. Taxon. Bot.* 1: 33–54.
- EDMONDS, J.M. 1972. A synopsis of the taxonomy of *Solanum* sect. *Solanum* (*Maurella*) in South America. *Kew Bull.* 27: 95–114.
- GRESSITT, J.L. (ed.) 1982. *Biogeography and ecology of New Guinea*. 2 Vols. Junk, The Hague.
- HAEGI, L.A.R. 1983. Systematic and evolutionary studies in the Australian Solanaceae. Thesis, Flinders Univ., S. Australia. 568 pp.
- HAWKES, J.G. & P. SMITH. 1965. Continental drift and the age of angiosperm genera. *Nature* 207: 48–50.
- HENDERSON, R.J.F. 1974. *Solanum nigrum* L. (Solanaceae) and related species in Australia. *Contr. Queensl. Herb.* no. 16: 78 pp.
- KUANG, Kō-zen & An-ming LU (eds.) 1978. Solanaceae. *Fl. Reipubl. Pop. Sinicae* 67: 1–175.
- MULLER, J. 1981. Fossil pollen records of extant angiosperms. *Bot. Rev.* 47: 1–142.
- PAIJMANS, K. (ed.) 1976. *New Guinea vegetation*. CSIRO & Aust. Nat. Univ. Press, Canberra. 213 pp.
- RANDELL, B.R. & D.E. SYMON. 1977. Distribution of *Cassia* and *Solanum* species in arid regions of Australia. *Search* 8: 206–207.
- RAVEN, P.H. & D.I. AXELROD. 1972. Plate tectonics and Australasian Paleobiogeography. *Science* 176: 1379–1386.
- SCHUSTER, R.M. 1972. Continental movements, 'Wallace Line', and Indomalayan Australasian dispersal of land plants. Some eclectic concepts. *Bot. Rev.* 38: 3–86.
- STEENIS, C.G.G.J. van. 1979. Plant-geography of East Malesia. *Bot. J. Linn. Soc.* 79: 97–178.
- SYMON, D.E. 1979. Fruit diversity and dispersal in *Solanum* in Australia. *J. Adelaide Bot. Gard.* 1: 321–331.
- 1981a. The Solanaceous genera, *Browallia*, *Capsicum*, *Cestrum*, *Cyphomandra*, *Hyoscyamus*, *Lycopersicon*, *Nierembergia*, *Physalis*, *Petunia*, *Salpichroa* and *Withania*, naturalised in Australia. *J. Adelaide Bot. Gard.* 3: 133–166.
- 1981b. A revision of the genus *Solanum* in Australia. *J. Adelaide Bot. Gard.* 4: 1–367.
- 1982. *Solanum* (Solanaceae) in arid Australia. In: *Evolution of the flora and fauna of arid Australia* (ed. W.R. Barker & P.J.M. Greenslade). Peacock Publ., Adelaide.
- 1985. The Solanaceae of New Guinea. *J. Adelaide Bot. Gard.* 8: 1–171.
- & J.R. CLARKSON. 1984. The re-instatement of *Solanum shanesii* F. Muell. Section *Lycianthes* (Solanaceae) with discussion of its significance. *J. Adelaide Bot. Gard.* 7: 201–206.
- WALKER, D. (ed.) 1972. *Bridge and barrier: the natural and cultural history of Torres Strait*. Publ. BG/3, Aust. Nat. Univ. Canberra.
- WALLACE, A.R. 1890. *The Malay Archipelago*. Ed. 10. Macmillan & Co., London.
- WHALEN, M.D. 1984. Conspectus of species groups in *Solanum* subgenus *Leptostemonum*. *Gentes Herbarum* 12: 179–282.
- , D.E. COSTICH & C.B. HEISER. 1981. Taxonomy of *Solanum* section *Lasiocarpa*. *Gentes Herbarum* 12: 41–129.
- WHITMORE, T.C. (ed.) 1981. *Wallace's Line and plate tectonics*. Clarendon Press, Oxford. 91 pp.