

PLACENTATION PATTERNS AND SEED NUMBERS IN *SOLANUM* (SOLANACEAE) FRUITS

D.E. Symon

C/- State Herbarium, Botanic Gardens,
North Terrace, Adelaide, South Australia 5000

Abstract

Placenta patterns of about 100 species of *Solanum* are presented. Considerable diversity occurs with elaboration and eventual division of the placenta. The septum may disintegrate or the development of extra septa and intrusions of the pericarp may occur. Elaboration of the placenta is closely correlated with high seed numbers and disintegration of the septum is found mostly in species with small red fruits. In section *Archaeosolanum* the seeds become embedded in an enlarged placenta which appears to occupy the free space in the locule completely and in some species of section *Leiodendra* a reticulum develops which separates the numerous seeds singly or in small groups. In subgenus *Lycianthes* several species have intrusions from the pericarp partially separating the seeds.

Introduction

The ovary of species of the Solanaceae is usually described as bicarpellate with axile placentation. The common exception noted is *Nicandra physalodes* (L.) Gaertner which may have 3, 4 or 5 locules.

After studying examples of 14 genera and 21 species of the Solanaceae, Murray (1946) concluded that the placentae are axile in position while the carpel walls, the septa and ovule bearing portions of the placentae are foliar in origin. It was noted that in some species, e.g. *Capsicum frutescens*, the growth of the placenta did not keep pace with the growth of the pericarp and the septum so that the upper parts of the locules are not isolated, i.e. the septum is incomplete. Other works, cited by Murray, note that the ovule bearing tissue of the gynoecium (in *Lycopersicon esculentum*, *Lycium*, *Capsicum* and *Solanum tuberosum*) appears to be a prolongation of the axis, the outer portion of the carpels arch over the central axile prolongation and then fuse, the apex prolonged into the style. The time of carpel fusion differed in different genera.

In a detailed study of many genera and species by Huber (1980), the late fusion of the carpel apex is clearly demonstrated and the ovary is mostly bicarpellate at least in its lower half. In addition to *Nicandra* a multiloculate ovary was also shown for *Jaborosa*. In all cases only a single species per genus was investigated. Both these studies showed that central axile placentation was often well developed and that the upper part of the septum is developed late or weakly.

Few studies of the mature fruits of *Solanum* on a broad scale have been located. An early paper by Perlova (1946) considered the morphology of the berries as a taxonomic character but confined this to tuber-bearing species. She concluded that the berries were taxonomically useful even within the restricted group she investigated. The nature of the placenta was not investigated.

Roth (1977) has assembled much of the published information on fruits of the Solanaceae. The interpretation of the significance of the stone cell concretions was not advanced beyond that of Bitter (1911, 1914) who considered them evolutionary relics of a once stony endocarp or, according to Kaniewski (1966) in Roth, of an ancestral fruit type. This may have had both a stony endocarp and stony outpart as the stone cell masses are mostly in the outer fleshy pericarp. The biology of the stone cell concretions is still not satisfactorily understood. Stone cells are believed to be wholly absent from subgenus *Leptostemonum* and from other sections except where mentioned.

The placentae and septa may be enlarged and proliferations which form the bulk of the intra-locular flesh develop from these. Houghtaling (1935) in a study of the size and shape of tomato fruits states that the placental tissue grows up around the ovules and that the cells of

this outgrowth eventually become very large and rupture as the fruit becomes ripe. However Czaja (1963) in Roth, has demonstrated that in tomato, at least, the jelly-like (slimy) material enveloping the seeds, so conspicuous in fruits of many *Solanum*, is in fact developed from the epidermis of the testa. In other cases the endocarp may proliferate and developmental studies will be needed to distinguish which of these is predominant. In the capsular fruited species, e.g. *S. rostratum*, the inner half of the pericarp develops a collenchymatous hypoderm and the differential shrinking as the berry dries, causes the fruit to open as a capsule. The majority of species produce fleshy berries in which the pericarp wall and the placentae are well developed. Both may proliferate into the locule so that all free space is occupied. At maturity the cell walls of the proliferations become thin and the cells partially collapse to become succulent, juicy and finally deliquescent. The abscission of some fruits, generally with their pedicel, e.g. *S. opacum*, *S. macoorai*, *S. xantii*, is facilitated by layers of specially modified cells in the pedicel which hydrolyse and enable separation to occur. A study of fruit types and their dispersal was published by Symon (1979) and a censer fruit form was described by Symon (1984); for further details of the latter see under section *Melongena*.

At the 1982 Conference on the Solanaceae held at St Louis Dr M. Nee and I found that, quite independently, we had both been making transverse sections of mature fruits and were surprised at the variety of placenta patterns revealed. Nee (1986) has now presented an array of placenta patterns observed in five genera of the Solanaceae and in 13 species of *Solanum*. He showed that the multiloculate condition occurred in several species of *Solanum* in addition to cultivars of the species *S. melongena*, *S. aethiopicum*, (*S. gilo*) and *Lycopersicon esculentum* (*S. lycopersicum*). In addition the septum appears to be absent in the mature fruits of a number of species.

Material and method

Transverse sections of full-sized or ripe fruits of *Solanum* were made at about midpoint of the fruit and scale drawings of the sections were sketched. In a few cases sections of ovaries were also made and fruits were dissected to explore the ramifications of the placenta and septum. About 100 species have been sectioned and to these have been added some redrawn from Nee (1986) and one from Hassler (1917) to enlarge the taxonomic coverage.

Limitations on the numbers of fruits and the range of species available mean that this study must be considered an introductory survey only. Herbarium specimens are frequently unavailable or unsuitable for use. The convention used in the illustrations has been to indicate the pericarp, septum, placenta and seeds in white space and the locule space in black. However in many cases the locule is occupied by cellular tissue developed from the inner wall of the pericarp, or from the placenta, or when jelly-like, apparently from the testa of the seeds. When the fruits are finally dry the locule space may be empty except for the seeds, e.g. *S. cinereum* (Fig. 10a, b) or *S. petrophilum* (Fig. 9d). Botanical authorities for all *Solanum* names used are given in the list of voucher material.

Subgenera, sections & species of *Solanum* examined

Subgenus *Solanum* (syn. subgenus *Pachystemonum*) section *Solanum* (Black Nightshades)

Species examined: *S. americanum*, *S. nigrum*, *S. physalifolium*, *S. opacum*, *S. retroflexum*, *S. villosum*. Fig. 1a-f, Table 1.

This section which contains the type species of the genus has its greatest diversity in South America and is now cosmopolitan. At maturity all fruits are relatively small (6-12 mm diam.), globular and succulent, green, purple-black or yellow to red in colour. Without exception these have been bilocular with the placenta not elaborated. The pulp is invariably succulent and

some species may contain stone cell concretions, e.g. *S. americanum*, *S. furcatum*, *S. opacum*, *S. physalifolium*, which are usually peripheral in position (in the pericarp) and may be confined to the apex of the berry in some cases. The green, aromatic fruit of *S. opacum* is shed with its pedicel at maturity.

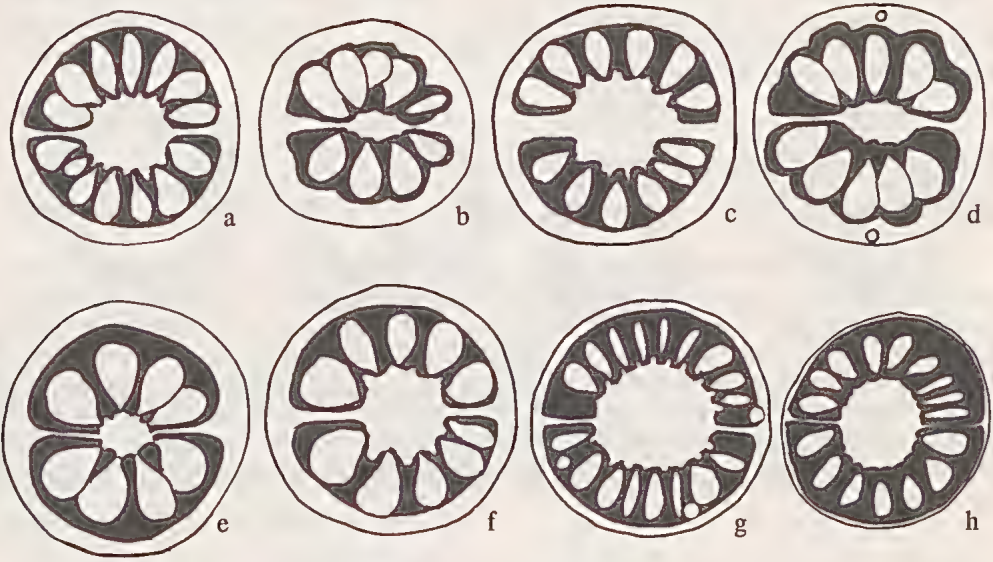


Fig. 1a, *S. americanum*; b, *S. nigrum*; c, *S. opacum*; d, *S. physalifolium*; e, *S. retroflexum*; f, *S. villosum*; g, *S. triflorum*; h, *S. xanthii*.

All the species examined in Fig. 1a-f, had a simple septum and central axile placenta and did not display much variation. A summary of seed numbers recorded is given in Table 1.

Table 1

Species	No. of fruits	Range and mean			
		Seeds		Stone cells	
<i>S. americanum</i>	76	(30-)	52	(-90)	2.4(-8)
<i>S. chenopodioides</i>	10	(22-)	49	(-64)	0
<i>S. furcatum</i>	8	(16-)	20	(-25)	10
<i>S. nigrum</i>	111	(10-)	37	(-72)	0
<i>S. nigrum</i> (green frtd)	10	—	43	—	0
<i>S. opacum</i>	56	(7-)	42	(-68)	2
<i>S. physalifolium</i>	60	—	19	—	4
<i>S. scabrum</i>	6	(79-)	103	(-126)	0

Subgenus *Solanum* section *Parasolanum* Child

Species examined: S. triflorum. Fig. 1g.

A small section of 10-13 species (in need of revision) from temperate North and South America. Considered close to section *Solanum*. One species *S. triflorum* has become weedy in a number of temperate areas. This has a green, succulent berry with abundant stone cells. The placenta is axile and though large, is not elaborated. Twenty fruits provided a mean and range of (78-) 129 (-163) seeds and (20-) 28 (-35) stone cell granules.

Subgenus *Solanum*; *S. xantii* group

Species examined: *S. xantii*. Fig. 1h.

S. xantii together with *S. parishii* and *S. umbelliferum* form a small group of species from southern North America that are not satisfactorily placed at the moment. They may have distant relationships with the tuber-bearing species. *S. xantii* has a green, aromatic, succulent berry that is shed with pedicel at maturity. The large central placenta is not elaborated. Three fruits provided a mean of 48 seeds per berry.

Subgenus *Solanum* section *Leiodendra* Dunal

Species examined: *S. callium*, *S. nudum*. Fig. 2a & b.

This section is concentrated in Central America and northern South America. Three species are widely disjunct or were dispersed very early after the European discovery of the Americas. viz. *S. callium* in Australia, *S. superficiens* in Java and *S. spirale* (= ?*S. antillarum* in Central America) in India. The two species examined *S. callium* (Aust.) and *S. nudum* (Central America), Fig. 2a-b, have unusual berries in which the septum and placenta are not at all distinct. The berry is filled with a reticulum which separates the seeds individually or in very small groups. No other berries like these were seen, but in subgenus *Lycianthes* several were seen in which intrusions developed from the pericarp and extended into the locule partially separating the seeds.

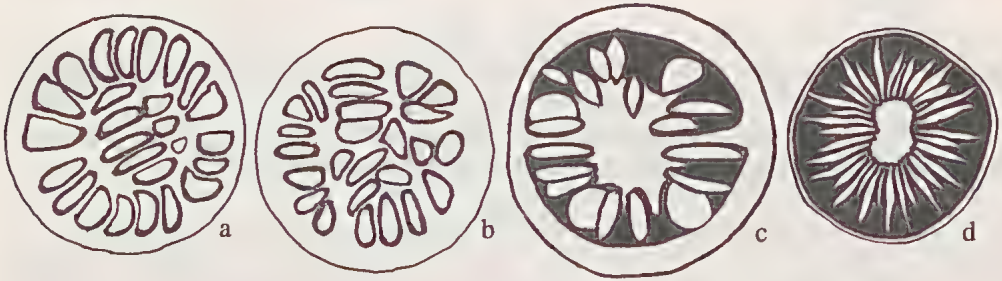


Fig. 2a, *S. callium*; b, *S. nudum*; c, *S. pseudocapsicum*; d, *S. pugiunculiferum*.

Subgenus *Potatoe* (G. Don) D'Arcy section *Petota* Dumort

Species examined: *S. tuberosum* cv. Coliban. Fig. 3a & b.

Species of this large and well known section are concentrated along the Andes of South America and extend to southern North America. All have green fruits some being attractively aromatic as in this species. They are succulent at maturity. The seeds are embedded in the periphery of the large placenta which completely fills the locule. They do not contain stone cells. Seed were counted on fruits from field grown plants in South Australia as no wild material has been available; 16 berries from 3 cultivars yielded a range and mean of (70-) 128 (-200) seeds.

Subgenus *Potatoe* (G. Don) D'Arcy section *Neolycopersicon* Correll

Species examined: *S. pennellii*. Fig. 3c.

This interesting species forms a connecting link between *Lycopersicon* and *Solanum* and occurs in Peru. The berry is distinctly bilobed, green, pubescent and with well developed calyx lobes. The locule is filled with green flesh which must be developed from the placenta as it is separate from the inner wall of the pericarp. Like *S. tuberosum* the placenta is well developed with the seeds on the periphery. Eight berries (52-) 112 (-155) seeds.

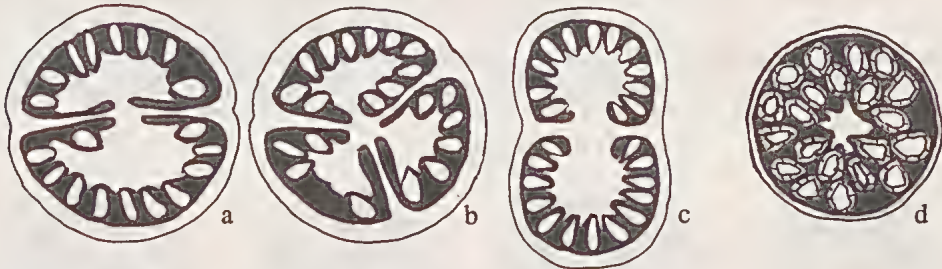


Fig. 3a & b, *S. tuberosum*; c, *S. pennellii*; d, *S. seaforthianum*.

Subgenus *Potatoe* (G. Don) D'Arcy section *Jasminosolanum* Bitter ex Seithe

Species examined: *S. seaforthianum*. Fig. 3d.

The species of this section are mainly found in South America and are climbers or lianes. Several species have been widely grown as ornamentals and *S. seaforthianum* has become established in several tropical areas. At maturity the berries are red and succulent. The septum is not apparent in fully ripe seeds. The seed number is relatively low, 15 berries yielding a range and mean of (22-) 27 (-30) seeds. The seeds have a conspicuous envelope during development which at maturity breaks down to leave a 'fuzz' of vertical cell walls giving the appearance of a pubescent seed.

Subgenus *Lycianthes* (Dunal) Bitter

Species examined: *S. amatitlanense*, *S. biflorum*, *S. bitterianum*, *S. escuintlense*, *S. geminiflorum*, *S. guianense*, *Lyc. hawkesiana*, *Lyc. howardiana*, *S. lycioides*, *S. moskowskii*, *S. oliverianum*, *S. rantonnei*, *S. sanctaclarae*, *S. shanesii*, *S. synantherum*, *S. vitiense* and *S. umbonatum*. Figs 4a-p.

Species included by me in this subgenus are at times maintained at the rank of genus, viz. *Lycianthes* Hassl. and were monographed by Bitter (1919). The type of the genus is *S. lycioides*. One of the distinguishing features of the genus as defined by Hassler was the reduction in seed number to about 8 per fruit and the enclosure of each seed in a bony endocarp, Fig. 4a. This is quite exceptional among the many species included in the genus in the emended and enlarged concept of Bitter (1919). The genus (or subgenus) was divided by Bitter into several subgenera and sections:

"*Lycianthes* subgenus 1. *Eulycianthes*" from S. America of two species and including the type of the genus *L. lycioides* (L.) Hassl. As stated above this has about 8 seeds per berry each enclosed in a bony endocarp (Fig. 4a), which is distinct from any other species included in the genus by Bitter (or indeed unlike any other *Solanum* I have seen). Bitter's second subgenus *Polymeris* from C. and S. America was further divided into 7 sections: 1. *Eupolymeris* including

S. guianense (Fig. 4b), *Lyc. hawkesiana* (Fig. 4c), *Lyc. howardiana* (Fig. 4d), *S. rantonnei* (Fig. 4e), *S. sanctaeclarae* (Fig. 4f). It may be noted that of these *S. rantonnei* is distinct with abundant stone cell masses and that the remaining three species have distinctive intrusions partially separating the seeds which will be seen in other species of subgenus *Lycianthes*. Sections *Kittoides*, *Perennans* and *Asaropsis*, all American, are not represented. In section *Simplicipila*, *S. amatitlense* (Fig. 4g) has the H-shaped placenta seen in other sections of *Solanum* (no stone cells nor intrusions). Section *Asiomelanesia* from S.E. Asia, e.g. *S. biflorum* and *S. bitterianum* (Fig. 4h & i), has no stone cells nor intrusions and moderately developed placentae; section *Synantheroides* from C. America, e.g. *S. escuintlense* (Fig. 4j), *S. geminiflorum* (Fig. 4k), the first with quadrilocular berry and dispersed placentae, the second with a very narrow placenta at right angles to the septum and weakly developed intrusions. The third subgenus *Cypellocalyx* is confined to Malesia and includes

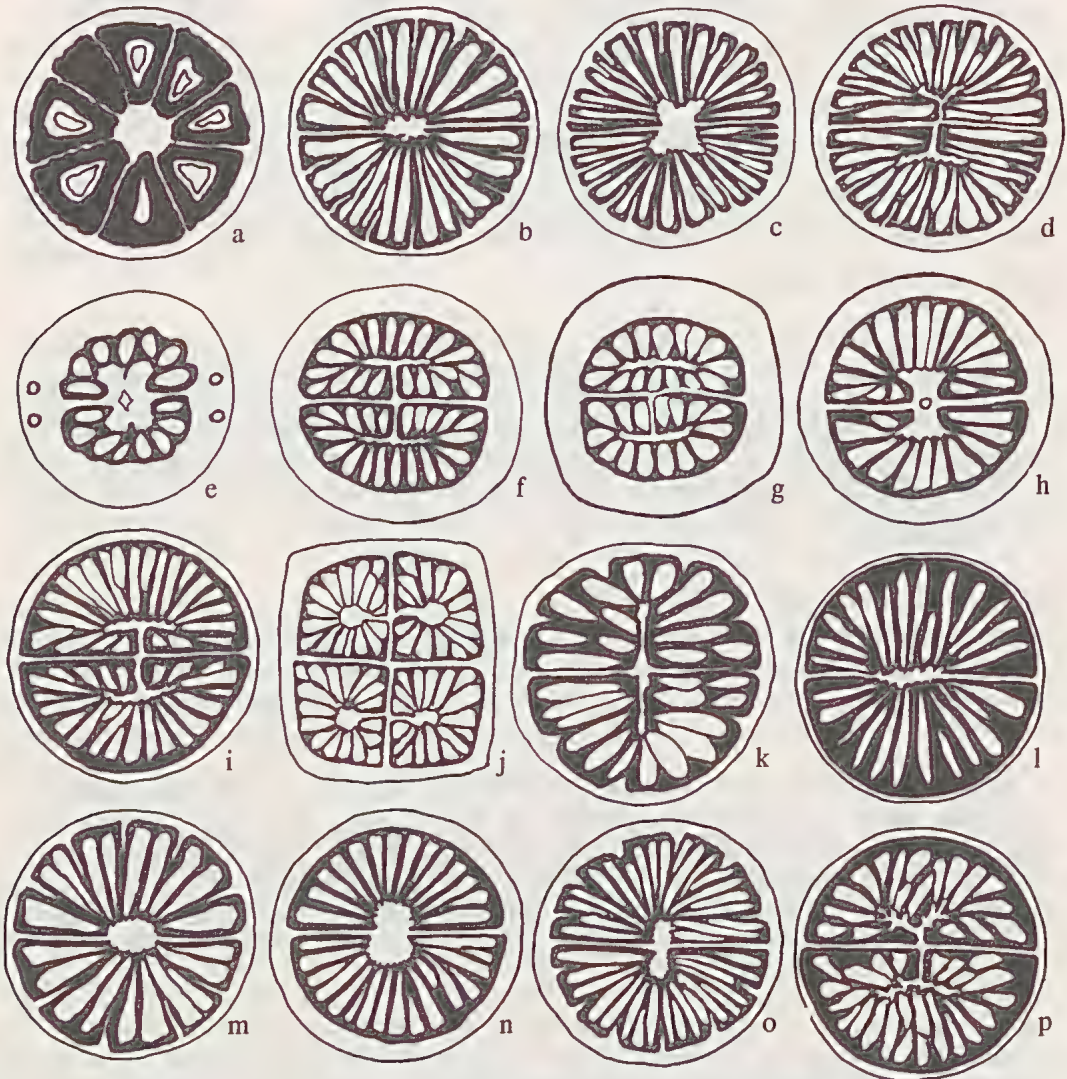


Fig. 4a, *S. lycioides*; b, *S. guianense*; c, *Lyc. hawkesiana*; d, *Lyc. howardiana*; e, *S. rantonnei*; f, *S. sanctaeclarae*; g, *S. amatitlense*; h, *S. biflorum*; i, *S. bitterianum*; j, *S. escuintlense*; k, *S. geminiflorum*; l, *S. moszkowskii*; m, *S. oliverianum*; n, *S. umbonatum*; o, *S. shanesii*; p, *S. vitiense*.

S. moszkowskii, *S. oliverianum*, *S. umbonatum* and probably *S. shanesii* and *S. vitiense* (Fig. 4l-p). All these have bilocular fruits with moderately developed placentae and it may be significant that two of these, *S. oliverianum* and *S. shanesii*, also have the intrusions developed from the pericarp partially separating the seeds.

Seed numbers are given in Table 2 but unfortunately few fruits have been available in many cases. The seeds vary as much as the fruits and range from thick blocky seeds of *S. rantonnei* to the highly compressed, papery seeds with a membranous wing of *S. moszkowskii* which are similar to the otherwise unrelated *S. capsicoides*.

It will be seen then that the subgenus (or genus) *Lycianthes* contains a wide array of fruit and seed forms all remarkably different from the type species.

Table 2

Species	No. of fruits	Range and mean	
		Seeds	Stone cells
<i>S. biflorum</i>	8	(66-) 120 (-178)	0
<i>S. bitterianum</i>	7	(45-) 110 (-198)	0
<i>S. geminiflorum</i>	1	114	0
<i>S. lycioides (ex literature)</i>		8	0
<i>S. moszkowskii</i>	1	51	0
<i>S. rantonnei</i>	3	80	20
<i>S. sanctaeclarae</i>	1	461	0
<i>S. shanesii</i>	22	(5-) 40 (-56)	0
<i>S. synantherum</i>	2	220	0

Subgenus *Archaeosolanum* Marz. section *Archaeosolanum* (Marz.) Danert (Kangaroo Apples).

Species examined: *S. aviculare*, *S. capsiciforme*, *S. linearifolium*, *S. laciniatum*, *S. simile*, *S. symonii*, *S. vescum*. Fig. 5a-h, Table 3.

An Australasian subgenus of 8 species with green (sometimes flushed purple) orange or vermilion succulent berries which are relatively large, 1.5-5 cm long. They may be conical

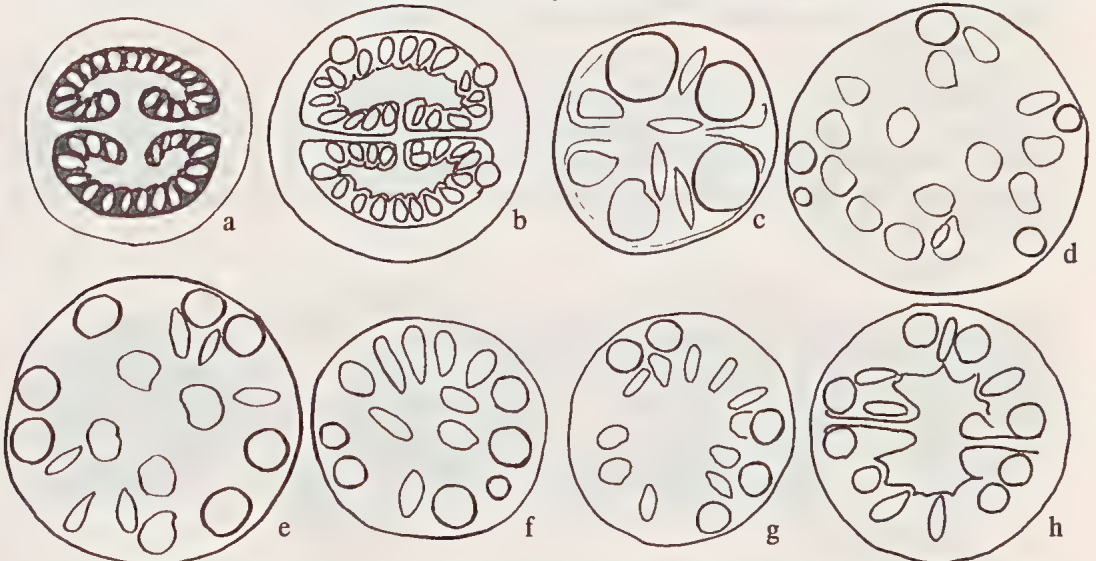


Fig. 5a, *S. aviculare* (ovary); b, *S. aviculare* (berry); c, *S. capsiciforme*; d, *S. laciniatum*; e, *S. linearifolium*; f, *S. simile*; g, *S. symonii*; h, *S. vescum*.

(*S. capsiciforme*), globular, or elliptical in shape. In most species stone cell concretions are abundant and seed numbers high, e.g. *S. multivenosum* may contain up to 1,200 seeds and 180 stone cell concretions per berry. The placenta may be enlarged to an H-shape bearing seeds on the inner face as well as the outer surface. At maturity the septum is often not readily distinguished, the placenta proliferates so that the seeds appear embedded in placental tissues and the locule is not clearly distinguished. The section has provided a coherent group with no other species looking quite like them which reinforces its distinction.

Seed numbers and stone cells are summarised in Table 3.

Table 3

Species	No. of fruits	Range and mean			
		Seeds		Stone cells	
<i>S. aviculare</i>	18	(388-)	648	(-845)	(27-) 40 (-69)
<i>S. capsiciforme</i>	10	(82-)	99	(-132)	(31-) 40 (-48)
<i>S. laciniatum</i>	20	(116-)	211	(-344)	(33-) 47 (-78)
<i>S. linearifolium</i>	15	(46-)	187	(-232)	(17-) 25 (-38)
<i>S. multivenosum</i>	3	(1003-)	1110	(-1196)	(138-) 162 (-186)
<i>S. simile</i>	84	(29-)	99	(-260)	(15-) 34 (-87)
<i>S. symonii</i>	20	(100-)	174	(-258)	(26-) 54 (-77)

Subgenus *Brevantherum* (Seithe) D'Arcy section *Pseudocapsica* Roem. & Schult.

Species examined: S. pseudocapsicum. Fig. 2c.

This small section comes from Mexico and South America. The species has been widely cultivated as an ornamental and is now naturalised in mesic warm-temperate sites. The few or solitary, red, succulent berries are held erect. At maturity the locules are not clearly defined. A count of seeds in 24 fruits provided the range and mean (18-) 48 (-79) per berry.

Subgenus *Brevantherum* (Seithe) D'Arcy section *Brevantherum* Seithe

Species examined: S. erianthum, S. mauritianum. Fig. 6a & b.

A Central American section of about 30 species two of which are now pan-tropic weeds. The fruits are generally held erect in dense corymbose cymes, are succulent, ochre yellow and of medium size, about 1 cm diam. They are known to be eaten by birds and fruit bats. The placenta is H-shaped with numerous seeds; stone cells are absent. Seed numbers in the two species examined were: *S. erianthum*, 6 fruits, (143-) 215 (-300) and *S. mauritianum*, 6 fruits (158-) 191 (-228).

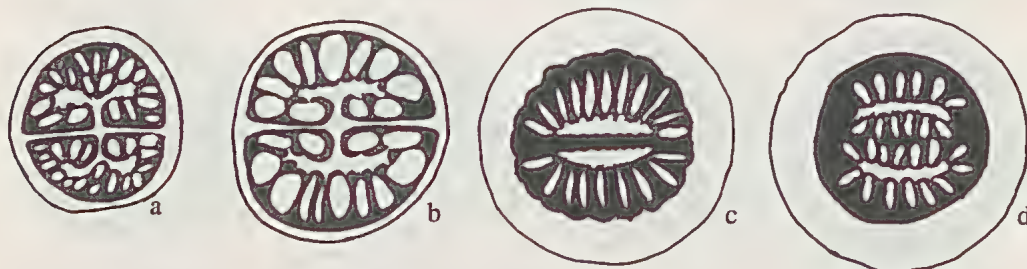


Fig. 6a, *S. erianthum*; b, *S. mauritianum*; c, *S. capsicoides*; d, *S. mammosum*.

Section *Pugiunculiferum* Symon Fig. 2d.

This monotypic section contains the anomalous species, *S. pugiunculiferum*, which has dryish fruits which are purplish green at maturity and contain little flesh. They do not appear to become succulent. No septum is apparent at maturity and the strongly flattened papery seeds (cf. *S. capsicoides*) are packed on edge around the placenta. A count of 27 fruits provided the range and mean (26-) 39 (-57) seeds per berry.

Subgenus *Leptostemonum* (Dunal) Bitter section *Acanthophora* Dunal

Species examined: *S. capsicoides*, *S. mammosum*. Fig. 6c & d.

This section of about 20 species is centred in Central and South America. The two species above have frequently been cultivated as ornamentals and have become widely naturalised in tropical zones. In both it will be seen that the septum has degenerated and the two placenta bodies stand erect and separated. In *S. capsicoides* the flesh is crisp and white and the seeds strongly flattened and paper-like. In *S. mammosum* the seeds are thicker and rounded. Fourteen fruits of *S. capsicoides* yielded the wide range and mean (73-) 188 (-346) seeds per fruit and four fruits of *S. mammosum* yielded (215-) 279 (-352) seeds per berry.

Subgenus *Leptostemonum* (Dunal) Bitter section *Dunaliana* (Bitter) Symon

Species examined: *S. tetrandrum*, *S. viride*, *S. viridifolium*, and *S. mankiense*. Fig. 7a, b, c, e.



Fig. 7a, *S. mankiense*; b, *S. tetrandrum*; c, *S. viride*; d, *S. missimense*; e, *S. viridifolium*; f, *S. chenopodium*; g, *S. corifolium*; h, *S. discolor*; i, *S. ferocissimum*; j, *S. parvifolium*; k, *S. semiarmatum*; l, *S. persicaefolium*.

A section of about 8 species centred on New Guinea with a few species extending to northern Australia and to the Pacific Islands. The species have smallish (less than 1 cm), red, succulent fruits often crowded in corymbose cymes which are held erect. As with the other small red-fruited species the septum appears to disintegrate and the seeds are arranged about the central placenta. Seed numbers are relatively low. Sixteen fruits of *S. tetrandrum* yielded a range and mean (7-) 12 (-18), fifteen fruits of *S. viridifolium* (12-) 19 (-36) and two of *S. mankiense* 61, 63.

Subgenus *Leptostemonum*, *S. ferocissimum* group Whalen (1984), section *Gracilliflorum* sensu Symon (1981) non (Dunal) Seithe

Species examined: *S. chenopodium*, *S. corifolium*, *S. ferocissimum*, *S. parvifolium*, *S. persicaefolium*, *S. semiarmatum* and *S. stelligerum*. Fig. 7f-l, Table 4.

This group is well represented in Australia, New Guinea and New Caledonia. Two closely related groups, *S. crotonoides* and *S. bahamense* of Whalen (1984) are reported from the Greater Antilles and Caribbean Islands respectively. Only one fruit of the latter group has been available to me. They are characterised by having small to medium sized, red (to black), succulent berries. Seed numbers are less than 100 and the placenta is little elaborated. However in most, including the single example from the Caribbean (*S. persicaefolium*), the septum disintegrates by maturity and the berries appear unilocular. Some are known to be dispersed by birds, Symon (1979) and a succulent pulp with minimum structure is likely to pass through the gut of a bird quickly and with least damage. Unfortunately none of the red fruited African species have been available to see whether this phenomenon occurs there. Seed numbers are given in Table 4.

Table 4

Species	No. of fruits	Seeds	
		Range	and mean
<i>S. chenopodium</i>	58	(4-) 7	(-14)
<i>S. corifolium</i>	10	(40-) 57	(-93)
<i>S. densevestitum</i>	24	(6-) 21	(-35)
<i>S. expedunculatum</i>	7	(30-) 43	(-62)
<i>S. ferocissimum</i>	23	(8-) 29	(-52)
<i>S. parvifolium</i>	9	(17-) 30	(-37)
<i>S. persicaefolium</i>	1	—	13
<i>S. semiarmatum</i>	22	(36-) 60	(-75)
<i>S. stelligerum</i>	33	(23-) 54	(-96)

Subgenus *Leptostemonum* (Dunal) Bitter section *Torva* Nees

Species examined: *S. hispidum* and *S. torvum*. Fig. 8a & b.

Perhaps 50 species (currently under study) from Central America to mainly South America. The fruits are of medium size, yellowish to orange-yellow to brownish, mucilaginous and with numerous seeds. Both examples were quadrilocular and particularly with the weedy *S. torvum*, packed with seeds. Six fruits of *S. hispidum* yielded a mean of 176 seeds and twelve fruits of *S. torvum* yielded a range and mean (235-) 345 (-409) seeds per berry.

Subgenus *Leptostemonum* (Dunal) Bitter section *Leprophora* Dunal, pro parte (*S. ellipticum* group, Whalen [1984])

This section is well represented in Australia with a few species also in the Americas. The following species are illustrated: *S. coactiliferum*, *S. dianthophorum*, *S. dimidiatum*, *S. eardleyae*, *S. echinatum*, *S. ellipticum*, *S. esuriale*, *S. karsensis*, *S. lacunarium*, *S. lucani*, *S. nummularium*, *S. oldfieldii*, *S. orbiculatum*, *S. petrophilum*, *S. quadriloculatum* and *S. sturtianum*. Fig. 8c-o, 9a-d.

Most species have medium sized, firm mucilaginous berries that are yellow at maturity. *S. eardleyae*, *S. petrophilum* and *S. quadriloculatum* are hard and bony at maturity. All have a simple bilocular berry with variously enlarged placenta except that quadrilocular examples have been seen in *S. ellipticum*, *S. lucani* and *S. quadriloculatum*.



Fig. 8a, *S. hispidum*; b, *S. torvum*; c, *S. dimidiatum*; d, *S. orbiculatum*; e, *S. nummularium*; f, *S. oldfieldii*; g, *S. coactiliferum*; h, *S. esuriale*; i, *S. lacunarium*; j, k, *S. dianthophorum*; S. *ellipticum*; m, *S. echinatum*; n, *S. lucani*; o, *S. sturtianum*.

The seed numbers recorded for this Section, Table 5, show a range of means from 4 to 341. With only one exception, *S. petrophilum*, all those with mean seed numbers greater than 100 have expanded placentae.

Table 5

Species	No. of fruits	Seeds Range and mean
<i>S. centrale</i>	7	(17-) 54 (-94)
<i>S. cleistogamum</i>	51	(27-) 55 (-119)
<i>S. coactiliferum</i>	8	(27-) 49 (-106)
<i>S. dianthophorum</i>	11	(116-) 219 (-291)
<i>S. dimidiatum</i>	4	(46-) 72 (-97)
<i>S. eardleyae</i>	17	(82-) 156 (-281)
<i>S. echinatum</i>	14	(41-) 107 (-185)
<i>S. ellipticum</i>	17	(23-) 131 (-323)
<i>S. esuriale</i>	35	(18-) 51 (-204)
<i>S. gabriele</i>	9	(164-) 232 (-278)
<i>S. gilesii</i>	5	(13-) 32 (-55)
<i>S. horridum</i>	5	(130-) 341 (-498)
<i>S. lachnophyllum</i>	8	(10-) 34 (-55)
<i>S. lacunarium</i>	14	(10-) 35 (-76)
<i>S. lasiophyllum</i>	4	(50-) 67 (-78)
<i>S. lucani</i>	35	(33-) 112 (-224)
<i>S. nummularium</i>	8	(5-) 18 (-33)
<i>S. oligacanthum</i>	27	(2-) 4 (-7)
<i>S. orbiculatum</i>	30	(20-) 38 (-95)
<i>S. petrophilum</i>	19	(13-) 66 (-250)
<i>S. quadriloculatum</i>	28	(59-) 156 (-336)
<i>S. seitheae</i>	8	(204-) 253 (-330)
<i>S. sturtianum</i>	23	(22-) 55 (-73)
<i>S. tetrahecum</i>	7	(165-) 236 (-291)

Subgenus *Leptostemonum* (Dunal) Bitter, *S. macoorai* and *S. hystrix* groups of Whalen (1984).

Species examined: *S. dallachii*, *S. dimorphispinum*, *S. furfuraceum*, *S. inaequilaterum*, *S. leopoldensis*, *S. macoorai*, *S. oedipus* and *S. prinophyllum*. Fig. 9e-k, Table 6.

The species listed here combine two all Australian groups separated by Whalen (1984). They generally have largish fruits (greater than 2 cm) and are mostly succulent, (*S. leopoldensis* dry and bony, *S. oedipus* dry and membranous) and are green or orange-red when ripe.

Most have high seed numbers, Table 6, and enlarged placentas. Exceptions are *S. inaequilaterum* which has an enlarged placenta with a mean of 49 seeds and *S. oedipus* with an axile placenta and a mean of 39 seeds. As these are large chunky seeds the figures may be representative, but the seed numbers for *S. inaequilaterum*, *S. macoorai* and *S. multiglochidiatum* are based on cultivated plants where full pollination may not have occurred.

Subgenus *Leptostemonum* section *Campanulata* Symon Fig. 9l.

S. campanulatum is an isolated species that has a relatively large (3 cm diam.), yellowish, firm fruit which may finally darken to almost black. It does not appear to be succulent when ripe. The septum persists in the fruit and the placenta is enlarged. The black seeds are numerous and the counts of nineteen berries have yielded the range and mean (147-) 568 (-947) seeds per berry.

Table 6

Species	No. of fruits	Seeds Range and mean
<i>S. cookii</i>	5	(251-) 367 (-563)
<i>S. dallachii</i>	1	168
<i>S. dimorphispinum</i>	3	(68-) 115 (-156)
<i>S. furfuraceum</i>	36	(48-) 173 (-246)
<i>S. hystrix</i>	6	(118-) 153 (-204)
<i>S. inaequilaterum</i>	16	(14-) 49 (-124)
<i>S. leopoldensis</i>	15	(200-) 428 (-620)
<i>S. macoorai</i>	17	(58-) 100 (-178)
<i>S. multiglochidiatum</i>	3	(16-) 23 (-33)
<i>S. oedipus</i>	4	(25-) 39 (-56)
<i>S. prinophyllum</i>	71	(101-) 376 (-647)



Fig. 9a, *S. karsensis*; b, *S. quadriloculatum*; c, *S. eardleyae*; d, *S. petrophilum*; e, *S. prinophyllum*; f, *S. macoorai*; g, *S. furfuraceum*; h, *S. inaequilaterum*; i, *S. dallachii*; j, *S. furfuraceum*; k, *S. dimorphispinum*; l, *S. campanulatum*.

Subgenus *Leptostemonum* (Dunal) Bitter section *Cryptocarpum* Dunal

Species examined: S. sisymbriifolium. Fig. 11o.

A small section from South America. The species listed has been cultivated as an ornamental and is sparingly naturalised in Australia. The immature fruit is largely protected by a prickly calyx until mature after which the bright red succulent berry is exposed. In the local example the berry is quadricellular with the placenta well separated from the septum. Counts of 29 fruits yielded the range and mean (33-) 116 (-205) seeds per berry.



Fig. 11a, *S. asymmetriphyllum*; b, c, *S. dioicum*, d, e, *S. leopoldensis*; f, g, *S. petraeum*; h, *S. tudunungae*; i, *S. citrinum*; j, *S. grandiflorum*; k, *S. repandum*; l, *S. quitense*; m, *S. aethiopicum*; n, *Lycopersicon esculentum*; o, *S. sisymbriifolium*.

Subgenus *Leptostemonum* (Dunal) Bitter, *S. crinitum* group Whalen (1984)

Species examined: *S. crinitum*, *S. grandiflorum*. Fig. 11i & j.

A small group of about 8 species from the north of South America. The species are often relatively large growing. One, *S. grandiflorum* has been widely grown in the tropics for its showy, rapidly fading changeable flowers. The fruits tend to be large (to 5 cm diam.) drab green with a firm rind. Both examples have been 4-locular with greatly modified placentas, in the case of *S. grandiflorum* being almost parietal in position. A single fruit of *S. grandiflorum* yielded 258 seeds.

Subgenus *Leptostemonum* (Dunal) Bitter section *Lasiocarpum* (Dunal) D'Arcy

Species examined: *S. quitoense*, *S. repandum*. Fig. 11k & l.

A section of 12 species centred in the northern Andes of South America but three species extending to the Pacific and south east Asia. The berry is often large, usually densely pubescent, succulent, orange, with numerous seeds. The berries of this section may have highly elaborated septa and placentae in some species, e.g. *S. quitoense* (Fig. 11l), or *S. repandum* (Fig. 11k). Not only are they multilocular but the placentae may be dispersed. Three species are cultivated for their fruits eg. *S. lasiocarpum*, *S. quitoense* and *S. repandum*. *S. quitoense* has a long history as a cultigen and it is not known whether wild type fruits with simpler placentas occur. Seed numbers in the two species available have been *S. lasiocarpum*, grown from seed from Thailand, 4 fruits (186-) 215 (-256) and *S. repandum*, four fruits yielded (224-) 232 (-248).

Subgenus *Leptostemonum* (Dunal) Bitter section *Melongena* Dunal

Species examined: (I) Andromonoecious species a. *S. beagleholei*, b. *S. chippendalei*, c. *S. cinereum*, d. *S. clarkiae*, e. *S. heteropodium*, f. *S. incanum*, g. *S. linnaeanum* (*S. sodomenum*), h. *S. marginatum*, i. *S. melanospermum*. Fig. 10a-j.

(II) Dioecious species a. *S. asymmetriphyllum*, b & c. *S. dioicum*, d & e. *S. leopoldensis*, f & g. *S. petraeum*, h. *S. tudununggae*. Fig. 11a-h.

This section with species in Afro-Asia and Australia has generally large fruits, commonly 2-3 cm diam. They tend to be firm and mucilaginous in texture rather than succulent and pulpy. The colours are generally shades of yellow though some may darken to almost black or may finally become dry and bony. In almost all cases the seeds are high in number, often dark in colour and stone cell concretions are absent. Elaboration of the placenta is quite common and quadrilocular forms occur. Several distinct variations occur. The most common form represented here by *S. marginatum*, *S. incanum* and *S. linnaeanum* from Afro-Asia and by *S. beagleholei*, *S. chippendalei*, *S. clarkiae* and *S. melanospermum* from Australia have the large yellowish fruits referred to above. In all except *S. melanospermum* the placenta is elaborate, a false septum may develop and the seeds are numerous. *S. cinereum* (Fig. 10a & b), is most distinctive as the fruit, which is at first yellow and finally almost black, is a globe with the seeds densely clustered on the central axile placenta. When ripe all septa have disintegrated, though marginal bumps indicate where the transverse septum originated. The mature dried fruit of *S. cinereum* Fig. 10b is unique in this section.

S. tudununggae Fig. 11a and *S. vansittartensis* both have the unusual censer mechanism described by Symon (1984). The placenta is enlarged to an H-shape. The mature berry is circumcissile above its base and shrinks and separates becoming a cap remaining within the



Fig. 10 a & b, *S. cinereum*; c, *S. linnaeanum*; d, *S. incanum*; e, *S. marginatum*; f, *S. beagleholei*; g, *S. chippendalii*; h, *S. melanospermum*; i, *S. clarkiae*; j, *S. heteropodium*; k, *S. oedipus* (ovary); l, *S. oedipus* (fruit).

enlarged coriaceous now globular calyx tube from which orifice the seeds escape on shaking. Most capsular and dehiscent fruits fracture along major structural junctions. Rethke (1946) in examining the anatomy of circumcissile dehiscence in *Hyoscyamus* (Solanaceae) showed that a zone of mechanical weakness is formed between the lid and base due to the alignment of the cells. Fracture was due to the differential shrinkage of the two parts. A glance at the illustrations will indicate the many placenta variations are found in this section. *S. chippendalii* Fig. 10g, is similar to the two species of section *Acanthophora* Fig. 6c-d.

Table 7 summarises the seed numbers recorded for some of these species.

Table 7

Species	No. of fruits	Seeds	
		Range and mean	
<i>S. asymmetriphyllum</i>	8	(302-)	429 (-639)
<i>S. beaugleholei</i>	16	(63-)	628 (-1164)
<i>S. chippendalei</i>	50	(66-)	208 (-785)
<i>S. cinereum</i>	1		384
<i>S. clarkiae</i>	29	(50-)	182 (-272)
<i>S. dioicum</i>	10	(40-)	417 (-907)
<i>S. incanum</i>	1		158
<i>S. linnaeanum</i>	13	(130-)	323 (-456)
<i>S. marginatum</i>	19	(657-)	1397 (-2206)
<i>S. melanospermum</i>	8	(68-)	93 (-109)
<i>S. petraeum</i>	3		463

Subgenus *Leptostemonum* (Dunal) Bitter section *Oliganthes* (Dunal) Bitter (*Anguivi* group Whalen [1984])

Species examined: S. aethiopicum (*S. gilo*). Fig. 11m:

A complex section of varied species from Africa. The fruits are red or orange, succulent and generally bilocular. In the example studied which is a subcultivar 6-locules are well developed and the placentae are dispersed. This is probably the result of domestication and the selection for larger, fleshier fruits. Six fruits of *S. aethiopicum* yielded the range and mean (111-) 171 (-218) seeds per berry.

Summary

Trends which are evident in this survey may be summarised as follows.

1. The basic condition appears to be axile placentation with a simple septum. All other forms can be developed from this.
2. Retention of axile placentation with little elaboration, but with degeneration of the septum at least at maturity. This may be seen especially in section *Dunaliana* (Fig. 7a, b, c), section *Jasminosolanum* (Fig. 2d), *S. ferocissimum* (Fig. 7d-k) and *S. bahamense* (Fig. 7l) groups. These all have relatively small, succulent, red fruits and seed numbers are never high.
3. Species with low seed numbers have simple non-elaborated placentas and those with high numbers have without exception some elaboration though this may take many forms. The potential for high seed numbers is thus greatly increased. A further septum may develop to form a 4-locular berry. This has occurred in several widely separated sections e.g. Fig. 4, 8, 11. However, high seed numbers also occur in subgenus *Archaeosolanum* (Fig. 5), where the seeds are apparently immersed in an enlarged placenta.
4. Separation of the placenta into two erect lobes with degeneration of the septum and of the link between the two lobes. This development is not so common and may be seen in section *Acanthophora* (Fig. 6c, d), and also in section *Melongena* (Fig. 10g).
5. Elaboration and migration of the placenta arms along the 'false' septum to form a 4-locular berry with, at times, near parietal placentation. Seed numbers are then generally very high. This has been found in several sections e.g. *Lycianthes* (Fig. 4), *Torva* (Fig. 8),

Melongena (Fig. 10-11), *Oliganthes* (Fig. 11), *Lasiocarpum* (Fig. 11) and *S. crinitum* group (Fig. 11).

6. Elaboration of multilocular fruits with dispersed placentae, which occurs under domestication may be seen in domesticates like *S. aethiopicum* (Fig. 11m), in *Lycopersicon esculentum* (*S. lycopersicum*) (Fig. 11n), *S. quitoense* and *S. repandum* (Fig. 11k & l).

7. Intrusions of the pericarp occur in some species of subgenus *Lycianthes* (Fig. 4b, c, d, k, m, o) and the two species of section *Leiodendra* (Fig. 3a, b) have distinctive intrusions separating the seeds.

8. Clear cut differences of taxonomic significance between subgenus *Solanum* and subgenus *Leptostemonum* are not apparent. Fruits like those of subgenus *Archaeosolanum* were not seen in other groups. No fruits with pericarp intrusions, nor stone cells were found in subgenus *Leptostemonum*. The elaboration of the placenta was, with few exceptions, more developed and more varied in subgenus *Leptostemonum*.

References

- Hassler, E. (1917). Solanaceae Austro-Americanae. *Annuaire Conserv. Jard. Bot. Geneve*. 20: 173-189.
- Huber, A.K. (1980). Morphologische und entwicklungsgeschichtliche Untersuchungen an Blüten und Blütenständen von Solanaceen und von *Nolana paradoxa* Lindl. (Nolanaceae). *Dissertationes Botanicae*, Vol. 55, J. Cramer, Vaduz.
- Bitter, G. (1911). Steinzellkonkretionen im Fruchtfleisch beerentragender Solanaceen und deren systematische Bedeutung. *Bot. Jahrb. Syst.* 45: 483-507.
- Bitter, G. (1914). Weitere Untersuchungen über das Vorkommen von Steinzellkonkretionen im Fruchtfleisch beerentragender Solanaceen. *Abh. Naturwiss. Vereine Bremen*. 23: 114-163.
- Bitter, G. (1919). Die Gattung *Lycianthes*. *Abh. Naturwiss. Vereine Bremen*. 24: 292-520.
- Houghtaling, H.B. (1935). A developmental analysis of size and shape in tomato fruits. *Bull. Torrey Bot. Club* 62: 243-252.
- Miller, R.H. (1969). A morphological study of *Solanum mammosum* and its mammiform fruit. *Bot. Gaz.* 130: 230-237.
- Murray, M.A. (1945). Carpellary and placentae structure in the Solanaceae. *Bot. Gaz.* 107: 243-260.
- Nee, M. (1986). Placentation patterns in the Solanaceae. In W.G. D'Arcy Edit. "Solanaceae: biology & systematics". (Columbia Univ. Press: New York), pp 169-175.
- Perlova, R.L. (1946). Morphology of the berries as a taxonomic character of tuber bearing *Solanum*. *Bot. Zurn. S.S.S.R.* 31: 19-32.
- Rethke, R.V. (1946). The anatomy of circumcissile dehiscence. *Amer. J. Bot.* 33: 677-683.
- Roth, I. (1977). "Fruits of Angiosperms". (Gebrüder Borntraeger: Berlin).
- Symon, D.E. (1979). Fruit diversity and dispersal in *Solanum* in Australia. *J. Adelaide Bot. Gard.* 1: 321-331.
- Symon, D.E. (1984). A new form of *Solanum* fruit. *J. Adelaide Bot. Gard.* 7: 123-126.
- Symon, D.E. (1985). The re-instatement of *Solanum shanesii* F. Muell. Section *Lycianthes* (Solanaceae) with discussion of its significance. *J. Adelaide Bot. Gard.* 7: 201-206.
- Whalen, M.D. (1984). Conspectus of species groups in *Solanum* subgenus *Leptostemonum*. *Gentes Herbarum* 12: 179-282.

Voucher material

- S. aethiopicum* L. (*S. gilo* Raddi) redrawn from Nee (1986), Fig. 11m.
- S. amatitanense* Coult. & Donn. Sm., Berlin 1773, Quebrada Huampami, Peru, Fig. 4g.
- S. americanum* Miller, grown from Constable 5633, Kogarah N.S.W., Fig. 1a.
- S. antillarum* O.E. Schultz.
- S. asymmetriphyllum* Specht, Symon 12138, near Alligator Riv. N.T., Fig. 11a.
- S. aviculare* G. Forster, grown from Eichler 18243, Mt Wilhelm, P.N.G., Fig. 5a, b.
- S. bahamense* L.
- S. beagleholei* Symon, Symon 12107, Napier Range, W.A., Fig. 10f.
- S. biflorum* Lour., Symon 10652, Bulolo, P.N.G., Fig. 4h.
- S. bitterianum* Symon, Symon 10651, Bulolo, P.N.G., Fig. 4i.

- S. callium* C.T. White ex R. Henderson, *Webb & Tracy 10741*, Levers Plateau N.S.W., Fig. 2a.
S. campanulatum R. Br., grown from *Whitehead s.n.*, Kulnara, N.S.W., Fig. 9l.
S. capsiciforme (Domin) Baylis, grown Waite Inst., Glen Osmond, S.A. Fig. 5c.
S. capsicoides All., redrawn from Nee (1986), Fig. 6c.
S. centrale J.M. Black, seed from *Latz 178*.
S. chenopodinum F. Muell., *Symon 5972*, Old Moolawatna, S.A., Fig. 7f.
S. chenopodioides Lam., seed grown from *Beauglehole 37803*.
S. chippendalei Symon, *Symon 2272*, Sir Frederick Range, W.A., Fig. 10g.
S. cinereum R. Br., *Symon 9851*, Cootamundra, N.S.W., Fig. 10a, b.
S. citrinum M. Nee, redrawn from Nee (1986), Fig. 11i.
S. clarkiae Symon, *Symon 12133*, Alligator River, N.T., Fig. 10i.
S. cleistogamum Symon, seed from *Symon 5418, 10611*.
S. coactiliferum J. Black, *Symon 4481*, Kyancutta, S.A., Fig. 8g.
S. cookii Symon, seed grown from *Tracey s.n.*
S. corifolium F. Muell., *Tracey s.n.*, Mt Glorious, Qld, Fig. 7g.
S. crinitum Lam.
S. crotonoides Lam.
S. dallachii Benth., grown from *Hyland 7367*, Wyvuri Holding, Qld, Fig. 9i.
S. densevestitum F. Muell., seed from *Symon s.n.*
S. dianthophorum Dunal, grown from *Redgen 044*, Glen Morgan, Qld, Fig. 8j, k.
S. dimidiatum Raf., grown from roots from *Everist s.n.*, Bundaberg, Qld, Fig. 4c.
S. dimorphispinum C. White, *Webb & Tracey 8352*, Mt Lewis, Qld, Fig. 9k.
S. dioicum W.V. Fitz., *Latz 4019*, Sturt Creek, N.T., Fig. 11c.
S. dioicum W.V. Fitz., *Symon 5336*, near Fitzroy Crossing, W.A., Fig. 11b.
S. discolor R. Br., *Moriarty 879*, Yarraman, Qld, Fig. 7h.
S. eardleyae Symon, *Latz 5058*, Mt Fraser, N.T., Fig. 9c.
S. echinatum R. Br., *Symon 7189*, Pine Creek, N.T., Fig. 8m.
S. ellipticum R. Br., grown from *Symon s.n.*, Ayer's Rock, N.T. Fig. 8l.
S. erianthum D. Don, grown from *Tracey s.n.*, Johansons Cave, Qld, Fig. 6a.
S. esculintense (Coult.) Hunz., *Gilmartin 235*, Santo Domingo, Fig. 4j.
S. esuriale Lindl., *Symon 115777*, near Renmark, S.A., Fig. 8h.
S. expedunculatum Symon, seed from *Symon 10700*.
S. ferocissimum Lindl., grown from *Tracey s.n.*, Narayen, Qld, Fig. 7i.
S. furcatum Dunal, seed grown from *Edmonds s.n.*
S. furfuraceum R. Br., *Webb & Tracey 10740*, Lever's Plateau, Qld, Fig. 9g, j.
S. gabriele Domin, seed from *Symon 5399, 10036*.
S. geminiflorum Mart. & Gal., *Nee 23551*, NW of Teocelo, Veracruz, Fig. 4k.
S. gilesii Symon, seed from *Latz 4035*.
S. grandiflorum Ruiz & Pavon, redrawn from Nee (1986), Fig. 11j.
S. guianense Dun., *Gentry 6229*, Cerro Tute, Panama, Fig. 4b.
S. hawkesiana D'Arcy, *Croat 9901*, near Guasimo, Panama, Fig. 4c.
S. heteropodium Symon, *Kenneally 9604*, W. Kimberleys, W.A., Fig. 10j.
S. hispidum Pers., grown from *Howard s.n.*, near Brisbane, Qld, Fig. 8a.
S. horridum Dunal, seed grown from *Symon 5403*.
Lyc. howardiana D'Arcy, *Dressler & D'Arcy 5505*, Cerro Campana, Panama, Fig. 4d.
S. hystrix R. Br.

- S. inaequilaterum* Domin, grown from *Henderson 1304*, Levers Plateau, Qld, Fig. 9h.
S. incanum L., grown from seed ex Kyambogo, Africa, Fig. 10d.
S. karsensis Symon, grown from roots *Pearce 63*, Kars Stn., N.S.W., Fig. 9a.
S. lachnophyllum Symon, seed from *Symon 9971*.
S. laciniatum Aiton, *Symon 10562*, Waitpinga, S.A., Fig. 5d.
S. lacunarium F. Muell., *Symon 11579*, Chowilla Creek, S.A., Fig. 8i.
S. lasiocarpum Dunal, seed ex *Aree*, Thailand.
S. lasiophyllum Dunal, seed from *Howard 5806*.
S. leopoldensis Symon, grown from *Symon 7028*, Mt Broome, W.A., Fig. 11d, e.
S. linearifolium Herasim. ex Symon, grown from *Myers C.P.I. 1163*, A.C.T., Fig. 5e.
S. linnaeanum Hepper & Jaeger, *Symon s.n.*, Myponga, S.A., Fig. 10.
S. lucani F. Muell., *Symon 6976*, near Mary River, N.T., Fig. 8n.
S. lycioides L., redrawn from Hassler (1917), Fig. 4a.
S. macoorai Bailey, grown from *Symon 4752*, Atherton, Qld, Fig. 9f.
S. mammosum L., redrawn from Nee (1986), Fig. 6d.
S. mankiense Symon, grown from *Symon 13857*, Manki, P.N.G., Fig. 7a.
S. marginatum L.f., grown from *D. of A. 562*, Nuriootpa, S.A., Fig. 10e.
S. mauritianum Scop., *Browning s.n.*, Waterfall Gully, S.A., Fig. 6b.
S. melanospermum F. Muell., grown from *Symon 5064*, Robinson River Stn, Qld, Fig. 10h.
S. missimense Symon, grown from *Symon 13844*, Mt Missim, P.N.G., Fig. 7d.
S. moszkowski Bitter, *Symon 10631*, Aseki Road, P.N.G., Fig. 4l.
S. multiglochidiatum Domin, seed from *Symon 4873*.
S. multivenosum Symon, seed from *Symon 10697*.
S. nigrum L., Waite Arboretum, Glen Osmond, S.A., Fig. 1b.
S. nudum Humb. & Bonpl., *D'Arcy 10958*, La Popa, Panama, Fig. 2b.
S. nummularium S. Moore, grown from *Symon 5478*, Kalgoorlie, W.A., Fig. 8e.
S. oedipus Symon, (ovary) grown from *Symon 7119*, Kalumburu, W.A., Fig. 10k.
S. oedipus Symon, (mature fruit) grown from *Symon 7119*, Kalumburu, W.A., Fig. 10l.
S. oldfieldii F. Muell., *Symon 5450*, N of Geraldton, W.A., Fig. 8f.
S. oligacanthum F. Muell., seed from *Barlow 1518, 1523, Symon 5891*.
S. oliverianum Lauterb. & Schumann, *Schram BW10620*, Manokwari, P.N.G., Fig. 4m.
S. opacum A. Braun & Bouché, grown from *Beaglehole 33110*, Bonang, Vic., Fig. 1c.
S. orbiculatum Dunal, *Symon 3420*, Commonwealth Hill, S.A., Fig. 4d.
S. parishii Heller
S. parvifolium R. Br., grown from *Moriarty 1557*, near Injune, Qld, Fig. 7j.
S. pennellii Correll, garden grown, *Symon s.n.*, Fig. 3c.
S. persicaeifolium Dun., *D'Arcy 4767*, Tortola Island, Fig. 7l.
S. petraeum Symon, *Symon 7139*, Pt Warrender, W.A., Fig. 11f, g.
S. petrophilum F. Muell., *Symon 8175*, Waltinga Dam, Gawler Ranges, S.A., Fig. 9d.
S. physalifolium Rusby, *Paton s.n.*, Launceston, Tas., Fig. 1d.
S. prinophyllum Dunal, grown from *Pearce s.n.*, near Healesville, Vic., Fig. 9e.
S. pseudocapsicum L., *Symon s.n.*, Willunga, S.A., Fig. 2c.
S. pugiunculiferum C.T. White, grown from *Chippendale 506*, Eley Stn., N.T., Fig. 2d.
S. quadriloculatum F. Muell., *Symon 6004*, Paralana, S.A., Fig. 9b.
S. quitoense Lam., drawn from slide of fruit, Fig. 11l.
S. rantonnei Carriere, Adelaide Bot. Gard. classground, Fig. 4e.

- S. repandum* G. Forster, cult. Adelaide Bot. Gard., *Symon 14297*, Fig. 11k.
S. retroflexum Dunal, grown from *Alcock s.n.*, Pilli Waterhole, S.A., Fig. 1e.
S. sanctaeclarae Greenm., *Croat 44230*, Sarapigui, Costa Rica, Fig. 4f.
S. scabrum Mill., seed grown from *Dept. Agric. s.n.*
S. seaforthianum Andrews, *Symon 4754*, Atherton, Qld, Fig. 3d.
S. seithae Symon, seed from *Symon 4959*.
S. semiarmatum F. Muell., grown from *Tracey s.n.*, Narayen, Qld, Fig. 7k.
S. shanesii F. Muell., *Clarkson 4217*, Palmer River, Qld, Fig. 4o.
S. simile F. Muell., grown from *Alcock 7543*, Marble Range, S.A., Fig. 5f.
S. sisymbriifolium Lam., grown from seed ex Kew, U.K., Fig. 11o.
S. spirale Roxb.
S. stelligerum Sm., origin lost.
S. sturtianum F. Muell., *Symon 5423*, Yanrey Stn., W.A. Fig. 8o.
S. superficiens Adelb.
S. symonii H. Eichler, grown from *Symon 4696*, Ceduna, S.A., Fig. 5f.
S. synantherum Sendtn., *Croat 26254*, near Concepcion, Panama.
S. tetrathecum F. Muell., seed from *Redgen 044*, *Symon 6721*.
S. tetrandrum R. Br., grown from *Symon 7774*, Gove, N.T., Fig. 7b.
S. torvum Sw., grown from *Symon 4755*, near Hockley, Qld, Fig. 8b.
S. triflorum Nutt., grown from *Whissen s.n.*, Tintinara, S.A., Fig. 1g.
S. tuberosum L. cv. Virginia, S. Aust. no voucher, Fig. 3a, b.
S. tudununggae Symon, grown from *Symon 10181*, Kalumburu, W.A., Fig. 11h.
S. umbelliferum Eschsch.
S. umbonatum Symon, *Symon 10630*, Aseki Road, P.N.G., Fig. 4n.
S. vansittartensis C.A. Gardner
S. vescum F. Muell., from *Carrodus 1161072*, Grampians, Vic., Fig. 5h.
S. villosum Miller, grown from D. of A. Strathalbyn, S.A., Fig. 1f.
S. viride G. Forster ex Sprengel, grown from *Buelow & Sykes 172*, Late Island, Pacific, Fig. 7c.
S. viridifolium Dunal, *Webb & Tracey 8351*, Bingal Bay, Qld, Fig. 7e.
S. vitiense Seemann, *Kajewski 2451*, Guadalcanal, Fig. 4p.
S. xantii A. Gray, grown from seed from San Francisco, U.S.A., Fig. 1h.
Lycianthes hawkesiana D'Arcy
Lycianthes howardiana D'Arcy, *Dressler & D'Arcy 5505*, Cerro Campana, Panama, Fig. 4d.
Lycianthes escuintlensis (J. Coulter) D'Arcy, *Gilmartin 235*, Touchi, Santo Domingo, Fig. 4j.
Lycianthes guianense (Dunal) Bitter, *Gentry 6229*, Cerro Tute, Panama, Fig. 4b.
Lycopersicon esculentum Miller, domestic garden, Adelaide, S.A. Fig. 11n.