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**The Sociology, Taxonomy and Ecology of the Passifloras and Factors
Influencing the Long-term Storage and Germination of their Seed.**

R. J. R. Vanderplank

Philosophy Doctorate Thesis

Discipline: Plant Physiology

2001

Vol. 1 of 2

Author No: M7188613
Submission date: 24 April 2001
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The Open University

The Oxford Research Unit

2001

Dedication

I dedicate this work to my best friend, Penny.

26 MAY 2004

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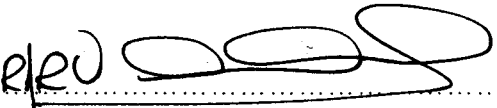
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Abstract

The longevity and long-term storage of *Passiflora* seed are investigated. Dehydrated seed were stored at temperatures from 30⁰C to -196⁰C for periods of up to five and a half years. It was determined that seed from most species should be treated as semi-orthodox for seed storage purposes, but seed from species in the section *Quadrangularis* should be treated as semi-recalcitrant. High temperatures during fruit maturation of *P. subpeltata* were shown to induce seed coat-imposed dormancy. The presence of seed coat-imposed dormancy was confirmed in seed of two other *Passiflora* species. Prolonged periods of seed washing in tepid water were shown to be successful in breaking seed coat-imposed dormancy. Factors influencing the successful germination of quiescent *Passiflora* seed were investigated. The seed coat morphology of *Passiflora* species produced by interspecific hybridisation was found to be in keeping with the variations found in seed produced by intra-specific hybridisation. The seed coat morphology of *Passiflora* cultivars was found to be an intermediary of the seed coat morphology of their parents. A new classification of the genus *Passiflora* using only the morphological features of their seed is presented using seed from 360 accessions. The results of this study support the karyotypic evidence of $x = 6$ and $x = 9$ and otherwise shadow the conventional taxonomic classification of *Passiflora*, with the exception of species in the subgenus *Astropheia* and sections *Quadrangularis*, *Serratifolia*, *Passiflora*, and *Tiliifolia* in the subgenus *Passiflora*. The seed coat morphology of *Passiflora* species is compared with that of *Adenia* species and the probability of parallel evolution of *Passiflora* from several ancient archetypal *Adenia* species is proposed. Aspects of the sociology and ecology of *Passiflora* species are presented. Evidence of insect and plant mimicry is demonstrated. Detailed descriptions of new *Passiflora* species and subspecies are presented.

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1 Introduction

Passiflora is the largest genus in the family Passifloraceae with 485 of its 675 species. The second largest genus is *Adenia*, with 102 species, leaving the remaining 17 genera with only 88 species. *Passiflora* is primarily an American genus with the overwhelming majority of species endemic to South and Central America and two species (*P. incarnata* and *P. lutea*) endemic to the temperate zones of southern North America. Twenty species are recorded in Asia and Malaysia and a few are native to Australasia. *Passiflora* comprise mostly climbing vines with a few small weak tropical trees like *P. macrophylla* and the medium-sized tree *P. lindeniana*.

The name *Passiflora* is derived from the Latin name 'Flos Passionalis' for the flower that tells the story of Christ's Passion or Crucifixion. The earliest literary record of a passion flower is believed to be that of Pedro Cieza de Leon in 1553 after his voyage to the New World. The work of Giacomo Bosio, a monastic scholar, promoted the 'Flos Passionalis' or 'Flower of the Five Wounds' as a symbol of Christianity in his poems and treatise on the Cross of Calvary (1610). This powerful symbolism of the religious importance of this flower is shown in Simone Parlasca's drawing in 1609. The species depicted in his drawing is believed to be *P. incarnata*, which was common in the West Indies and the mainland of southern North America at that time. The discovery of this 'stupendously marvellous' flower was taken by the Jesuits as a sign that Christianity should be brought to the peoples of the New World. When natives were observed eating the fruit of this vine, this was taken as a further sign that they were hungry for the word of Christ.

The origins of some of the modern symbolism of the parts of the flower and the vine itself are unknown. The fruit illustrations are of a plant similar to *P. incarnata* but the later passion flower story or legend is based on a species with lanceolate leaves, and subsequently on *P. caerulea* with palmate leaves. Many other additions and omissions have been made to the story over the years but the most widely known version is that the three stigmata represent the three nails that were used in the Crucifixion. The five stamens or anthers represent the five wounds of Christ and the corona filaments, the Crown of Thorns. The ten petals and sepals represent the ten apostles present at the Crucifixion (Judas and Peter were absent). The three bracts represent the Trinity, the five-lobed leaves of *P. caerulea*, the hands of the prosecutors and the tendrils, the cords that bound Christ. The blue of the flower represents Heaven and the white, purity. In some stories, based on an unknown species, spots on the leaves represented the thirty pieces of silver, and pink or red colouration in the flower represented the blood of Christ. In 1612 a detailed and botanically accurate drawing of *P. incarnata*, which had been cultivated in France, was published under the name 'Flos Passionalis, sive Grenadille ex India'. However it wasn't until 139 years later, when Linnaeus published his work in 1753, that the genus *Passiflora* as we know it today was born.

The name 'passion flower' is now being exploited using the modern common understanding of the word 'passion'. Passion fruit, particularly *P. ligularis*, are increasingly being marketed as 'Love Fruit' and 'Love Apple' and are heavily promoted for 14 February, 'Valentines Day'. This trend has now spread to include the plants as gifts of love alongside the more traditional gifts of red roses or jewellery.

Thousands of tonnes of fruit are now harvested each year from many countries throughout the tropics and subtropics of Africa, America, Asia and Australasia for the fresh fruit trade. This results in the production of drinks, sherbets and sweets and more recently fragrances in a wide range of products such as soaps, shower gels, perfumes, candles and incense sticks. The introduction of *P. mollissima* into Hawaii and New Zealand for fruit production in the early part of the 20th century is now giving cause for concern as it has escaped into the wild and is covering vast mountain areas, destroying the less robust native species to such an extent that it is now classified as a pernicious weed (Green, 1991). Similarly, *P. edulis* Sims. escaped into the wild in East Africa in the 1950s but to date no adverse effects have been reported.

The by-product of pulp, which is left after the juice has been extracted from the fruit, is used in cattle feed as an additional source of protein (Morton, 1987). The dried young leaves and shoots of *P. incarnata* contain passiflorine, a sedative or tranquilliser that is prepared as a drink, in a similar way to tea, or processed into more sophisticated forms (powders or tablets) and taken to aid natural sleep. The extraction of passiflorine and identification of further flavonoids from other species has been a subject of widespread research in recent years. A study of 114 species has been completed by the University of Mississippi (Abourashed, Vanderplank & Khan, 2002) and a larger study is planned. Various parts of plants from several species are used medicinally by native tribes of the Americas. The roots of *P. foetida* are reputed to be anti-spasmodic, and those of *P. quadrangularis* to be antihelmintic, while the seed of *P. coriacea* is used to kill insects in Guatemala (Killip, 1938).

The horticultural trade in the UK and Europe now produces over 500,000 passion flower plants in pots for sale each year and the popularity of these vines as garden and conservatory climbers and houseplants is still increasing. In southern parts of North America their popularity is similarly increasing as garden plants.

Popular belief suggested that the seed of *Passiflora* were short-lived and difficult to germinate. Various solutions were offered to overcome these problems; seed should be sown straight from the fruit with arils still attached, seed will only germinate if they have been scarified, seed should be soaked in warm tea or water for 24 hours prior to sowing and so on. Seed were said to be short-lived with a viability of less than one year. Seed storage was best at room temperature and seed would not survive sub-zero temperatures. No comprehensive study had been conducted on *Passiflora* seed, with the exception of *P. edulis*, which is of considerable agricultural importance.

Following a trip to Venezuela and seeing first-hand the rapid expansion of its population and the loss of the natural habitats of *Passiflora* species, including the rare tree *P. lindeniana*, of which there were only four mature specimens known in the Merida area at that time, the future of many *Passiflora* species seemed threatened. Six years later, one taxon, *P. cuneata* var. 'Miguel Molinari', has been lost from the wild and only two mature specimens of *P. lindeniana* are known in the Merida area. The possibility that seed of all *Passiflora* species could be collected and stored for long periods of time to guard against the possible loss of their genotype from the wild was a prime motivating force for this research.

The results from preliminary seed storage and germination tests suggested that seed from separate species behaved differently. The reasons for this were unclear, although it seemed reasonable for plants from different geographical areas to produce seed with varying needs. However, the diversity of seed from such closely related species of the same genus was unexpected. The possibility that the genus *Adenia* had evolved from a single archetypal species was proposed by de Wilde (1972) and the theory that the closeness of *Adenia* and *Passiflora* might hold some answers to the seed behaviour of *Passiflora* has been considered and examined.

The close similarities of the seed morphology of species within a subgenus was very distinct, and the similarities in morphological details between *Passiflora* seed and the seed of some *Adenia* species was striking. The classification of *Passiflora* seed using seed morphology alone and the comparison of these seed with the seed of some *Adenia* species was undertaken. The results were then compared with the traditional classification of *Passiflora* using conventional taxonomy.

Continuing results of seed germination tests from freshly harvested seed suggested the possibility of seed coat-imposed dormancy in *P. subpeltata*. This was investigated and after confirmation, methods of breaking seed coat-imposed dormancy were tested.

The inclusion of many personal observations and the ecology of some *Passiflora* is intended to give a better understanding of this wonderful and diverse genus and the possible effects this ecology might have on their seed and seed storage behaviour. The complex relationship between *Passiflora* species and the *Heliconius* butterflies

has been mentioned only briefly as this is the subject of extensive ongoing zoological research.

1.1 Traditional classification of Passifloraceae with special reference to

Passiflora, Adenia and Hollrungia

Passifloraceae Juss. ex Kunth.

Dicots, Dilleniidae, Violales (Mabberley, 1987)

Comprising 19 genera with 719 species almost entirely confined to the tropics of Africa, America, Asia, and Australasia.

Genera of Passifloraceae

<u>Genus</u>	<u>Author</u>	<u>Number of species</u>
<i>Abatia</i>		11
<i>Adenia</i>	Forssk.	106
<i>Aphaerema</i>		1
<i>Ancistrothyrsus</i>	Harms	2
<i>Androsiphonia</i>	Stapf.	1
<i>Basananthe</i>	Peyr.	33
<i>Barteria</i>	Hook.	1
<i>Crossostemma</i>	Planch. ex Benth.	1
<i>Deidamia</i>	Noronha ex Thouars	5
<i>Dilkea</i>	Mast.	5
<i>Efulensia</i>	C. H. Wright	2
<i>Hollrungia</i>	K. Schum.	1
<i>Mitostemma</i>	Mast.	3
<i>Paropsia</i>	Noronha ex Thouars	11
<i>Paropsiopsis</i>	Engl.	7

<u>Genus</u>	<u>Author</u>	<u>Number of species</u>
<i>Passiflora</i>	L.	525
<i>Schlechterina</i>	Harms	1
<i>Smeathmannia</i>	Sol. ex R. Br.	2
<i>Viridivia</i>	J. H. Hemsl. & Verdc.	1

1.1.1 Adenia

Adenia Forssk. (1775), with 106 species, is primarily an Old World genus found in Africa and Asia. Species vary from small desert or semi-desert plants with swollen stems and thorns in East and South Africa to giant forest climbers that climb by the use of tendrils in West Africa and Asia.

1.1.2 Hollrungia

Hollrungia K. Schum. (1988) has one species, found in the rainforests of Malesia, which is related to *Passiflora tetrandra* Banks and Sol. (1828), formerly *Tetrapathaea tetrandra* from New Zealand (J. J. O. de Wilde, 1972).

1.2 Classification of *Passiflora*

Passiflora L. *Sp. Pl.* 955 (1753). Lectotype: Britton and Brown, 1913, *Passiflora incarnata* L.

Passiflora is a genus with 23 subgenera and 525 species, and more than 236 named and described interspecific hybrids (Vanderplank, 2003). It is primarily a New World

genus, endemic to the Americas with only 17 species found in Asia and Australasia. None are endemic to Africa. Most plants are climbers, climbing by the use of axillary tendrils, and range from large robust species growing to over 50 metres high (*P. quadrangularis* L.) to small slender climbers found growing over grasses and small shrubs (*P. allantophylla* Mast.). Occasionally they form small trees or spreading shrubs (*P. lindeniana* Tr. & Planch.). Most are tropical and subtropical plants but rarely they are temperate, found at elevations up to 4,200 metres in the Andes Mountains. Most plants are perennial evergreens with one notable exception, *P. gracilis* Jacq. (ex Link.), which is a true annual. *P. lutea* L. and *P. incarnata* L. are endemic to North America and are both very herbaceous, dying back to ground level in the autumn and overwintering by means of thick fleshy roots.

***Passiflora* subgenera and sections**

<i>Apodogyne</i>	Killip (1938)	1 species
<i>Astephia</i>	Killip (1938)	1 species
<i>Tryphostemmatoides</i>	(Harms) Killip (1938)	4 species
<i>Decaloba</i>	(DC.) Reichenback (1828)	177 species in 13 sections
Section 1	<i>Cieca</i>	
Section 2	<i>Decaloba</i> with 8 series	
	Series <i>Apetalae</i>	
	Series <i>Auriculata</i>	
	Series <i>Heterophyllae</i>	
	Series <i>Luteae</i>	
	Series <i>Miserae</i>	

Series *Organenses*

Series *Punctatae*

Series *Sexflorae*

- Section 3 *Deidamioides*
- Section 4 *Discophora*
- Section 5 *Distemma*
- Section 6 *Eueidipabulum*
- Section 7 *Hahniopathanthus*
- Section 8 *Hollrungiella*
- Section 9 *Mayapathanthus*
- Section 10 *Octandrathus*
- Section 11 *Pseudogranadilla*
- Section 12 *Pseudodysosmia*
- Section 13 *Xerogona*

<i>Chloropathanthus</i>	(Harms) Killip (1938)	2 species
<i>Murucuja</i>	(Medic) Mast (1871)	4 species
<i>Pseudomurucuja</i>	(Harms) Killip (1938)	7 species
<i>Psilanthus</i>	(Juss.) Killip (1938)	3 species
<i>Adenosepala</i>	Killip (1938)	1 species
<i>Rathea</i>	(Karst.) Killip (1938)	3 species
<i>Tacsonia</i>	(Juss.) Tr. & Planch. (1873)	49 species in 10 sections
Section 1	<i>Ampullacea</i>	
Section 2	<i>Bolivana</i>	
Section 3	<i>Bracteogama</i>	
Section 4	<i>Colombiana</i> with 3 series	

Series *Colombianae*

Series *Leptmischae*

Series *Ouindiensae*

Section 5 *Fimbriatistipula*

Section 6 *Parritana*

Section 7 *Poggendorffia*

Section 8 *Tacsonia*

Section 9 *Tacsoniopsis*

Section 10 *Trifoliata*

Manicata (Harms) Escobar (1988a) 6 species

Distephana (Juss.) Killip (1938) 16 species

Tacsonioides (DC.) Killip (1938) 6 species

Passiflora 138 species in 17 sections

Section 1 *Digitata*

Section 2 *Imbricata*

Section 3 *Kermesina*

Section 4 *Laurifolia*

Section 5 *Lobatae*

Section 6 *Macdougaliana*

Section 7 *Marginata*

Section 8 *Menispermifolia*

Section 9 *Pachyantha*

Section 10 *Palmatisecta*

Section 11 *Passiflora*

Section 12 *Pedata*

	Section 13	<i>Quadrangularis</i>	
	Section 14	<i>Serratifolia</i>	
	Section 15	<i>Setacea</i>	
	Section 16	<i>Simplicifolia</i>	
	Section 17	<i>Tiliifolia</i>	
<i>Calopathanthus</i>		(Harms) Killip (1938)	1 species
<i>Dysosmia</i>		(DC.) Killip (1938)	13 species
<i>Dysosmioides</i>		Killip (1938)	5 species
<i>Polyanthea</i>		Killip (1938)	1 species
<i>Astrophea</i>		(DC.) Mast. (1871)	57 species in 5 sections
	Section 1	<i>Botryastrophea</i>	
	Section 2	<i>Dolichostemma</i>	
	Section 3	<i>Euastrophea</i>	
	Section 4	<i>Leptopoda</i>	
	Section 5	<i>Pseudoastrophea</i>	
<i>Tetrapathaea</i>		(DC.) Green (1972)	1 species
<i>Tetrastylis</i>		(Barb. Robr.) Hutchins	1 species
<i>Porphyropathanthus</i>		Escobar (1989b)	1 species

An additional twenty-two species were awaiting formal description in December 2003, giving a total of 525 species. With the exception of the former subgenera *Deidamioides* and *Tacsoniopsis*, with only one species each, which have been reduced to sections of the subgenera *Decaloba* and *Tacsonia* respectively by E. Kugler in B. & T. Ulmer (1997a), the only alterations to the classification of E. P. Killip (1938) which are included are those published in *Index Kewensis* 2 (1997).

2 Literature survey

2.1 Historical Survey: *Passiflora* as a genus

The earliest known published reference to a plant now be considered to be a *Passiflora* is that of Pedro de Cieza (1553), followed by that of Jose de Acosta (1591). The earliest illustration is that of Simone Parlasca (1609). This is a very symbolised drawing of the religious aspects of this Holy Flower, 'Flos Passionalis', which told the story of Christ's Passion and gave the name to the genus. In 1610 Jacomo Bosio published his work of writings, poems and drawings of this 'Flos Passionalis' and is generally credited with promoting this flower as being a sign that the native people of the New World should be brought to Christianity (Plate 1). In 1612 the first truly botanical illustration of a passion flower (*P. incarnata*) was published under the title 'Flos Passionalis, sive Grenadilla' (Plate 2). This plant was in cultivation in France at this time.

The first use of the name *Passiflora* is in a table by Cesi published in 1651 (MacDougal, 1994) but it was not until Linnaeus (1745) that the genus *Passiflora* as we know it today was born. Under the direction of Linnaeus, John G. Hallman presented 22 *Passiflora* species with direct reference to earlier synonyms (Linnaeus, 1745). In 1753 Linnaeus described 24 species in *Species Plantarum*, which included the original 22 species. By this time passion flowers were already becoming a popular garden or greenhouse climber. Lamarck (1789) recognised 35 species and Cavanilles (1790) presented the first extensive monograph of the genus. By 1828 de Candolle had recognised 145 American species. Less than twenty years later Roemer (1846) published a monograph on Passifloraceae in which he regarded *Passiflora* as a



Jacomo Bosio's drawing of 1610, which is very similar to Simone Parlasca's drawing of 1609.

The first known illustration of a passion flower is by Simone Parlasca, 1609, with this highly symbolised drawing.

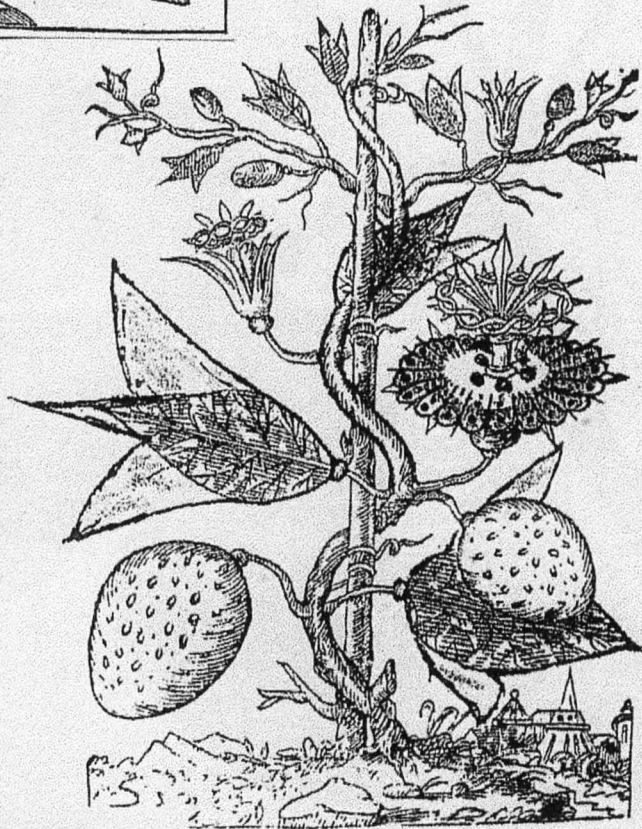


Plate 1. Early concepts of the passion flower

Flos Passionalis, sive Granadille
Ex India.

Floruit mense Augusto Anni, 1612. in horto
 Iohannis Robini Herbarij Regiæ Majest. in Gallia,
 vidiq; depictum à quodam, qui vocatur Angelus:
 conspectus est à multis Religiosis præsertim
 Capucinis et alijs: affirmat aut Robinus
 sibi allatam ex Insula Canada.

N. Descamps herborista
 de la Reine Regente.

Capita (clavorum instar) in summitate
 viridia sunt: cauliculi superiores
 cum umbilico et parte inferiore
 media exalbido-virescent, sangui-
 nis inspersi punctulis.

Folia 5 exteriorius luteo; in-
 terius albo colore, quorum
 cauliculi in totum virides sunt,
 inspersi ibidem sang. punct.

Circulus umbilico proximus, cum reli-
 quis staminibus ut et flammulis purpureo-violaceo.

Majora io. folia albo: lacinae eorum ut et aculej, viridi colore.

Seria huius ala, cum nervis, rubescit.



This illustration, 'Flos Passionalis', of 1612 is undoubtedly *P. incarnata*, which was already in cultivation in France by this time.

Plate 2. Earliest botanical illustration of *P. incarnata*

separate genus from *Dysosmia* (D.C.) and *Decaloba* (D.C.), which had been considered as sections of *Passiflora* by the early authors.

In 1872 M. T. Masters presented his comprehensive monograph of the American species in *Flora Brasiliensis*, which covered 202 species of *Passiflora* and reunited *Dysosmia* and *Decaloba* as sections of *Passiflora*. Triana and Planchon (1873) described 66 Colombian species of *Passiflora*. Harms (1893b and 1898) revised the classification of Passifloraceae. In 1925, in his second edition, Harms did not recognise subgenera and *Passiflora* was instead divided into many sections. E. P. Killip's complete revision of 'The American Species of Passifloraceae' in 1938 took over 12 years to complete and included all the 355 known species of *Passiflora* of the Americas. In 1960 he revised this edition to include a further 11 species (Killip & Cuatrecasas, 1960). Since this time no complete revision of the genus has been attempted but minor revisions have been made and many new species included.

In 1972 W. J. J. O. de Wilde described eight Asian or Australian species that were not included in Killip's works. In 1972 P. S. Green included the genus *Tetraphaeta* in *Passiflora*. L. B. Holm-Nielsen *et al.* (1988) described several new species and made minor revisions in 'Flora of Ecuador'. L. K. Escobar (1986, 1987, 1988a and b, 1989a-d, 1990, 1992 and 1994) contributed much to the understanding of *Passiflora* from Colombia, particularly the subgenus *Tacsonia*, and made several minor revisions to this subgenus. J. M. MacDougal (1988a and b, 1989a-e, 1992, 1994 and 1995) has published numerous papers including additional new species. His major work, 'Revision of *Passiflora* subgenus *Decaloba* section *Pseudodysosmia*', published in 1994, is the most significant revision since Killip's in 1938. Many new species have

been described since this work and by the end of 2003 there were 503 described species of *Passiflora* and 22 confirmed new species awaiting formal description.

In August 1999, C. Feuillet and J. M. MacDougal presented a paper at the International Botanical Congress in which they proposed a complete reclassification of *Passiflora*. They suggested reducing the original 25 subgenera with 45 sections presently in operation to four subgenera with super-sections and sections. The four proposed subgenera are:

1. *Astrophea* The stout-stemmed or tree-like species (unchanged from Killip, 1938) with 57 species
2. *Deidamioides* To include 13 species that do not belong in the other three subgenera
3. *Decaloba* With 213 species, mostly $x = 6$, $2x = 12$ (chromosome counts)
4. *Passiflora* With 220 species, mostly $x = 9$, $2x = 18$

The divisions within these four subgenera are units of subgenera, series or sections taken from Killip (1938), Escobar (1986-1994), Holm-Nielsen *et al.* (1988) and Green (1972). Although recent studies of the phylogeny of *Passiflora* using DNA sequencing broadly support the division by chromosome studies of the two major subgenera, *Decaloba* ($x = 6$) and *Passiflora* ($x = 9$), there is little evidence to support the remaining two subgenera (S. E. Vanderplank, unpublished). The possibility of reclassification or making major revisions to the traditional classification of *Passiflora* using the evidence from the morphology of their seed is presented in the following pages. This gives some support to the Feuillet and MacDougal subgenera *Decaloba* and *Passiflora* but also gives an insight into the phylogeny of many species,

particularly those placed by Feuillet and MacDougal (unpublished, 1999) in the subgenera *Astrophea* and *Deidamioides*.

2.2 Historical Survey of *Passiflora* Seed and their Germination

The earliest published account of passionfruit is believed to be that of Pedro de Cieza in his '*Historiae Peruvianae*' of 1553 in which he praised the odour and taste of passionfruit but made no reference to the seed. An illustration of a flowering and fruiting vine, *Passiflora incarnata* L., with an open half-fruit showing arilled seed appears in Donato d'Eremita's '*Vera effigie della Grandiglia detta fior della passione*' of 1619. It was a hundred years later before any real scientific work was undertaken. This was a microscopic examination of the pollen of *Passiflora* (Badcock 1748a and b). Only a few years later in 1753 Linnaeus, in '*Species Plantarum*' described 24 species of *Passiflora* but in spite of these detailed plant descriptions there is no detailed account of their seed. The first real attention to the visible appearance of *Passiflora* seed is found in Joseph Gaertner's '*De fructibus et seminibus plantarum*' of 1788.

Some 40 years later, in 1830, F. T. G. Bartling recorded *Passiflora* seed germination to be epigeal and the seedlings as having elliptic foliaceous cotyledons, which are now considered to be the most common type of dicotyledonous plants (de Vogel, 1980). In 1871 M. J. Masters' '*Contributions to the Natural History of Passifloraceae*' shows detailed drawings of many individual parts of *Passiflora* flowers, including ovules, and ovules surrounded by their arils, of *Passiflora alba* (Link and Otto, 1828) which is now considered to be synonymous with *Passiflora*

subpeltata (Ortega, 1798). Also described are the variations in seed size and sculpturing of a few species including *P. alata* Dryand., *P. quadrangularis* L. and *P. racemosa* Brot..

J. Lubbock's 'A contribution to our knowledge of seedlings' of 1892 gives a very detailed description of seed and seedlings of several *Passiflora* species including *P. leschenaultii* DC., *P. macrocarpa* Mast. (now considered to be synonymous with *P. quadrangularis* L.), *P. caerulea* L., *Tacsonia ignea* Hort. and *Tacsonia van-volxemii* Hook. The genus *Tacsonia* Juss. has now been demoted to a subgenus of *Passiflora* L. and the species *P. van-volxemii* is considered to be synonymous with *P. antioquiensis* Karst.

'Passion-vine rearing from seed' by S. Hermann (1899) advocates soaking seed in urine for 24 hours before sowing to promote germination. It is noteworthy that this article was published in 'The Agricultural Gazette' of New South Wales, Australia. This marks the start of research work on *Passiflora* funded by government-run agricultural research stations with a positive agenda to assist farmers and growers in the new passionfruit production industry, which was becoming increasingly important economically. The purely botanical interest in this genus is now largely superseded by commercial interests from many countries in the tropics and subtropics of Asia, Africa, Australia and America.

In 1925, Harms published a major work on *Passifloraceae*, 'Die Natürlichen Pflanzenfamilien', his first for 27 years. This included detailed descriptions of seed of many *Passifloraceae* species including *Adenia* Forsk. and *Tryphostemmatoides*

Harm., which is now demoted to being a section of subgenus *Decaloba* (DC.)

MacDougal in *Passiflora* L.. In 1935, in the Hawaii Agricultural Experimental Station Bulletin, W. T. Pope recommended that for optimal germination, seed of *P. edulis* Sims should be sown immediately after harvesting of the fruit.

In 1938 E. P. Killip published his comprehensive work, 'The American Species of Passifloraceae'. This included brief descriptions of seed of most of the *Passiflora* known at that time. Using this data Killip tried to correlate the two main types of *Passiflora* seed with a prominent vegetative feature of each group. He noted that seed that had transverse ridges and grooves came from species that had glandless petioles whereas species that had glandiferous petioles produced reticulated or pitted seed. The exceptions to this rule were the species in subgenus *Plectostemma* Mast., which is now the subgenus *Decaloba* (DC.) (Rchb.) MacDougal (1994), section *Hahniopathanthus* Harms, with reticulated seed, and species in the section *Decaloba* that have large auriculate glands.. Killip dramatically redefined the section *Cieca* to encompass those species in the subgenus *Decaloba* (previously *Plectostemma*) that have reticulated seed coats and petiole glands as these were considered primitive characteristics for the genus (MacDougal, 1994). Unfortunately Killip was unable to examine seed of species in the subgenera *Tacsonia* Juss., *Astropheia* DC. and *Granadilla* Medic. (which is now subgenus *Passiflora*), because seed were not presented with the original herbarium specimens. This is still, too often, the case today. When new species are described and herbarium specimens commissioned, fruit and seed are not considered to be of sufficient importance for diagnostic and taxonomic purposes and are often not included. It may be difficult to obtain ripe fruit of large-fruited species as they tend to have shorter flowering periods and fewer fruit

than the smaller-fruited species, and the large, sweet, fleshy fruit may be immediately consumed by mammals on ripening.

In the 'Department of Agriculture and Stock' pamphlet, 1948, J. M. Wills suggests that seed of *Passiflora edulis* Sims should be allowed to remain in the fruit until they have dried naturally and kept inside the fruit until they are required for sowing. They should then be soaked overnight in warm water at 180°F. However this technique was condemned as nonsense by A. M. W. Grieg in the New Zealand Department of Agriculture Bulletin, 1948. In 1954 J. S. Pruthi and L. Girdhari repeated Will s' experiments using *Passiflora edulis* Sims seed and water with an initial temperature of 180°F for overnight soaking. Their results showed only a minor reduction of 1-2% in germination using this method and a similar percentage loss in viability was recorded for one-year-old seed.

In 1955 in 'Embryology of Passifloraceae', M. V. S. Raju described a detailed investigation into the gametogenesis and seed development of *Passiflora calcarta* Mast. F. A. Kuhne, in 1968 in 'Cultivation of Granadillas', suggests that even fresh seed of *P. edulis* Sims and *P. edulis* f. *flavicarpa* Deg. are best scarified by lightly rubbing the seed on fine-grained sandpaper before sowing. He also recommends that seed with their juices and arils should be allowed to ferment for three days before washing and drying prior to storage in closed containers. Problems were being experienced in germinating the seed of both varieties. This may have been due to the fact that as world cultivation increased the vines were being grown at lower elevations. Traditionally *P. edulis* Sims was grown at elevations of approximately 5-6,000 ft where the mean daytime temperature is significantly lower than the

temperatures found in the tropics at sea level. High temperatures during fruit maturation may have triggered seed coat imposed dormancy.

In 'Passion Fruit Culture' in 1956, E. K. Akamine recorded that *Passiflora* seed were probably best stored undisturbed in whole fruit at 55⁰F (13⁰C) for short periods of up to two months. Lower storage temperatures delayed subsequent germination and freezing of fruit killed their seed. Artificial dehydration of seed for between half an hour and two hours at 108-140⁰F (42-60⁰C) with a forced draught did not harm germination providing seed were sown within a few days of drying, but a temperature of 158⁰F (70⁰C) was detrimental to germination.

S. G. Torne and N. P. Raut Desai (1975) investigated the effect of ionising radiation on seed germination of *Passiflora* species. They used twelve levels of gamma rays ranging from 1kr. to 30kr. on seed of *P. edulis* Sims and *P. foetida*. Results showed that lower levels of gamma radiation increased germination and the survival percentage for seedlings also improved after radiation.

In 'The Seeds of Dicotyledons' in 1976, E. J. H. Corner examined the relationship between *Cucurbitales* and *Passiflora* with detailed examination of the seed of *P. edulis* Sims as a type species. In 1977, T. Y. Teng, in 'Storage of passion fruit seeds (*Passiflora edulis* forma *flavicarpa* Deg.)', stated that seed viability was retained better when seed were stored at 9.1% moisture in sealed containers in an air-conditioned room. Seed had 72% viability after 12 months, while seed stored at 5.2% moisture in sealed containers at ambient room temperature lost 100% viability after only ten months. Teng also suggests the critical moisture content for seed of

Passiflora edulis f. *flavicarpa* Deg. to be above 6.2% and advocates using alternating temperatures of 20⁰C and 30⁰C for 16 and 8 hours respectively for seed germination.

In 1979, in 'Germination of hard-to-start xerophyte seeds', Schutzman found that both thiourea at 5% solution and gibberellic acid at 200ppm improved germination percentages.

M. J. S. Morley-Bunker in 'Seed Coat Dormancy in *Passiflora* Species' (1980) conducted a series of experiments investigating the seed coat structure of *Passiflora edulis* Sims to discover whether or not the hard bony testa was so impermeable to water and gases that it caused dormancy, 'seed coat imposed dormancy'. His dormancy-breaking experiments included trials with various temperature regimes. He found that a dual temperature treatment of 12 hours at 20⁰C followed by 12 hours at 30⁰C worked best. Seeds whose coats were cracked before sowing also showed an increased percentage of germination. The use of sulphuric acid, chipping and gibberellic acid did not enhance germination. Finally he recorded that seed from some sources did not require any dormancy-breaking treatment for germination to take place; they germinated readily. However seed obtained from Kenya, although fresh and healthy, would not respond to any dormancy-breaking treatment. He recorded 0% germination for all attempts and was most perplexed by this. It seems that he had discovered seed coat-imposed dormancy that was due not to the mechanical restraints of water uptake or gaseous exchange by the seed coat, but to the supply of inhibitors to the embryos, but he failed to recognise this.

In 1983, M. R. Becwar, P. Stanwood and K. W. Leonhardt investigated the 'Dehydration effects on freezing characteristics and survival in liquid nitrogen of desiccation tolerant and desiccation sensitive seed'. This included work on *P. edulis* f. *flavicarpa* Deg.. Seed moisture content was reduced to 2% (percentage of the fresh mass) and seed were then subjected to liquid nitrogen at -196°C . The survival rate was high at over 70%. They concluded that this was sufficient proof that *Passiflora* seed should be considered 'orthodox' for storage requirements. Longevity of orthodox seed is increased by storage at low moisture and temperature conditions (Ellis, Hong & Roberts, 1990). This was partly confirmed by J. C. de Oliveira *et al.* in 1984 in 'Effect of age on the emergence and vigour of yellow passion-flower seed'. Seed of *Passiflora edulis* f. *flavicarpa* collected over a ten-year period and stored in a dry chamber at ambient temperature survived for up to five years. One exceptional year (1981) was noted because of a particularly low percentage of seed germination. No explanation for this was offered.

In 'The Handbook of Seed Technology for Genebanks', volume II, (1985), by Ellis, Hong and Roberts there is a very short chapter (chapter 55) on *Passifloraceae* which reviewed previous literature on *Passiflora* seed. It confirms the work of Morley-Bunker (1980) by recording that 'seed may show considerable dormancy' and suggests 'dormancy-breaking treatments' of scarification for *Passiflora edulis* Sims and other 'germination regimes for non-dormant seed'. Three other *Passiflora* species are covered: *P. ligularis* Juss., *P. maliformis* L. and *P. quadrangularis* L..

P. Worley, in 'Passionflowers from seed' (1989) suggests that seed of *Passiflora incarnata* L. may have inhibitors in their seed coat that prevent them from

germinating. This is the first reference to the possibility of true seed coat imposed dormancy in *Passiflora*. Worley also suggests that the best dormancy-breaking treatment is to soak seed for 4-8 hours in dilute tannic acid found in cold black tea. This is made from the leaves of the tea plant (*Camellia sinensis* T.) and soaking is followed by high temperature and high humidity conditions as found in a sealed propagation chamber.

In 'Storage of Passionfruit Seeds', by J. Nakagawa, C. Cavariani and W. A. Amaria (1991) the best seed survival rates were achieved by storing seed of *P. edulis* Sims in paper bags in a 'cool chamber'. Seed stored in ambient laboratory conditions recorded 0% germination after 32 months. H. Tsuboi and J. Nakagawa (1992) investigated the effects of the scarification with sandpaper, sulphuric acid and hot water on the germination of passion fruit seeds (*Passiflora edulis* f. *flavicarpa* Deg.). They concluded that scarification produced faster germination than non-scarified seed and that germinating the seed with arils and juices also improved the speed of germination. Treatment with sulphuric acid and hot water (80⁰C) decreased germination rates.

J. MacDougal, in his 'Revision of *Passiflora* subgenus *Decaloba* section *Pseudodysosmia*, *Passifloraceae*', 1994, suggests a general correlation between testal morphology and fruit type. Highly compressed and finely punctate-foveolate seed are found in species that have ripe green fruit and clear arils. Slightly compressed and foveate to coarsely reticulate seed are found in species with orange arils and purple fruit. Large, slightly compressed, very coarsely foveate-areolate seed occur in orange-arilled, red-fruited species.

In most species of *Passiflora* germination is epigeal but there are some exceptions. *P. exsudans* Zuccarini produces seed that are epigeal in most cases but it has a variant in which germination is hypogeal. The advantage of this may be that late germination from beneath thick leaf litter in cold deciduous forests may protect the cotyledonary axillary buds within the testa from late frosts, thereby giving the seedling a second chance should the primary shoot become frosted. In *P. lutea* L., *P. discophora* Jorg. and *Tetrastylis ovalis* Vell. Germination is also recorded as being hypogeal. *Tetrastylis* Vell. is now included as a subgenus of *Passiflora* L. *P. discophora* Jorg. and *Tetrastylis ovalis* Vell. are both found growing wild in thick forests where leaf litter may cause problems with epigeal germination.

W. R. Bruner (1998) proposed a technique for germinating seed of *P. incarnata* L. and *P. lutea* L. Seed should be soaked in water at room temperature for four or five days, the water being emptied and replaced by hot tap water once or twice daily. On the fourth or fifth day the water is replaced by hot tap water with an added tea-bag (containing dried chopped leaves from *Camellia sinensis* T.). This is then refrigerated for four or five more days. Finally the cold water and tea-bag are removed and discarded and hot tap water is immediately poured over the seed. This causes the hard testa or seed coat to burst open, making an audible cracking sound. Seed are then sown in a conventional manner and germinate in seven to ten days. Unfortunately Bruner does not give any precise temperatures for this technique. The first four or five days of this treatment may successfully wash out any chemical inhibitor contained in the seed coat and the second four or five days may be helpful to fully imbibe the seed, culminating in the fracture of the seed coat.

3 Morphology and ecology

3.1 General morphology of *Passiflora*

Passiflora L. *Sp. Pl.* 955 (1753). Lectotype: Britton and Brown, 1913, *Passiflora incarnata* L.

Most *Passiflora* are opportunist climbers that may rapidly become established in open areas on the edge of gallery forests (MacDougal, 1994) or in clearings made by falling trees in tropical rainforests. They are often found growing on waste ground or derelict sites in southern USA, for example *P. incarnata*. Although most species occur in the tropical rainforests, particularly at lower elevations, many species, such as *P. truxillensis*, have adapted to the harsh conditions of the high Andes and are recorded at elevations of up to 4,200 metres (Killip, 1938). A few species, like *P. morifolia*, are found in the semi-deserts of southern North America (MacDougal, 1994) and some species, such as *P. nitida*, have successfully adapted to the contrasting seasons of the flood plains of Brazil and Venezuela (Tillett, 1988). A few weak tree *Passiflora* species have been recorded and one small stout tree species, *P. lindeniana*, is found in Venezuela (Killip 1938). Apart from one annual species, *P. gracilis*, all *Passiflora* species are perennials (Killip, 1938), most of which are common or rare wild plants with the exception of a few species, like *P. tarminiana*, wrongly recorded as *P. mollissima* until 2001 (Jorgensen & MacDougal, 2001), that are regarded as pernicious weeds (Green, 1972).

3.1.1 Roots

The roots are mostly fibrous but rarely tuberous as in *P. tuberosa*. Taproots have been recorded in *P. karwinskii* (MacDougal, 1994). Fleshy shallow spreading roots may occasionally be invasive, and produce sucker growths as seen in *P. pulchella* (Tillett, 1988), *P. incarnata* and *P. caerulea* in cultivation (Vanderplank, 1996a).

3.1.2 Stem

The stems can be robust, woody and perennial as in large vines like *P. vitifolia* (Plate 3c) or slender annual stems growing from perennial roots as seen in *P. morifolia*, or woody trunks as in *P. lindeniana*, a small tree. Stems may be thick and corky as in *P. suberosa* and *P. holosericea* (Plate 3b) and very angular, square-stemmed, as in *P. quadrangularis*, triangular as in *P. trialata* or hexangular in *P. biflora* (Plate 3a) and many other species in the subgenus *Decaloba* (MacDougal, 1994). The stems of *P. laurifolia* are renowned for their durability and are used to make fish traps in the West Indies and Lesser Antilles (Killip, 1938).



a. The stems of *P. biflora* Lam., 1789 (NCP 1026) may be the only parts of the plant that photosynthesise for many months after defoliation by insect herbivores; b. Corky-barked stem of *P. holosericea* L., 1753 (NCP 1110, McD 3317); c. Woody base of large multi-stemmed vine *P. vitifolia* Kunth, 1817 (NCP 1251).

3.1.3 Node

The node in *Passiflora* (and the rest of Passifloraceae) consists of a leaf, two stipules and two axillary buds in vertical series. The lower bud gives rise to a tendril or tendril-tipped inflorescence. The upper bud (accessory bud) is vegetative. In most species the peduncle of the inflorescence does not develop and the flower or flowers appear to arise on either side of the tendril (Harms, 1893a and 1925, de Wilde, 1971b and MacDougal, 1994).

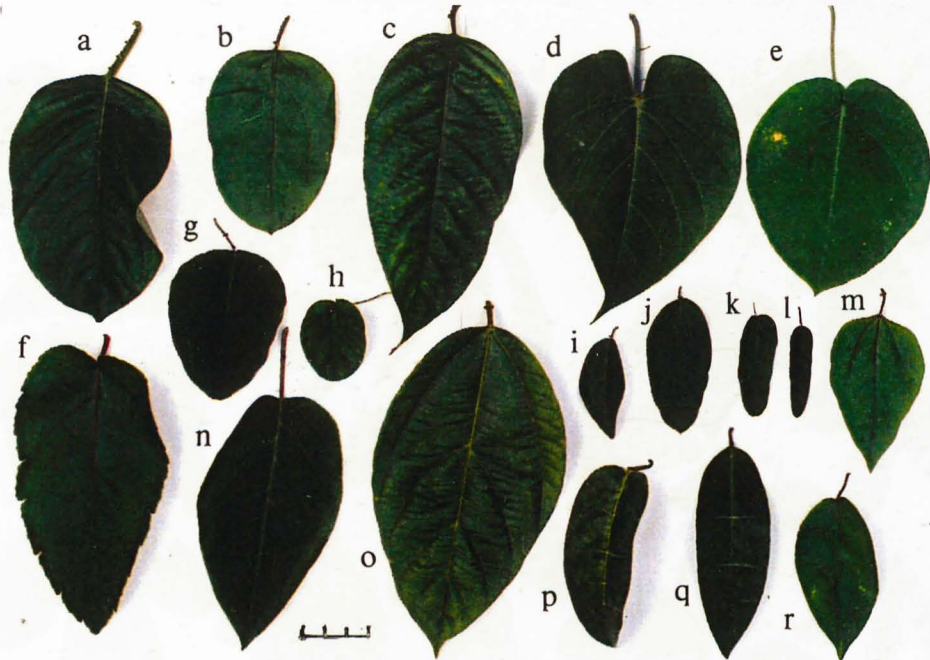
3.1.4 Stipules

The stipules are very variable and are used taxonomically to distinguish between groups of species. Their margin can be entire, toothed or deeply cleft and occasionally pinnatisect as in *P. foetida*. They may be foliaceous, as in *P. caerulea*, or setaceous and in many species, like *P. biflora*, are deciduous (Killip, 1938).

3.1.5 Leaves

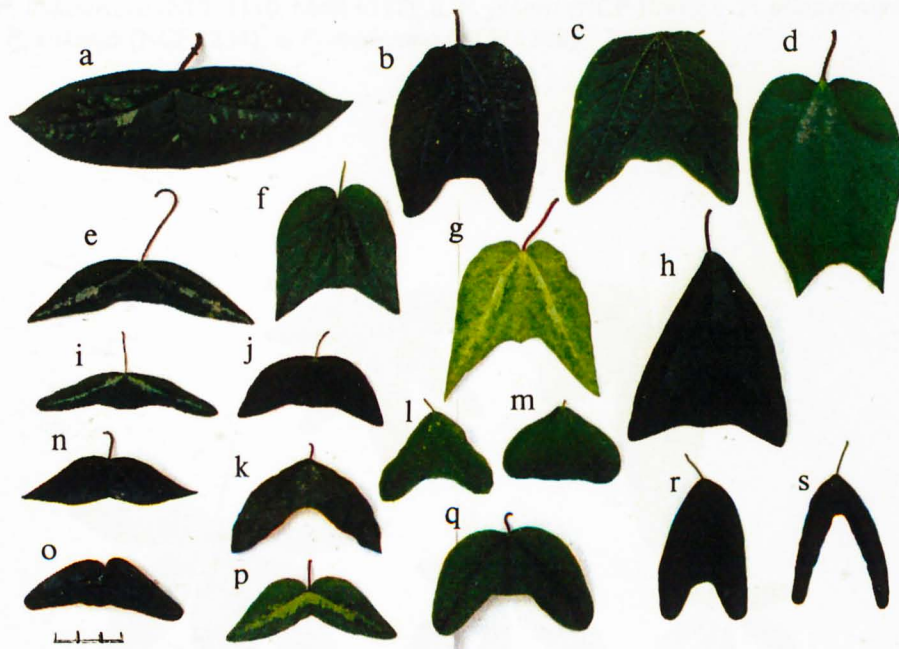
Leaves are always alternate and usually simple, very rarely compound as in *P. cirrhiflora*. The petiole often bears extrafloral nectary glands, usually opposite and numbering two to ten although sometimes scattered (Killip, 1938) and more numerous as in *P. tarminiana* (Vanderplank, 1996a). These may resemble Lepidoptera eggs and are considered to be egg mimic glands (Gilbert, 1982). The genus *Passiflora* exhibits perhaps the most diverse range of leaf shapes of any genus of angiosperms (Plates 4 and 5), probably due in part to selection pressures from visually searching butterflies

(Gilbert, 1975, 1982). Leaves may vary wildly in shape even on a single plant, as seen in *P. obtusifolia* (Killip, 1938). They may be simple, as in *P. alata*, orbicular as in *P. gracillima*, bilobed as in *P. standleyii* or transversely elliptic as in *P. coriacea*. They may be trilobed, as in *P. incarnata*, or palmate with five or seven lobes as in *P. caerulea*. Leaf laminas can be coriaceous, membranous, downy, hirsute, waxy or rugose (Killip, 1938) and may have uncinata trichomes as in *P. morifolia* (MacDougal, 1994). There may be two or many inconspicuous or conspicuous nectarous glands, which may be brightly coloured, yellow or red, on either leaf surface and are considered to be egg mimic glands in several species such as *P. boenderii* (Gilbert, 1982). Like the petiole glands the nectarous glands secrete a sugary, nectar-like syrup, which is a rich source of food for many insects, including ants which in turn protect the vines from predators including Lepidoptera larvae and eggs which they unceremoniously remove (Bentley, 1977). Leaf colour is also quite varied and many species show variegations or mottling of cream, yellow or red as in *P. trifasciata*. The underside of the leaves may be deep red or purplish as in *P. organensis*. The leaf margin is often entire but can be toothed or even pectinate (Killip, 1938). Leaves are predominantly three-nerved or obscurely five-nerved, the nerves reaching the margin and terminating in a mucro. The shape of the leaf lobes and their individual geometry is considered an important taxonomic feature for many species, especially those in the subgenus *Decaloba*, section *Pseudodysosmia* (Harms), (Killip), MacDougal (1994).



Representative simple leaves of *Passiflora* species from the subgenera *Decaloba*, *Apodogyne*, *Tryphostemmatoides*, *Murucuja*, *Passiflora* and *Distephana*:

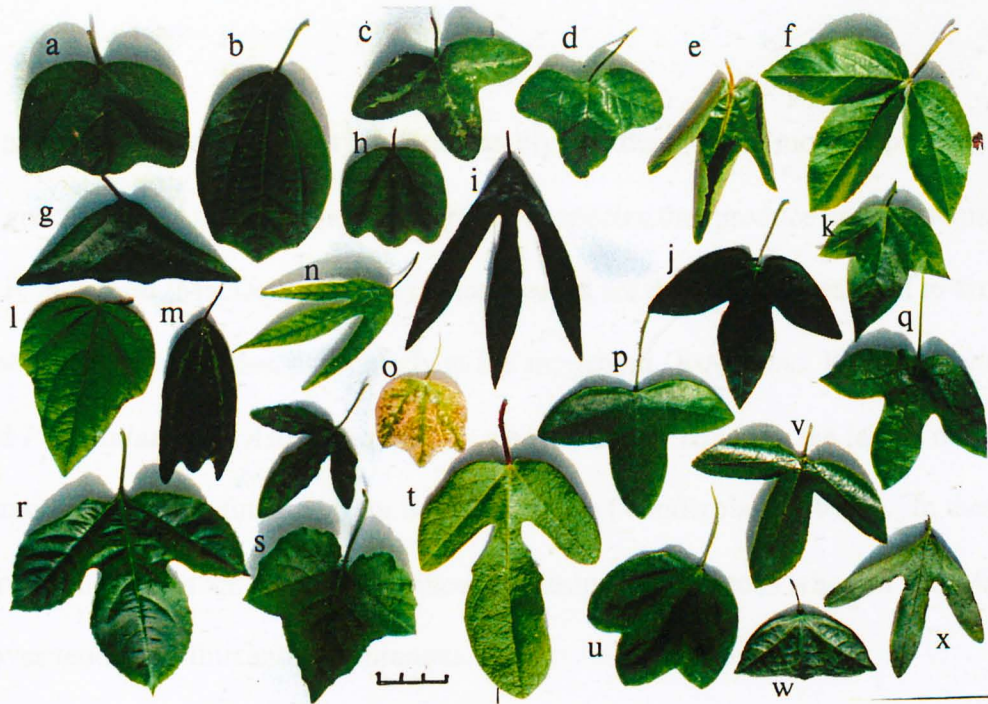
- a. *P. quadrangularis* (NCP 1368); b. *P. phoenicia* (NCP 1175); c. *P. pergrandis* (NCP 1353);
 d. *P. ligularis* (NCP 1133); e. *P. lancetillensis* (NCP 1124); f. *P. coccinea* (NCP 1051);
 g. *P. actinia* (NCP 1003); h. *P. gracillima* (NCP 1097); i. *P. tridactylites* (NCP 1245);
 j. *P. multiflora* (NCP 1142); k. *P. discophora* (NCP 1065); l. *P. cuprea* (NCP 1050);
 m. *P. auriculata* (NCP 1020); n. *P. maliformis* (NCP 1283); o. *P. jatunsachensis* (NCP 1346);
 p. *P. laurifolia* (NCP 1127); q. *P. variolata* (NCP 1264); r. *P. serratifolia* (NCP 1227).



Representative two-lobed leaves of *Passiflora* species from the subgenera *Decaloba* and *Pseudomurucuja*:

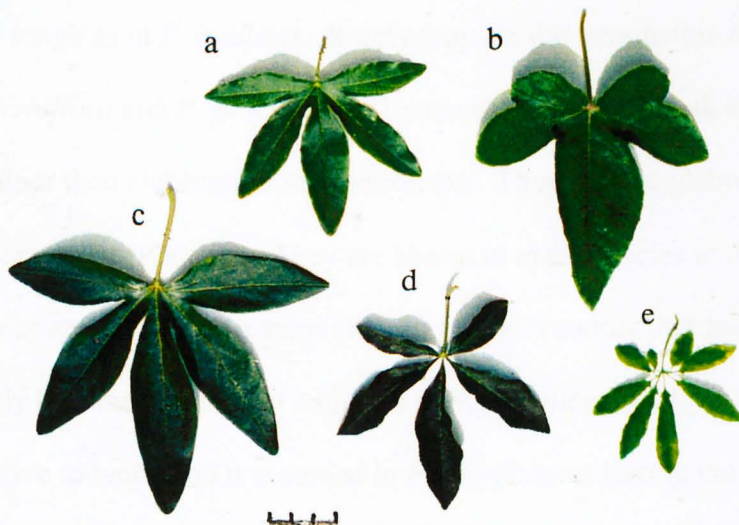
- a. *P. coriacea* (NCP 1037); b. *P. tuberosa* (NCP 1243); c. *P. jorullensis* (NCP 1119);
 d. *P. rovirosae* (NCP 1200); e. *P. colinvauxii* (NCP 1047); f. *P. capsularis* (NCP 1045);
 g. *P. rubra* (NCP 1196); h. *P. talamancensis* (NCP 1286); i. *P. amalocarpa* (NCP 1002);
 j. *P. punctata* (NCP 1178); k. *P. biflora* (Costa Rica) (NCP 1267);
 l. *P. biflora* var. Lamarck (NCP 1024); m. *P. yucatanensis* (NCP 1255); n. *P. misera* (NCP 1150);
 o. *P. perfoliata* (NCP 1180); p. *P. sanguinolenta* (NCP 1213); q. *P. biflora* (Trinidad) (NCP 1026);
 r. and s. *P. cuneata* var. 'Miguel Molinari' (NCP 1044).

Scale bar in cm



Representative three-lobed leaves of *Passiflora* species from the subgenera *Decaloba*, *Passiflora*, *Tacsonia*, *Manicatae* and *Distephana*:

- a. *P. sexflora* (NCP 1214); b. *P. helleri* (NCP 1105); c. *P. lutea* (NCP 1132); d. *P. gracilis* (NCP 1094);
 e. *P. vitifolia* (NCP 1251); f. *P. trisecta* (NCP 1244); g. *P. anfracta* (NCP 1005);
 h. *P. subpurpurea* (NCP 1345); i. *P. tricuspis* (NCP 1229); j. *P. exura* (NCP 1326);
 k. *P. suberosa* (NCP 1208); l. *P. menispermifolia* (NCP 1151); m. *P. gilbertiana* (NCP 1089);
 n. *P. gritensis* (NCP 1387); o. *P. membranacea* (NCP 1301); p. *P. amethystina* (NCP 1022);
 q. *P. cinnabarina* (NCP 1043); r. *P. edulis* (NCP 1069); s. *P. morifolia* (NCP 1148);
 t. *P. holosericea* (NCP 1110, McD 3317); u. *P. giberti* (NCP 1092); v. *P. pilosicorona* (NCP 1185);
 w. *P. xiikzodz* (NCP 1254); x. *P. mooreana* (NCP 1308).



Representative five- to nine-lobed leaves of *Passiflora* species from the subgenera *Passiflora*, *Dysosmia* and *Polyanthea*:

- a. *P. tenuifolia* (NCP 1242); b. *P. foetida* var. *hibiscifolia* (NCP 1087); c. *P. caerulea* (NCP 1034);
 d. *P. cincinnata* (NCP 1059); e. *P. cirrhiflora* (NCP 1329).

Scale bar in cm.

In most species, leaf longevity is considerably less than twelve months, particularly in *P. gracilis*, the 'Annual passion flower' and in species that produce annual stems such as *P. morifolia* (MacDougal, 1994) whose leaves are deciduous after eight to sixteen weeks. In some species, particularly in the subgenera *Distephana*, like *P. glandulosa* and *P. variolata*, and *Astrophea*, like *P. amoena* and *P. candida*, the leaves may remain healthy and functional for over 24 months (Vanderplank, 1996a). In these species the leaves are generally coriaceous, fleshy and glaucous whereas short-lived leaves tend to be thin and membranous.

The leaves illustrated in Plates 4 and 5 are taken from plants held by the National Collection of Passiflora (NCP) and are shown with NCP accession numbers.

3.1.6 Tendril

The tendrils are solitary and arise from the leaf node. They can be very robust and extremely tough as in *P. ligularis*. Rarely they are the termination of an inflorescence as in *P. cirrhiflora* and *P. gracillima*. Occasionally they are weak and used for holding rather than climbing as in *P. murucuja*. They may be glabrous or hirsute as in *P. menispermifolia* (Plate 6a). They are absent in many species in the subgenus *Astrophea* or are reduced to a spine (Killip, 1938). Tendrils that fail to gain purchase may rapidly become flaccid and wither as in *P. multiflora* (Plate 6c). The tendril is very sensitive to touch and is recorded in *P. morifolia* as having the most rapid movement of any climbing plant by completing a revolution of the tendril in 43 minutes (Junker & Reinhold, 1975). Rarely tendrils are branched as in *P. gracillima* and even more unusually they affix themselves to a host tree using adhesive discs as

in *P. discophora* (Plate 6d). Mutant flowering at the distal end of the tendril is recorded in *P. phoenicea* (Plate 6b). In this species one flower per leaf node is normal. The tendril flowers are additional and lack bracts.

3.1.7 Peduncles

In most species peduncles are borne solitarily or in pairs from the leaf axils and are one-flowered (Killip 1938). There are exceptions: *P. multiflora* has many flowers from each axil, *P. racemosa* flowers in long leafless racemes and in *P. cirrhiflora* and a few other species the peduncle has two flowers and terminates in a tendril.

Occasionally the peduncles are borne in pairs on short axillary branches as in *P. biflora*.

3.1.8 Bracts

In the majority of species three bracts are present on the peduncle just below the flower, although in some species they are very soon deciduous. Their size and shape and their position on the peduncle constitute a very important character for the differentiation of subgenera, sections and species (Killip, 1938). Bracts are linear to setaceous and scattered along the peduncle in some species in the subgenera *Murucuja* and *Astropheia*. They are leaf-like in many species especially within the subgenus *Passiflora* (Killip, 1938). In the subgenus *Distephana* they may be vivid red and the margins have many large nectar-bearing glands similar to the petiole and leaf lamina glands as in *P. quadrifaria*.



a. *P. menispermifolia* Kunth, 1817 (NCP 1151). Tendrils are densely hirsute. Coiling is initiated at mid-tendrils; b. *P. phoenicia* Lindley, 1833 (NCP 1175). Flowering is on the distal end of coiling tendrils. Note flower bracts are absent on these blooms; c. *P. multiflora* L., 1753 (NCP 1142). Young tendrils that fail to gain purchase become flaccid and rapidly wither; d. *P. discophora* Jorg. & Law, 1987 (NCP 1065) with palmate tendrils that form attachments using adhesive pads. The tendrils and branches then tension by coiling, thus holding the vine close to its large tree host.



Scale bar in cm.

Ants of several species have been observed feeding on the sweet secretions of the glands and in return protect the developing fruit from insect larval predation (Bentley, 1977). In *P. foetida* and its many varieties the bracts are pinnatisect, bipinnatisect or even tripinnatisect and encapsulate the developing flower bud. After flowering they encapsulate the fertilised ovary. These bracts have numerous glands that ooze a sticky secretion, which shows high protease and acid phosphatase activity similar to that found in the digestive enzymes in the traps of carnivorous plants. Insects attracted to these glands become trapped in the secretion, are digested by the plant and so provide additional amino acids (Radhamani, Sudershana & Krishnan, 1995). When the fruit is fully developed and ripe it changes colour from green to bright yellow or red and the bracts become deciduous and fall away to allow access to the fruit by birds and mammals. In some species, especially in subgenus *Decaloba*, section *Hahniopathanthus*, only two very foliaceous, often brightly coloured bracts are present as in *P. membranacea* (Killip, 1938).

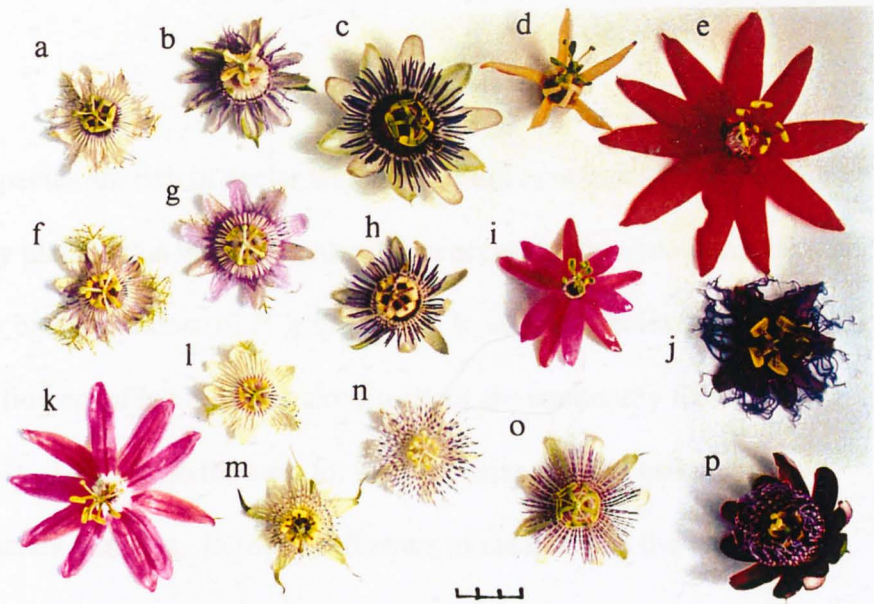
3.1.9 Flowers

Flowers of many species, including all the species in the subgenus *Decaloba*, section *Miserae*, and the species in subgenus *Distephana*, such as *P. glandulosa* and *P. coccinea* ssp. *Cacao*, and in subgenus *Dysosmia*, *P. foetida*, which are endemic to the lowland forests of South America, are held vertically for insect pollination but remain open for less than six hours, from dawn to approximately midday. This short period when they are available for pollination is necessitated by the need of the flower to protect the fertile stigmas from heavy rainfall during thunderstorms, which would otherwise wash off the unestablished pollen grains. Heavy afternoon rain is a regular

occurrence throughout the wet season and often in the dry season in these lowland forests. Flowers of the majority of species, including the large showy species in the subgenera *Tacsonia* and *Passiflora*, such as *P. mollissima* and *P. caerulea* (Plate 7c, top), remain open for approximately twelve hours, and longer during cooler periods, especially when under cultivation. The flowers of a few species endemic to Australasia stay open for a second or third day. In *P. aurantia* the flowers are yellow or pale orange on the first day, orange on the second day and deep orange on the third day. True night flowering is recorded in *P. trisecta* and *P. mucronata*, which are pollinated by small nectar-feeding bats, and in *P. penduliflora*, which is moth-pollinated.

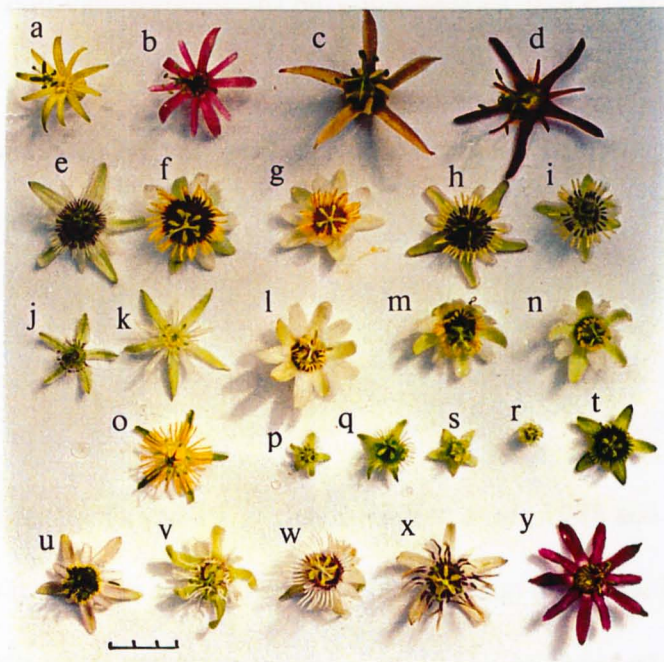
Flowers can be large, fleshy and over 125mm in diameter, as in *P. quadrangularis*, or small and fragile and less than 12mm in diameter as in *P. allantophylla*. They may be richly multicoloured and highly fragrant such as *P. alata*, inconspicuous greenish white like *P. apetala* or monocoloured and odourless like *P. coccinea*.

Open flowers may be presented with a horizontal attitude or angled slightly above or below the horizontal. They are occasionally held vertically as in *P. misera*, *P. coccinea*, *P. foetida* and *P. tuberosa* or may be very pendant like *P. tarminiana*, *P. penduliflora* and *P. yucatanensis*. These variations are probably due to adaptations to climatic variations and specific specialist pollinating animals (Vanderplank, unpublished).



a. *P. foetida* var. *hibiscifolia* (NCP 1087); b. *P. incarnata* (NCP 1113); c. *P. caerulea* (NCP 1034); d. *P. aurantia* (NCP 1008); e. *P. vitifolia* (NCP 1251); f. *P. foetida* var. *hirsutissima* (NCP 1078); g. *P. urbaniana* (NCP 1248); h. *P. mooreana* (NCP 1308); i. *P. reflexiflora* (NCP 1369); j. *P. quadrangularis* (NCP 1368); k. *P. palmeri* var. *sublanceolata* (NCP 1287); l. *P. foetida* var. *galapagensis* (NCP 1388); m. *P. giberti* (NCP 1092); n. *P. naviculata* (NCP 116); o. *P. sprucei* (NCP 1376); p. *P. alata* (NCP 1037).

P. aurantia is included in both flower sets to demonstrate comparative sizes.



a. *P. citrina* (NCP 1058); b. *P. sanguinolenta* (NCP 1213); c. *P. aurantia* (NCP 1008); d. *P. cinnabarina* (NCP 1043); e. *P. morifolia* (NCP 1148); f. *P. holosericea* (NCP 1106); g. *P. holosericea* (NCP 1109); h. *P. punctata* (NCP 1178); i. *P. colinvauxii* (NCP 1047); j. *P. gracilis* (NCP 1094); k. *P. capsularis* (NCP 1045); l. *P. yucatanensis* (NCP 1255); m. *P. biflora* (NCP 1026); n. *P. biflora* (NCP 1027); o. *P. gilbertiana* (NCP 1089); p. *P. suberosa* (NCP 1208); q. *P. juliana* (NCP 1116); r. *P. suberosa* (NCP 1207); s. *P. obtusifolia* (NCP 1171); t. *P. coriacea* (NCP 1037); u. *P. cuneata* var. 'Miguel Molinari' (NCP 1044); v. *P. rubra* (NCP 1196); w. *P. quinquangularis* (NCP 1189); x. *P. karwinskii* (NCP 1120); y. *P. tacsonioides* (NCP 1321).

Representative flowers of *Passiflora* species from the subgenera *Decaloba*, *Pseudomurucuja*, *Distephana*, *Tacsonioides*, *Passiflora* and *Dysosmia*:

Flowers of most species are rich in nectar and have a faint or sometimes strong odour that is usually very pleasant, as in *P. colinvauxii*, but occasionally obnoxious, like the sulphur dioxide or bad eggs odour of *P. gilbertiana*. In certain species in section *Pseudodysosmia*, flowers of lower nodes along a shoot are commonly female-sterile (MacDougal, 1994). This is also the case for many species that are glasshouse cultivated in temperate climates. In the first flowers of each season the ovary is discoloured, yellowish or pinkish, and cannot be fertilised. The stamens of these early flowers may also appear sterile and fail to produce ripe pollen. This same scenario is repeated with species like *P. colinvauxii* that are still flowering after the autumn equinox as the temperature and light levels fall. At first sight it would appear that this is solely due to physical cultivation conditions but some species, like *P. auriculata*, that flower during the long daylight hours at the time of the summer solstice, when temperature and light conditions are very settled, also show this behaviour (Vanderplank, unpublished).

3.1.10 Hypanthium

The hypanthium (de Wilde, 1971a and 1972, Holm-Nielsen *et al.*, 1988 and MacDougal, 1994), also referred to as the flower-tube, floral-cup (Masters, 1871, Brizicky, 1961 and Tillett, 1988) and calyx tube (Killip, 1938, Jorgensen *et al.*, 1984 and Vanderplank, 1991 and 1996a), is quite variable in structure and appearance. It is often bowl-shaped or cup-shaped, particularly in the subgenus *Decaloba*. It is campanulate in the subgenera *Murucuja* and *Distephana*, and long-cylindrical in the subgenus *Tacsonia* and its allies (Killip, 1938). It is often green or greenish in small

flowered species and brightly coloured in the larger flowered species (mauve, pink, yellow, red, orange or white).

3.1.11 Sepals

There are always five sepals, all approximately the same size and shape, attached to the upper edge of the hypanthium. They are usually brightly coloured, violet, blue, mauve, purple, red, pink, orange, yellow, green or white on the upper surface and green on the undersurface. In the subgenera *Passiflora* and *Tacsonia*, and to a much lesser extent in other subgenera, they are dorsally keeled with a terminal awn which may be up to 20mm long as in *P. amethystina*. The margins of the sepals of *P. variolata* bear five to seven pairs of nectariferous glands that are visited by *Ectatomma tuberculatum* ants that protect the flower and ovary from herbivore attack in Peru (Moffett, 1999).

3.1.12 Petals

Flowers of most species have five petals, all of the same shape and size. They are very delicate membranous appendages attached to the upper edge of the hypanthium above the sepals (MacDougal, 1994). They are usually the same colour as the sepals on both the upper and underside surfaces. A few species, such as *P. suberosa*. and *P. apetala*, lack petals.

3.1.13 Corona

The corona is the hallmark of the genus *Passiflora*, and although present in varying degrees in all genera of this family, it is most highly developed and differentiated in this genus (MacDougal, 1994). The corona consists of outgrowths from the hypanthium consisting of various series of threads, filaments, membranes or rings and is regarded as being of appendicular origin (Friedel, 1914, Puri, 1947 and 1948, and MacDougal, 1994). The threads or filaments may be in one, two, three or many series or ranks. They may be very decorative and brightly coloured, usually banded, and may act as a visual signal to birds and bats that nectar is on offer and thereby encourage widespread cross-pollination of the flowers. In most species the outer series or the outer two series are the longest and may be longer than the petals or less than half their length. The third and subsequent series are usually very short thread-like or even tubercle-like processes. In the subgenus *Murucuja* the corona is a membranous tube surrounding the androgynophore as in *P. tulae*. In the subgenus *Distephana* the first and second series are filaments for all or most of their length and the innermost series is a membranous tube surrounding the androgynophore as in *P. vitifolia* and *P. coccinea*. This serves to protect the nectar chamber from heavy rainfall that may dilute or contaminate the nectar (Vanderplank, unpublished).

3.1.14 Operculum

In the subgenus *Decaloba* the operculum is a pilate or folded membrane with its margin incurved towards the androgynophore. It is absent in the subgenus *Astephia*. In many species it is inclined inward and the margin is erect. In the subgenus *Passiflora* there is considerable diversity, from a row of free filaments to a fringe or entire membrane (Killip, 1938).

3.1.15 Nectary

Under the operculum as a circular trough is the floral nectary. This is usually a raised annular ridge within the nectar trough (MacDougal, 1994). It is lacking in many species such as *P glandulosa*.

3.1.16 Limen

Between the nectary and the base of the androgynophore, the limen consists of a thin membranous ring or cup-like structure. The limen may be white, cream or greenish, spotted and streaked with red or purple, or uniformly dark purple as in *P. morifolia* (MacDougal, 1994).

3.1.17 Androgynophore

The androgynophore is composed of connate staminal filaments, themselves adnate to an elongate gynophore. It is straight in almost all species except four carpellate species, including *P. lobata*, and a few others, including *P. discophora* and *P. ovalis*.

3.1.18 Androecium

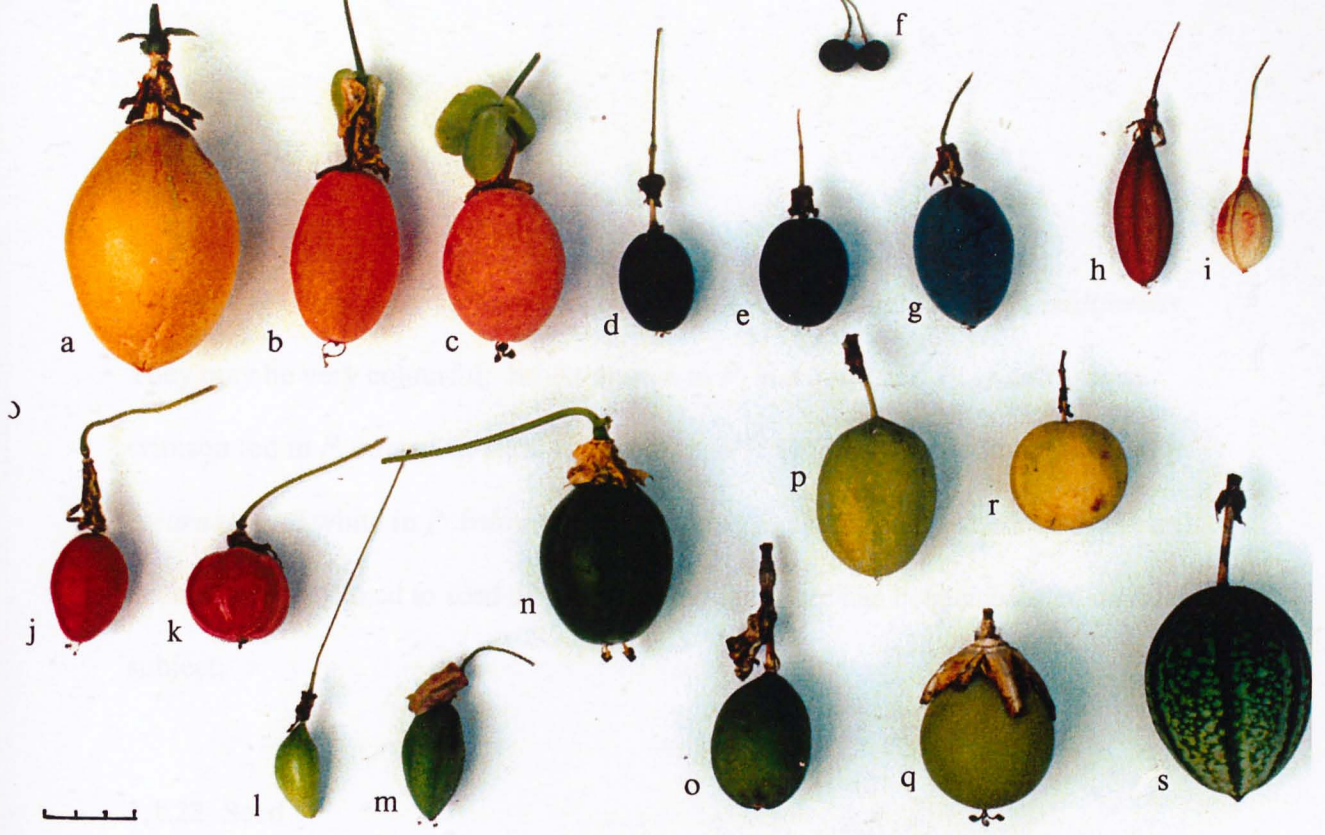
The androecium is composed of five stamens, generally arranged in radial symmetry but asymmetric in a few species which seem to be bird or bat-pollinated (*P. trisecta*, *P. dioscoreifolia* and *P. lobata*). The anthers are presented on the lower side of the column, always facing the outermost sepal (MacDougal, 1994).

3.1.19 Gynoecium

The ovary has one locule and parietal placentation (Adanson, 1763, Cronquist, 1981 and MacDougal, 1994). There are usually three styles but occasionally four as in *P. tetrandra* and *P. lobata*. The styles are free to the base, very slender and green, yellow-green or pinkish green in small flowered species, especially in the subgenus *Decaloba*. In the larger flowered species they may be speckled reddish or purple, or a single bright colour, for example red in *P. vitifolia*. The styles move from an erect position in the bud and opening flower to a horizontal position while the flower is most widely open, and then downwards to a level at or below the anthers, and finally back to their original vertical position as the flower closes (Linnaeus, 1745 and Morren, 1842). The stigma is usually pale green, olive green or yellowish green.

3.1.20 Fruit

Fruit of *Passiflora* are usually pendular or semi-pendular but held vertically in a few species as in *P. quadrifaria*. They may be small and berry-like, usually deep purple or black, occasionally red when ripe, often with only a few arillate seeds. In extreme conditions fruit may be one-seeded as in *P. suberosa* (MacDougal, 1994). In contrast, the most seed-laden fruit are those of *P. herbertiana*, which produces comparatively small seed in fruit the size of a hen's egg. On average 1,000 seed per fruit are recorded but as many as 1,342 seed have been found in a single fruit produced by a vine in cultivation. Individual fruit can be long, tapering and capsulate, circular or hexagonal in cross-section, and green, red, mauve or purple when ripe (Plate 8). The fruit often burst at their distal end to disperse their seed singly, as in *P. gracilis*, or in groups or clusters as in *P. capsularis*. Larger fruit may be the size of a small hen's egg or as large as a small melon, spherical or oval, sometimes banana-shaped like *P. mollissima*, and triangular like *P. truxillensis* or square like *P. quadrangularis* in cross-section. The pericarp may be soft as in *P. mixta*, fragile and brittle as in *P. foetida*, or very hard and brittle as in *P. ligularis*, sometimes with a thick and fleshy mesocarp like *P. quadrangularis*, which is prepared and eaten as a vegetable in South America. These large fruit are usually brightly coloured, yellow, red, pink, purple or mottled green like *P. vitifolia*. In some fruit the endocarp wall is suspended by threads of the mesocarp tissue, as in *P. subpeltata* (Tillett, unpublished), *P. giberti*, *P. naviculata* and *P. pallens* (Vanderplank, unpublished).



Representative mature fruit and halved fruit showing arils and seed of *Passiflora* species from the subgenera *Decaloba*, *Distephana*, *Dysosmia* and *Passiflora*.

- a. *P. alata* NCP 1037; b. *P. tenuifolia* NCP 1242; c. *P. caerulea* NCP 1034; d. *P. yucatanensis* NCP 1255
 e. *P. biflora* NCP 1026; f. *P. suberosa* NCP 1208; g. *P. morifolia* NCP 1148;
 h. *P. capsularis* NCP 1045; i. *P. rubra* NCP 1196; j. *P. palmeri* var. *sublanceolata* NCP 1287;
 k. *P. foetida* var. *hirsutissima* NCP 1078; l. *P. colinvauxii* NCP 1047; m. *P. gracilis* NCP 1094;
 n. *P. incarnata* NCP 1113; o. *P. manicata* NCP 1258; p. *P. subpeltata* NCP 1223;
 q. *P. maliformis* NCP 1283; r. *P. naviculata* NCP 1161; s. *P. vitifolia* NCP 1251.



Scale bar in cm

3.1.21 Arils

The arils are often very aromatic, sweet and juicy as in *P. edulis* and *P. maliformis*. They may be very colourful: bright orange in *P. morifolia* and *P. gracilis*, deep crimson red in *P. caerulea*, clear pale yellow in *P. biflora*, clear without pigment in *P. incarnata* and white in *P. rubra* and *P. capsularis*. The colour and odour of the arils is undoubtedly linked to seed dispersal but no literature has been published on this subject.

3.1.22 Seed

The seed are usually laterally compressed, rectangular or oblong to suborbicular in general outline and occasionally semi-spherical as in *P. discophora* or almost ovoid as in *P. truxillensis*. Most have a chalazal beak but one notable exception is *P. lancetillensis* (sp. nov. ined., Meerman). The seed coat or testa (Corner, 1976 and Lubbock, 1892) or sarcotosta (MacDougal, 1994) is two or three cells thick. The external sculpturing on the testa is caused by the sculpturing of the lower surface cells or tegman (Corner, 1976) or sclerotesta (MacDougal, 1994). In Lubbock (1892) the testa includes the cells of the tegman or sclerotesta. The size and sculpturing of the testa presents many useful taxonomic characters in species of *Passiflora* (MacDougal, 1994). In section *Pseudodyosmia* these features are distinctive enough to be diagnostic for almost all species (MacDougal, 1994). General correlation between testal morphology and fruit type has been suggested. Highly compressed and finely punctate-foveolate seed are found in species that have green fruit and clear arils. Slightly compressed and foveate to coarsely reticulate seed are found in species with

orange arils and purple fruit. Large, slightly compressed, very coarsely foveate-areolate seed occur in the orange-arilled red-fruited species (MacDougal, 1994). The depressions and foveae in the testa project downward into the abundant endosperm and give rise to a moderately ruminate endosperm that has been called 'the *Passiflora* type of rumination' (MacDougal, 1994). E. P. Killip (1938) recorded a correlation between seeds with a series of transverse ridges and grooves and plants with glandless petioles and between seeds that were reticulated or pitted and species with generally glanduliferous petioles. However, this does not hold strictly true for species in the subgenus *Decaloba*, sections *Hahniopathanthus* and *Decaloba*, or for those in the subgenera *Passiflora*, *Tacsonia* and *Astrophea*.

3.2 Flowering and pollination

3.2.1 Flowering

In most *Passiflora* species only one or two flower buds develop from each leaf node on separate peduncles, although there are some exceptions, including *P. sexflora*, *P. multiflora* and *P. rovirosae*. As fertile shoots develop, these buds mature and flower in succession down the flowering branch, usually at a rate of one or two flowers per node every one to three days, depending on climatic conditions. This time scale may be extended greatly for plants in cultivation subjected to low temperatures and poor light conditions during winter months. The flowering duration of every species is determined by the number of flower buds produced on a fertile stem and the time between opening flowers on each node. Flowering racemes of *P. coriacea* can have in excess of 230 flowers and stems of *P. vitifolia* may have over 250 flowering nodes

during the year (Vanderplank, 1996a) but flowering on a single stem is arrested if the stem becomes laden with fruit. This process is virtually continuous in some species, especially those found in the lowland tropics such as *P. vitifolia*, *P. glandulosa* and *P. coccinea*, which flower throughout the year. In many species, particularly those found in the subtropics and those that are subjected to prolonged wet and dry seasons, flowering is seasonal and may last only a few weeks or several months as in *P. morifolia*, *P. adenopoda* and *P. cuprea*. Those that are endemic to temperate regions are very herbaceous in habit and regrow from fleshy roots annually, as do *P. lutea* and *P. incanata*. Flowering is spasmodic in some species like *P. menispermifolia* and *P. nephroides* with many, often short, flowering periods. Under glasshouse cultivation conditions natural flowering times and flowering duration are usually very different from those found in the wild. In four species within the section *Decaloba*, *P. ferruginea*, *P. rufa* (sp. nov. ined., Feuillet), *P. jatunsachensis* and particularly *P. auriculata*, the flower buds become fully developed in succession down fertile branches but remain as buds until the majority have reached maturity, then over a period of 2 or 3 days all the flowers on the entire plant simultaneously open, making a spectacular display known as 'orgy flowering' or 'mass flowering', which is common in other genera in South America (S. Tillett, unpublished). The advantages of this flowering strategy are not clear but in Venezuela many plants of *P. auriculata* in the same vicinity have been recorded as flowering on the same few days (S. Tillett, unpublished). This mass flowering may cause frenzied insect feeding ensuring better cross pollination (*P. auriculata* is not self fertile) and the resulting fruit maturing simultaneously on many vines may be an evolutionarily advanced strategy for greater seed survival and distribution. Alternatively this may be another strategy to cope with the severe predation from larvae of numerous *Heliconiinae* species including *Agraulis*

vanillae, *Dryas julia*, *Heliconius numata*, *H. hecale*, *H. cydno*, *H. erato*, *H. sara* and *H. pachinus*.

3.2.2 Pollination

All *Passiflora* species are ideally cross-pollinated by animal visitation but a few species, such as *P. caerulea*, *P. capsularis* and *P. morifolia*, have evolved self-pollination in the absence of animal pollinators.

3.2.2.1 Self-pollination

The mechanism for self-pollination of autocompatible species has been documented by Linnaeus (1745), Medikus (1790), Sprengel (1793), Morren (1842) and MacDougal (1994). After a time period that varies from species to species, the styles, which have moved from a vertical position within the bud to a horizontal position in the fully open flower, start moving downwards towards the base of the androgynophore. This positions the stigmas at or below that of the stamens, which have now become very loosely pendant on the filaments. This ensures that any shaking movements of the flowers will dust pollen from the stamens onto the stigma. This may be caused by a late visit from a nectar or pollen feeding animal or by a larger mammal or reptile brushing against the vine or its support, or by a perching bird. Even the movement caused by a gentle breeze is sufficient for this purpose. This has been observed in *P. gracilis* and *P. morifolia* under glasshouse cultivation conditions when insect pollination was not possible. The resulting fruit from self-

pollination were of good size and laden with many healthy viable seed. Finally the styles return to their original vertical position as the flower closes.

In *P. foetida* in Argentina anthesis occurs between 6am and 11am, varying with local temperature and latitude (Garcia and Hoc, 1998b). Under glasshouse cultivation during average seasonal temperatures for June and July in the UK, anthesis occurs between dawn and 9.30am in many species including *P. foetida* var. *hirsuta*, *P. foetida* var. *hirsutissima*, *P. foetida* var. *hibiscifolia*, *P. biflora* and *P. biflora* var. *lamark*.

The majority of *Passiflora* species are self-incompatible and need cross pollination by a separate genotype plant. Self-incompatibility in *P. edulis* f. *flavicarpa* is controlled by two loci, the *s*-gene and another (do Rogo, Bruckner, da Silva, Finger, de Siqueira, and Fernandes, 1999).

In studies of *P. edulis* f. *flavicarpa* at the College of Agriculture of Jaboticabal, Sao Paulo, Brazil, it was found that there are three types of flowers according to the curvature of the styles: totally curved, partly curved and upright styled. Those with upright styles produced fertile pollen but did not set fruit due to the attitude of their styles (Morton, 1987). The precise physical and chemical mechanisms that prevent self-pollination in most species of *Passiflora* have not been investigated at this time.

3.2.2.2 Wind pollination

Wind pollination is ineffective because of the heaviness and stickiness of the pollen, which is instead well suited for transportation from flower to flower, caught on insect hairs, animal fur or bird feathers.

3.2.2.3 Animal pollination

A wide variety of animals have been identified as pollinators or possible pollinators of various *Passiflora* species but the downward movement of the styles in the ageing flower is important. It aids pollination by reducing the distance between the stigma and the corona platform where a potential pollinator would need to venture to be able to reach the nectaries at the base of the androgynophore. This ensures that any pollen from a neighbouring plant that was caught on the back of a late visitor would be transferred to the still receptive stigma. The stigma remains receptive until styles start to move upwards to their original vertical position (MacDougal, 1994).

3.2.2.4 Insect pollination

Extensive studies have been conducted on the entomophily of *P. edulis* and *P. edulis* f. *flavicarpa* (Nishida, 1954, 1963, Akamine & Giralami, 1959 and Cox, 1957). Many insects have been positively identified as being important or less important pollinating species in commercial passionfruit vineyards. The two most important pollinating insects are the honey bee, *Apis mellifera*, and the larger carpenter bee *Xylocopa sonorina*. Three other insect species may also be effective pollinators in commercial

crops but to a much lesser extent: the hover flies *Volucella obesa* and *Eristalis arvorum* and the oriental blow-fly *Chrysomya megacephala*. In Florida, USA, the carpenter bees *Xylocopa megaxylocopa frontatis* and *Xylocopa neoxylocopa* are considered to be the most effective pollinating insects (Morton, 1987). In Hawaii Nishida (1954) recorded many insects visiting passionflower blooms which appeared to do very little to assist their pollination including beetles (Coleoptera), thrips (Thysanoptera), grasshoppers (Orthoptera), two species of wasps (Hymenoptera) and eight species of flies (Diptera). In Argentina *P. caerulea* flowers are primarily pollinated by four species of bees (Hymenoptera): *Xylocopa augusti*, *Xylocopa frontalis*, *Xylocopa artifex* and *Xylocopa nigrocincta* (Garcia & Hoc, 1998a).

The size of the blooms of individual *Passiflora* species, particularly the distance between the corona platform and the anthers and stigmas, dictates the size of a successful pollinator. Many small insects, including wasps, beetles, flies and even butterflies, must be regarded as nectar or pollen thieves only (Christensen, 1995). In Ecuador and Colombia the only insect large enough to pollinate *P. bahinifolia* (syn. *P. alnifolia*) is a species of Thygater bee (*Anthophoridae*) (Christensen 1995, 1998).

In El Salvador three species of bumble bees (*Bombus*), five species of parasitic wasps (*Trigonia*) and four species of social bees (*Xylocopa*) are recorded as feeding on the nectar of passionflower blooms and as being effective pollinators (Berry, 1957). In Brazil two genera of bees are recognised as pollinating insects, *Epicharis* and *Xylocopa* (Hurd, 1955). In Brazil and Venezuela the flag bug and the American leaf-footed bug (Coreidae) have often been observed visiting passionflowers and may be pollinators but are more likely to be nectar thieves (Molinari, unpublished).

In Mexico some species of small wasps (Hymenoptera) are thought to be the primary pollinating insects of smaller flowered species like *P. suberosa* (MacDougal, 1994). In French Guyana a very large bee, *Ptilotopus americanus*, was observed visiting the flowers of *P. coccinea* ssp. *tortue* (ssp. nov. ined.) and *P. glandulosa* before midday (Vanderplank, unpublished). Its large size caused its upper thorax and head to become laden with pollen as it forced its way between the anthers, stigma and corona filament platform to reach the abundant nectar provided at the base of the corona tube. Flowers of both these species are traditionally considered to be hummingbird pollinated (Gentry, 1981) because they are bright red (the colour most associated with bird pollination) and because their close relative *P. vitifolia* is indisputably confirmed as being hummingbird pollinated (Skutch, 1964 and Snow, 1982). However the open flowers of *P. coccinea* ssp. *tortue* (ssp. nov. ined.) and *P. glandulosa* are presented vertically on strong peduncles, providing a horizontal landing platform for large insects like *Bombus* (Plate 9b). The horizontally held petals and sepals assist in creating a larger and more conspicuous landing platform. The distance between the corona platform and the underside of the anthers/stigmas is approx 10-12mm and the anthers/stigmas are held outstretched horizontally covering the corona platform, creating a low roof above the entrance to the nectar chamber, which would have to be negotiated by any nectar feeder/pollinator visitor (Vanderplank, unpublished). The fully open flowers of *P. vitifolia* and *P. manicata*, however, which are both hummingbird pollinated (Skutch, 1964, Snow, 1982, Snow & Gross, 1980, Escobar, 1985 and Christensen, 1998), are presented at an angle of approximately 45° to the vertical and the petals and sepals reflex to become almost parallel to the peduncle. (The *P. coccinea* shown in the Christensen study is *P. vitifolia*.)



a



b

a. *P. reflexiflora* Cav., 1799 (NCP 1348). Flowers are presented at 30° or more above the horizontal corresponding to the direction of the peduncle. This is the most convenient orientation for hummingbird visitation. The open throat of the hypanthium provides easy access to the nectarines and the distance between the rim of the hypanthium and the androecium and gynaecium is critical to avial pollination. After pollination the flowers are re-orientated through 90° into an inverted position to protect the developing fruit from adverse weather conditions; b. *P. coccinea* subsp. *brownsberg* subsp. nov. ined. presents its flowers in a vertical orientation, providing a convenient landing stage for large insects. The corona filaments protecting the throat of the hypanthium delay visiting nectar feeders. This ensures prolonged contact between their upper thorax and the androecium and gynaecium region of the flower, increasing the chances of successful pollination. The distance between the rim of the hypanthium and the androecium and gynaecium is critical to large insect pollination. The fertilised ovary and developing fruit remain in a vertical position and are protected by large folious bracts that will encase them within a few hours of pollination.

The above photographs of *P. reflexiflora* and *P. coccinea* show pendular shoots with their distal parts towards the base of each photograph.

This substantially reduces the size of the corona platform making it difficult for an insect to land and gain purchase. The outer rank of corona filaments in *P. vitifolia* also helps to act as a barrier to visiting insects (Vanderplank, unpublished). The distance between the anthers/stigma and the corona platform is more than twice as great in *P. vitifolia* (28mm) and *P. manicata* (23mm) as in *P. coccinea* subsp. *Tortue* and *P. glandulosa*. The anthers/stigma are held in a more vertical position thereby creating a higher, smaller roof above the entrance to the nectar chamber.

Hummingbirds are forced close to the centre of the flower alongside the androgynophore to gain access to the nectar chamber, inadvertently pollinating the flower. The flowers of these species are adapted for hummingbird pollination and discourage insect pollination. The reflexed state of the petals and sepals allows hummingbirds to hover close to the flower while collecting nectar without any danger of wing contact, as in *P. reflexiflora* (Plate 9). The angle of the flower, orientated at 45°, ensures that the bird has good visibility and ease of manoeuvrability. Also, the distance between the anthers/stigma and the corona platform corresponds to the head and beak size of these small birds. In *P. coccinea* ssp. *tortue* (ssp. nov. ined.) and *P. glandulosa*, however, all these factors are reversed. The nectar reward is made more accessible to a large insect and bird pollination is discouraged. The horizontal sepals and petals would cause wing damage, the vertical flowers impair visibility when hovering and make manoeuvring more difficult, and the hummingbird would have to risk eye damage to get its head through the anther/stigma roof to reach the nectar chamber at the base of the hypanthium (Vanderplank, unpublished).

In Argentina *P. foetida* is primarily pollinated by a member of Hymenoptera, *Ptiloglossa tarsata* (Colletidae). The flowers are also visited by an *Augochlorella*

species (Halictidae), which collects pollen without touching the stigmas and is considered to be a pollen thief (Garcia & Hoc, 1998a).

In the UK under glasshouse cultivation many insect species have been observed visiting a large number of passionflowers. These include Hymenoptera, bumble bees (*Bombus*), cuckoo bees (*Psithyrus*), honey bees (*Apis mellifera*), leaf cutter bees (*Megachile*), the common wasp (*Vespula vulgaris*), social wasps (Vespidae), ants (Formicidae), true flies (Diptera) and hoverflies (Syrphidae) (Vanderplank, unpublished). Plants visited include species from the subgenera *Decaloba*, *Distephana*, *Dysosmia*, *Manicata*, *Tacsonia* and *Passiflora*. The precise effectiveness of those insects as pollinators is not known but the fact that insect pollination is successful under these artificial conditions is verified by the successful pollination of several species that are not self fertile. These include *P. colinvauxii* and *P. adenopoda*, which produced seed-laden fruit at the end of the 1998 summer without hand pollination. The precise pollinator species for these taxa is still unconfirmed (Vanderplank, unpublished).

During warmer summer conditions in the UK the leaf cutter bees *Megachile* are active and are the only insects that are able to feed on the nectar from passionflowers of the subgenus *Tacsonia* in cultivation. These species have a very long hypanthium (calyx tube) that may be over 100mm long, as in *P. mixta* and *P. tarminiana*. Being unable to feed on the nectar at the base of the hypanthium in the conventional way (from the opening at the apex of the tube) they cut one or more small holes at the base of the hypanthium just above the bowl, giving them access to all the available nectar. These holes generally cause the flower to collapse (Vanderplank, unpublished). This

activity does not generally assist in the pollination of the flower although the inexperienced leaf cutter bee will often visit the top of the tube in an attempt to reach the nectar and must occasionally assist pollination. *P. cumbalensis* and *P. mixta* have jointed bracts surrounding the base of the hypanthium to prevent these nectar raids in the wild (Escobar, 1989a) but these bracts are ineffective against the European leaf cutter bee when in cultivation (Vanderplank, unpublished).

P. allantophyla and several similar species with few yellow tipped corona filaments are possibly pollinated by small beetles that are attracted to the flowers from a distance by their scent and from nearby by the visual signal. On reaching the flower the beetles search for their nectar reward in the corona filaments and their backs and heads carry pollen from flower to flower and deposit it (Alastair Culham, unpublished).

P. penduliflora is a night flowering species with green flowers 4.5-5mm in diameter presented on long (80-100mm), fragile, pendular peduncles. It is thought to be pollinated by a hovering hawkmoth (Sphingidae). In all other species of *Passiflora* with pendular flowers the operculum acts as a dam preventing the nectar from leaking from the nectar chamber. *P. penduliflora* lacks an operculum and limen and for this reason was placed in the monospecies subgenus *Astephia* by E. P. Killip in 1938. The nectar is held in the nectar chamber by surface tension (Vanderplank, unpublished). This is assisted by the deeply undulating inner hypanthium surface, which provides five narrow fissures as part of this chamber.

Koschnitzke & Sazima (1997) suggest that in Brazil the flowers of *P. capsularis* are nocturnal and are pollinated by an unidentified moth. I have not found nocturnal flowering in this species or in closely related species.

The Longwing or Passionflower Butterflies from the subfamily *Heliconiinae* are closely associated with many *Passiflora* species and have been observed landing on their flowers. Benson *et al.* (1975) suggest that the flowers of two species are pollinated by these insects but this hypothesis is discounted by MacDougal (1994) who points out that the two *Passiflora* species in question are the main food plant for the larvae of the *Heliconius* butterflies and that these two *Passiflora* are recorded as being pollinated by hummingbirds. In captivity the butterflies *Idea leuconoe*, *Parthenos sylvia*, *Heliconius melpomere* (the postman butterfly) and *Heliconius charitoni* (the zebra butterfly) have been observed taking nectar from the flowers of *P. biflora*, and both the flowers and leaf petiole nectaries of *P. vitifolia* (John Calvert, unpublished). It therefore seems reasonable to assume that some pollination may be executed by various butterfly species.

3.2.2.5 Pollination by mammals

A small monkey, *Samiri oerstedii*, that feeds on the large flowers of *P. quadrangularis* in Costa Rica is believed to be partly responsible for its pollination (Happel, 1983 and MacDougal, 1994).

3.2.2.6 Bat pollination

Several species of *Passiflora* are night flowering with zygomorphic flowers and are recorded as being bat pollinated (chiropterophily). *P. mucronata* is pollinated by the bat *Glossophaga soricina* and another species of *Phyllostomid* bat (Sazima & Sazima, 1978). *P. ovalis* is also bat pollinated (Buzato & Franco, 1992). Other night flowering species with zygomorphic flowers are unconfirmed as being bat pollinated. *P. trisecta* has large robust white flowers with abundant nectar which are conspicuous in moonlight. Christensen (1998) suggests that *P. discophora*, *P. micropetala*, *P. dioscoreifolia* and *P. lobata* are likely candidates for the same reasons. Stephen Tillet (unpublished) suggests that pollination of *P. fieldiana* may be assisted by fruit bats, which have been observed interacting with this large vine which may attain a height of over 30m. The flowers are large with an open bowl-like hypanthium over 50mm in diameter, which makes the abundant nectar accessible to an animal with a comparatively short tongue like a bat. Although this is not a true night flowering species the flowers remain open into the late evening when fruit bats are active. The fruits of this species are known to be eaten by bats and seed from other unidentified species of *Passiflora* have been found in the stomach of various fruit bats (Jesus Molinari, University of Merida, Venezuela, unpublished).

3.2.2.7 Hummingbird pollination

Bird pollination (ornithophily) by hummingbirds is recorded in several subgenera, including *Tacsonia*, *Tacsonioides*, *Distephana*, *Astrophea*, *Dysosmia* and *Decaloba* (Lindman, 1906, Janzen, 1968, Escobar, 1980, 1985 & 1989a, Snow & Snow, 1980,

Feinsinger, 1983, Christensen, 1998, MacDougal, 1994, Fjeldsa & Krabbe, 1990 and Skutch, 1964). *Passiflora* species pollinated by hummingbirds are generally characterised by an elongated androgynophore and hypanthium, a poorly developed or small corona and odourless white, red, purple or pink flowers (Escobar, 1980 and MacDougal, 1994). The high mountain species of subgenus *Tacsonia* like *P. tarminiana* and *P. mixta* are found wild at altitudes up to 4,200m. They have a particularly long hypanthium that prohibits all but the sword-billed hummingbird, *Ensifera ensifera*, from feeding on its nectar and thereby ensures cross-pollination over a wide area (Escobar, 1980).

The activity of social bees like *Apis mellifera* is greatly reduced in the high altitude cooler conditions of the Andes mountains and although the solitary bees *Megachile* are better suited to cooler conditions they are not active at these elevations. It is proposed that the evolutionary pressures on these birds and *Passiflora* have accelerated this particular flower design (MacDougal, 1994) not only to provide nectar as a reward for the pollinating hummingbird but also to make it difficult for nectar thieves to gain access to the nectar via the extended hypanthium. The pendular orientation of the flower also assists in this cause.

All *Passiflora* species which are truly hummingbird pollinated flower throughout the year with only brief interludes (Escobar, 1980). The same plant would be visited daily and any open flowers visited two or three times a day. The flowers of many species from the subgenus *Tacsonia* stay open a second and third day during cooler conditions and would continue to be visited until the nectar supply was exhausted. This is referred to as trap-lining pollination (Newstrom *et al.*, 1994). Newstrom also

suggests that some large bees (*Bombus*), *Xylocopa centris* and hawkmoths, Sphingidae species, may do the same.

In Jamaica the Western Streamertail Hummingbird or Doctor Bird, *Trochilus polytmus*, has been observed visiting the flowers of *P. perfoliata* from midday onwards. The Red-billed Hummingbird is similarly thought to be responsible for the pollination of *P. oblongata* (Kay, 1999).

In Costa Rica the Longtailed Hermit, *Phaethornis superciliosus*, is the pollinator of *P. vitifolia* (Skutch, 1964, Snow & Snow, 1980, Gentry, 1981 and Janzen, 1968). In Peru, the White-bearded Hermit, *Phaethornis hispidus*, and the Reddish Hermit, *Phaethornis ruber*, are the primary pollinators of *P. coccinea* and *P. vitifolia* (Christensen, 1998).

In Colombia *P. ampullacea* is pollinated by the Shorter-billed Hummingbird (Escobar, 1980) and *P. manicata* is pollinated by an unknown hummingbird (Escobar, 1985), as are *P. longiracemosa* (Snow & Snow, 1980), *P. sanguinolenta* (MacDougal, 1994) and *P. amoena* (Escobar, 1994).

3.2.2.8 Flower presentation

Most *Passiflora* species present their flowers boldly on the extremities of fertile shoots in conspicuous colours as a signal to attract animal visitors with a reward of nectar. *P. discophora*, which is endemic in the dense tropical rainforests of Ecuador, has several unusual features (Plate 6d). These include hypogeal seed germination and

palmate tendrils that terminate in adhesive discs which enable it to climb on the bark of the largest forest trees to gain a favourable position high above the forest floor. In cultivation the flowers are presented on long mature pendular shoots hidden beneath the younger growths and generally with the face of the flower towards the tree support (Vanderplank, unpublished). Flowering is usually on pendular stems halfway between the base and the apex of the vine. It has been suggested that the flowers are pollinated by bats (Christensen, 1998). This seems most unlikely on three counts: the flowers are open during the morning and close soon after midday; the flower attachment to the peduncles is very fragile and would fracture before being discovered by a foraging bat; the flowers are negatively presented to a flying visitor. It seems more likely that this species is pollinated by a small flightless or poorly flighted animal that inhabits this darkened world between the canopy and the forest floor and spends most of its time on the bark of trees under the many competing vines; from this vantage point the flowers would be more conspicuous.

3.2.2.9 Climatic effects

All methods of pollination may be adversely affected by rainfall. If rain occurs up to one and a half hours after pollination there will be no fruit set. However if rainfall occurs two hours after pollination there will be no detrimental effect (Morton, 1987). Carpenter bees *Xylocopa megaxylocopa* and *Xylocopa neoxylocopa* will not work flowers of *P. edulis* and *P. edulis* f. *flavicarpa* if the nectaries are wet (Morton, 1987).

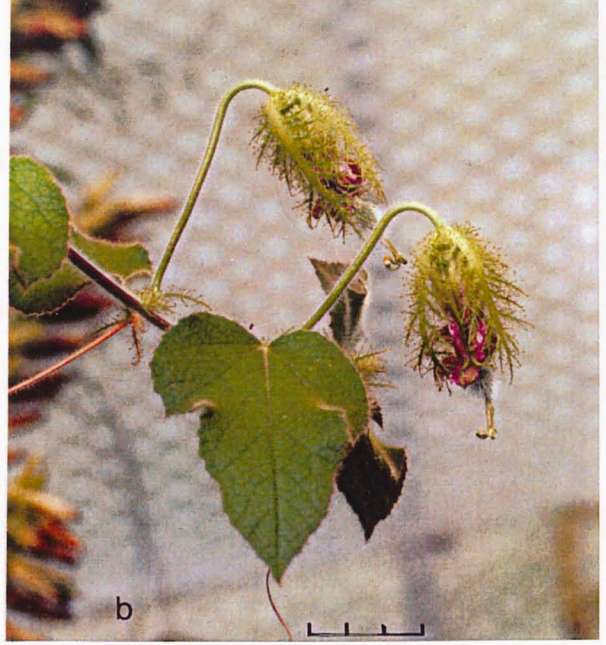
The evolution of flower design including the time of opening, the duration of opening and the method of pollination must be closely linked to natural variations in local

climatic conditions. The extended duration of the open flowers of *P. tarminiaina* and *P. mixta* to three days in the high Andean mountains would be pointless if these flowers were vertically held. They would quickly become flooded, the nectar would be lost, and the pollen would be washed off the anthers and stigma alike. This problem is overcome by having pendular flowers with large sepals and petals that help protect the vital organs from frequent mountain showers and heavy morning dew. Daily afternoon rain is a feature of the lowland tropical rainforests of South America. *Passiflora* species here that flower throughout the year close their flowers by midday to shelter them from these often heavy downpours. This behaviour also seems to be the survival strategy of many species that are endemic to the lowland tropics.

3.2.2.10 Flower and fruit orientation

The necessity to present flowers boldly and openly at the most advantageous angle, to allow easy access to visiting nectar-feeding animals that will inadvertently ensure successful cross-pollination, has one major disadvantage. The fertile parts of the flowers (the anthers and stigmas) are then exposed to the vagaries of the weather. To reduce the constant problem of rainfall, either as heavy showers or light drizzle, that will wash the freshly deposited pollen from the stigmas, some *Passiflora* species re-orientate the closing flowers to an inverted position where the petals and sepals umbrella the stigmas from being washed clean. In *P. reflexiflora* the stipe (the region of the peduncle between the bracts and the base of the hypanthium) turns the flower through 90° soon after it closes (usually within six to twelve hours depending on the temperature) to an inverted position (Vanderplank, unpublished) (Plate 9a).

In *P. palmeri* the distal section of the peduncle below the bracts turns the fading flower through 90° - 130° to an inverted position (Plate 10b). In *P. auriculata* the entire length of the peduncle turns the withering flower through 180° so that the developing ovary is inverted and brought back close to the stem, below the fertile node (Vanderplank, unpublished). In each case, once fertilization is completed, the ovary develops and matures in this inverted position.



a. Flower and flower buds are presented within 20° of the vertical corresponding to the direction of the peduncle (pedicel). Feathery bracts are reflexed beneath the sepals and petals; b. 24 hours after pollination the distal section of the peduncle below the bracts has re-orientated the flower and the fertilised ovary (which is now enclosed by the bracts) through 90° into an inverted position where it remains; c. Immature fruit are now only partially enclosed by the still healthy glanduliferous bracts; d. Mature fruit. The deciduous bracts have withered and fallen away leaving the flower remnants visible.

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Scale bar in cm

3.3 Natural fruit harvest and seed dispersal

There is very little information in the literature on the dispersal of *Passiflora* seed. Whole seed of *P. incarnata* have been observed in the droppings of rabbits and skunks during the fruit-fall season in the USA (MacDougal, unpublished) and *P. subpeltata* seed has been found in abundance in skunk droppings in Mexico (MacDougal, 1994). Various un-named rodents are recorded as being responsible for seed dispersal of un-named *Passiflora* species (Abramsky, 1983 and MacDougal, 1994). In French Guyana fallen fruit of *P. coccinea*, *P. glandulosa*, *P. cerasina*, *P. candida*, *P. nitida* and *P. crenata* have been observed devoid of arils and seed, with the remains of the fruit-shell showing marks made by the teeth of a sizeable mammal, probably the coati (*Nasua nasua*), which is very common in this region of the Guyanas (Vanderplank, unpublished). This mammal may also be primarily responsible for the seed distribution of many other *Passiflora* species. Fertile flowering branches of *P. amoena* occur predominantly within one metre of the ground and occasionally beneath the leaf litter. Their fruit are within easy reach of the coati, but more elevated maturing fruit of *P. coccinea* subsp. *tortue* (subsp. nov. ined) and *P. coccinea* subsp. *cacao* (subsp. nov. ined) remain untouched until fully ripe when they become deciduous and fall to the forest floor (Vanderplank, unpublished). Several species of bats in Venezuela have been confirmed as feeding on passion fruit by close examination of the contents of their stomachs (J. Molinari, unpublished). Seed are unharmed and excreted, often while the bat is in flight. The fruit of *P. fieldiana*, which is endemic to Venezuela, have long been considered to be eaten by, and have their seeds dispersed by bats. The hard-shelled fruitcases are often found

with teeth and claw marks that have been identified by Stephen Tillett (unpublished) as having been made by bats.

Seed of *P. coccinea* ssp. *bolivia* (ssp. nov. ined.) are thought to be distributed by monkeys, which are known to feed on their fruit, commonly known as 'monkey guzzle', in Bolivia. *P. vitifolia* is also said to be a favourite fruit of monkeys in Brazil. Surprisingly, there is no published data on which species of birds feed on passion fruit although it is generally accepted that many do. In French Guyana ripe fruits of *P. nitida* have been observed with large peck marks from unidentified birds that have penetrated the tough pericarp to access the sweet arils and seed (Vanderplank, unpublished). *Passiflora* species that flower and produce large brightly coloured fruit at the top of the forest canopy are most closely associated with large fruit-eating birds. Like the bats, the primary food of the birds is the fleshy arils that surround each individual seed. The seed passes unharmed through their digestive tract to be excreted randomly over a wide area, often while the bird is still in flight.

The terrestrial fate of the seed excreted by birds and mammals is not clear and must depend largely on where the seed fall. Further distribution and better positioning of the seed for successful germination may be inadvertently aided by insects which are primarily interested in the faeces (droppings) and subsequently help to bury the seed in the leaf litter. Seed eating mammals (small rodents) may also assist distribution by collecting and burying seed for later consumption and failing to retrieve their hidden stores. No reptiles or amphibians have been recorded as eating passion fruit, but this should not be discounted as a possibility.

The wet lowland tropical forests of South America are honeycombed by rivers and tributaries. During the wet season many rivers burst their banks to swamp the vast flood plains. Most fruits of *Passiflora*, especially those found in these lowland forests, are very positively buoyant and after fruit fall are undoubtedly transported downstream, where they become stranded on riverbanks and flood plains as the water recedes. *P. nitida* is a well known flood plain species and mature plants will tolerate having their roots and lower stems submerged for many weeks each year. Whether or not any aquatic animal is involved in seed dispersal has not been recorded, but many species of fish are known to feed on vegetable matter and fruits and may, like birds and mammals, digest only the fleshy arils and excrete unharmed seed. Alternatively, they may feed on the fruit but spit out the hard-shelled seed. These seed are negatively buoyant and would sink to the riverbed where they may germinate in the river shallows or on the flood plain as the floods recede.

In cultivation in the UK the fruit and seed of any *Passiflora* that is left accessible will be removed and devoured by various rodents such as the House Mouse (*Mus musculus*), the Wood Mouse (*Apodemus sylvaticus*), the Bank Vole (*Clethrionomys glareolus*), the Field Vole (*Microtus agrestis*), the Common Rat (*Rattus norvegicus*), and the Grey Squirrel (*Sciurus carolinensis*) (Vanderplank, unpublished). It is generally the transportation of the fruit that affects seed dispersal and the distance travelled from the mother plant may be considerable. Often the offending animal is disturbed while eating the fruit and fails to return to it. The whole or partly eaten fruit may be transported and buried for later consumption but not reclaimed, allowing the seeds to germinate at a later date (Plate 12b). Only fragments of the seed coat of *Passiflora* seed have been observed in rodent faeces in the UK. The House Mouse

and Wood Mouse have been observed cracking the seed-case open and ingesting only the soft embryos (Vanderplank, unpublished). Even the small seed of *P. rubra* and *P. capsularis* are treated in this way. It is probable that other rodents mentioned also follow these eating habits.

In some species the fully mature ripe fruit remains the same colour as the immature fruit. In *P. coccinea* ssp. *bolivia* (ssp. nov. ined.) and *P. vitifolia* the fruit has a hard tough shell and is variegated or mottled pale and dark green, rendering it inconspicuous against the deep green foliage of the vine. This camouflage colouration and the failure to change to a bright vivid colour on ripening is probably a defence against discovery by keen-eyed birds. This would only be an advantage if the birds were seed-eaters rather than fruit-eaters or if another animal was preferred for the task of seed distribution. No change in odour from unripe to ripe fruit is detectable to human olfactory senses but to the more discerning primates, perhaps a change in odour is easily detected. The opened fruit is very aromatic and sweetly scented even to poorly developed olfactory senses. Primary seed distribution of these species is performed by perhaps many species of monkeys that can crack open the hard-shelled fruit to feed on the soft juicy flesh and seeds, and later excrete the undigested unharmed seeds over a wide area away from the mother plant. It is possible that seed deposited by primates on the forest floor has a much better chance to germinate and become established with the help of monkey manure than seed deposited in bird or bat manure. This evolutionary pressure may have culminated in the production of camouflaged fruit. These fruit have also developed a camouflage defence against being eaten by bats. Instead of the hard surface of the fruit being glaucous, as in *P. fieldiana* and *P. ligularis*, the fruit of which are food to various bats

(Tillett, unpublished), the surface of the fruit of *P. coccinea* ssp. *bolivia* (ssp. nov. ined.) and *P. vitifolia* is pilose and tomentose (like velvet). This surface absorbs the ultrasound used by the bat for echo-location and thereby helps the fruit avoid detection (Vanderplank, unpublished). If the ripe fruits are not discovered on the vine, after several weeks the abscission layer becomes fragile and at the slightest movement the fruit fall to the forest floor or waterway below. Secondary seed dispersal is probably performed by terrestrial mammals, water movement or fish, which may assist in the transportation of the fruit and seed away from the mother plant. However, they will probably not be dispersed as widely as if primary dispersal had been effective (Vanderplank, unpublished).

In some species, like *P. quadrifaria* and *P. coccinea* ssp. *tortue* (ssp. nov. ined.), developing fruit are kept hidden and protected from premature harvest inside large folious bracts which have numerous large nectariferous glands along the margin. These attract and are attended by vicious biting ants that vigorously defend their nectar source and thereby act as a deterrent to any unwanted inquisitive visitor (Bentley, 1977). In *P. quadrifaria* the bracts remain bright scarlet throughout fruit development and become deciduous soon after fruit maturation. In *P. coccinea* ssp. *tortue* (ssp. nov. ined.) the bracts turn from scarlet to folious green as the fruit develops. They are most inconspicuous at the time of fruit maturation when the nectarous glands cease to function and are deserted by their protecting ants (Vanderplank, unpublished). The mature fruit, still inside the intact bracts, becomes deciduous and is easily dislodged from the surrounding bracts by clumsy movement. In both species the fruit are reddish brown and inconspicuous and are possibly a food of several species of primate. However, if the ripe fruit are approached too

vigorously, by mammals or birds, they may be lost and fall to the ground to be devoured by a ground dwelling animal like the coati (*Nasua nasua*). This may be either a dual approach to seed distribution or an example of a transition from one strategy to another, superior, strategy (Vanderplank, unpublished). In *P. quadrifaria* the bracts remain brightly coloured, inviting attention constantly up to and during fruit maturation whereas in *P. coccinea* ssp. *tortue* (ssp. nov. ined.) the bracts turn green during fruit development and remain green and intact after the fruit has ripened and become deciduous. The development of bright red bracts would seem to be an earlier evolutionary feature and the further colour change to green again in *P. coccinea* ssp. *tortue* (ssp. nov. ined.) is perhaps a more recent evolutionary event, favouring a ground-based animal for seed distribution (Vanderplank, unpublished).

In some *Passiflora* species, including *P. urbaniana* and the many varieties of *P. foetida*, the developing soft-bodied fruit is enclosed in bipinnatisect or tripinnatisect feathery bracts that are glandular at their apex (Plate 11a). These glands ooze a sticky secretion which shows high protease and acid phosphatase activity similar to that found in the digestive enzymes within the traps of carnivorous plants. Insects that become trapped in this secretion are digested by the plant, which obtains extra amino acids (Radhamani, Sudarshana & Krishnan, 1995). As the fruit ripens it changes colour from folious green to bright red or yellow, the glandular secretion is terminated and the bracts become brown and deciduous, leaving the ripe fruit accessible to birds and small mammals (Plate 11b and c). The glandular secretion on the bracts seems also to act as a deterrent to birds and mammals that may otherwise be tempted to sample the fruit while still immature.



a



b



c

P. foetida var. *hirsutissima* Killip, 1936 (NCP 1078)

a. Immature fruit surrounded by protective feathery glanduliferous bracts; b. Ripening fruit. Bracts are withered and redundant; c. Ripe fruit. Deciduous bracts have fallen away.

Scale bar in cm

In Peru the sepals of *P. variolata* have five to seven pairs of large nectariferous glands that are visited by *Ectatomma tuberculatum* ants which protect the flowers and developing ovary from herbivore predation (Moffett, 1999).

In *P. tarminiana* and closely related species fully mature fruit may remain on the vine for many weeks after ripening. The fruits are soft-skinned when ripe and easily bruised and, although they are ovoid (banana-shaped) and a pale or deep dull yellow, they can be quite inconspicuous and well hidden amongst the tangled stems and dead or dying leaves of the wild-growing vine. The arils are sweet, juicy and aromatic. This suggests that primary seed distribution is performed by a climbing mammal or a bird that is a fruit-eater rather than a seed-eater. After several weeks over-ripe fruit fall to the ground. This species and its close relatives are usually found at higher elevations or in lower rainfall areas often on steep mountain slopes and secondary seed distribution is performed by a terrestrial mammal, probably a ruminant that is attracted to the now fermenting fruit and can digest the flesh surrounding the seed and allow the seed to pass through its digestive system unharmed. Finally, smaller mammals, primarily seed-eaters, may affect seed distribution by burying seed for later consumption and later failing to retrieve their hidden store. Perhaps the success of *P. tarminiana*, which is now classified as an invasive weed in Hawaii (Green, 1972), and the proliferation of many species and natural hybrids of the subgenera *Tacsonia* and *Manicata* demonstrate the merit of this strategy of having three mechanisms of seed distribution (Vanderplank, unpublished).

In other species that produce large fruit with sweet fleshy aromatic arils, the fruit colouration is drab, when fully ripe, yellowish green in *P. incarnata* and sombre deep

dull purple in *P. edulis* Sims. As soon as the fruit of these species is fully ripe it falls from the vine. In commercial vineyards the ripe fruit of *P. edulis* Sims and *P. edulis* f. *flavicarpa* Deg. are collected from the ground beneath the vine and never picked (Morton, 1987). This suggests that seed distribution in the wild is solely dependent on terrestrial mammals, such as rabbits, skunks and other small rodents. The possibility that ground-scavenging birds may also assist in seed distribution is not discounted but this must be considered as being very secondary to mammalian distribution.

In a few *Passiflora* species, like *P. morifolia*, fully ripe fruit remain on the vine and if they are not discovered by foraging animals they dehydrate and shrivel but remain firmly attached to the parent plant (Plate 12a). Seed of this species is well adapted to becoming dehydrated and in this state can withstand severe frosts, even temperatures as low as -196°C in liquid nitrogen (Vanderplank, unpublished). This reluctance of *P. morifolia* to release its drying fruit suggests that the seed are safer suspended on the plant than subjected to the hazards on the ground. The annual stems of *P. morifolia* die back after fruiting and the shrivelled fruit do eventually fall to the ground as spring arrives. By this strategy seed is saved from becoming food for ground dwelling animals during the colder drier months when germination is not possible until conditions favour germination and time on the open ground is minimised (Vanderplank, unpublished). Primary seed dispersal is by an agile climbing rodent or small bird that can negotiate the tangled stem of these vines. Secondary seed dispersal may well be performed by the same rodents and other less agile mammals that accidentally devour the dried fruit and pass the unharmed seed in their droppings.



a



b

a. Fruit of *P. morifolia* Mast., 1872 (NCP 1148) may remain attached to the vine long after annual stems are redundant; b. Fruit remains of *P. morifolia* after arils and seed have been harvested by mice (*Mus musculus*).



c



d

c. and d. Seedlings of (c.) *P. vitifolia* Kunth, 1817 (NCP 1251) and (d.) *P. subpeltata* Ortega, 1798 (NCP 1223) that have grown from unclaimed seed buried by mice (*Mus musculus*).

Scale bar in cm.

Many of the small-flowered species (less than 25mm in diameter) produce small black or red berry-like fruit with white or yellow, moderately sweet and fleshy, arils. The ripe fruit are less accessible to small rodents than species like *P. morifolia* on account of their often long, pendular peduncles. The mature fruit drops from the vine after a number of days if they are not discovered. This suggests that small birds or small monkeys may be primarily responsible for seed dispersal. Ground-dwelling mammals may help to accomplish secondary seed dispersal after the fruit has fallen to the forest floor.

In some species, particularly in the subgenus *Decaloba* section *Pseudodysosmia*, like *P. dioscoreifolia* and *P. lobata* and section *Xerogona*, such as *P. capsularis* and *P. rubra*, the fully mature fruit burst open from the distal end while still attached to the vine, releasing the aril-covered seed to fall to the ground. The arils of these species are much less fleshy than the arils of large-fruited or berry-like fruited species and separate from each other very readily. They are odourless, bland to the taste and may be white, orange or bright red, as in *P. gracilis*. Seed dispersal is by a ground-dwelling mammal, probably a rodent. Arilled seed may become entangled with body hair and transported some distance from the mother plant. Birds and climbing mammals would dislodge the seed from the ripe fruit while clambering about, before they reach the fruit, and for this reason are thought to play only a minor role in seed dispersal.

3.4 Herbivorous pests and pathogens

3.4.1 Fruit Flies

The Oriental Fruit Fly *Dacus dorsalis*, the Melon Fly *Dacus cucurbitae* and the Mediterranean Fruit Fly *Ceratitis capitata* are serious pests of *Passiflora* in Hawaii and Australia (University of Hawaii, 1979). These pests puncture the immature developing fruit and cause it to shrivel and prematurely abort. An unidentified fruit fly has been causing devastation in all endemic species in Venezuela since 1995 (Tillett, unpublished).

3.4.2 Mites

The Spider Mites *Brevipalpus phoenicis* and *Tetranychus telarius* and the Broad Mite *Hemitarsonemus latus* are now found in most tropical and subtropical countries and in ornamental species cultivated in protected environments. Although most species may suffer damage from these mites, species in the subgenera *Tacsonia* and *Manicata* are particularly susceptible when in cultivation. An unidentified mite that causes stem galls on *P. suberosa* in southern Florida, USA, is reported to be devastating the wild population of this native species (Jeffery Stotts, unpublished).

3.4.3 Aphids

Aphididae are a common pest worldwide. *Myzus persicae* and *Macrosiphum solanifolii* are serious pests in Hawaii (University of Hawaii, 1979). In cultivation

most *Passiflora* species are vulnerable to attack, particularly *P. caerulea*, *P. vitifolia*, *P. helleri* and *P. coriacea* which are otherwise virtually untroubled by insect predators. *Aphis gossypii* and *Myzus persicae* attack *P. edulis* Sims and *P. edulis flavicarpa* in Florida, USA, and are responsible for transmitting the virus that causes 'woodiness' (Morton, 1987).

3.4.4 Scale Insects (Coccoidea)

Many species of Coccoidea occur naturally in the wild and particularly in ornamental plants produced by commercial nurseries. The Barnacle Scale, *Ceroplastos cistudiformis*, is recorded as a pest of *Passiflora* in Hawaii (University of Hawaii, 1979).

3.4.5 Mealy Bugs (Pseudococcidae)

These are primarily pests of ornamental or glasshouse cultivated taxa. Infestations are usually worse during the winter months when growth rates are reduced by poor light and lower temperatures, and natural predators are less active. Many species are susceptible to these pests and may be completely destroyed if left untreated, especially species in the subgenera *Passiflora*, *Dysosmia* and *Tacsonia*. In cultivation the uncinata trichome, or hooked hair, defences of *P. lobata*, *P. adenopoda*, and *P. morifolia* of subgenus *Decaloba* section *Pseudodysosmia* are a positive disadvantage to the effective natural control of this herbivorous pest. Both the larvae and the adult Mealy Bugs are small enough to be able to move freely beneath these sharp stiff hairs, but their principal predator, a small ladybird-like beetle *Cryptolaemus montrouzieri*, is

much larger and has difficulty traversing the trichomes to feed and deposit its eggs. Although the young larvae of *C. montrouzieri* are able to move freely and feed on the juvenile Mealy Bug larvae, their mobility becomes increasingly hindered as they grow and the danger of becoming impaled on the sharp hairs increases. A few *Passiflora* species (*P. holosericea*, *P. discophora* and *P. gracillima*) appear to be completely immune to attack. The Citrus Mealy Bug *Planococcus citri* is a major pest of *P. edulis* Sims and *P. edulis* f. *flavicarpa* in Australia during the summer months (Morton, 1987).

3.4.6 Thrips (Thripidae and Aeolothripidae)

These are primarily glasshouse pests which can quickly devastate ornamental passionflowers during the warmer summer conditions. The Red-banded Thrip *Selenothrip rubrocinctus* is recorded as being a serious pest of passion flowers in Hawaii (University of Hawaii, 1979).

2.2.4.1 Bugs

The Passion Vine Leaf Hopper (*Scolypopa australis*) attacks the leaves. The Passion Vine Bug (*Leptoglossus australis*) feeds on the flowers and immature fruit. The Green Vegetable Bug or Stinkbug (*Nezara viridula*) feeds on the foliage and young fruit. The Brown Stinkbug (*Boerhavia maculata*), the Large Black Stinkbug (*Anoplocnemis* sp.) and the Small Black Stinkbug (*Leptoglossus membranaceus*) are also sap-suckers of many passion flowers, feeding mainly from the leaves and stems.

The stinkbug *Chrorodocera laticornis* is recorded in Florida, USA, attacking *P. edulis* Sims and *P. edulis* f. *flavicarpa* (University of Hawaii, 1979).

3.4.8 Ants

In glasshouse cultivation in the UK an unidentified ant (Formicidae) has been observed stealing nectar from *P. 'Pura Vida'* flowers by cutting a small hole through the operculum to reach the nectar chamber. The ants did not make any contact with the stigmas and did not steal any of the abundant pollen and are therefore considered to be only opportunist nectar thieves and not pollinators (Vanderplank unpublished).

3.4.9 Lepidoptera

Under glasshouse cultivation conditions in temperate climates, cutworms or 'surface caterpillars', the larvae of *Noctua* and *Agrotis* species of moths, may cause severe damage to major roots near the base of the vine (Vanderplank, 1996a). The larvae of a similar unidentified species of Lepidoptera are recorded by MacDougal (1994) as attacking *P. morifolia* roots in Mexico and Guatemala.

3.4.10 Coleoptera

The larvae of flea beetles (*Phyllotreta* species) cut small holes in the surface of the leaves. Although unsightly, the damage is not fatal (Vanderplank, 1996a). In Central America and Mexico severe damage from flea beetles of the genus *Monomacra* has been recorded on *P. lobata*, *P. adenopoda*, *P. morifolia*, *P. bryonoides* and *P.*

pterocarpa (MacDougal, 1994). Flea beetles from the genus *Parchicola* have been observed on *P. adenopoda* in Ecuador (MacDougal, 1994). A trial plot of *P. incarnata* at the University of Mississippi, USA, in 1999 was completely demolished in less than four days by an infestation of adult ‘Spanish Fly’ or Three Striped Blister Beetles (*Epicauta occidentalis*) (Charles Burandt, unpublished).

3.4.11 Leaf Miners

Leaf miners also cause unsightly, but not fatal, damage. Passion flowers with thick leaves are most affected, for example *P. quadrangularis*, *P. edulis* Sims, *P. alata*, *P. racemosa*, *P. x allardii* and *P. x violacea*. The larvae of various insects, including Hymenoptera (*Fenusa* species), Coleoptera (*Orchestes* species), Lepidoptera (*Lithocolletis* species) and Diptera (*Phytomyza* and *Euleia* species) are recorded in the wild on *P. exsudans* and other species in the section *Pseudodysosmia* in Mexico and other parts of Central America (MacDougal 1994).

3.4.12 Vine Weevils

The larvae of vine weevils (*Otiiorhynchus sulcatus*) can be a particular problem in pot grown plants. A few larvae may cause the fatality of a large vine within several weeks (Vanderplank, 1996a). Vine weevils are also recorded attacking *P. adenopoda* and *P. sicyoides* in Mexico (MacDougal, 1994).

3.4.13 Whitefly

Whitefly or Snowy Flies (*Trialeurodes vaporariorum*) can be a major problem on most species during warmer periods, particularly on *P. racemosa*, *P. caerulea*, *P. subpeltata* and many species in the subgenus *Decaloba* (Vanderplank, 1996a).

3.4.14 Leaf Roller Moths

Larvae of the Leaf Roller Moths (*Tortrix* moths), particularly *Clepsia spectrana* (Cyclamen Tortrix), may cause extensive damage to glasshouse-cultivated plants in the UK but this is rarely fatal (Vanderplank, 1996a). A similar unidentified leaf-rolling larva (Lepidoptera) is recorded attacking *P. exsudans* in Mexico (MacDougal 1994).

3.4.15 Nematodes

Several species of nematodes cause severe damage to most commercial passionfruit species and cultivars in the tropics. The *P. edulis* f. *flavicarpa* is very resistant to this pest and is now cultivated in preference to other commercial species where eelworm infestation is known to exist. It is also used as a rootstock species for *P. edulis* Sims. The fruit of this purple passionfruit, although smaller, are much preferred to the larger but more acid yellow fruit of *P. edulis* f. *flavicarpa*. *P. edulis* Sims has significantly lighter cropping yields and is more prone to disease than f. *flavicarpa* and this has accelerated the introduction of many hybrids that have improved fruit quality but are still resistant to nematodes (Vanderplank, 1996a). Root Knot Nematodes

(*Meloidogyne javanica*) and Spiral Nematodes (*Scutellonema truncatum*) are particular problems in the Republic of South Africa. *P. tarminiana* is particularly vulnerable when planted in poorly drained soils (Morton, 1987).

3.4.2 Fungal diseases

Brown Spot is caused by *Alternaria passiflorae*, *A. tenuis* and *A. tomato*, particularly in damp conditions in Hawaii, Australia, New Zealand and East Africa (Morton, 1987). Stem Rot or Collar Rot (*Phytophthora cinnamomi* and *nicotinae*) is recorded in Fiji, South Africa and Australia in *P. edulis* Sims but not in *P. edulis* f. *flavicarpa*. Fusarium Wilt (*Fusarium oxysporium*) also attacks primarily *P. edulis* Sims in Uganda (Morton, 1987). Stem End Rot, caused by *Botryodiplodia theobromae*, is recorded attacking *P. quadrangularis* in East Africa (Morton, 1987). Under glasshouse cultivation conditions, powdery and downy mildews may cause heavy losses in all seedlings and soft-stemmed species like *P. apetala*, *P. organensis* and *P. palmeri* (Vanderplank, 1996a).

3.4.3 Viruses

Several viruses have been recorded in *Passiflora* species including Passion Fruit Mottle Virus in *P. edulis* f. *flavicarpa* in Sri Lanka (Dassanayake and Hicks, 1992) and Passiflora Latent Carlavirus in many ornamental species and cultivars, including *P. x allardii*, *P. x violacea*, *P. 'Amethyst'*, *P. caerulea*, *P. foetida* and *P. 'Incense'* (Hicks *et al.*, 1996). Others include 'Bullet' or Passion Fruit Woodiness Potyvirus in *P. edulis* Sims and *P. aurantia*, Passiflora Ringspot Potyvirus in *P. foetida*, Citrus

tristeza closterovirus in *P. gracilis* (Hicks et al., 1996), Cucumber Mosaic Virus in an un-named *Passiflora*, possibly *P. caerulea*, in the UK (Anon, 1972) and Passionfruit Yellow Blotch Virus in *P. edulis* f. *flavicarpa* (Seneviratne & Wickramasingha, 1974). Many of these viruses are also recorded in commercial plantations in Hawaii, Australia, Fiji, New Zealand, Samoa, Malaysia, South and East Africa, and North and South America (Morton, 1987).

3.5 *Heliconius* butterflies

Most of the complex relationships between *Passiflora* and their many herbivores have not been studied and even the identification and documentation of most of these leaf eaters is very limited. Pests that cause economic damage are the exception but in these cases generally only their efficient eradication or control has been investigated. Another exception to this general rule of thumb is when there are other commercial interests or when the host plant or predator has been elevated into mythology or the general public's awareness because of perceived beauty, variety or the basically bizarre. The relationship between *Passiflora* and the *Heliconius* butterflies satisfies all these criteria admirably. The exclusivity of *Passiflora* taxa as larval food plants for these exotic butterflies has earned them the common name 'Passionflower butterflies' or 'Longwing butterflies' on account of their extended wing span. This mysterious and fascinating relationship between *Heliconius* butterflies and *Passiflora* is a subject of extensive and often contradictory ongoing research. Any definitive answer that may be forthcoming from these investigations may well be applicable to many other angiosperm-herbivore interactions.

The main hypothesis is that these herbivorous insects have caused sufficient evolutionary pressure to dramatically alter the outward form of some *Passiflora* species. Turner (1973) and Benson, Brown and Gilbert (1975) concluded that plant and insect show considerable parallel evolution but Mitter and Brooks (1983) conclude that some or all of the diversification of *Passifloraceae*, including *Passiflora*, happened before the recent evolution of *Heliconius* butterflies. The parallel evolution theory would however seem to be supported by the fact that none of the *Passiflora* species that are endemic to Asia, and particularly species in the subgenus *Decaloba* in Australasia such as *P. herbertiana*, *P. aurantia* and *P. cinnabarina*, have evolved the brightly coloured leaf lamina nectaries, 'egg mimicry glands', so closely associated with the ova of the *Heliconius* butterflies as these butterflies are not endemic to these continents. These brightly coloured leaf lamina nectaries are found on many *Passiflora* species, particularly in the subgenus *Decaloba*. Their function is to reduce herbivore attack by deceiving ovipositing females into thinking that the plant in view has already been visited and eggs deposited.

A similar strategy is successfully used by species in the subgenus *Passiflora*, section *Quadrangularis*, such as *P. phoenicea* and *P. alata*. These plants produce three dimensional petiole glands that closely resemble Lepidoptera eggs. These are most striking at the growth points on juvenile leaves where *Heliconius* butterflies prefer to deposit their eggs (Gilbert, 1982 and 1983, Smiley, 1985, Spencer, 1987 and 1988, Bowers, 1988 and McLain, 1983). Other defences against herbivore attack include the stiff hooked hairs or trichomes on the leaves and stems of species in the subgenus *Decaloba*, section *Pseudodysosmia*. These make it difficult for marauding insects to

traverse the plant and impale the unwary soft bodied *Lepidoptera* larvae that attempt to feed on the leaves (Levin, 1973, Gilbert, 1971 and MacDougal, 1994).

Leaves of some species are chemically unpalatable to most herbivores. This specialised chemistry and the presence of hooked trichomes are both considered to be recent developments in evolutionary terms (Gilbert, 1971). However, the larvae of one *Heliconiinae* species, *Dione moneta*, still manage to successfully feed on *Passiflora* species in this particular group. The small young larvae can walk between the trichomes and the larger larvae manage to walk over the hairs without becoming impaled (Benson *et al.*, 1975, MacDougal, 1994)

The butterfly *Heliconius charitonius* oviposits on the immature or developing tendrils of *P. suberosa* and *P. viridiflora* in Mexico. This is thought to give better protection for the ova and emerging larvae against searching symbiotic ants. These ants feed from various nectar-exuding glands on the leaves, petioles and flower bracts and in return protect the vine from herbivores, especially *Heliconius* larvae (Bentley, 1977). The numerous nectarous glands on the flower bracts of *P. foetida*, *P. quadrifaria* and *P. vitifolia*, and the distribution success of these species demonstrates that this strategy works. The greater the activity of ants on or near the developing fruits, which is encouraged by these nectar producing glands, the less the chance of loss or damage from predators, including mammals or birds. When the fruit is fully ripened, these glands cease to produce nectar and the bracts still surrounding the ripe fruit become deciduous, leaving a conspicuous invitation to fruit eating animals that a free meal is on offer.

The possibility of mimicry between *Passiflora* species of the section *Pseudodyosmia* and sympatric *Cucurbitaceae* as a strategy to avoid predation by *Heliconius* larvae is proposed by MacDougal (1994).

P. biflora is very variable throughout its extensive range from the Bahamas to the Antilles and from Mexico through Central America to Colombia, Venezuela and Ecuador. *P. misera* is distributed from Panama through north eastern South America to northern Argentina. Both species are predated by a range of *Heliconius* species (larvae). In cultivation, when exposed to *Heliconius* larval attack they are rapidly defoliated but the stems remain unharmed (Plate 3a). They do not immediately start foliage regeneration but remain seemingly dormant for weeks or months. Suddenly they start vegetative regeneration simultaneously from numerous primary and secondary growth buds, totally refoliating the vine in a few days (Vanderplank unpublished). (Most *Passiflora* species become stressed when totally defoliated, resulting in root damage or loss and poor, weak foliage regeneration.) Older plants of *P. biflora* in the wild have generally established an extensive web of tangled angulate stems over tall grasses and small shrubs. These remain healthy, although leafless, for some years, unlike species in the subgenera *Passiflora* and *Distephana* where lower or pendular shoots wither and die after flowering and fruiting (Plate 3a). These are then replaced on an annual basis by more elevated shoots as seen in *P. caerulea*, *P. vitifolia* and *P. maliformis*. The rate of photosynthesis by the stems of *P. biflora* and *P. misera* is sufficient not only to maintain a healthy vine in the short term but to enable the plant to build up energy reserves to restart new growth rapidly and vigorously when conditions are favourable. The plant can then extend its dominance over other support plants to flower and fruit before it is defoliated again by

Lepidoptera larvae. *P. misera* is virtually unique amongst *Passiflora* in having very broad, flat stems that are almost leaf like and are presented with their broad side to the sky when the plant is growing horizontally, so maximising the area for photosynthesis. This is a very recent development in evolutionary terms which appears to solve its particular herbivore problem. Is this a harmonious solution that will endure? Or will the herbivore evolve to eat the stems and increase their speed of regeneration, which is already staggering, even for *Lepidoptera*. A complete metamorphosis of *H. melpomere* is less than 10 days (John Calvert, unpublished).

It is worth noting that this close association between *Passiflora* and *Heliconiinae* is recorded as being strictly one of host and predator. No symbiosis has been verified in the wild (MacDougal, 1994) but in captivity both *H. melpomere* (the Postman butterfly) and *H. charitonius* (the Zebra butterfly) have been observed visiting flowers of *P. biflora* for nectar (John Calvert, unpublished), which is the fundamental mechanism for insect or animal pollination.

3.6 Mimicry

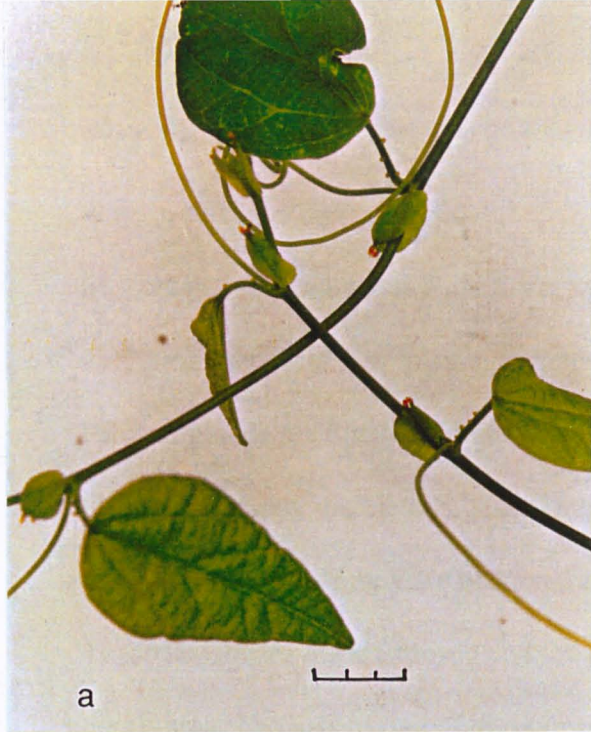
The occurrence of mimicry in some *Passiflora* species has been a subject of great interest to botanists and zoologists for many years. Prominent morphological features in some species of *Passiflora* are considered to have been greatly influenced by herbivore pressure (Turner, 1973, Benson, Brown and Gilbert, 1975, Williams and Gilbert, 1981 and Gilbert, 1983) and now form very effective defences against insect predation of vegetative parts. In one species, *P. morifolia*, fruits are protected against predation by tree climbing mammals (MacDougal, unpublished).

3.6.1 Stipule

The stipules of *P. caerulea* are modified to resemble slugs (molluscs) or caterpillars (Lepidoptera larvae) climbing along the main stems of the vine. This acts as a deterrent to adult female Lepidoptera depositing their eggs, as they are reluctant to risk the safety of their future offspring on a plant infested by slugs and caterpillars that may disturb or eat them (Rothschild, 1974 and 1984).

The acuminate points of the folious stipules of *P. garckeii* are bright yellow and closely resemble *Heliconius* butterfly eggs or newly hatched larvae in size, shape and colour. These bright yellow points are particularly prominent in the vigorous growing shoots (Plate 13a) and on juvenile stipules, which are in close proximity to each other before the young internodes elongate (Vanderplank unpublished), when viewed from above, as they would be by a searching butterfly, the points resemble a newly deposited cluster of eggs. Like the stipules of *P. caerulea*, this acts as a deterrent to the keen sighted female *Heliconius* butterflies from depositing their eggs and risking their future offspring on what appears to be an infested plant and encourages them to fly on in search of a suitable host plant.

The apex of the stipules of *P. maliformis*, *P. serrulata* and *P. platyloba* is also bright yellow when immature and may serve the same purpose as those of *P. garckeii* (Vanderplank unpublished).



a. Stipules of *P. garckeii* Mast, 1871, develop orange or yellow tips that are particularly colourful towards the apex of vigorous shoots; b. Fertile flowering stems of *P. gracillima* Killip, 1924, produce pedicels bearing a tendril and two bright orange modified flower buds towards their apex. These remain undeveloped while the fertile flower buds develop, blossom and set fruit, after which they are deciduous.



c. The petiole of *P. phoenicia* Lindl., 1883, produce two prominent, brightly coloured nectariferous glands near the leaf blade. When viewed from above, looking down the stem, these resemble clusters of eggs; d. *Passiflora* sp. nov. ined. from the subgenus *Decaloba* shows the most spectacular example of randomly distributed, brightly coloured leaf-lamina glands, considered to be egg mimicry.

Scale bar in cm.

3.6.2 Petiole glands

In species of the subgenus *Passiflora*, section *Quadrangularis*, the petiole glands are very prominent and may vary in number from one to four pairs along the petiole.

Pairs of glands are distributed unevenly along the petiole, usually towards the leaf blades in a highly visible position. These glands are egg shaped and very convincing as egg mimics when they are observed on young, vigorous, vertically growing shoots. These shoots are often exposed and are the most vulnerable to discovery by roaming herbivores. The loss of one of these prime growth shoots that have the potential to secure an improved and elevated position on the host plant would be very serious or even disastrous.

In *P. phoenicea* these petiole glands are bright yellow which is consistent with the colour of *Heliconius* butterfly eggs (Plate 13c). Adult *Heliconius* females are reluctant to deposit their eggs on occupied territory and so fly on in search of an uninfested plant (Gilbert, 1975 and Murawski, 1993). What attracts these butterflies to passion vines has not been proven but it is proposed that the keen sighted *Heliconius* butterflies recognise their larval food plants by the shape of their leaves (Gilbert, 1975). However the chemical signature of each *Passiflora* species may also have a role to play in unwittingly attracting *Heliconius* butterflies and the visual signals may have evolved to deter the predators from depositing their eggs on those species which have failed to evolve and change their chemical signature to deter their prime herbivore predator.

Research now being conducted by Miriam Rothschild is investigating the possibility that the volatiles released by these egg mimic petiole glands of *P. phoenicea* are identical to those released by the eggs of *Heliconius* butterflies, thereby proving that the complex relationship between *Passiflora* species and their most colourful herbivore is not just visual.

The immature petiole glands of *P. auriculata* may be orange or red near the apex of vigorous vertical shoots and resemble clusters of Lepidoptera eggs, possibly a *Heliconius* species (Vanderplank unpublished). Again this acts as a deterrent to female butterflies not wanting to lay their eggs on occupied shoots.

The petiole glands of *P. retipetala* may vary from two to four pairs of small sessile appendages which are bright yellow and, like the stipules of *P. garckeii*, resemble a cluster of newly laid Lepidoptera eggs when viewed from above the growing shoot (Vanderplank unpublished). As in previous examples, this may be enough to deter female butterflies from depositing their eggs.

3.6.3 Leaf lamina nectaries

Leaf lamina nectaries are found in many *Passiflora* species, particularly those in the subgenus *Decaloba* such as *P. pardifolia*, sp. nov. ined. (Plate 13d). They are usually found in two haphazard rows of seven glands or less between the three main veins of bilobed or trilobed leaves. In a few species these glands are bright yellow dots and are most conspicuous on the upper side of the leaf blade (*P. boenderi*, *P. gilbertiana* and *P. indecora*). On the underside of the leaf they are inconspicuous brown or

purple rings which exude a sweet, sticky nectar-like substance from their centre. In the above species the glands are flush with the leaf blade surface, but in *P. vespertillio* and *P. talamencensis* the glands are raised on volcano-shaped peaks 1-2mm high. Both types of glands are thought to be egg mimics (Gilbert 1975) and act in a similar way to the petiole glands of *P. phoenicea* and the stipules of *P. garckeii*. It is noteworthy that the glands of *P. boenderi* are not outwardly visible on the developing immature leaves whereas the leaf lamina glands of *P. cuneata* var. 'Miguel Molinari' are very striking at this early stage. The leaf lamina nectaries of many species are less conspicuous (*P. biflora*, *P. helleri*, *P. jorullensis* and *P. tuberosa*) but may still resemble insect eggs on the upper leaf surface and are nectariferous on the underside. It is suggested that parasitic wasps (Hymenoptera) are attracted to feed on this sweet secretion and are then available to parasitise any eggs that might be laid on the vine (Gilbert, L., unpublished).

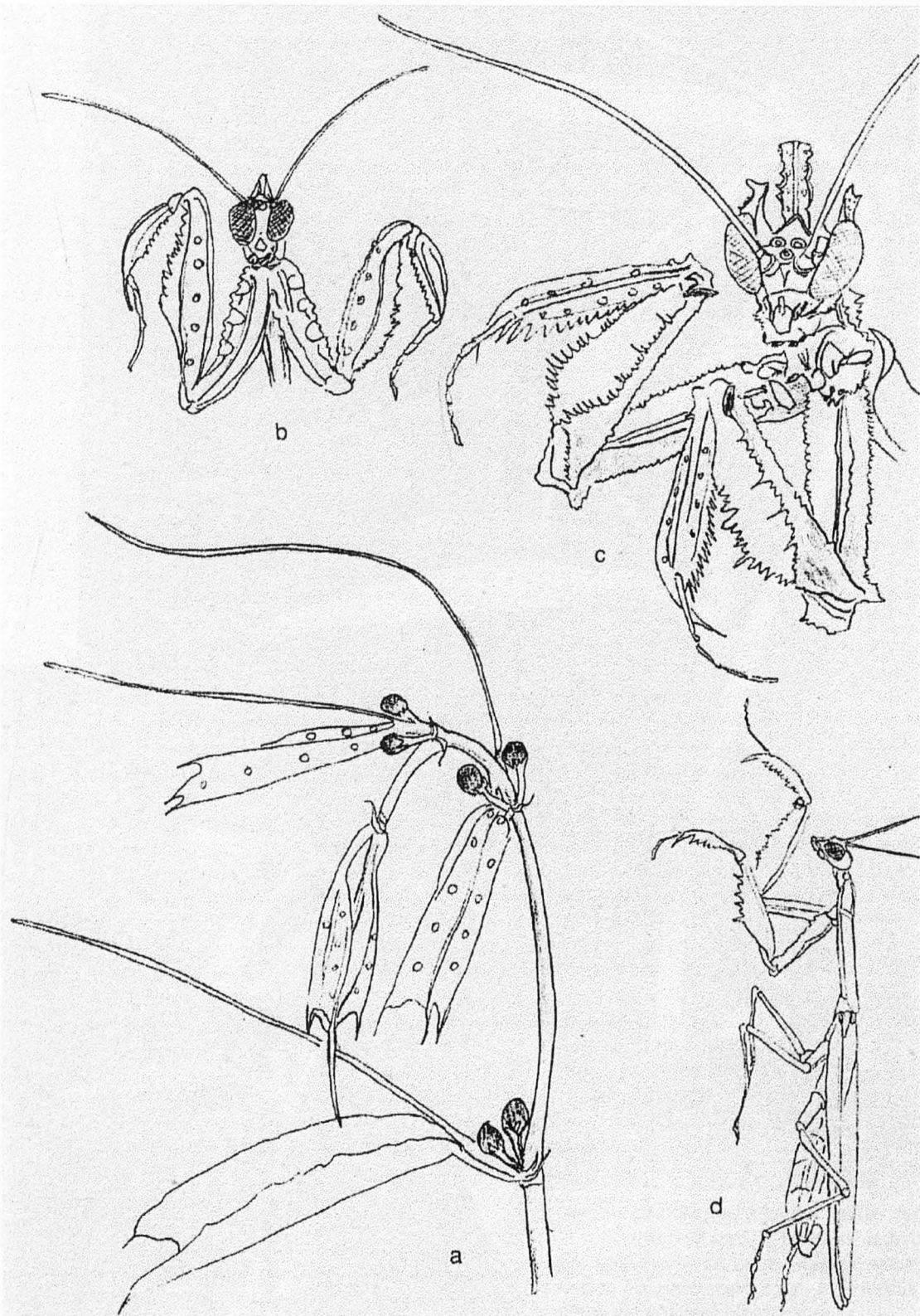
3.6.4 Fruit

The fruit of *P. morifolia* in the wild populations of Guatemala, Ecuador, Brazil and Peru are ovoid in general outline, 24-32mm wide and 33-38mm long and covered in minute sessile or raised trichomes less than 0.2mm high. However, in the population of *P. morifolia* found near Caracas, Venezuela, the fruits are smaller and the base of the trichome is greatly enlarged to 1-4mm high. As the jade green fruits approach maturity they resemble the fruits of *Datura* species, which are very toxic to mammals and are also found growing wild in close proximity to *P. morifolia* (MacDougal, unpublished).

This is an example of 'aide-mémoire mimicry', 'jog-memory mimicry' or 'recall-to-mind mimicry' (Rothschild, 1984). The spiky fruits of a non-toxic vine remind a would-be predator of a previous encounter with a fruit of the same design (*Datura*), which made it feel extremely unwell. Not wishing to repeat the experience, the herbivore leaves the non-toxic *Passiflora* fruits unmolested. The colour change of the unripe fruit from vivid green to deep purple-black on ripening seemingly breaks the association between these fruits and the poisonous *Datura* fruits, and the passion fruit are then greedily harvested by monkeys and other tree-climbing mammals (MacDougal, unpublished).

3.6.5 Primary growths

In *Passiflora cuneata* var 'Miguel Molinari' and some closely related species in the subgenus *Decaloba*, section *Decaloba*, the leaf orientation, design and colouration together with the orientation of immature tendrils, stipules and flower buds produces the appearance of a large carnivorous Praying Mantis (Mantidae family) (Plates 14 and 15). This insect-like appearance has only to trigger the memory of a previous unsuccessful attack by a vicious predator to be effective in deterring herbivore attack. Like the fruits of *P. morifolia* (Venezuela) this is an example of 'aide-mémoire mimicry' (Rothschild, 1984). Where the butterfly or other insect has had a terrifying encounter with a similar looking carnivore, rather than risk becoming a tasty snack, it may fly on in search of a safe site to lay its eggs.



a. *P. cuneata* var. 'Miguel Molinari'. A climbing shoot with flower buds; b., c. and d. Praying Mantids (*Mantidae*).

Plate 14. Insect mimicry (*Mantidae*)



P. cuneata var. 'Miguel Molinari' cultivated from wild collected seed. The visual impact of this species may be more dramatic when viewed in the same wavelength as it would be when seen by herbivorous insects.

Scale bar in cm

Plate 15. Insect mimicry in *P. cuneata* var. 'Miguel Molinari'

It seems possible that the leaf shape and overall design of the leaf lamina nectaries and tendrils have evolved primarily for this mimic display at the early stages of shoot development when the plant is most vulnerable, and that the later visible yellow leaf glands are only a secondary defence on the mature leaves.

3.7 Plant mimicry observations in the field

During a recent expedition to French Guyana collecting *Passiflora*, I observed that each time I thought I had found a wonderful new *Passiflora* species with giant three lobed leaves, on close examination it would turn out to be an unidentified Cucurbitaceae species. However, if I persisted with my search I would often find a familiar species of *Passiflora* with three lobed leaves, such as *P. garckeii* or *P. retipetala*, growing in close proximity. Initially I discounted the idea that plants might hide! But this thought returned when a keen eyed colleague and I had examined a large specimen of *P. glandulosa* growing over an unidentified tree with simple leaves of a similar design. This in itself was not remarkable but I was attracted back to the *P. glandulosa* to examine a flower, which was smaller and a paler pink than usual but was out of reach. When I finally climbed up to the bloom I realised that it was of a very different species, *P. amoena*, which is noted as being a small tree or weak climber. Here it was, however, covering a medium sized tree with strong, healthy vigorous climbing stems and flowering in a manner not recorded before, on young fertile stems. On one such stem, near the growing tip, were numerous *Heliconius* butterfly eggs. These were later identified by their larvae after hatching. *P. glandulosa* seems to be largely unmolested by herbivores in French Guyana. Is there an advantage for *P. amoena* when growing with a vine with almost identical

leaves? Do the leaves of *P. glandulosa* release volatiles that usually repel potential insect herbivores? Would it therefore be advantageous for a vulnerable species to grow in close proximity to, and even to entwine itself around, *P. glandulosa*? During the remaining four days of my visit I consistently found that if I found *P. glandulosa* I would often find *P. amoena* nearby as a robust climbing vine. Following this I examined each *Passiflora* I found to observe its host support and plants growing in close proximity. Most consistent and striking was the presence of *P. garckeii* and *P. retipetala* growing near large leafed Cucurbitaceae species and *P. candida* growing through and over an unidentified species of tree with very similar foliage.

In October 1999, during a visit to Florida, USA, I was searching for *P. multiflora*, which is native in the Everglades National Park at the southern part of the state. I found several examples of the simple leafed form of *P. suberosa* growing over West Indies Mahogany (*Swietenia mahogoni*) which has an almost identical leaf shape, although a little smaller (Plate 16). Perhaps this is a coincidence, because this species of mahogany is common in this area, or perhaps *P. suberosa* is less likely to be discovered by searching herbivores amongst leaves of the same design, which are of no interest to the insect herbivore (Plate 16). Plant mimicry between *Passiflora* subgenus *Decaloba* section *Pseudodysosmia* and sympatric Cucurbitaceae as a strategy for avoiding predation by *Heliconius* larvae is proposed by J. MacDougal (1994).



P. suberosa L., 1753 (simple-leaved form) growing over West Indies Mahogany (*Swietenia mahogoni*) in southern Florida.



P. suberosa shaded for identification

4 Hypotheses

4.1 Morphology of *Passiflora* seed

4.1.1 Interspecific cross pollination does not influence the morphology of the resultant seed.

4.1.2 Traditional classification of *Passiflora* into subgenera and sections would be more meaningful and the phylogeny more accurate if greater significance had been given to the morphology of their seeds.

4.1.3 The morphology of the seed of an interspecific hybrid closely resembles that of its maternal parent.

4.2 Moisture content of *Passiflora* seed

4.2.1 The strong woody testa of *Passiflora* seed is an effective barrier to successful dehydration of seed using drying agents (silica gel, di-phosphorus pentoxide and heat at 30⁰C).

4.3 Successful germination of *Passiflora* seed

4.3.1 The successful germination of *Passiflora* seed is primarily influenced by the temperature that is maintained during the germination period.

4.3.2 The successful germination of *Passiflora* seed is influenced by the acidity of the germination medium.

4.3.3 The seed of *Passiflora* species with pale colouration compared with their sibling seed have reduced viability.

4.3.4 Germination is improved in *Passiflora* seed that have been stored at 20⁰C by cooling of seed to 4⁰C for 30 days prior to germination.

4.4 Seed coat imposed dormancy

4.4.1 *Passiflora* seed that fail to germinate readily when subjected to ideal germination conditions are being influenced by seed coat imposed dormancy.

4.4.2 High environmental temperatures during fruit maturation induce seed coat imposed dormancy in *Passiflora subpeltata* seed.

4.4.3 Seed coat imposed dormancy in *Passiflora* seed can be broken by washing prior to sowing.

4.5 Status of *Passiflora* seed for storage purposes

4.5.1 *Passiflora* seed are best stored within their fruits or with their arils still attached.

4.5.2 *Passiflora* seed should be treated as recalcitrant or unorthodox for seed storage purposes as they are not capable of withstanding water loss of magnitude, are short-lived and are damaged during storage at low temperatures, which is consistent with Bewley & Black, 1994.

4.5.3 *Passiflora* seed should be treated as orthodox for seed storage purposes as their viability and longevity is extended by dehydration and storage in sub zero temperatures.

5 Materials and methods

5.1 Materials (non-biological)

5.1.1 Equipment

Incubator:	Genlab	Dual thermostat (94G037) Model E1C
Incubator:	Genlab	Single thermostat (94G168) Model M6C
Electronic balance:	Sartorius	1207 80.0000g
Beakers:	50ml Pyrex	Bibby Sterilin Ltd
Conical flasks:	50ml Pyrex	Bibby Sterilin Ltd
Petri dishes:	55mm Triple vent	Greiner Labortechnik
Storage jars:	700ml Glass	Anchor Hocking Co., Ohio, USA
Burettes:	100ml Class B 241/0120	Single-bore stopcock Valac
Thermometers:	Red Spirit BDH	Cat. 268/0069
Specimen bottles:	100ml polypropylene PS Azlon BGG 424	Bibby Sterilin Ltd
Specimen tube:	30ml Screw cap A215/0040	Bijou Polypropylene
Thermohydrograph:	Cassella	A1424
Charts (thermohydrograph):	Cassella	750/1209
Retort stands:	Stainless steel	Baird & Taplock
Clamp:	Three-pronged aluminium	Rexaloy
Bosshead:	Rexaloy	
Clamp (retort):	Rexaloy	
Filter papers:	Whatman No. 1	55mm circles No. 1001/055
Parafilm:	American National Can.	PM-992
Fridge:	programmable, domestic	M-eurotech

Freezer: programmable, domestic M-eurotech

Dissecting instruments

Protective gloves and goggles

Light microscope: Swift binocular 710162 Microinstruments Ltd

At the Department of Engineering & Applied Science, Electro-optics, at the University of Bath:

Dissecting microscopes Prior

Sputter coater Edwards 150B

Scanning electron microscope Joel JSM T330

Scanning electron microscope Joel JSM 6310

Funded by the Science & Engineering Research Council at the University of Bath

5.1.2

Chemicals

Water: Super purity solvent code H950, filtered to 0.5 microns, pH 6.8 to 6.9

Indicator strips: pH 6.5-10.0 BDH Prod. 31503

Indicator strips: pH 0-6 BDH Prod. 31505

Di-phosphorus pentaoxide P_2O_5 BDH Laboratory Supplies Prod. 295273Y

Gibberellic acid $C_{19}H_{22}O_6$ GA_3 BDH Laboratory Supplies Prod. 44047

Dimethyl sulphoxide CH_3SOCH_3 BDH Laboratory Supplies Prod. 28216 4K

Agar (Agar-Agar) Sigma Plant cell culture tested A 1296

Alginic acid Sigma Plant cell culture tested A 0682

Phlagel (Gellon gum) Sigma Plant cell culture tested P 8169

Silica gel BDH Laboratory Supplies Prod. 30062 7B

Ammonia solution 33% BDH Laboratory Supplies Prod. 271415 B

Domestic bleach Sodium hypochlorite less than 5% Tesco Stores Ltd

Ethanol 99.7-100% BDH Laboratory Supplies Prod. 10107

Garden lime	CaO	Vitax Ltd
Tea bags		Tesco Stores Ltd
Water (plant cultivation)	Domestic supply	pH 6.4-6.6
Nitric acid	BDH Laboratory Supplies	Prod. 10168
Blutac	Bostick Ltd	
Fertiliser	Vitax Q4	Vitax

5.2 Materials (biological)

5.2.1 Choice of species

Passiflora edulis Sims would have appeared to be the obvious first choice but so much work had already been published on this species that with only limited resources available for this research it was considered that species which had not been investigated so thoroughly might be more rewarding. The chosen species or varieties had to fulfill a number of essential criteria and if possible cover other criteria that were considered important but not essential.

Essential criteria:

1. Seed should be readily obtainable in quantity
2. Plants must be propagated from verified stock, preferably collected in the wild
3. Stock must be healthy and virus free
4. Seed must be true to type
5. Chosen species must be reluctant to hybridise with other species grown in close proximity
6. A species with economic importance was to be included.

Non-essential criteria:

1. Stock must be easy to cultivate under glasshouse conditions in the UK
2. Species with large seeds would be preferable but not essential
3. Species not requiring hand pollination would be preferable
4. Mature vines must be of a manageable size
5. Species should come from as diverse habitats as possible
6. Species should come from different subgenera if possible
7. A horticultural hybrid would be advantageous for some studies
8. A species with ecological importance would also be most beneficial

It was impossible to meet all these criteria but most were fulfilled admirably by the four species and one cultivar that were chosen.

5.2.2 Detailed description of the five primary taxa in this study

Descriptions are mainly from personal experience but from literature where stated.

5.2.2.1 *Passiflora vitifolia*

Subgenus *Distephana* (Juss.) Killip. *Field Museum of Natural History* (1938)

P. vitifolia H. B. Kunth *Nov. Gen. & Sp.* 2: 138 (1817)

Synonyms (recognised by Killip, 1938):

P. sanguinea J. E. Sm. in *Rees. Cycl.* 26: *Passiflora* No. 45 (1819)

P. punicea R. & P. ex DC. *Prodr.* 3: 329 (1828)

P. vitifolia var. *cassiquiarensis* M. Roemer, *Fam. Nat. Syn.* 2: 181 (1846)

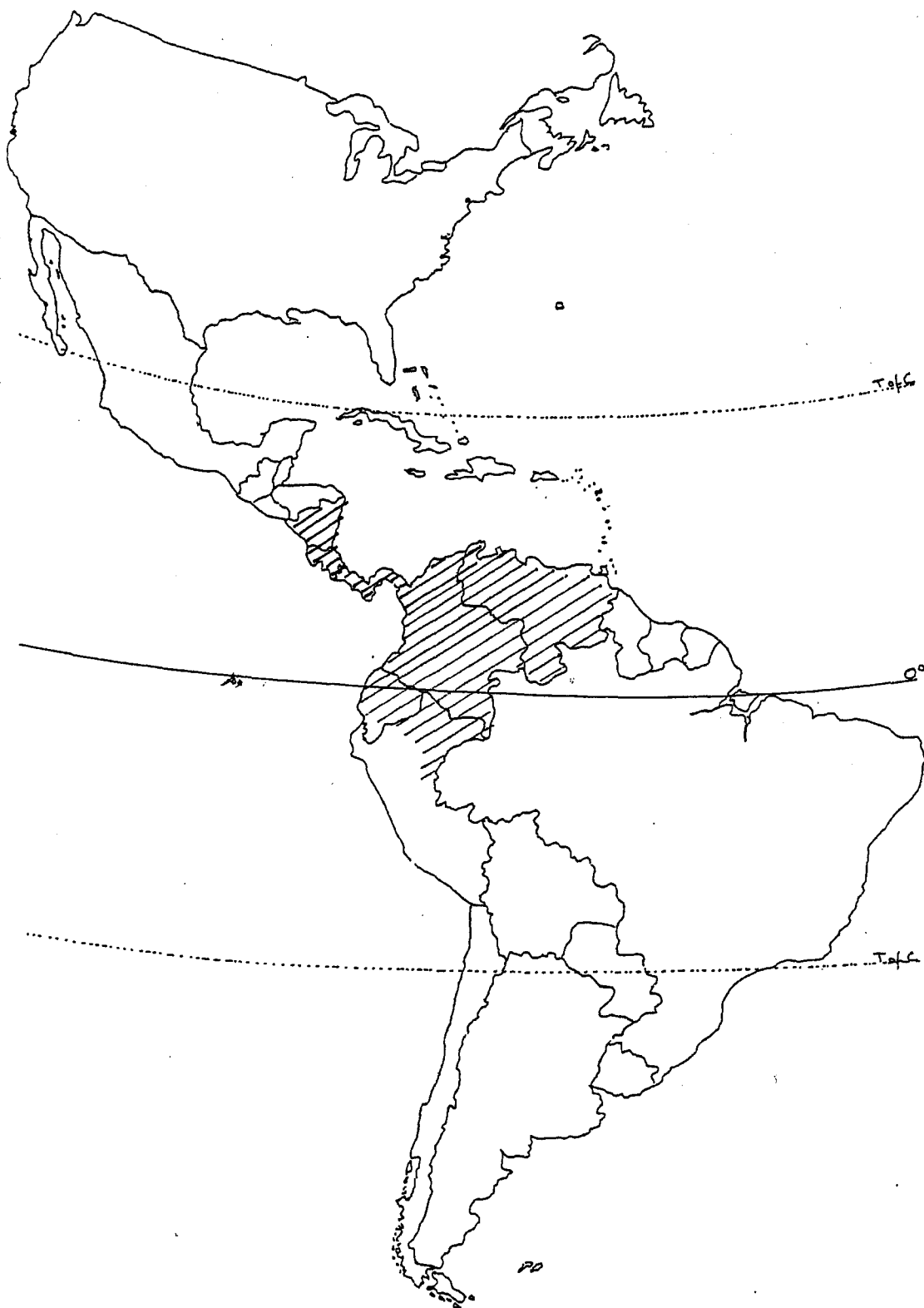
P. serrulata var. *pubescens* Griseb. *Bonplandia* 6: 7 (1858)

P. servitensis Karst. *Linnaea* 30: 163 (1859)

Large vine, 30m and above; roots fibrous, main roots produce sucker growths when damaged; stem terete, ferruginous-tomentose; stipules setaceous, 3 to 5 mm long, 1-1.5mm wide with two nectarous glands approximately halfway, soon deciduous; tendrils strong, 180-220mm long, tomentose; petiole 25-40mm long, biglandular at base, glands orbicular; leaves 70-160mm long, 110-180mm wide, three-lobed to below middle (lobes acuminate), 3-5 nerved, irregularly repand-dentate or crenate, membranous, lustrous above, tomentose on nerves above, densely puberulent or tomentose beneath; peduncles stout, 40-90mm long, 14-18mm wide with 4-10 nectarous glands on serrate margin; flowers scarlet, bright red or vermilion; hypanthium crateriform, margin crenate (in 10 segments), 9-11mm high, 14-17mm in diameter; sepals lanceolate, 52-68mm long, 14-18mm wide, carinate, the keel terminating in an awn, dull deep red without, bright red within, glabrous; petals linear-lanceolate, 48-53mm long, 11-16mm wide, obtuse, bright red both surfaces, glabrous; corona filaments in 3 or 4 series, outer series bright deep red, 16-24mm long, the next two series white, 10-14mm long, may be fused into one irregular series in some distinct populations, inner series white, 12-16mm long, erect, closely surrounding the androgynophore, 12-17mm long, the upper half cleft into numerous filaments, the lower part membranous, slightly fleshy; operculum deflexed, 6-10mm long, pink, crenate, apex fringed with 3mm-long fine filaments; androgynophore 36-48mm tall; stamina filaments greenish pink, 1mm long, 2mm wide; stamens 10-12mm long, 3mm wide, greenish pink towards the filament; pollen deep yellow; ovary ovate, 8mm long, 4mm wide, green; style 12-16mm long, bright red; stigma triangular, 4-5mm long, 4-5mm wide, pale green; fruit ovoid, 56-68mm long, 46-54mm wide, camouflaged with deep and pale green variegations in 6 distinct vertical sections, densely pilose; exocarp hard, becoming brittle with age, surface pilose; pericarp

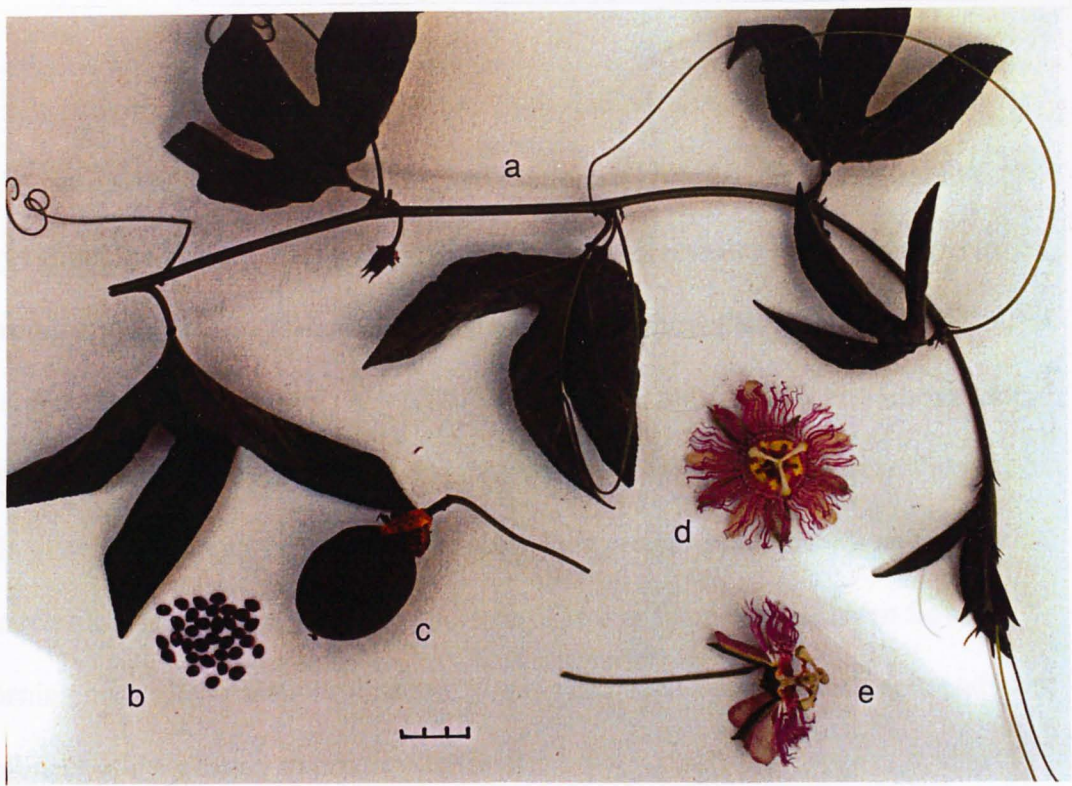
fleshy, pale green, 2.5-3.5mm thick; mesocarp white, fleshy, 2-3mm thick; endocarp tough, thin membrane 0.2-0.5mm thick, containing arilled seed; arils pale yellow, sweet and aromatic, juicy; seed symmetrical, obovate, very compressed with crenulated margin, acute at base, rotund at apex with depressed triangular chalazal beak, middle slightly convex with reticulate foveate surface on each side; seed per fruit 149 (190) 218, 6-7.5mm long, 3-4mm wide, 1.25-1.5mm thick, 100 seed 1.929g (Vanderplank, unpublished). Distribution: Nicaragua to eastern and southern Venezuela, Colombia, eastern Ecuador and northern Peru at low altitudes (Plate 17). Local names: 'guate-guate' (Panama), 'curuvito', 'granadilla' (Colombia) (Killip, 1938) (Plates 18, bottom, 24 and 27).

P. vitifolia has several closely related species which all have large red flowers and are confined largely to lowland tropical forests: *P. coccinea* Aubl., *P. glandulosa* Cav., *P. quadrifaria* Vanderplank, *P. speciosa* Gardn., *P. variolata* P. & E., *P. buchtienii* Killip, *P. quadriglandulosa* Rodschied and *P. involucrata* (Mast.) Gentry. Whereas *P. vitifolia* is endemic to northern South America only, its related species are common over a much larger area including the Guyanas, Brazil, Bolivia, Cuba and some Caribbean islands. The seed of these related species are morphologically very close to those of *P. vitifolia* and are expected to behave in a similar manner for seed storage purposes.



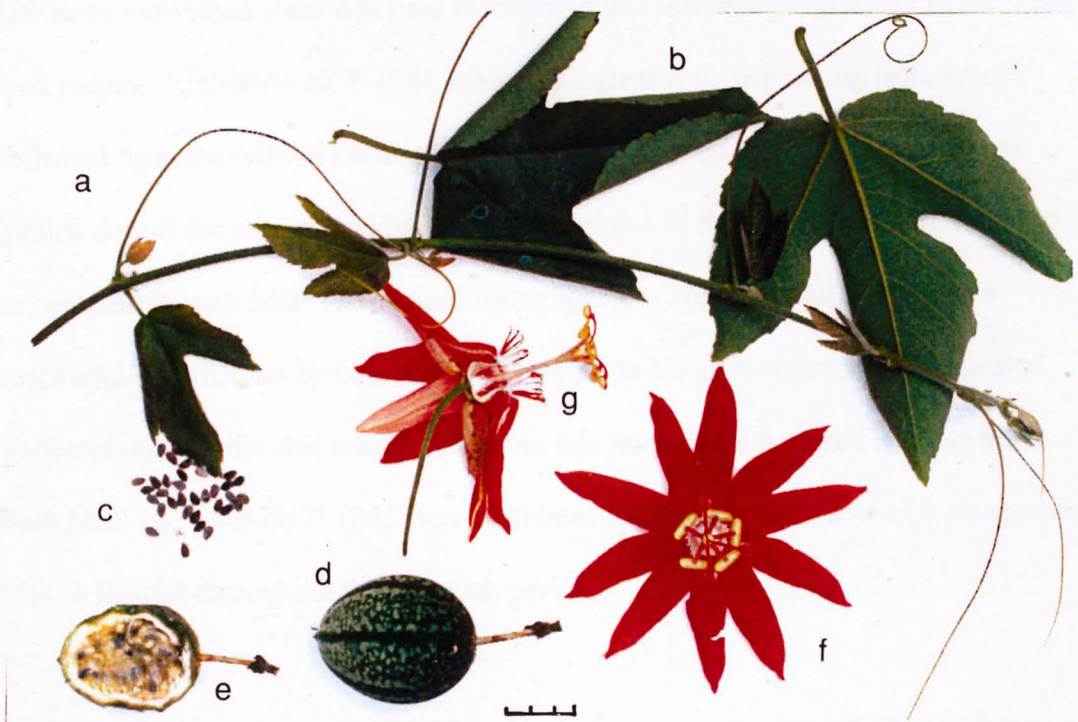
P. vitifolia distribution: Lowland rainforests of Nicaragua, Costa Rica, Panama, Venezuela, Colombia, Ecuador and northern Peru.

Plate 17. Distribution map for *P. vitifolia*



P. incarnata L., 1753 (NCP 1113)

a. Fertile shoot; b. Clean seed; c. Mature fruit; d. Flower viewed from above; e. Longitudinal section through flower showing internal structure.



P. vitifolia H. B. Kunth., 1817 (NCP 1251)

a. Fertile shoot with developing flower buds that are surrounded by colourful bracts from infancy to maturity; b. Mature leaves; c. Clean seed; d. Mature fruit; e. Longitudinal section through fruit showing seed within their arils; f. Flower viewed from above; g. Longitudinal section through flower showing internal structure.

Scale bar in cm

In its natural habitats, in lowland tropical rainforests, flowering is continuous throughout the year. This ensures daily visits from its primary pollination species of hummingbird, the Long-tailed Hermit, *Phaethornis superciliosus*, and the White-bearded Hermit, *Phaethornis hispidus* (Skutch, 1964, Snow, 1982, and Christensen, 1998). When in cultivation flowering may still be continuous throughout the year but if kept at temperatures below 10°C for prolonged periods plant growth and flowering are retarded, resulting in prolonged periods of two or three days between flowers opening on fertile shoots. Pollination is rarely achieved by insect visitation and hand pollination is necessary to produce fertile fruit.

P. vitifolia NCP 1252 is a single accession originating from Loggies Nurseries, USA, in 1989 and is believed to be from a selected seedling grown from wild collected seed. The same individual plant was used throughout this research programme as the female seed parent. *P. vitifolia* NCP 1251 is also a single taxon, originating from seed collected from the wild in Ecuador in 1991, and was used as the male seed parent (pollen donor) for research purposes. No other taxa in this collection were found to be compatible with NCP 1252 as pollinator species. However, NCP 1251 was successfully pollinated by two taxa, *P. quadrifaria* Vanderplank and *P. x piresae* Vanderplank, and for this reason seed from this taxon were not used in these trials. Both NCP 1251 and NCP 1252 were cultivated in the same glasshouse (6.7m span by 15m in length) throughout this research period.

Both plants were originally cultivated in large 20 litre pots in a well drained John Innes type loam-based compost. Once they had outgrown their pot they were allowed to root through the basal drainage holes of the pots to establish their roots in the

under-floor heated sand bed (125mm depth of pit sand). The vines were permitted to grow unhindered to the apex of the glasshouse roof (4.5m high) during the summer months and were pruned back during the winter after fruit harvest to occupy an area of 3m². The basal growth of NCP 1252 in 1999 was 290mm. Large main roots that became damaged during routine cultivation work produced vigorous sucker-growths that were regularly removed. Some of these growths were 4-5m from the vine base.

Plant fertiliser in the form of granules of the slow-release fertiliser Vitax Q4 were intermittently scattered over these plant beds during spring and summer months.

Minimum winter temperatures were maintained at 12⁰C and glasshouse ventilation started when the temperature reached 23⁰C. Maximum temperatures rarely exceeded 30⁰C.

Hand-pollination was essential and was completed between 12 noon and 3pm each day (British Summer Time) by removing fertile stamens from NCP 1251 and dusting the pollen onto the stigmas of open flowers of NCP 1252. Although hand-pollination is still possible throughout the year, the success rate during the winter months is greatly reduced due to several factors but mainly low temperatures, short day length and excessively high humidity.

Fruit were harvested from the glasshouse floor only after natural fruit fall. The movement in the vine created by the air circulation system of the glasshouse warm air boilers, which is continuous throughout the year, is sufficient to dislodge fruit when they are fully ripe.

Seed extraction and cleaning followed the same procedure as for *P. morifolia* but with a more gentle approach as the seed of *P. vitifolia* may be fractured by rough handling.

P. vitifolia has been cultivated in Europe since about 1880 and there were several publications around this period exalting its virtues. In subsequent years there were many attempts at hybridising this species with hardy species like *P. caerulea* and *P. incarnata* but although seed were produced and seedlings raised, their flowering was poor and flower buds aborted at an early stage. Hybrids produced with *P. coccinea* include *P. 'Cordelia'* and *P. 'Hot Shot'* which are of horticultural merit. The hybrid *P. x piresae* is from the cross with *P. quadrifaria* Vanderplank as the female seed parent.

No commercial cultivation of *P. vitifolia* has been recorded but fruit are sometimes offered for sale in local markets in Ecuador, Colombia and Central America.

5.2.2.2 *Passiflora incarnata*

Subgenus *Passiflora*

Series *Passiflora*

P. incarnata L. *Sp. Pl.* 959 (1753)

Synonyms (recognised by Killip, 1938):

P. Kerii Spreng. *Syst. Veg.* 3: 39 (1826)

P. incarnata var. *integriloba* DC. *Prodr.* 3: 329 (1828)

P. edulis var. *Kerii* Mast. *Trans. Linn. Soc.* 27: 637 (1871); in Mart. *Fl. Bras.* 13 (1): 610 (1872)

Plant very herbaceous, producing long annual climbing stems from subterranean crown, glabrous or usually finely pilosous; roots thick and fleshy producing sucker growths during late summer; stem terete, strong, vigorous; stipules setaceous, 2-3 mm long or glandular-serrulate with 1-3 small glands up to 4 mm long, very early deciduous; petiole 12-80 mm long, biglandular near apex, glands suborbicular, sessile; leaves 60-150 mm along mid-nerve, 50-120 mm along lateral nerves, 70-150 mm between apices of lateral lobes, three-lobed from three-quarters to four-fifths of their length, cordulate, finely serrate, three-nerved, membranous, dark green above, glaucescent beneath; lobes ovate-lanceolate or oblong-lanceolate, 20-50 mm wide, acute or acuminate, the middle lobe narrowed at base, rarely the lateral lobes bilobate; tendrils strong, 140-240 mm long; peduncles up to 100 mm long, stout; bracts spatulate or oblong, 4-7 mm long, 2.5-4 mm wide, obtuse or acute, minutely glandular-serrulate towards apex, conspicuously biglandular at base, borne approximately 5 mm below flower; flowers up to 70 mm wide; hypanthium short-campanulate; sepals lanceolate-oblong, 20-30 mm long, 8-12 mm wide, white, pale lavender or pinkish, slightly carinate, the keel terminating in an awn 2-3 mm long; petals usually slightly shorter than sepals, obtuse, white, pale lavender or pinkish; corona filaments in six series, lilac, mauve, pinkish, or pure white in *P. incarnata* var. *alba*, outer two series filiform, 15-25 mm long, crispate at apex, usually white for lower one-third and coloured towards apex, succeeding three series capillary, about 2 mm long, radiate or erect, usually with purple apex, innermost series membranous at base, filamentose above, filaments 4 mm long; operculum membranous, 2 mm long, incurved, fimbriate; nectar ring a low ridge midway between operculum and androgynophore; limen cupuliform closely surrounding the base of the androgynophore, crenulated; androgynophore 15 mm tall; staminal filaments flecked

deep purple on yellow-green; stamens pale yellow above; pollen pale yellow; style 15 mm long, pinkish; stigma olive-green, 4-5 mm diameter; ovary ovoid, densely brownish or whitish velutinous-tomentose; fruit deep green, ripening yellowish-green, sparsely pilose, 50-70 mm long, 40-60 mm diameter; exocarp flexible, 0.5 mm thick, sparsely pilose on surface; pericarp white, 1-2 mm thick; mesocarp spongy, white, with numerous fleshy mesocarp threads that attach to the endocarp, 5-7 mm thick; endocarp thin, translucent membrane 0.1 mm thick to which the arilled seed are secured; arils white or very pale yellow, translucent, flavour sharp like a lemon when unripe, sweet, juicy and aromatic when fully ripe, 15 mm long, 12 mm wide, 6 mm thick; seed golden brown to dark brown, symmetrical obovate, slightly compressed with smooth narrow margin, acute at base, rotund at apex with depressed chalazal beak; middle convex with numerous (more than 80) smooth shallow reticulations on each side; seed per fruit 65 (112) 163; seed size 5-6.5 mm long, 4-5 mm wide, 2-2.25 mm thick; 100 seed 2.689-3.818g (Vanderplank, unpublished) (Plate 18, top).

Distribution: USA from Virginia to Missouri and south to Florida and Texas, also a population in Bermuda (Killip, 1938) (Plate 19).

P. incarnata is often found growing on wasteland and railway embankments and is common in many of the southern states of the USA. Common names include 'May Apple', 'May Pops', 'Apricot-vine', 'Pasionaria', 'Virginian Passionflower', 'Purple Passionflower', 'Flesh Coloured Passionflower' and 'Wild Passionflower' (Killip, 1938).



P. incarnata distribution: USA, from Virginia to Missouri and south to Florida and Texas, and Bermuda.

Plate 19. Distribution map for *P. incarnata*

P. incarnata is one of two truly herbaceous species endemic to North America. It is of considerable economic importance and many hundreds of acres are cultivated each year in the USA. Fruit are harvested during the summer for processing into drinks, sweets and sherberts, and aromatic extractions are used in soaps, shower-gels and other toiletries. The young shoots and leaves are harvested during the growing season, particularly in the late summer when they are rich in various alkaloids (flavonoids) that have nerve-calming or sedative properties. Once dried, the leaves are used in many familiar preparations to aid natural sleep and relaxation, such as N.R.I. 'Night Tablets', Health and Heather 'Quiet Night', Lanes 'Quiet Life', Metabasic Products 'Su Nerven' and Health and Diet 'Passion Flower'. The dried flower heads are used to treat insomnia, neuralgia, diarrhoea and discharges from the vagina (Usher, 1974).

A number of decorative hybrids have been raised by interspecific hybridisation. *P.* 'Incense' (*P. incarnata* x *P. cincinnata*) is well known in the USA and Europe and tens of thousands are marketed each year as patio plants. Other notable hybrids are *P.* x *colvillii* (Sweet, 1825), (*P. incarnata* x *P. caerulea*), *P.* 'Medallion' (*P. incarnata* x *P. actinia*), *P.* x *nebulae* (*P. incarnata* x *P. serratodigitata*) and *P.* 'Karen Jacobson' (*P. incarnata* x *P. lehmanii*).

P. incarnata NCP 1113 was raised from wild collected seed harvested in 1987 and provided by Roy Cheek of the Cannington College of Agriculture and Horticulture. Individual plants are short-lived when cultivated in containers under glasshouse conditions and the original cultivated taxa have been gradually replenished by plants raised from seed harvested from these original plants. Minor variations were

observed in all these taxa, mainly in the size and colour of the flowers, but these were in keeping with variations in wild populations described by E. P. Killip in 1938.

Seedlings were potted on until they reached a final pot size of eight litres, which was sufficient to produce multi-stemmed flowering plants up to 1.75 metres high. A well-drained soil-based compost, similar in formulation to John Innes Potting Compost No. 3 was used but with 50% extra sharp sand or limestone chippings. 50-60 taxa were spaced at 0.5 m centres in double rows 0.5 m apart and trained over bamboo support canes 1.5 m high. These occupied a small section of a glasshouse 20.1 m x 28.8 m with heating capacity for frost protection but otherwise unheated. The cultivation temperature was between 4 and 8⁰C above the outside air temperature, rising to a maximum of 25⁰C during the long days of the summer months. Fertiliser was applied to vines between June and August using granules of the medium slow-release fertiliser Vitax Q4. These were hand broadcast over the tops of the pots every three weeks. Water was given as required during this period and subsequently reduced to nil by the end of October as the annual stems became deciduous and redundant. Only minimal water was given during the winter months in order to stop the thick fleshy roots from becoming dehydrated.

New vigorous shoots appear each year in early April with the first flowers appearing in May. Flowering continues through to October and possibly later in warmer weather conditions. Most individuals are not self-fertile and it was necessary to assist natural entomophily by daily hand-pollination using a small soft-haired paintbrush. Pollen was collected and distributed from flower to flower, most flowers obtaining a cocktail of pollen from many individuals as they would from a bee or other

pollination insect. Anthesis was completed by 3pm BST (British Summer Time). Insects observed visiting these flowers for nectar and pollen-gathering were various flies (Diptera) and members of *Apoidea* (Hymenoptera) including honey bees, bumble bees, cuckoo bees and humble bees. This small plant population was cultivated in isolation away from any species that may have been compatible and cross-pollinated by insect visitation. Fruits were collected from the glasshouse floor after natural fruit fall. The air movement in this well-ventilated glasshouse was sufficient to dislodge ripe fruit after the incision layer had been (activated). Seed extraction and cleaning followed the same procedure as described for *P. morifolia*. In general seed of *P. incarnata* were much easier to clean and prepare for storage than those of *P. morifolia* on account of their greater size and less persistent attachment of the arils.

5.2.2.3 *Passiflora morifolia*

Subgenus *Decaloba*

Section *Pseudodysosmia* (Harms) (Killip) J. M. MacDougal, *Am. Soc. Plant Tax.*

Vol. 41 (1994)

P. morifolia Mast. in Mart. *Fl. Bras.* 13 (1): 555 (1872)

Synonyms (recognised by Killip, 1938):

P. warmingii Mast. in Mart. *Fl. Bras.* 13 (1): 554-591 (1872)

P. weberiana Mast. in Andre, *Rev. Hort.* 57: 113 (1885)

P. erosa Rusby, *Bull. New York Bot. Gard.* 4: 363 (1907)

P. warmingii ssp. *chacoensis* R. E. Fries, *Arkiv. Bot.* 8 (8): 4 (1909)

P. heydei Killip, *J. Wash. Acad. Sci.* 12: 258 (1922)

Caespitose climbing vine with long annual stems from thickened woody roots, pubescent throughout with uncinatate trichomes; stem subterete, striate; stipules ovateo-

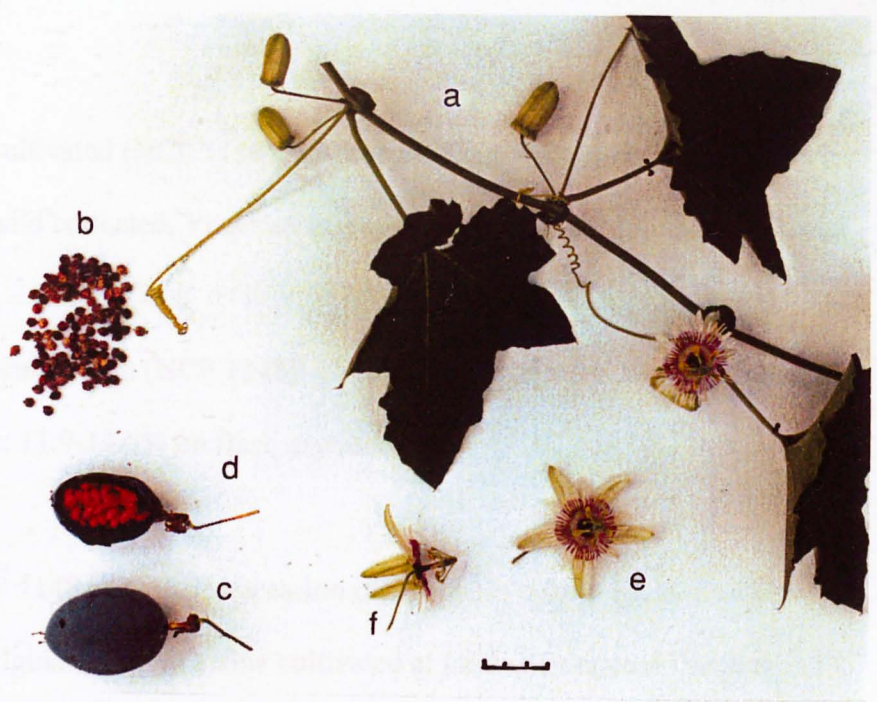
auriculate, caudate to long-caudate, the margin entire or rarely with denticulate to caudate teeth; petioles 2-7 mm long, biglandular near apex, nectaries urceolate to obovoid, nectarous surface directed downwards; leaves 3-5 lobed, 3.5-9.5 cm long, 4.5-12.5 cm wide, the lobes shallowly deltate to ovate, acute to obtuse or rounded; margins dentate to serrate; leaf-laminar nectaries usually absent; peduncles 12-30 mm long, solitary or in pairs, bearing scattered linear-triangular bracts; flowers 2.5-3 cm in diameter with slight sweet odour; hypanthium 7-12 mm diameter; sepals 13-20 mm long, 4.5-8 mm wide, lanceolate to triangular-ovate, slightly carinate near apex, green with whitish margin without and white within; petals 9-11 mm long, 3-4.5 mm wide, narrowly ovate, white on both surfaces; corona filaments 50-65 mm in one series, 7-11 mm long, white with a broad band of violet or purple distally; limen uniformly purplish; staminal filaments connate; anthers 3.3-5 mm long; ovary ellipsoid to widely ellipsoid or subglobose, pubescent with uncinuate trichomes, sometimes on raised bases; styles 6.5-9 mm long, 22-30 mm diameter, ellipsoid to subglobose, pubescent with sessile or raised trichomes or, in Venezuelan population, hispid on 0.8-4 mm long raised bases; ripe fruit deep purple-black and glaucous; pericarp 2-4 mm thick, very soft and purple throughout; arils orange-red, insipid to sour; seed widely obovate, very coarsely reticulate-foveate with 9-12 foveae per side, 4.3-4.8 mm long, 3.2-3.4 mm wide, 1.7-2.1 mm thick (Vanderplank, unpublished). Distribution: in Central America only one isolated population is recorded in Guatemala. In South America *P. morifolia* is found in Colombia, Venezuela to Peru (not in the Amazon basin), Bolivia, Paraguay, southern Brazil and northern Argentina (MacDougal, 1994), (Plate 20). In Guatemala flowering is from July to August with fruiting in September. In South American countries flowering is from December to March and fruiting from February to April (MacDougal, 1994)(Plate 21, top).

P. morifolia was cultivated in France as early as 1884 (Andre, 1885 and 1887) and is now well known in Europe and a favourite in many botanical gardens. It is also cultivated in parts of Asia, Australia, Africa and North America. In its native habitats *P. morifolia* is found in seasonal dry semi-temperate to tropical deciduous forest or on the edge of gallery forest and sometimes on open scrub or wet montane forest (MacDougal, 1994). No specific insect or other animal has been identified as being primarily responsible for pollination and no animal has been recorded as being responsible for seed dispersal, but it seems reasonable to assume that this is zoochory.

In cultivation under glass in the UK flowering is from May to October and fruiting from August to November. Many fruit become shrivelled on the vine but remain on deciduous redundant stems until January or February. Both aerial and fallen fruit are food for small rodents, including the Wood Mouse *Apodemus sylvaticus*, the House Mouse *Mus musculus* and the Field Vole *Microtus agrestis* (sometimes called the Short-tailed Field Mouse). These rodents are very effective at dispersing the seed by randomly burying surplus harvest. In the glasshouse seedlings are commonly found as far as 25 metres from the mother plant. The fruit of these cultivated vines are larger than those recorded from the wild population and may be 40 mm long and 32 mm in diameter. The seed are also larger, being 4.5-5.1 mm long, 3.1-3.7 mm wide and 1.9-2.1 mm thick. This is consistent with most other species. When in cultivation all their morphological features, including their seed, are enlarged (Vanderplank, unpublished).

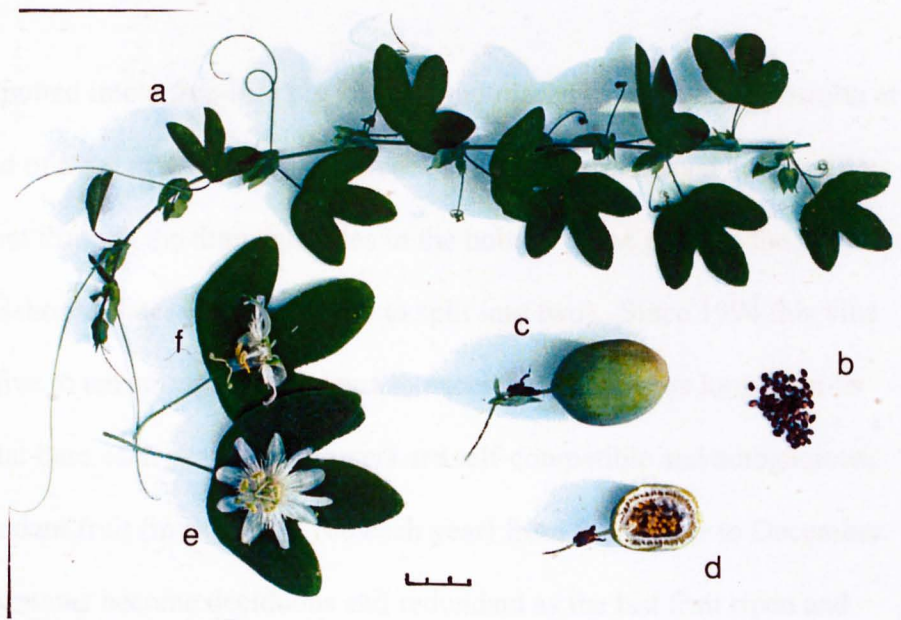


P. morifolia distribution: Guatemala, Colombia, Venezuela, Ecuador, Peru, Bolivia, Paraguay, Argentina and south-eastern Brazil.



P. morifolia Mast., 1872 (NCP 1148)

a. Fertile flowering shoot; b. Clean seed; c. Mature fruit; d. Longitudinal section through mature fruit showing arils; e. Flower viewed from above; f. Longitudinal section through flower showing internal structure.



P. subpeltata Ortega, 1798, NCP 1223

a. Fertile shoot; b. Clean seed; c. Mature fruit; d. Longitudinal section through mature fruit showing arils and threads of mesocarp tissue; e. Flower viewed from above; f. Longitudinal section through flower showing internal structure.

Scale bar in cm

Fresh dry seed, cultivated (NCP 1148): 100 seed 1.838g

Fresh dry seed, wild collected, Venezuelan population (Miguel Molinari): 100 seed
1.259g

Seed per fruit in cultivation (NCP 1148): 13-92, average content 57 (from 20 fruit)

Moisture content: 11.9-14.6% on fresh dry seed basis

P. morifolia NCP 1148 is a single accession raised in 1990 from horticulturally produced seed originating from a vine cultivated at Leiden Botanical Gardens in the Netherlands. No other accession records are available but this taxon is consistent with two other cultivated populations, from the Botanical Gardens at Cambridge University, England and the Royal Horticultural Society gardens at Wisley, under the name *P. warmingii* Mast., which is synonymous with *P. morifolia* Mast.

This vine was potted into a five-litre pot in 1992 and placed in an isolated position at the western end of a 6.7 m x 28.8 m glasshouse. It became established here and was permitted to root through the drainage holes in the bottom of the pot into the hardcore base of the glasshouse (later causing the pot to split into two). Since 1994 this vine has produced five to ten strong annual stems in excess of five metres long from its woody perennial base each year. The flowers are self-compatible and autogamous, producing abundant fruit (in excess of 100 each year) from September to December. These climbing stems become deciduous and redundant as the last fruit ripen and cooler winter temperatures are encountered, along with the poor light intensity and reduced daylight hours of an English winter. The minimum winter temperature was 1°C for short periods, the average temperature being approximately 6°C. The potting compost surrounding this woody base is left un-watered from October to April each

year but the roots that have penetrated the glasshouse hardcore base remain constantly wet due to the outdoor winter rainfall that seeps beneath this glasshouse. Old dead shoots are removed during winter and new growth begins in early April. The first flowers appear towards the end of May and growth is at its most vigorous during June and July when glasshouse temperatures may rise above 30⁰C during the day.

Fruit were harvested only when they were fully ripe (i.e. deep purple over all their surface, soft to the touch and when gently depressed between finger and thumb the indent did not reflate) and before they became withered.

The bright orange-arilled seed were extracted from each fruit with the aid of a pocket penknife. The flesh and seed were then molested in a coarse sieve with square holes of 2-3 mm in diameter using the back of the fingers in a circular motion. As the seed became detached from the arils the fractured flesh was washed through the sieve using clean tap water at 14⁰C. After 10-15 minutes of this treatment the new, partly clean seed were placed between soft paper tissue (kitchen roll) and rubbed to remove persistent arils and surface moisture. Clean seed were then spread on the top of five or six layers of newspaper and placed on a warm surface at 25⁰C to dry for up to three days. They were then taken from the paper and any remaining dried arils removed by hand. Seed were then considered to be ready for research purposes.

5.2.2.4 *Passiflora subpeltata*

Subgenus *Passiflora*

Series *Lobatae* Killip. *Field Museum of Natural History*, volume XIX (1938)

P. subpeltata Ortega, *Nov. Rar. Pl. Hort. Matrit.* **6**: 78 (1798)

Synonyms (recognised by Killip, 1938):

P. alba Link & Otto, *Icon. Pl. Rar.* **65** (1828)

P. stipulata Aubl. *Sensu Griseb. Bonplandia* **6**: 7 (1858)

P. adenophylla Mast. in Mart. *Fl. Bras.* **13** (1): 568 (1872)

P. atomaria Planch. in Mart. *Fl. Bras.* **13** (1): 570 (1872)

P. stipulata var. *atomaria* Planch. in Tr. & Planch. *Ann. Sci. Nat. V. Bot.* **17**: 153 (1873)

Vine glabrous; stem terete, striate; stipules semi-oblong, 10-45mm long, 5-23mm wide, micronulate, entire, glandular-crenulate at base; petioles 40-60mm long, slender, bearing 2 to 4 ligulate glands 0.5-1.0mm long; leaves 40-150mm long, 50-160mm wide, three-lobed to or below middle, lobes oblong, up to 60mm wide, rounded or obtuse, glandular-serrulate in sinuses, glands (frequently obsolescent) subcordate and often subpeltata at base, glabrous or slightly pulverulent above, glabrous beneath; peduncles round, 40-60mm; bracts ovate-oblong, 10-25mm long, 10-15mm wide, acute or obtuse, cordate and slightly serrulate at base, borne just below the base of the flower; flowers borne singly, 40-50mm wide; sepals oblong, 20-25mm long, 5-10mm wide, obtuse, green without, carnate, the keel terminating in a foliaceous awn 10-15mm long, 1-3mm deep, pure white within; petals linear-oblong 18-22mm long, 5-7mm wide, pure white both surfaces; corona filaments pure white in five series, outer two 20mm long, the succeeding two series semi-erect, 4mm long,

innermost 6mm long; operculum membranous, erect, incurved 2.5mm high, nectar ring narrow; limen tubular, closely surrounding gynophore, the margin reflexed, crenulated; ovary ovoid, glaucous; fruit whitish green ripening mustard yellow, globose or obovate, 51-60mm long, 43-60mm diameter, exocarp thin, 0.2mm thick, pericarp soft, fleshy, 2.5-3.5mm thick, white; endocarp thin and papery, translucent, 0.1mm thick suspended on sparse long threads of mesocarp tissue 4-8mm long; seed mass enclosed by endocarp bag; arils fleshy, pale yellow, translucent; seed symmetrical, obovate, slightly compressed with smooth margin, acute at base, rounded at apex with acute chalazal beak, middle convex with numerous reticulations on each side, light or dark brown (Plate 21, bottom); seed per fruit 155 (210) 252, size 4.5-5.0mm long, 3-3.5mm wide, 1.5-1.75mm deep, 100 seed 1.243g, fresh dry seed moisture content 8.3-9.8% (Vanderplank, unpublished). Distribution: central Mexico through central America to Colombia and Venezuela from sea level to 2,800m altitude (MacDougal, 1994). Now introduced into many countries including West Indies, Cuba, Hawaii, South Africa, Australia and Asia (Vanderplank, unpublished) (Plate 22); very common in horticultural collections in Europe and North America. Local names: 'Granadina', 'granada de zorra' (Mexico) (Killip, 1938).

Flowering is from May to October with fruit harvest from August to December when cultivated under glasshouse conditions in the UK.

P. subpeltata NCP 1223 originated from seed supplied by Gabriel Boissy in France in 1989. Only vegetatively propagated plants from this taxon have been used in this study. A number of individual plants have been cultivated in three distinct environments during their preflowering, flowering and fruit maturation periods.



P. subpeltata distribution: Mexico, Central America, Colombia, Venezuela, Cuba and Haiti from sea level to altitudes of 2,800 metres.

Plate 22. Distribution map for *P. subpeltata*

All plants were grown in a well-drained 'John Innes' type, soil-based compost in 10-15 litre pots and allowed to root through the base of the pot into the glasshouse 'pit sand' floor. Some individuals were cultivated in an unheated well-ventilated glasshouse which stayed at a constant 3⁰C above the outside air temperature during the night-time and up to 5⁰C in daylight hours (glasshouse 5). Other plants were cultivated in a heated glasshouse in more humid conditions with a minimum temperature of 8⁰C, (glasshouse 6). A final group were cultivated in stove-house conditions of high humidity and high temperature with a minimum night-time temperature of 15⁰C and up to 35⁰C during daylight hours (glasshouse 7).

Plants were trained up 2m canes and allowed to grow higher up supporting wires to 3m high. *P. subpeltata* is a medium-sized slender vine, well suited to pot cultivation and needing less than two cubic metres of growing space per mature vine. Pruning of old or redundant shoots was performed as necessary, mostly during the end of the winter months. Individual vines are comparatively short-lived in cultivation and were replaced by vigorous young plants vegetatively propagated from the original genotype plant every 3-4 years. The flowers of *P. subpeltata* are sweet-scented and abundant with nectar. They are self-compatible and autogamous. Anthesis was completed by 2pm BST (British Summer Time) each day without artificial interference and only limited insect visitation was observed, mostly small flies (Diptera) and 'solitary bees' (Hymenoptera), which undoubtedly assisted in pollination. None of the species that were grown in the same glasshouse as *P. subpeltata* were found to be pollen compatible with this species and so no precautions were taken to prevent possible interspecific pollination. Fruit fall was 45-65 days after anthesis and fruit were harvested from the glasshouse floor. The main support of each vine was gently

shaken daily to dislodge any entangled fruit. Ripe fruit are pale mustard yellow, soft and usually slightly shrivelled. All prematurely aborted juvenile and unripe fruit were discarded. Seed extraction and seed cleaning followed the same procedure as described for the fruit of *P. morifolia*.

The only notable hybrid of *P. subpeltata* is *P. 'St Rule'*, *Royal Hort. Soc.* 1896, (*P. alba* x *P. buonapartea*) or (*P. subpeltata* x *P. x decaisneana*).

P. subpeltata is cultivated widely in Europe and North America as an ornamental vine but there are no accounts of the fruit being used domestically or for any commercial plantations. In the wild seed are probably dispersed by small mammals. Seed of *P. subpeltata* have been found in skunk droppings in Mexico (MacDougal, 1994).

Various other rodents have also been recorded as being responsible for seed dispersal (Abramsky, 1983 and Baretal, 1984). In cultivation under glasshouse conditions the fruit and seed are fed upon and dispersed by several rodents including the Wood Mouse (*Apodemus sylvaticus*), the House Mouse (*Mus musculus*) and the Field Vole (*Microtus agrestis*). Unripe fruit within easy reach of ground-dwelling and climbing mammals retains a strong odour of cyanide until it is fully ripe and falls from the vine. This ill odour seems to afford complete protection from invertebrate herbivores and bird predation until the fruit has fully matured.

5.2.2.5 *Passiflora x decaisneana*

P. x decaisneana M. J. E. Planchon, *Fl. Des Serres Ser. 1*, **8**: 267 (1853)

(*P. alata* x *P. quadrangularis*)

Synonyms (Vanderplank, unpublished):

P. x buonapartea Naudin, *Journ. Hort. Ser. III*, xi: 383 (1885)

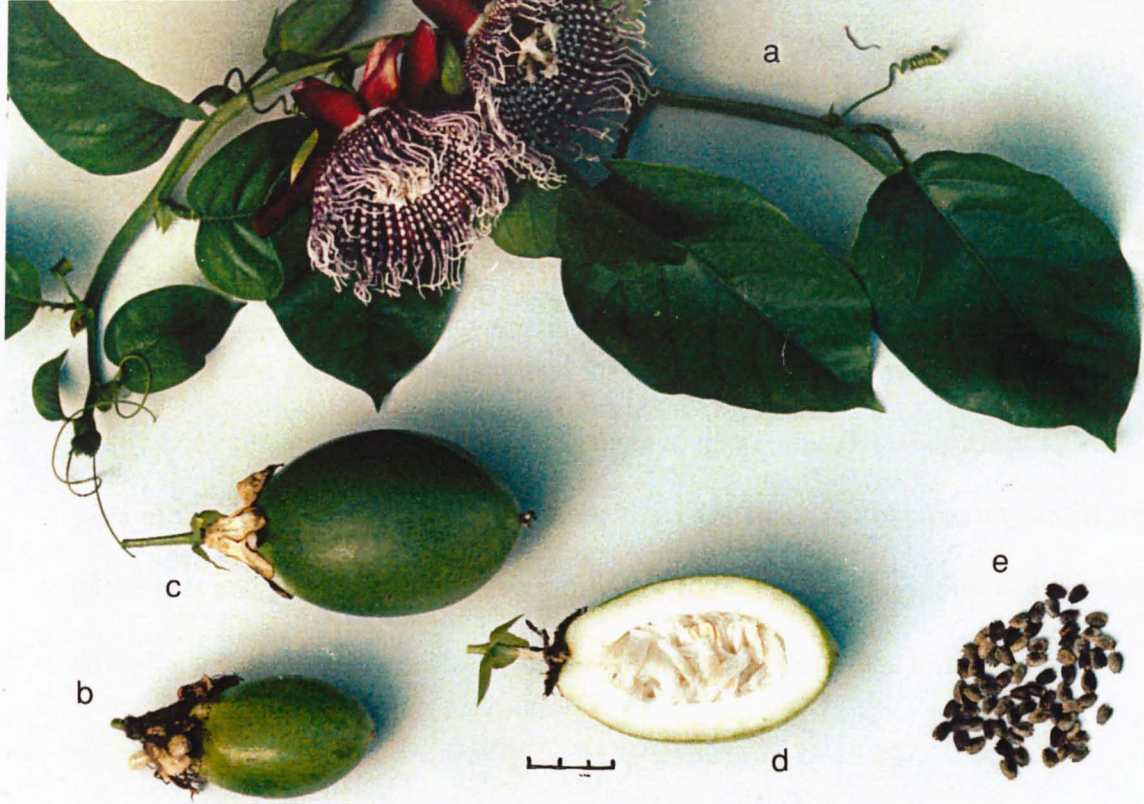
(*P. quadrangularis* x *P. alata*)

P. x innesii Mast., *Dict. Of Gard.* 3: 31 (1886)

Plant glabrous throughout; roots fibrous; stem stout, four-angled, angles conspicuously winged; stipules 18-22 mm long, 6-9 mm wide, ovate, margin serrulate; tendrils stout, strong, up to 350 mm long; petiole strong, carinate, 40-70 mm long, 5-7 mm diameter; petiole glands sessile, in pairs, four, occasionally five or six, 3 mm high, 2.5 mm diameter; leaves entire, broadly ovate or cordiform, 110-270 mm long, 80-160 mm wide, penninerved with prominent midnerve strongly elevated beneath, 8-10 secondary lateral nerves; peduncles 30-40 mm long, triangular in cross-section; bracts cordate-ovate, 25-30 mm long, 15-25 mm wide; flowers borne singly, up to 130 mm wide, deep red, violet and white (Plate 23); hypanthium campanulate; sepals ovate, 40-50 mm long, 18-24 mm wide, green without, keeled with a hair-like awn 2 mm long, deep brick red within; petals ovate-oblong, 45-55 mm long, 15-18 mm wide, deep brick red both surfaces; corona filaments in six series, outer two prominent and showy, fleshy, filiform, 65-75 mm long, 3-4 mm diameter at base, banded with red, purple, speckled mauve and white, crispate at apex, inner two series 4-5 mm long, banded purple and white; operculum membranous, 4 mm long; limen annular, yellow; androgynophore stout, enlarged near base with two annular processes; staminal filaments speckled red, 9 mm long, 3 mm wide; stamens pale, whitish green; pollen lemon yellow; style 12-14 mm long, whitish; stigma creamy white; ovary 10-12 mm long, 5-7 mm diameter, greenish white; fruit large, ovoid,

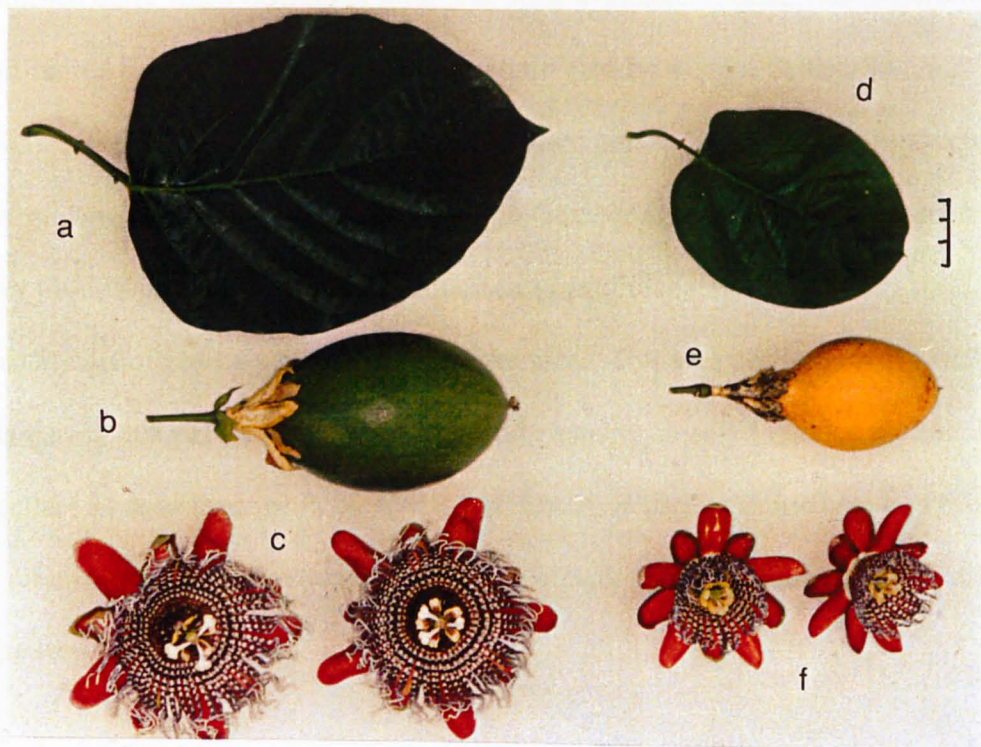
100-165 mm long, 65-95 mm diameter, bright green , ripening greenish mustard yellow; exocarp thin, 0.2 mm thick; pericarp thick, fleshy, greenish white ripening yellowish white, 12-16 mm thick; mesocarp membrane soft, white, 1.0-1.5 mm thick with mesocarp threads attached to the endocarp membrane that encloses the arilled seed; arils full of sweet aromatic juice, pale translucent yellowish white; seed large, symmetrical, obovate highly compressed, plane, with wide crenate margin, bidentate at base, tridentate at apex with triangular chalazal beak, middle slightly convex with reticulate-foveate surface on both sides, brown or dark brown; seed size 8-9 mm long, 6-6.5 mm wide, 1.75-2 mm thick; seed per fruit 54 (148) 237; 100 seed 3.9-4.2g. The morphological features of *P. x decaisneana* seed are intermediate between those of its parents *P. quadrangularis* and *P. alata* (Plate 23).

P. x decaisneana NCP 1064 is a horticultural hybrid which is distributed throughout the UK and Europe and is often on display in botanical gardens and private collections. In the 1980s and earlier it was often erroneously labelled *P. quadrangularis* and NCP 1064 originated under that name from the Royal Horticultural Society gardens at Wisley, Surrey. The species *P. quadrangularis* and its progeny *P. x decaisneana* are almost identical when considered from the written word but easily separated when viewed side by side. Both taxa were widely cultivated in the early part of the 20th century but as many collections became disrupted by war the more robust and enduring *P. x decaisneana* survived adverse conditions of low temperatures and general neglect and became confused with its seed parent. This confusion was aided by some publications that showed illustrations with the caption '*P. quadrangularis* var. *Decaisneana*' (Anon., 1855 and 1902).



P. x decaisneana Planchon, 1853 (NCP 1064)

a. Fertile shoot with flowers; b. immature fruit; c. Mature-sized unripe fruit d. Longitudinal section through unripe fruit showing thick fleshy mesocarp; e. Clean seed.



P. x decaisneana (NCP 1064), seed parent of *P.* 'Enigma'
 a. Leaf; b. Unripe fruit; c. Flowers viewed from above.
P. alata Dryand, 1781 (NCP 1037), pollen parent of *P.* 'Enigma'
 d. Leaf; e. Mature ripe fruit; f. Flowers viewed from above.

Scale bar in cm

Plate 23. Plant portraits of *P. x decaisneana* and *P. alata*

A small population of *P. x decaisneana*, raised by cuttings from the original single taxon, were cultivated in a heated glasshouse 28.8 m x 6.7 m which was maintained at a minimum temperature of 5⁰C, rarely rising above 25⁰C during summer. Plants were potted and cultivated as described for *P. morifolia* and permitted to root through the base of the pots into the glasshouse sand and gravel flooring. Fertilizer, in the form of the medium slow-release fertiliser Vitax Q4 was hand broadcast over the top of the pots and glasshouse floor every three to four weeks during spring and summer. After the plants were established, regular watering was not found to be necessary.

Flowering is from July to November. The flowers of *P. x decaisneana* are self-sterile but compatible with the pollen of *P. alata* NCP 1031, which flowers from August to December. Hand pollination was essential for successful fertilisation and this was performed daily when flowers of both taxa were available. Pollen was transferred on a soft-haired paintbrush and anthesis was completed by 4-5 pm British Summer Time (B.S.T.). The pollen of *P. alata* is seldom mature before 1 pm B.S.T. Fruit were harvested eight to ten weeks after anthesis in October and November. Although very heavy (400-600g), fruit stay loosely attached to pendular stems when fully ripe; they are easily dislodged by gentle shaking of the vine. This was performed on a daily basis during this period. Seed extraction and cleaning closely followed the same procedure as described for *P. morifolia* but, like *P. vitifolia*, the seed are less robust and require more gentle treatment. The hand cleaning was particularly easy because of the large size of the fruit.

Notable hybrids include the cultivar *P.* 'St Rule' (*P. alba* x *P. x buonapartea* or *P. subpeltata* x *P. x decaisneana*) which was raised by John Wilson in 1896. The progeny from the cross *P. x decaisneana* x *P. alata*, is *P.* 'Enigma' Vanderplank and was so called because the origins of *P. x decaisneana* were unclear at the time of the cross, as it was often confused with *P. quadrangularis*. After copies of the original papers describing *P. x decaisneana* and *P. x buonapartea* had been studied, and *P. quadrangularis* had been observed in cultivation in Venezuela, it became clear that the correct epigraph for this taxon was *P. x decaisneana*. The progeny *P.* 'Enigma' is an intermediate of its parents without any unusual or outstanding features and is of little horticultural value (Plate 31). The epithet *P.* 'Enigma' is used only for this study as it would be invalid as a variety name under the 1995 International Code of Nomenclature for Cultivated Plants.

5.2.3 Detailed descriptions of previously undescribed species, subspecies and cultivars of particular importance to this study:

The close similarities between many *Passiflora* have given rise to some confusion on the part of previous authors, particularly concerning the large red-flowered species found in the lowland tropics of South America and commonly known as the 'coccineas'. In order to avoid possible confusion as to the identity of the species *P. coccinea* Aubl. (1775) and the previously undescribed subspecies *tortue*, *bolivia*, *cacao* and *brownsberg*, and the species *P. quadrifaria* Vanderplank and *P. vitifolia* Kunth, all these taxa are described in detail with individual plant diagnoses. Also included are detailed descriptions of the cultivar *P. 'Enigma'* and the new species *P. gabrielliana* sp. nov. ined.

5.2.3.1 *P. coccinea* Aubl. (1775)

P. coccinea Aubl. *Pl. Guian.* 2: 828 pl. 324 (1775)

The *P. coccinea* described by Killip in his 1938 monograph is not consistent with that of F. Aublet (1775) found in French Guyana but is consistent with the plant of that name native to Bolivia, which is closely related to *P. vitifolia* H.B.K., because of the structure of its corona filaments, mottled six-striped downy fruit, flower bracts and seed morphology. The *P. coccinea* described by Escobar (1988b) is consistent with the plant found in Bolivia. Another race or subspecies of *P. coccinea* is endemic to the Brownsberg Hills of Surinam and is very closely related to the plants from French Guyana.

Five closely related species or subspecies of *P. coccinea* are briefly described here because of their importance to this work and to avoid possible confusion that might otherwise arise. The names of the four subspecies reflect the origin of each race, but the plants that are endemic to Bolivia and Surinam should be considered as separate species because of their major morphological differences. The botanical illustration of *P. vitifolia* Kunth is included to demonstrate the very close similarities between this species and the Bolivian *P. coccinea*, which seems to be more closely related to *P. vitifolia* than the *P. coccineas* of the Guyanas. The synonyms for *P. coccinea* listed by E. P. Killip (1938) are not consistent with any of the taxa described here and are therefore not included.

5.2.3.1.1 *P. coccinea* ssp. *tortue*, ssp. nov. ined. Vanderplank

Vine 15 m. and over, robust; stem stout, tomentose, becoming strong and woody; stipules narrow, linear, 9 mm long with 3-5 sessile glands; petiole 14-22 mm long, usually with 2 glands near the base, occasionally 4 glands with the second pair close to the leaf blade; glands nectarous; leaves ovate to oblong, 120-200 mm long, 35-80 mm wide, margin serrate with numerous tiny nectarous glands; peduncles robust, 60-70 mm long; bracts dull red, 65-85 mm long, 30-50 mm wide, ovate, concave, margin with numerous large nectarous glands; bracts enclose the developing fruit and turn deep green, tinged reddish, and remain attached until the fruit has fallen; flowers 140 mm diameter, bright red; hypanthium campanulate, red, glaucous; sepals 65 mm long, 15 mm wide, bright red, keeled with terminal awn 14 mm long; petals 60 mm long, 14 mm wide, bright red both sides; corona filaments in 2 series, outer rank pinky red outside, white inside, 12 mm long, inner rank pinky white, 8 mm long; operculum

10 mm long, pendant, curved and filamentose for 2-3 mm, pinky white; limen ragged fringe 4-5mm above the base of the hypanthium; androgynophore 26-30 mm long; ovary dull green, pyriform; fruit 35-45 mm long, 20-25 mm diameter at widest part, pyriform, ripening pale brown, held vertically with bracts surrounding fruit, nectarous glands stay active until fruit matures; arils white, sweet, juicy, aromatic; seed broadly obovate, symmetrical, compressed with granulate testa surface, dark brown (Plates 24c and 25). Mass of 100 seed 0.619-0.888g. Distribution: Tortue and most of coastal French Guyana.

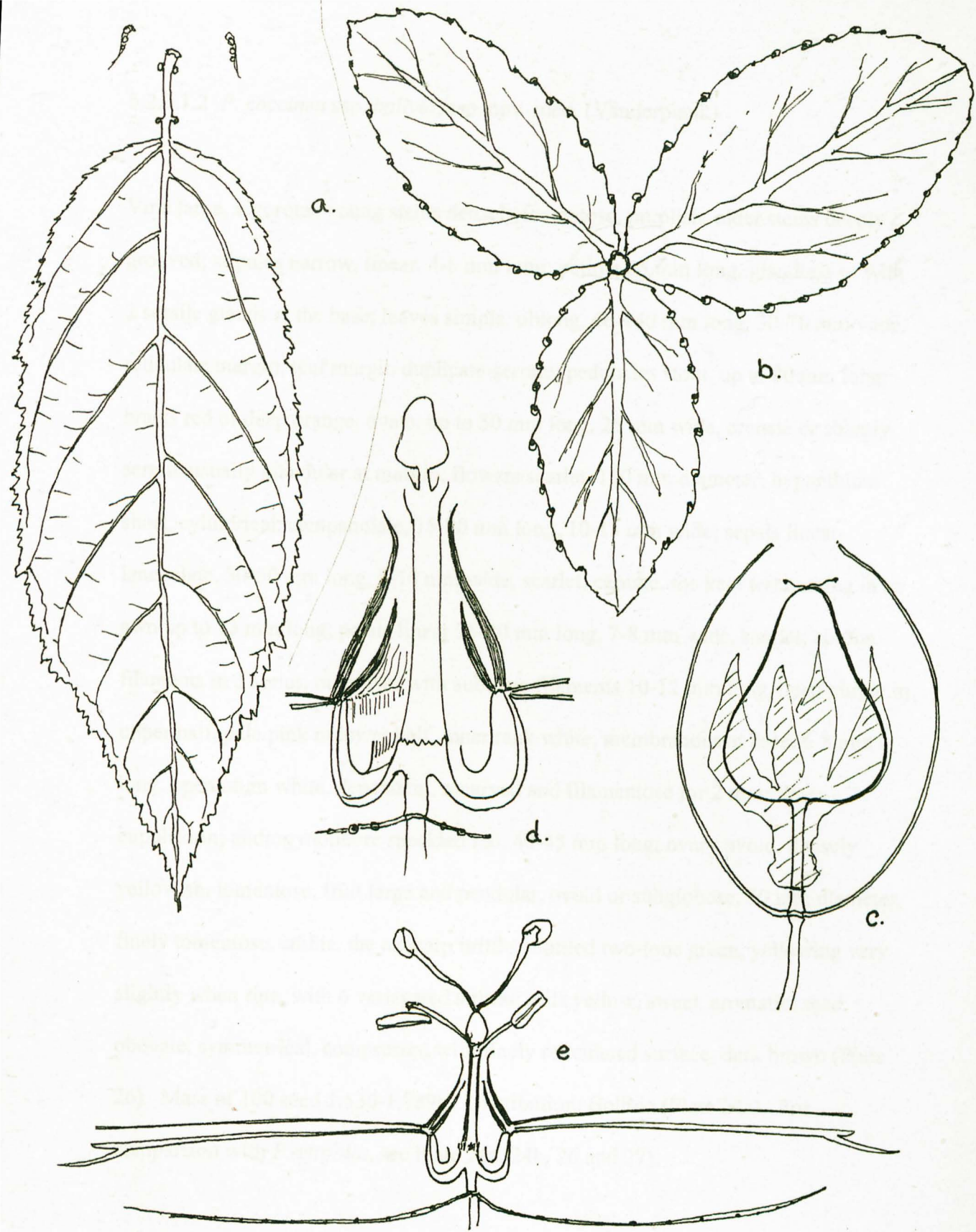


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a. *P. coccinea* ssp. *bolivia* ssp. nov. ined. (NCP 1051); b. *P. vitifolia* Kunth, 1817 (NCP 1251); c. *P. coccinea* ssp. *tortue* ssp. nov. ined. (NCP 1324); d. *P. quadrifaria* Vanderplank, 1996 (NCP 1191); e. *P. coccinea* ssp. *brownsburg* ssp. nov. ined. (NCP 1658);

Plate 24. *P. coccinea* sub-species and its close relatives



P. coccinea subsp. *tortue* subsp. nov. ined.

a. Leaf with stipules; b. Flower bracts; c. Fruit with withered remains of flower and surrounded by bracts; d. Section through flower and bracts; e. Enlarged section through hypanthium and androgynophore regions of flower. (x 2.5).
All illustrations are life size except where stated.

Plate 25. Plant diagnoses: *P. coccinea* ssp. *tortue*

5.2.3.1.2 *P. coccinea* ssp. *bolivia*, ssp. nov. ined. (Vanderplank)

Vine large, vigorous; young stems densely tomentose, purplish, older stems deeply grooved; stipules narrow, linear, 4-6 mm long; petiole 35 mm long, glandless or with 2 sessile glands at the base; leaves simple, oblong, 60-140 mm long, 30-70 mm wide, reticulate margin, leaf margin duplicate-serrate; peduncles stout, up to 80 mm long; bracts red or deep orange, ovate, up to 50 mm long, 25 mm wide, crenate or sharply serrate, usually glandular at margin; flowers scarlet, 110 mm diameter; hypanthium short, cylindrical, campanulate, 15-20 mm long, 10-13 mm wide; sepals linear-lanceolate, 30-50 mm long, 8-10 mm wide, scarlet, carnate, the keel terminating in an awn up to 13 mm long; petals linear 35-40 mm long, 7-8 mm wide, scarlet; corona filaments in 3 series, outer two with subulate filaments 10-12 mm long, deep purple in upper half, pale pink in lower half, inner rank white, membranous at base, 6-8 mm long; operculum white, dependent, recurved and filamentose for 2 mm; limen cupuliform; androgynophore speckled red, 40-45 mm long; ovary ovoid, densely yellowish, tomentose; fruit large and pendular, ovoid or subglobose, 50 mm diameter, finely tomentose, edible, the exocarp brittle, mottled two-tone green, yellowing very slightly when ripe, with 6 variegated stripes; arils yellow, sweet, aromatic; seed obovate, symmetrical, compressed with finely reticulated surface, dark brown (Plate 26). Mass of 100 seed 1.536-1.789g. Distribution: Bolivia (Plate 24a). For comparison with *P. vitifolia*, see Plate 24a, 24b, 26 and 27).



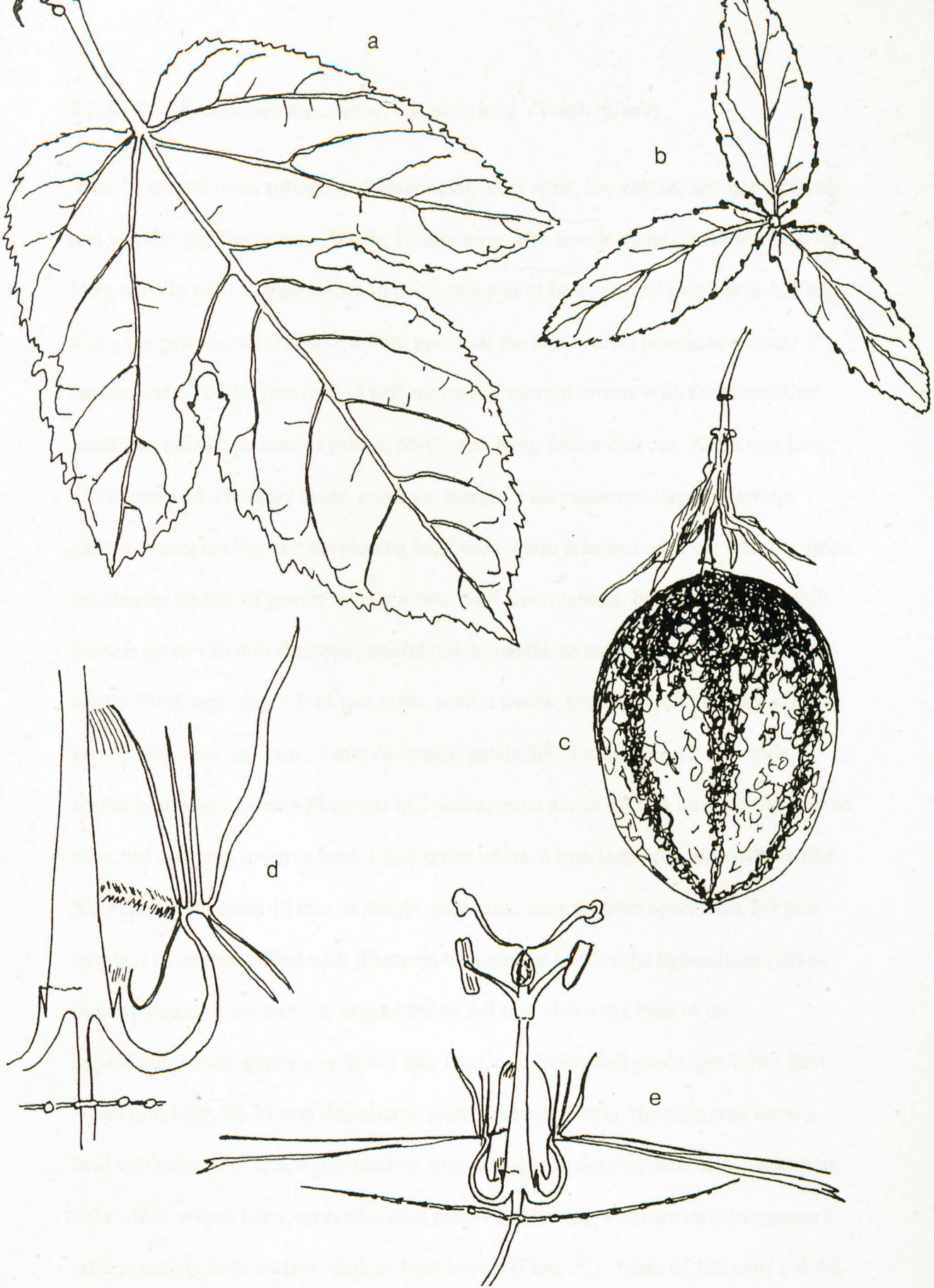
P. coccinea subsp. *bolivia* subsp. nov. ined.

a. Leaf with stipules; b. Flower bracts; c. Fruit with bracts; d. Section through flower and bracts;

e. Enlarged section through hypanthium and androgynophore regions of flower (x 2.5).

All illustrations are life size except where stated.

Plate 26. Plant diagnoses: *P. coccinea* ssp. *bolivia*



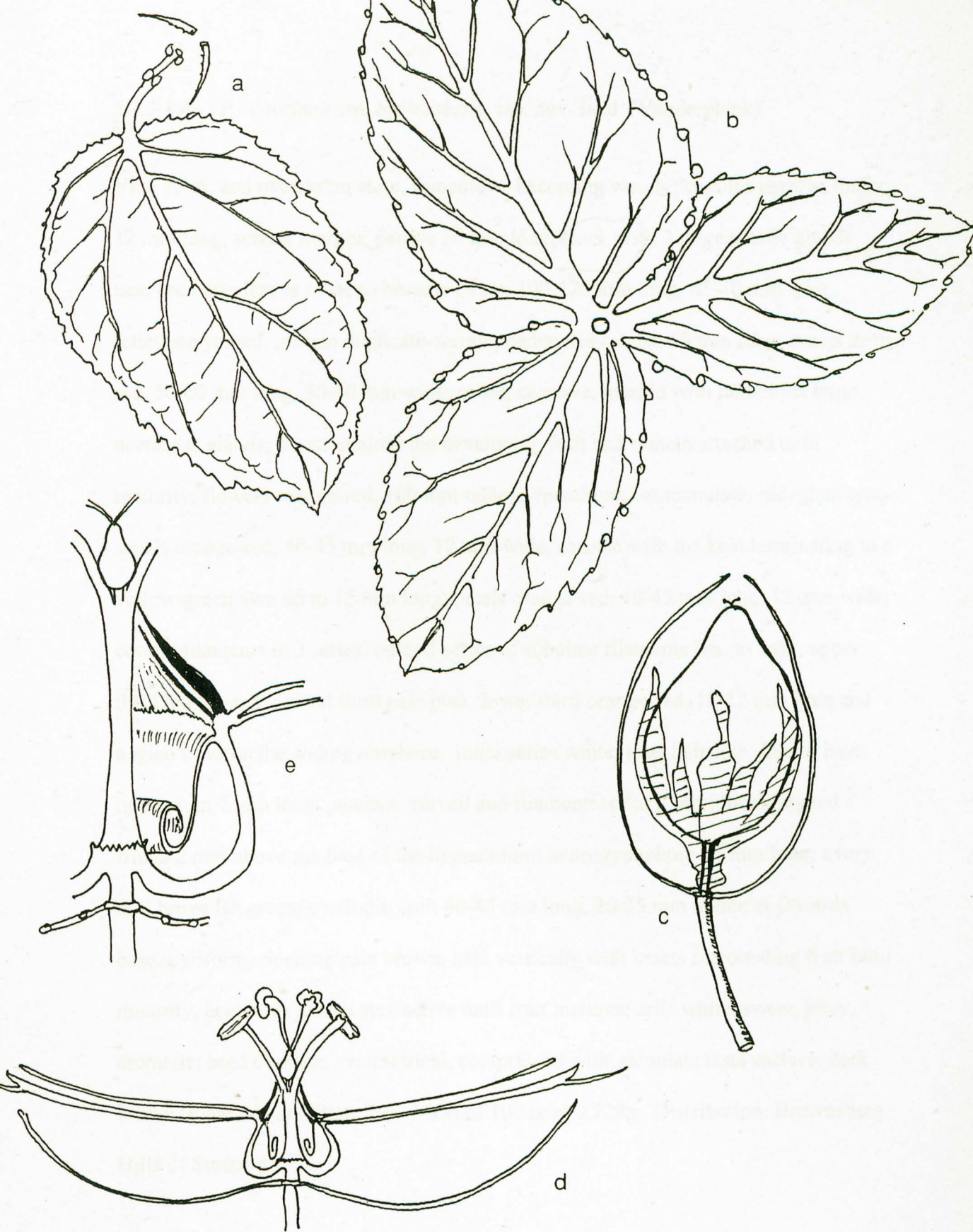
P. vitifolia Kunth, wild collected in Ecuador (NCP 1251)

a. Mature leaf with stipules; b. Flower bracts; c. Mature fruit with withered remains of flower. Bracts are deciduous; d. Enlarged section through hypanthium and androgynophore region of flower (x 2.5); e. Longitudinal section through flower and bracts.

Plate 27. Plant diagnoses: *P. vitifolia*

5.2.3.1.3 *P. coccinea* ssp. *cacao*, ssp. nov. ined. (Vanderplank)

Vine 15 m. and over, robust; multi-stemmed, stem stout, tomentose, becoming strong and woody; stipules narrow, linear, 10 mm long with sessile glands; petiole 15-20 mm long, usually with 4 large glands in pairs, one pair at base, second pair below halfway along the petiole, occasionally a third pair near the leaf blades; glands nectarous; leaves ovate, 70-100 mm long, 45-65 mm wide, margin serrate with numerous tiny nectarous glands; peduncles robust, 55-65 mm long; bracts dull red, 70-85 mm long, 40-60 mm wide, broadly ovate, concave, margin with numerous large nectarous glands; bracts enclose the developing fruit and remain attached until the fruit becomes deciduous; nectarous glands remain active until fruit matures, but not after fruit fall; flowers up to 120 mm diameter, scarlet red; hypanthium campanulate, red, glaucous; sepals 50-55 mm long, 13-14 mm wide, scarlet inside, brownish red beneath, carnate, keeled with terminal awn 12 mm or longer; petals 50-55 mm long, 12 mm wide, scarlet both sides; corona filaments in 2 series, outer series 10 mm long, fleshy, free to base, red and pink towards base, inner series white, 8 mm long with narrow hair-like filaments; operculum 10 mm or longer, pale pink, membranous apart from 2-3 mm terminal filaments, coiled with filaments towards the base of the hypanthium; limen inconspicuous, membranous, ragged fringe 3-4 mm above the base of the hypanthium; androgynophore 20-25 mm long, red; ovary dull green, pyriform; fruit 30-40 mm long, 20-25 mm diameter at widest part, pyriform, ripening pale brown, held vertically with bracts surrounding fruit throughout development and maturation; arils white, sweet, juicy, aromatic; seed narrowly obovate, symmetrical, compressed with granulate testa surface, dark or light brown (Plate 28). Mass of 100 seed 0.436g. Distribution: Cacao and probably most of French Guyana.



P. coccinea subsp. *cacao* subsp. nov. ined.

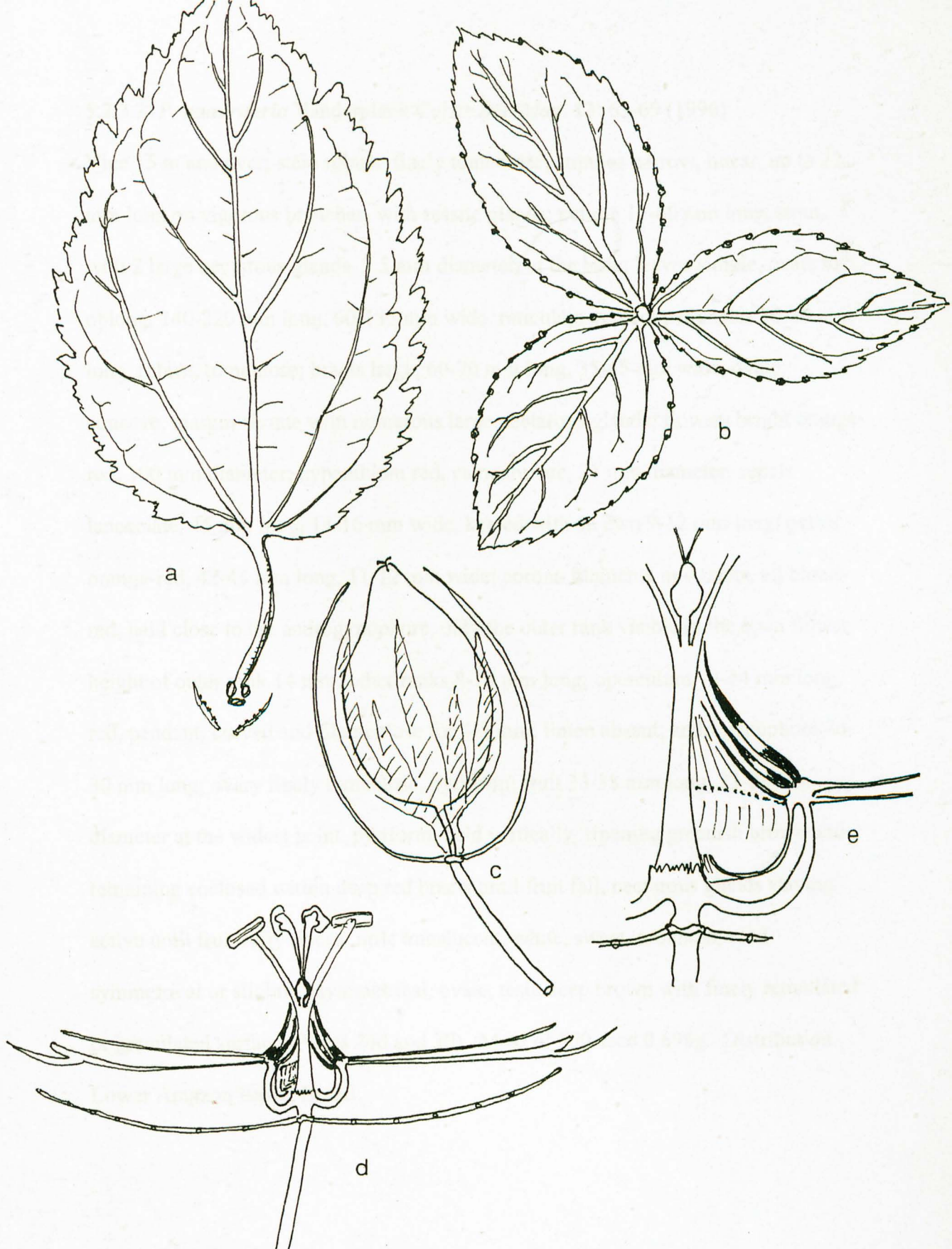
a. Leaf with stipules; b. Flower bracts; c. Fruit with remains of flower and surrounded by bracts; d. Section through flower and bracts; e. Enlarged section through hypanthium and androgynophore regions of flower. (x 3).

All illustrations are life size except where stated.

Plate 28. Plant diagnoses: *P. coccinea* ssp. *cacao*

5.2.3.1.4 *P. coccinea* ssp. *brownsberg*, ssp. nov. ined. (Vanderplank)

Vine 15 m. and over; stem stout, tomentose, becoming woody; stipules narrow, linear, 12 mm long, serrate margin; petiole 30 mm long, stout, with 2 large sessile glands near the base; leaves ovate to broadly ovate, 100-120 mm long, 65-80 mm wide, reticulate veined, margin duplicate-serrate; peduncles robust, 60 mm long; bracts deep red, 50-60 mm long, 30-40 mm wide, ovate, concave, margin with numerous large nectarous glands; bracts enclose the developing fruit and remain attached until maturity; flowers orange-red, 100 mm wide; hypanthium campanulate, red, glaucous; sepals orange-red, 40-45 mm long, 12 mm wide, carnate with the keel terminating in a yellow-green awn up to 15 mm long; petals orange-red, 40-45 mm long, 12 mm wide; corona filaments in 3 series, outer 2 series of subulate filaments free to base, upper third orange-red, central third pale pink, lower third orange-red, 10-12 mm long and angled towards the androgynophore, inner series white, fine, hair-like, free to base; operculum 7 mm long, pendant, curved and filamentose for 2 mm; limen ragged fringe 2 mm above the base of the hypanthium; androgynophore 25 mm long; ovary dull brownish green, pyriform; fruit 40-45 mm long, 20-25 mm diameter towards base, pyriform, ripening pale brown, held vertically with bracts surrounding fruit until maturity, nectarous glands stay active until fruit matures; arils white, sweet, juicy, aromatic; seed obovate, symmetrical, compressed with granulate testa surface, dark brown (Plate 24e and Plate 29). Mass of 100 seed 0.728g. Distribution: Brownsberg Hills of Surinam.



P. coccinea subsp. *brownsberg* subsp. nov. ined.

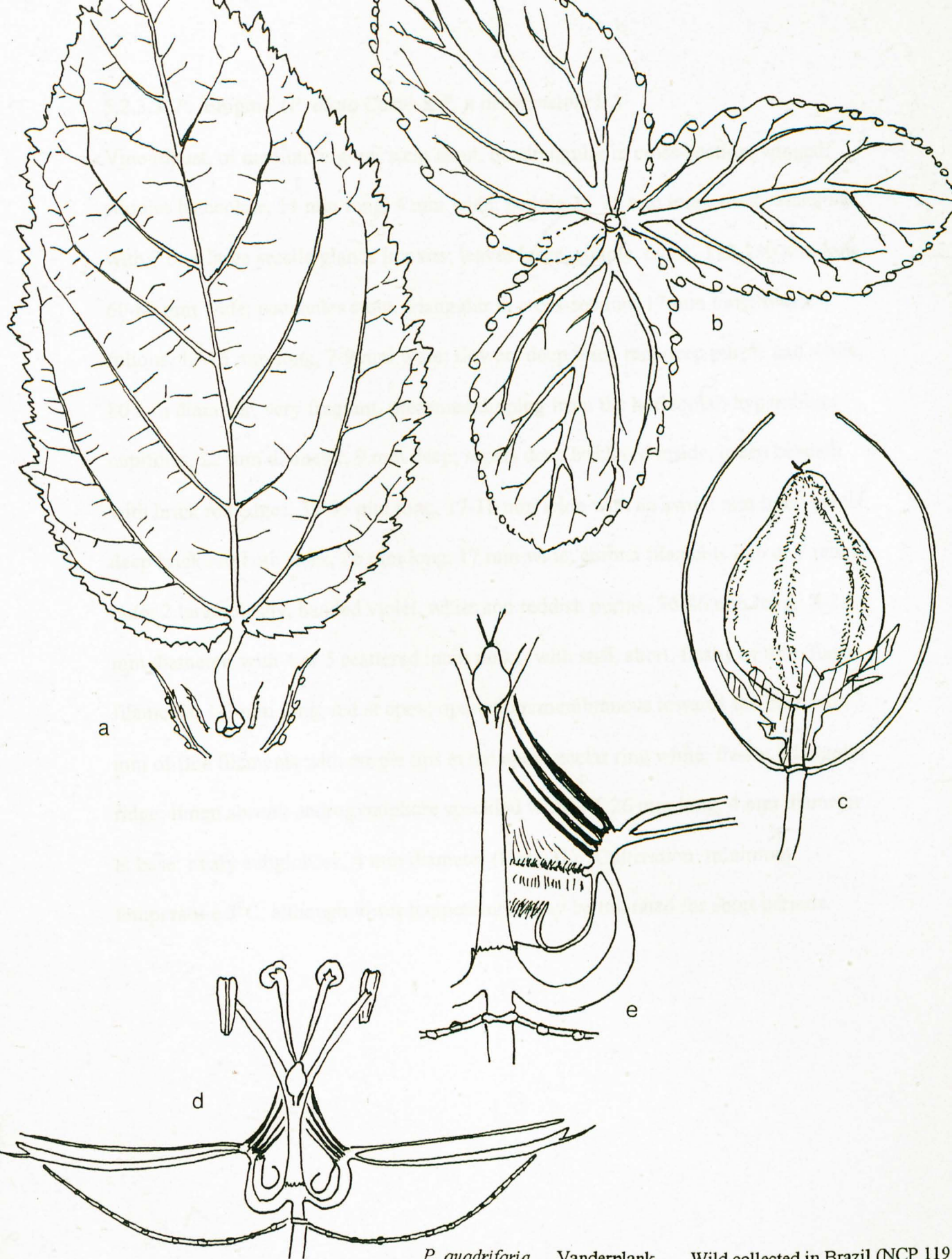
a. Leaf with stipules; b. Flower bracts; c. Fruit with remains of flower and surrounded by bracts; d. Section through flower and bracts; e. Enlarged section through hypanthium and androgynophore regions of flower. ($\times 2.5$).

All illustrations are life size except where stated.

Plate 29. Plant diagnoses: *P. coccinea* ssp. *brownsberg*

5.2.3.2 *P. quadrifaria* Vanderplank *Curtis Bot. Mag.* **13**: 63-69 (1996)

Vine 15 m and over; stem robust, finely tomentose; stipules narrow, linear, up to 22 mm long on vigorous branches, with sessile glands; petiole 15-60 mm long, stout, with 2 large nectarous glands, 2.5 mm diameter, at the base; leaves simple, ovate to oblong, 140-220 mm long, 60-135 mm wide, reticulate-veined; peduncles 70-80 mm long, robust, tomentose; bracts large, 60-70 mm long, 35-45 mm wide, ovate, concave, margin serrate with numerous large nectarous glands; flowers bright orange-red, 100 mm diameter; hypanthium red, campanulate, 21 mm diameter; sepals lanceolate, 45 mm long, 14-16 mm wide, keeled with an awn 9-12 mm long; petals orange-red, 42-45 mm long, 11-12 mm wide; corona filaments in 4 ranks, all blood-red, held close to the androgynophore, only the outer rank visible in the open flower, height of outer rank 14 mm, other ranks 8-12 mm long; operculum 12-14 mm long, red, pendant, curved and filamentose for 4-5 mm; limen absent; androgynophore 26-30 mm long; ovary finely tomentose, pyriform; fruit 33-38 mm long, 23-26 mm diameter at the widest point, pyriform, held vertically, ripening greenish brown and remaining enclosed within deep red bracts until fruit fall, nectarous glands staying active until fruit fully ripens; arils translucent, white, sweet, aromatic; seed symmetrical or slightly asymmetrical, ovate, testa deep brown with finely reticulated or granulated surface (Plates 24d and 30). Mass of 100 seed 0.698g. Distribution: Lower Amazon Basin, Brazil.



P. quadrifaria Vanderplank Wild collected in Brazil (NCP 119)

a. Leaf with stipules; b. Flower bracts; c. Fruit with remains of flower and surrounded by bracts; d. Section through flower and bracts; e. Enlarged section through hypanthium and androgynophore regions of flower (x 2.5).
 All illustrations are life size except where stated.

Plate 30. Plant diagnoses: *P. quadrifaria*

5.2.3.3 *P. 'Enigma'* (*P. alata* Curtis x *P. x decaisneana* L.)

Vine robust, of medium vigour; stem stout, quadrangular in cross-section, winged; stipules lanceolate, 11 mm long, 4 mm wide; petiole 25-35 mm long, stout, triangular, with 2 or 4 large sessile glands in pairs; leaves large, simple, ovate, 110-140 mm long, 60-80 mm wide; peduncles stout, triangular in cross-section, 17 mm long; bracts foliaceous, 12-15 mm long, 7-9 mm wide; flowers deep brick red, deep purple and white, 80 mm diameter, very fragrant, presented dipping from the horizontal; hypanthium cupiform, 22 mm diameter, 9 mm deep; sepals deep brick red inside, green beneath with brick red edges, 32-35 mm long, 17-18 mm wide with an awn 2 mm long; petals deep brick red both sides, 26 mm long, 17 mm wide; corona filaments in 6 or 7 ranks, outer 2 large, fleshy, banded violet, white and reddish purple, 36-40 mm long, 2-2.5 mm diameter, with 4 or 5 scattered inner ranks, with stiff, short, fleshy or thin, fleshy filaments, 1-2 mm long, red at apex; operculum membranous towards the base with 2 mm of fine filaments with purple tips at the apex; nectar ring white, fleshy, triangular ridge; limen absent; androgynophore speckled with red, 26 mm long, 4 mm diameter at base; ovary subglobose, 4 mm diameter (Plate 31). Cultivation: minimum temperature 5°C, although lower temperatures may be tolerated for short periods.



P. 'Enigma' (*P. alata* x *P. x decaisneana*)

a. Bracts; b. Plan of flower; c. Cross-section of flower; d. Enlarged cross-section of hypanthium; e. Stipules; f. Leaf with petiole bearing two pairs of glands; g. Petiole with one pair of glands; h. Flower and foliage. Drawings are life size except where stated.

Plate 31. Plant diagnoses: *P.* 'Enigma'

5.2.3.4 *Passiflora gabrielliana*: a new species from French Guyana

P. gabrielliana sp. nov. ined. was found by Cor Laurens during his visits to French Guyana in 1997, 1999 and February 2000. Several plants were found growing along roadside verges near the Rivieres des Cascades at Tonnegrande, and also near Sinnamary in Circad Territory and near Roura beside the Crique Gabrielle, after which it is named. The leaves and general habit of this vine are very similar to several other species endemic to French Guyana, mainly *P. laurifolia*, *P. variolata*, *P. citrifolia*, *P. aimae* and *P. cerasina*. The short flowering season of less than two months may explain why this species has not previously been recorded. Large, spectacular, fragrant flowers hang in bunches from pendular branches during January and February and are followed by golden yellow fruit during February and March. The fruit are probably eaten by coati, which inadvertently distribute their seed.

P. gabrielliana sp. nov. ined.

Vine medium-sized, 8 metres and above; stems stout, terete; stipules narrow, linear; petiole robust, 12 mm long, with two oval sessile glands close to leaf blades; leaves tough, leathery, 80-150 mm long, 30-75 mm wide, upper surface glaucous, underside dull; simple, with major vein and five to seven secondary veins; tendrils strong, 114-220 mm long; peduncles strong, terete, 50 mm long; bracts ovate, deep purplish, margin with few large glands; flowers pendular, borne singly but presented in clusters on fertile pendular branches; large and heavy, very showy, deep red, violet, mauve and white; hypanthium campanulate; sepals fleshy, ovate, 50 mm long, 18 mm wide, naviculate, deep dull red inside, paler outside, slightly keeled with short hair-like awn; petals ovate-oblong, 50 mm long, 15 mm wide, deep dull red both sides; corona filaments two major series, the outer held almost horizontally beneath the petals,

fleshy, up to 20 mm long, banded violet-mauve and white; second series large, fleshy, pendular, up to 60 mm long, 2-3 mm in cross-section, banded with four or five bands of red and white towards the base, two bands of violet-mauve and white mid-way, then violet-mauve for the remainder towards the apex; androgynophore stout, greenish-white; staminal filaments 8 mm long, 1.5 mm wide, pale green; pollen pale yellow; ovary subglobose, whitish yellow; fruit green, ripening orange-yellow, subglobose or oviform, 50-75 mm long, 35-42 mm diameter; exocarp forms thin shell less than 0.25 mm thick; mesocarp white, fleshy, 5-6 mm thick; arils translucent, white, sweet, juicy, aromatic; seed pale or dark brown, symmetrical or very slightly asymmetrical; testa shallowly reticulate-foveate; triangular chalazal beak; 100 seed 0.949g. Distribution: coastal regions of French Guyana at low elevations, found growing along roadsides and tracks amongst shrubs and small trees.

5.2.4 List of *Passiflora* species in this study in subgeneric and section order

The *Passiflora* species that have been cited in this study are listed with authors, publication details in subgeneric and section order and are in keeping with Killip's 1938 monograph and supplemental notes in 1960 as set out on pages 9-12. Each subgenus and section is numbered and these are used as a code (subgenus number/section number) in the brief details in Table 1 of the 360 accessions included in this study. Other details, including the authority, date of publication, country of origin, the collector, the seed mass and the colour of ripe arils and fruit are also included. Further details of the cultivars included in this study showing the author, publication date, publication and parentage are included in Appendix I.

Passiflora L., *Sp. Pl.* 955 (1753)

Subgenus 1: *Apodogyne* Killip, *Field Mus. Nat. Hist. Bot.* (1938)

P. multiflora L., *Sp. Pl.* 956 (1753)

Subgenus 2: *Astephia* Killip, *Field Mus. Nat. Hist. Bot.* (1938)

P. penduliflora Bert. in DC., *Prodr.* 3: 326 (1828)

Subgenus 3: *Tryphostemmatoides* (Harms) Killip, *Field Mus. Nat. Hist. Bot.* (1938)

P. gracillima Killip, *Journ. Wash. Acad. Sci.* 14: 112 (1924)

P. tryphostemmatoides Harms, *Bot. Jahrb.* 18 Beibl. 46: 6 (1894)

Subgenus 4: *Decaloba* MacDougal (DC.) Rchb., (1828)

Section 1: *Cieca* (Medic) Mast., *Trans. Linn. Soc.* 27: 630 (1871)

P. coriacea Juss., *Ann. Mus. Hist. Nat.* 6: 109 (1805)

P. gracilis Jacq. ex Link., *Enum. Pl.* 2: 182 (1822)

P. holosericea L., *Sp. Pl.* 958 (1753)

P. juliana MacDougal, *Novon* 2: 363 (1992)

P. obtusifolia Sesse & Moc., *Pl. Nov. Hisp.* 156 (1887)

P. pallida L., *Sp. Pl.* 955 (1753)

P. suberosa L., *Sp. Pl.* 958 (1753)

P. tridactylites Hook., *Trans. Linn. Soc.* 20: 222 (1851)

Section 2: *Decaloba* (DC.) Mast., *Trans. Linn. Soc.* 27: 631 (1871)

P. affinis Engelm., *Bost. Journ. Nat. Hist.* 6: 233 (1850)

- P. allantophylla* Mast., *Bot. Gaz.* **16**: 7 (1891)
- P. alnifolia* H.B.K., *Gen. & Sp.* **2**: 136 (1817)
- P. amalocarpa* Barb. Rodr., *Vellosia* **1**: 25 (1891)
- P. apetala* Killip, *Journ. Wash. Acad. Sci.* **12**: 255 (1922)
- P. auriculata* H. B. K., *Nov. Gen. & Sp.* **2**: 131 (1817)
- P. bauhinifolia* H. B. K., *Nov. Gen. & Sp.* **2**: 132 (1817)
- P. biflora* Lam., *Encycl.* **3**: 36 (1789)
- P. candollei* Tr. & Planch.
Ann. Sci. Nat. V. Bot. **17**: 161 (1873)
- P. colinvauxii* Wiggins, *Maulronc.*, **xx**: 251 (1970)
- P. cuneata* Willd., *Enum. Hort. Berol.* 696 (1809)
- P. cuneata* var. 'Miguel Molinari' Vanderplank,
Curtis's Bot. Mag. **15** (2): 109 (1998)
- P. fanchonae* Feuillet, *Candollea* **41**: 175-177 (1986)
- P. ferruginea* Mast. in Mart., *Fl. Bras.* **13** (1): 556 (1872)
- P. filipes* Benth., *Pl. Hartw.* 118 (1843)
- P. gilbertiana* MacDougal, *Ann. Missouri Bot. Gard.* **76**: 610 (1989)
- P. helleri* Peyr., *Linnaea* **30**: 54 (1859)
- P. jorullensis* H. B. K., *Nov. Gen. & Sp.* **2**: 133 (1818)
- P. lancearia* Mast., *Journ. Bot. Brit. & For.* **23**: 114 (1885)
- P. lutea* L., *Sp. Pl.* 958 (1753)
- P. malletii* MacDougal, *Ann. Missouri Bot. Gard.* **76**: 1172 (1989c)
- P. misera* H. B. K., *Nov. Gen. & Sp.* **2**: 136 (1817)
- P. nubicola* MacDougal, *Ann. Missouri Bot. Gard.* **76**: 608 (1989)
- P. organensis* Gardn., *London Journ. Bot.* **4**: 104 (1845)

- P. ornithoura* Mast., *Bot. Gaz.* **16**: 8 (1891)
- P. punctata* L., *Sp. Pl.* 957 (1753)
- P. sanctae-mariae* MacDougal, *Novon* **5**: 48-51 (1995)
- P. sexflora* Juss., *Ann. Mus. Hist. Nat.* **6**: 110 (1805)
- P. standleyii* Killip, *Journ. Wash. Acad. Sci.* **14**: 110 (1924)
- P. talamancensis* Killip, *Journ. Wash. Acad. Sci.* **12**: 260 (1922)
- P. tricuspis* Mast. in Mart., *Fl. Bras.* **13** (1): 587 (1872)
- P. trifasciata* Lemaire, *Illus. Hort.* **15**: pl. 544 (1868)
- P. tuberosa* Jacq., *Pl. Hort. Schonbr.* **4**: 49 (1804)
- P. vespertilio* L., *Sp. Pl.* 957 (1753)
- P. viridescens* L. K. Escobar, *Phytologica* **66**: 81 (1989)
- P. yucatanensis* Killip, *Field Mus. Bot.* **8**: 26 (1930)
- Section 4: *Discophora* Jorg. & Law., *Nordic J. Bot.* **7** (2): 129 (1987)
- P. discophora* Jorg. & Law., *Nordic J. Bot.* **7** (2): 129 (1987)
- Section 5: *Distemma* Lem., *Hort. van Houtte* fasc. ii t. 11 (1847)
- P. aurantia* Forst., *Florulae Ins. Austr.* (1786)
- P. cinnabarina* Lindl., *Gard. Chron.* 724 (1855)
- P. herbertiana* Ker-Gawl, *Edwards' Bot. Reg.* **9** (1823)
- Section 7: *Hahniopathanthus* (Harms) Killip,
Field Mus. Nat. Hist. Bot. (1938)

P. guatemalensis Wats., *Proc. Amer. Acad.* **22**: 473 (1887)

P. hahnii Fourn., *Rev. Hort.* **41**: pl. 430 (1869)

P. membranacea Benth., *Pl. Hartw.* 83 (1841)

Section 8: *Hollrungiella* (K. Sch.) de Wilde, *Blumea* **20**: 1 (1972)

P. hollrungia K. Sch., *Engl. Bot. Jahrb.* 9 (1888)

Section 11: *Pseudogranadilla* (Harms) Killip,

Field Mus. Nat. Hist. Bot. (1938)

P. indecora H. B. K., *Nov. Gen. & Sp.* **2**: 134 (1818)

P. kalbreyeri Mast., *Journ. Bot. Brit. & For.* **21**: 36 (1883)

P. pulchella H. B. K., *Nov. Gen. & Sp.* **2**: 134 (1817)

Section 12: *Pseudodyosmia* (Harms)(Killip) MacDougal,

Sys. Bot. Mon. (1994)

P. adenopoda DC., *Prodr.* **3**: 330 (1828)

P. bryonoides H. B. K., *Nov. Gen. & Sp.* **2**: 140 (1817)

P. colimensis Mast. & Rose, *Contr. U. S. Natl. Herb.* **5**: 181 (1899)

P. dioscoreifolia Killip, *Journ. Wash. Acad. Sci.* **14**: 110 (1924)

P. dolichocarpa Killip, *Journ. Wash. Acad. Sci.* **20**: 374 (1930)

P. exsudans Zuccarini,

Abh. Math-Phys. Cl. Konigl. Bayer Akad. Wiss. **2**: 342 (1837)

P. karwinskii Mast. in Mart., *Fl. Bras.* **13**: 555 (1872)

P. lobata (Killip) J. Hutchinson ex MacDougal,

Phytologia **60**: 446(1986)

- P. morifolia* Mast. in Mart., *Fl. Bras.* **13**: 555 (1872)
- P. oaxacensis* MacDougal, *Sys. Bot. Mon.* vol. 41 (1994)
- P. pendens* MacDougal, *Sys. Bot. Mon.* **41** (1994)
- P. pilosa* Ruiz & Pavon ex DC., *Prodr.* **3**: 330 (1828)
- P. podadenia* Killip, *Journ. Wash. Acad. Sci.* **14**: 109 (1924)
- P. pterocarpa* MacDougal, *Sys. Bot. Mon.* **41** (1994)
- P. quercetorum* Killip, *Field Mus. Nat. Hist. Bot.* **19**:113 (1938)
- P. sicyoides* Schlechtendal & Chamisso, *Linnaea* **5**: 88 (1830)

Section 13: *Xerogona* (Raf.) Killip, *Field Mus. Nat. Hist. Bot.* **19**:113 (1938)

- P. brevifila* Killip, *Field Mus. Nat. Hist. Suppl. Notes* **35** (1) (1960)
- P. brevipes* Killip, *Carnegie Inst. Wash. Publ.* **461**: 312 (1936)
- P. capsularis* L., *Sp. Pl.* 957 (1753)
- P. citrina* MacDougal, *Ann. Missouri Bot. Gard.* **76**: 608 (1989)
- P. conzattiana* Killip, *Journ. Wash. Acad. Sci.* **17**: 425 (1927)
- P. costaricensis* Killip, *Journ. Wash. Acad. Sci.* **12**: 257 (1922)
- P. quinquangularis* Calderon, *Passifloras Dilobatas del Salvador* **6**
- P. rovirosae* Killip, *Journ. Wash. Acad. Sci.* **12**: 259 (1922)
- P. rubra* L., *Sp. Pl.* 956 (1753)
- P. sanguinolenta* Mast., *Gard. Chron.* (1868)

Subgenus 5: *Chloropathanthus* (Harms) Killip, *Field Mus. Nat. Hist. Bot.* (1938)

- P. viridiflora* Cav., *Icon Pl.* **5**:15 pl. 424 (1799)

Subgenus 6: *Murucuja* (Medic.) Mast., *Trans. Linn. Soc.* **27**: 626 (1871)

P. murucuja L., *Sp. Pl.* 957 (1753)

P. tulae Urban., *Symb. Ant.* 1: 374 (1899)

Subgenus 7: *Pseudomurucuja* (Harms) Killip, *Field Mus. Nat. Hist. Bot.* (1938)

P. cuprea L., *Sp. Pl.* 955 (1753)

P. oblongata Swartz., *Prodc. Veg. Ind. Occ.* 97 (1788)

P. perfoliata L., *Sp. Pl.* 956 (1753)

Subgenus 11: *Tacsonia* (Juss.) Tr. & Planch., *Ann. Sci. Nat. V. Bot.* 17: 126 (1873)

Section 1: *Ampullacea* L. K. Escobar, *Fl. Colombia* (1988)

P. ampullacea (Mast.) Harms,
in Engl. & Prantl., *Pflanzenfam.* 3 (6a): 91 (1893)

Section 3: *Bracteogama* L. K. Escobar, *Fl. Colombia* (1988)

P. cumbalensis (Karst) Harms, *Bot. Jahrb.* 18: 13 pl. 46 (1894)

P. mollissima (H.B.K.) Bailey, *Rhodora* 18:156 (1916)

P. tarminiana P. M. Jorgensen & J. M. MacDougal
Novon 11: 8-15 (2001)

P. zamoriana Killip, *Suppl. Notes Am. Sp. Pass.*,
Contr. U.S. Natl. Herb. 35: 11-12 (1960)

Section 4: *Colombiana* L. K. Escobar, *Fl. Colombia* 10: 41 (1988)

P. antioquiensis Karst., *Linnaea* 30: 162 (1859)

P. cuatrecasasii Killip, *Suppl. Notes Am. Sp. Pass.*,

Contr. U.S. Natl. Herb. **35**: 7 (1960)

P. rugosa (Mast.) Tr. & Planch.,

Ann. Sci. Nat. V. Bot. **17**: 136 (1873)

P. tenerifensis L. K. Escobar, *Fl. Colombia* **10**: 34 (1988)

P. triariae Killip, *Field Mus. Nat. Hist. Bot.* **19**: 136 (1938)

P. truxillensis Planch. & Lind., *Ann. Sci. Nat. V. Bot.* **17**: 135 (1873)

Section 6: *Parritana* L. K. Escobar, *Fl. Colombia* **10**: 58 (1988)

P. parritae (Mast.) Bailey, *Rhodora* **18**: 156 (1916)

Section 7: *Poggenдорffia* L. K. Escobar, *Fl. Colombia* **10** (1988)

P. pilosicorona Sacco, *Bradea* **1** (33): 350 (1973)

P. pinnatistipula Cav., *Icon. Pl.* **5**: 16, pl. 428 (1799)

Section 8: *Tacsonia* (Juss)(Tr. & Planch.) L. K. Escobar,

Fl. Colombia **10** (1988)

P. matthewsii (Mast.) Killip, *Journ. Wash. Acad. Sci.* **17**: 428 (1927)

P. mixta L. *Fil. Suppl.* 408 (1781)

P. schlimiana Tr. & Planch., *Ann. Sci. Nat. V. Bot.* **17**: 130 (1873)

Section 9. *Tacsoniopsis* (Tr. & Planch.) Killip *Stat. Nov.* (1938)

P. bracteosa Planch. & Lind., *Ann. Sci. Nat. V. Bot.* **17**: 137 (1873)

Subgenus 12: *Manicata* (Harms) L. K. Escobar, *Fl. Colombia* **10**: 92 (1988)

P. macropoda Killip, *Suppl. Notes Am. Sp. Pass.*,

Contr. U.S. Natl. Herb. **35**: 1 (1960)

P. manicata (Juss.) Pers., *Syn. Pl.* **2**:221 (1807)

P. trisecta Mast. in Mart., *Fl. Bras.* **13** (1): 564 (1872)

Subgenus 13: *Distephana* (Juss.) Killip, *Field Mus. Nat. Hist. Bot.* (1938)

P. aimae Annonay & Feuillet *Adansonia* ser. 3 (1998)

P. buchtienii Killip, *Journ. Wash. Acad. Sci.* **14**: 115 (1924)

P. coccinea Aubl., *Pl. Guian.* **2**: 828 (1775)

P. coccinea ssp. *bolivia* ssp. nov. ined.

P. coccinea ssp. *brownsberg* ssp. nov. ined.

P. coccinea ssp. *cacao* ssp. nov. ined.

P. coccinea ssp. *tortue* ssp. nov. ined.

P. glandulosa Cav., *Diss.* **10**: 453, pl. 281 (1790)

P. involucrata (Mast.) Gentry, *Pl. Syst. Evol.* **137**: 95-105 (1981)

P. quadrifaria Vanderplank, *Curtis's Bot. Mag.* **13**: 63 (1996)

P. quadriglandulosa Rodschied., *Med. Chir. Bemerk Esseq.* **77** (1796)

P. speciosa Gardn. in Fielding & Gardn., *Sert. Pl.* pl. 17 (1844)

P. variolata Poepp. & Endl., *Nov. Gen. & Sp.* **2**: 58 (1835)

P. vitifolia H.B.K., *Nov. Gen. & Sp.* **2**: 138 (1817)

Subgenus 14: *Tacsonioides* (DC.) Killip, *Field Mus. Nat. Hist. Bot.* **19** (1938)

P. reflexiflora Cav., *Icon. Pl.* **5**: 15 (1799)

P. umbilicata (Griseb) Harms in Engl. & Prantl.,

Pflanzenfam. **3** (6a): 91 (1893)

Subgenus 15: *Passiflora*

Section 1: *Digitatae*

P. serratodigitata L., *Sp. Pl.* 960 (1753)

Section 3: *Kermesinae*

P. kermesina Link & Otto

Verhandl. Ver. Gartenb. Preuss. 2: 403 Pl. 15 (1826)

Section 4: *Laurifoliae*

P. acuminator DC., *Prodr.* 3: 328 (1828)

P. ambigua Hems., *Bot. Mag.* 128 (1902)

P. crenata Feuillet & Crem., *Bot. Pro.* 4: 378-381 (1984)

P. guazumaefolia Juss., *Ann. Mus. Hist. Nat.* 6: 112 (1805)

P. laurifolia L., *Sp. Pl.* 956 (1753)

P. nigradenia Rusby, *Mem. N. Y. Bot. Gard.* 7: 311 (1927)

P. nitida H.B.K. *Nov. Gen. & Sp.* 2: 130 (1817)

P. riparia Mart. Ex Mast., *Fl. Bras.* 13 (1): 599 (1872)

Section 5: *Lobatae*

P. amethystina Mikan., *Delect. Fl. & Faun. Bras. Fasc.* 4 (1825)

P. caerulea L., *Sp. Pl.* 959 (1753)

P. eichleriana Mast. in Mart., *Fl. Bras.* 13: 616 (1872)

- P. elegans* Mast. in Mart. *Fl. Bras.* **13** (1): 621 (1872)
- P. exura* Feuillet, *Novon* **4**: 236-241 (1994)
- P. garckeii* Mast., *Trans Linn. Soc.* **27**: 639 (1871)
- P. giberti* N. E. Brown, *Trans. & Proc. Bot. Soc. Edinb.* **20**:58 (1896)
- P. gritensis* Karst., *Linnaea* **30**: 163 (1859)
- P. mooreana* Hook., *Bot. Mag.* **66** (1840)
- P. naviculata* Griseb., *Abh. Ges. Wiss. Gottingen* **19**: 149 (1874)
- P. pallens* Poepp. ex Mast. in Mart., *Fl. Bras.* **13** (1): 567 (1872)
- P. resticulata* Mast. & Andre., *Journ. Linn. Soc.* **20**: 42 (1883)
- P. retipetala* Mast., *Kew Bull. Misc. Inf.* (1893)
- P. sprucei* Mast. in Mart. *Fl. Bras.* **13** (1): 568 (1872)
- P. stipulata* Aubl., *Pl. Guian.* 830 (1775)
- P. subpeltata* Ortega, *Nov. Rar. Pl. Hort. Matrit.* **6**: 78 (1798)
- P. tenuifila* Killip, *Journ. Wash. Acad. Sci.* **17**: 430 (1927)

Section 8: *Menispermifoliae*

- P. menispermifolia* H.B.K., *Nov. Gen. & Sp.* **2**: 137 (1817)
- P. nephrodes* Mast., *Bull. Torrey Club* **17**: 282 (1890)

Section 11: *Passiflora*

- P. cincinnata* Mast., *Gard. Chron.* (1868)
- P. edulis* Sims, *Bot. Mag.* **45** (1818)
- P. incarnata* L., *Sp. Pl.* 959 (1753)
- P. mayarum* MacDougal, *Ann. Missouri Bot. Gard.* **76**: 615 (1989)

Section 12: *Pedatae*

P. pedata L., *Sp. Pl.* 960 (1753)

Section 13: *Quadrangulares*

P. alata Dryand., *Bot. Mag.* 2: 66 (1781)

P. phoenicea Lindl., *Bot. Reg.* 19: pl. 1603 (1833)

P. quadrangularis L., *Syst. Ed.* 10: 1248 (1759)

Section 14: *Serratifoliae*

P. serratifolia L., *Sp. Pl.* 955 (1753)

Section 16: *Simplicifoliae*

P. actinia Hook., *Bot. Mag.* 69 (1843)

P. mucronata Lam., *Encycl.* 3: 33 (1789)

P. oerstedii Mast. in Mart., *Fl. Bras.* 13 (1): 562 (1872)

Section 17: *Tiliifoliae*

P. ligularis Juss., *Ann. Mus. Hist. Nat.* 6: 113, pl. 40 (1805)

P. magnifica L. Escobar, *Phytologia* 69 (5) (1990)

P. maliformis L., *Sp. Pl.* 956 (1753)

P. platyloba Killip, *Journ. Wash. Acad. Sci.* 12: 260 (1922)

P. seemannii Griseb., *Bonplandia* 6: 7 (1858)

P. serrulata Jacq., *Obs. Bot.* 2: 26, pl. 46 (1767)

P. tiliaefolia L., *Sp. Pl.* 956 (1753)

P. triloba R. & P. ex DC, *Prodr.* 3: 330 (1828)

Subgenus 16: *Calopathanthus*

P. racemosa Brot., *Trans. Linn. Soc.* **12**: 71, pl. 6 (1817)

Subgenus 17: *Dysosmia* (DC.) Killip, *Field Mus. Nat. Hist.* **19** (1938)

P. foetida L., *Sp. Pl.* 959 (1753)

P. foetida var. *galapagensis* Killip, *Field Mus. Nat. Hist.* **19** (1938)

P. foetida var. *gossypifolia* (Desv.) Mast.,

Trans. Linn. Soc. **27**: 631 (1871)

P. foetida var. *hibiscifolia* (Lam.) Killip,

Field. Mus. Nat. Hist. **19** (1938)

P. foetida var. *hirsuta* Mast., *Trans. Linn. Soc.* **27**: 631 (1871)

P. foetida var. *hirsutissima* Killip,

Carnegie Inst. Wash. Publ. **461**: 326 (1936)

P. foetida var. *hispida* (DC.) Killip ex Gleason,

Bull. Torrey Club **58**: 408 (1931)

P. foetida var. *lanuginosa* Killip,

Carnegie Inst. Wash. Publ. **461**: 325 (1936)

P. foetida var. *maxoni* Killip,

Carnegie Inst. Wash. Publ. **461**: 326 (1936)

P. foetida var. *monitziana* (Planch) Killip ex Pulle

Fl. Suriname **3** (1): 318 (1937)

P. foetida var. *orinocensis* Killip in Bailey, *Gent. Herb.* **2**: 205 (1930)

P. foetida var. *parvifolia* Killip, *Field. Mus. Nat. Hist.* **19** (2) (1938)

P. foetida var. *riparia* (C. Wright) Killip,

Field Mus. Nat. Hist. **19** (1938)

P. foetida var. *subpalmata* Killip,

Carnegie Inst. Wash. Publ. **461**: 326 (1936)

P. foetida var. *vitacea* Mast. in Mart., *Fl. Bras.* **13**(1): 583 (1872)

P. palmeri Rose, *Contr. U.S. Nat. Herb.* **1**: 131, pl. 14 (1892)

P. palmeri var. *sublanceolata* Killip,

Carnegie Inst. Wash. Publ. **461**: 322 (1936)

P. urbaniana Killip, *Journ. Wash. Acad. Sci.* **17**: 426 (1927)

Subgenus 19: *Polyanthea* (DC.) Killip, *Field Mus. Nat. Hist.* **19** (1938)

P. cirrhiflora Juss. *Ann. Mus. Hist. Nat.* **6**: 115, pl. 41 (1805)

Subgenus 20: *Astrophea* (DC.) Mast., *Trans. Linn. Soc.* **27**: 629 (1805)

Section 1: *Botryastrophea* (Harms) Killip, *Field Mus. Nat. Hist.* **19** (1938)

P. amoena L. Escobar, *Syst. Bot.* **19** (1994)

P. fuchsiiflora Hemsl. In Hook., *Icon Pl.* **26** (1898)

P. longiracemosa Ducke, *Archiv. Jard. Bot. Rio* **3**: 221 (1922)

Section 2: *Dolichostemma* Killip, *Field Mus. Nat. Hist.* **19** (1938)

P. pittieri Mast., *Bot. Gaz.* **23**: 246 (1897)

Section 3: *Euastrophea* (Harms) Killip, *Field Mus. Nat. Hist.* **19** (1938)

P. lindeniana Tr. & Planch., *Ann. Sci. Nat. V. Bot.* **17**: 182 (1873)

P. macrophylla Spruce ex Mast., *Journ. Linn. Soc.* **20**: 31 (1883)

P. ovata Martin ex DC., *Prodr.* **3**: 322 (1828)

Section 5: *Pseudoastrophea* (Harms) Killip, *Field Mus. Nat. Hist.* **19** (1938)

P. candida (Poepp. & Endl.) Mast., *Trans. Linn. Soc.* **27**: 629 (1871)

P. ceratocarpa Silveira, *Archiv. Jard. Bot. Rio de Janeiro* **5**:217 (1930)

P. costata Mast. in Mart., *Fl. Bras.* **13** (1): 573 (1872)

Subgenus 21: *Tetrapathaea* (DC.) P. S. Green, *Kew Bull.* **26** (3): 553 (1972)

P. tetrandra Banks & Sol. Ex DC. (Candolle), *Prodr.* **3** (1828)

Subgenus 22: *Tetrastylis* Barb. Rodr., *Rev. Engenharia* **4**: 260 (1882)

P. ovalis (Vell.) Killip, *Journ. Wash. Acad. Sci.* **17**: 426 (1927)

5.2.5 *Passiflora* accessions in this study in alphabetical order (Table 1)

Column 1 Species, authority and date

Column 2 Collector of seed and collection number

Column 3 Origin of seed; cultivated seed are recorded as 'cultivated' with the country of cultivation. Where no other information is recorded, seed have been collected from the wild in that country. Seed from cultivars are recorded as 'cultivar'.

Columns 4

The mass of 100 seed has generally been obtained from fresh dry seed cultivated in the UK. These seed have been given a NCP collection number (column 2). The age of other seed samples varies considerably and a loss of mass of up to 10% due to dehydration between the date of collection and the date of weighing must be considered a possibility.

Columns 5 and 6

The colour of fruit and arils has been suggested by J. M. MacDougal in his 1994 monograph to be a taxonomically diagnostic feature of *Passiflora*.

Table 1. *Passiflora* accessions in this study.

Species, authority & date	Collector & collection no.	Origin of seed	Mass per 100 seed (g)	Colour of arils (when ripe)	Colour of fruit (when ripe)	Subgenus and section number	New seed group number
<i>actinia</i> Hook (1843)	J. Vanderplank NCP 1003	Cultivated UK (1998)	1.342	Clear	Yellow	15 / 16	5 - 1
<i>acuminata</i> DC. (1828)	L. Gilbert 9156 NCP 1609	Cultivated USA	3.006			15 / 4	5 - 3
<i>adenopoda</i> DC. (1828)	M. Molinari NCP 1492	Venezuela (1994)	1.555	Orange	Purple and green	4 / 12	2
<i>adenopoda</i> DC. (1828)	J. Vanderplank BW 90-060 NCP 1004	Cultivated USA	1.688	Orange	Purple and green	4 / 12	2
<i>adenopoda</i> DC. (1828)	J. Vanderplank NCP 1661	Costa Rica (2001)	0.962	Orange	Purple and green	4 / 12	2
'Adularia' Vanderpl. (1994)	J. Vanderplank NCP 1016	Cultivar UK (1996)	0.357	White	Greeny yellow		9 - 2
'Adularia' Vanderpl. (1994)	J. Vanderplank NCP 1641	Cultivar UK (1999)	0.419	White	Greeny yellow		9 - 2
<i>affinis</i> Engelm. (1850)	P. Schappert NCP 1551	Texas USA	0.422	Pale Yellow	Black	4 / 2	9 - 1
<i>aimae</i> Annonay & Feuillet (1998)	J. Vanderplank NCP 1616	French Guyana (2001)	0.691	White	Brown	13	4
<i>alata</i> Dryand (1788)	J. Vanderplank NCP 1031	Cultivated UK (1997)	2.941	Pale yellow	Orange	15 / 13	1 - 1

Species, authority & date	Collector and collection no.	Origin of seed	Mass 100 seed (g)	Colour of arils (when ripe)	Colour of fruit (when ripe)	Subgenus /section	New seed group no.
<i>alata</i> Curtis (1781)	J. Mann	Cultivated Seychelles (1993)	2.193	Pale yellow	Orange	15 / 13	1 - 1
<i>alata</i> Curtis (1781)	J. Vanderplank	Cultivated UK (1996)	2.449	Pale yellow	Orange	15 / 13	1 - 1
<i>alata</i> 'Shannon'	J. Vanderplank NCP 1010	Cultivated UK (1997)	3.005	Pale yellow	Orange	15 / 13	1 - 1
<i>allantophylla</i> Mast. (1891)	J. Vanderplank NCP 1612	Cultivated UK (1991)	0.419	Clear white	Black	4 / 2	9 - 1
<i>alnifolia</i> H.B.K. (1817)	L. Gilbert 8022 NCP 1631	Cultivated USA	3.006			4 / 2	9 - 1
<i>amalocarpa</i> Rodriguez (1891)	M. Duffell NCP 1002	Cultivated UK (1998)	0.158	Clear white	Black	4 / 2	9 - 1
<i>ambigua</i> Hems (1902)	J. Meerman NCP 1605	Belize	4.914	Yellow	Orange	15 / 4	1 - 2
<i>ambigua</i> Hems (1902)	J. Vanderplank	St. Lucia	3.205	Yellow	Orange	15 / 4	1 - 2
<i>ambigua</i> Hems (1902)	J. Vanderplank	Venezuela	3.716	Yellow	Orange	15 / 4	1 - 2
'Amethyst' Vanderpl. (1991)	J. Vanderplank NCP 1012	Cultivar UK 1996	0.989	Orange	Orange		5 - 1
<i>amethystina</i> Mikan (1825)	J. Vanderplank NCP1022	Cultivated UK (2000)	1.610	Clear white	Yellow/green	15 / 5	7
<i>amethystina</i> Mikan (1825)	A. Frank NCP 1627	Bolivia	1.117	White	Black	15 / 5	7
<i>amoena</i> Escobar (1994)	P. Pomie	French Guyana	1.112	White	Pink	19 / 1	13

Species, authority & date	Collector and collection no.	Origin of seed	Mass 100 seed (g)	Colour of arils (when ripe)	Colour of fruit (when ripe)	Subgenus /section	New seed group no.
<i>amoena</i> Escobar (1994)	J. Vanderplank NCP.1555	French Guyana	0.919	White	Pink	19 / 1	13
<i>ampullacea</i> (Mast.) Harms (1893)	B. Bowden	Colombia	1.840	Yellow	Yellow	11 / 1	5 - 2
<i>antioquiensis</i> Karst (1859)	C. Laurens NCP 1597	New Zealand	1.556	Yellow	Yellow	11 / 4	8
<i>apetala</i> Killip (1922)	T. Fox NCP 1570	Costa Rica (2000)	0.435	White	Black	4 / 2	9 - 1
<i>arida</i> var. <i>pentaschista</i> Killip (1938)	J. M. MacDougal NCP 1553	Arizona USA	0.418	White	Yellowing green	17	1 - 4
<i>aurantia</i> Forst (1786)	J. Vanderplank NCP 1008	Cultivated UK (1997)	0.506	White	Green	4 / 5	6
<i>aurantia</i> Forst (1786)	D. Ellison NCP 1370	Wild Australia	0.463	White	Green	4 / 5	6
<i>auriculata</i> Kunth (1817)	M. Molinari	Venezuela (1994)	0.612	White	Dark brown	4 / 2	9 - 3
<i>auriculata</i> Kunth (1817)	R. Boender	Cultivated Florida USA	0.683	White	Dark brown	4 / 2	9 - 3
<i>auriculata</i> Kunth (1817)	P. Pomie	French Guyana	0.574	White	Dark brown	4 / 2	9 - 3
<i>auriculata</i> Kunth (1817)	J. Vanderplank NCP 1331	Trinidad	0.413	White	Dark brown	4 / 2	9 - 3
Aurora Vecchia	J. Vanderplank NCP 1636	Cultivated UK (2001)	1.341	Yellow	Red		1 - 4
<i>bauhinifolia</i> Kunth (1817)	K. Kingma	Venezuela	0.389			4 / 2	9 - 1

Species, authority & date	Collector and collection no.	Origin of seed	Mass 100 seed (g)	Colour of arils (when ripe)	Colour of fruit (when ripe)	Subgenus /section	New seed group no.
<i>biflora</i> Lam. (1789)	J. Vanderplank NCP 1026	Trinidad (1999)	0.350	Yellow	Black	4 / 2	9 - 1
<i>biflora</i> Lam (1789)	T. Fox	Costa Rica	0.766	Orange/yellow	Black	4 / 2	9 - 1
<i>biflora</i> Lam (1789)	Royal Bot.Gard., Kew 1992/3560		0.355	Orange/yellow	Black	4 / 2	9 - 1
<i>biflora</i> var Lamarck Lam (1789)	J. Vanderplank NCP 1024	Cultivated UK	0.611	Orange/yellow	Black	4 / 2	9 - 1
<i>boenderi</i> MacDougal (2003)	R. Boender NCP 1029	Costa Rica	0.650	White	Black	4 / 2	9 - 1
<i>bracteosa</i> Planch & Lind (1873)	L.E. Escobar	Colombia				11 / 9	5 - 2
<i>brevifila</i> Killip (1960)	J. Vanderplank NCP 1450	Costa Rica (2001)	0.963			4 / 13	1 - 2
<i>brevipes</i> Killip (1936)	M. Feather NCP 1450	Belize	0.312			4 / 13	9 - 3
<i>bryonioides</i> Kunth (1817)	J.M. MacDougal NCP 1558	Mexico	0.331	White	Whitey green	4 / 12	5 - 2
<i>caerulea</i> L. (1753)	J. Vanderplank NCP 1035	Cultivated UK	1.041	Orange-red	Orange	15 / 5	5 - 1
<i>caerulea</i> L. (1753)	G. Bossey (1992)	Brazil	1.002	Orange-red	Orange	15 / 5	5 - 1
<i>caerulea</i> 'Constance Elliott'	J. Vanderplank NCP 1033	Cultivated UK	0.993	Orange-red	Orange		5 - 1
<i>candida</i> Mast. (1871)	C. Laurens	French Guyana	2.467			19 / 5	12

Species, authority & date	Collector and collection no.	Origin of seed	Mass 100 seed (g)	Colour of arils (when ripe)	Colour of fruit (when ripe)	Subgenus /section	New seed group no.
<i>candida</i> Mast. (1872)	J. Vanderplank NCP 1569	French Guyana (2001)	1.140	White	Pale yellow	19 / 5	12
<i>candollei</i> Triana & Planch. (1873)	R. Stepansky NCP1355	Bolivia	0.205	Yellow	Black	4 / 2	9 - 1
<i>capsularis</i> L. (1753)	J. Vanderplank NCP 1045	Cultivated UK	0.336	White	Purple	4 / 13	9 - 2
<i>capsularis</i> L. (1753)	J. Vanderplank NCP 1384	Cultivated UK	0.378	White	Purple	4 / 13	9 - 2
<i>cerasina</i> Annonay & Feuillet (1997)	Cor Laurens NCP 1610	French Guyana (2001)	2.691	White	Deep red	15/11	5 - 1
<i>cerasina</i> Annonay & Feuillet (1997)	J. Vanderplank & S. Vanderplank NCP 1638	French Guyana	1.768			15 / 11	5 - 1
<i>ceratocarpa</i> Silveira (1930)	P. Pomie NCP 1659	Brazil	2.780			20 / 5	5 - 4
<i>cincinnata</i> Mast. (1855)	J. Vanderplank NCP 1059	Cultivated UK	3.194	White	Orange	15 / 11	5 - 1
<i>cincinnata</i> Mast. (1855)	J. Vanderplank NCP 1565	Costa Rica (2001)	2.395	White or pale yellow	Orange	15 / 11	5 - 1
<i>cinnabarina</i> Lind (1855)	C. Schulz	Germany	0.835	White	Green	4 / 5	6
<i>cinnabarina</i> Lind (1855)	J. Vanderplank NCP 1341	Cultivated UK	0.721	White	Green	4 / 5	6
<i>cirrhiflora</i> Juss (1805)	J. Vanderplank NCP 1650	French Guyana	3.102	White	Green	4 / 5	9 - 3

Species, authority & date	Collector and collection no.	Origin of seed	Mass 100 seed (g)	Colour of arils (when ripe)	Colour of fruit (when ripe)	Subgenus /section	New seed group no.
<i>citrina</i> MacDougal (1989)	J.M. MacDougal 4636.NCP 1058	3469 x 3048	0.345	White	Yellow	4 / 13	9 - 2
<i>citrina</i> MacDougal (1989)	J. Vanderplank NCP 1651	Cultivated UK	0.395	White	Yellow/green	4 / 13	9 - 2
<i>cobanensis</i> Killip (1924)	Cor Laurens	Belize (2000)	1.950			4 / 13	9 - 1
<i>coccinea</i> ssp. <i>bolivia</i> ssp. nov. ined.	Royal Bot.Gard., Kew (1987) NCP 1051	Bolivia	1.789	Pale yellow	Variegated green	13	4
<i>coccinea</i> ssp. <i>bolivia</i> ssp. nov. ined.	Craig Daniels	Bolivia	1.536	Pale yellow	Variegated green	13	4
<i>coccinea</i> ssp. <i>brownsberg</i> ssp. nov. ined.	J. Vanderplank NCP 1658	Surinam	0.728	White	Brown	13	4
<i>coccinea</i> ssp. <i>cacao</i> ssp. nov. ined.	J. Vanderplank NCP 1354	French Guyana	0.436	White or pale yellow	Yellow-brown	13	4
<i>coccinea</i> ssp. <i>tortue</i> ssp. nov. ined.	J. Vanderplank NCP 1323	French Guyana	0.619	White or pale yellow	Yellow-brown	13	4
<i>coccinea</i> ssp. <i>tortue</i> ssp. nov. ined.	P. Pomie (1998) NCP 1356	French Guyana	0.888	White or pale yellow	Yellow-brown	13	4
<i>coccinea</i> ssp. <i>tortue</i> ssp. nov. ined.	C. Laurens (1999) NCP 1324	French Guyana	0.846	White or pale yellow	Yellow-brown	13	4
<i>x colvillii</i> Sweet (1825)	J. Vanderplank NCP 1042 (1992)	Cultivated UK	0.194	White	Yellow/green		5 - 1
<i>colimensis</i> Mast. & Rose (1899)	J.M. MacDougal	Mexico		White	Whitey green	4 / 12	5 - 2

Species, authority & date	Collector and collection no.	Origin of seed	Mass 100 seed (g)	Colour of arils (when ripe)	Colour of fruit (when ripe)	Subgenus /section	New seed group no.
<i>colinvauxii</i> Wiggins (1970)	J. Vanderplank NCP 1590	Cultivated UK	0.434	White	Black	4 / 2	9 – 1
<i>comte A</i> sp. nov. ined.	J. Vanderplank NCP 1615	French Guyana (2001)	2.263	Clear white	Deep yellow		1 – 2
<i>comte B</i> sp. nov. ined.	J. Vanderplank NCP 1620	French Guyana (2001)	1.761	Clear white	Orange		5 – 2
<i>comte C</i> sp. nov. ined.	J. Vanderplank NCP 1618	French Guyana (2001)	4.502	Clear white	Deep yellow		1 – 2
<i>conzattiana</i> Killip (1927)	J. Vanderplank NCP 1040	Cultivated UK (2001)	0.519	White	Yellow	4 / 3	9 – 3
<i>coriacea</i> Juss (1805)	J. Vanderplank NCP 1039	Cultivated UK	1.321	White	Black	4 / 1	3
<i>coriacea</i> Juss (1805)	Leiden Bot. Gard.	Belize	0.847	White	Black	4 / 1	3
<i>costaricensis</i> Killip (1922)	C.W. Howell	USA	0.260			4 / 13	9 – 2
<i>costaricensis</i> Killip (1922)	Royal Bot.Gard., Kew. (1993) 126 NCP 1602	Costa Rica	0.398			4 / 13	9 – 2
<i>crenata</i> Feuillet & Crem. (1984)	P. Pomie NCP 1645	French Guyana (1999)	4.003			15 / 4	1 – 2
<i>crenata</i> Feuillet & Crem. (1984)	C. Feuillet 1632	French Guyana	3.828			15 / 4	1 – 2
<i>cuatrecasasii</i> Killip (1960)	L.E. Escobar	Colombia				11 / 4	5 – 2
<i>cumbalensis</i> (Karst) Harms (1894)	L.E. Escobar	Colombia		Yellow	Yellow	11 / 3	5 – 2

Species, authority & date	Collector and collection no.	Origin of seed	Mass 100 seed (g)	Colour of arils (when ripe)	Colour of fruit (when ripe)	Subgenus /section	New seed group no.
<i>cuneata</i> Willdenow (1809)	M. Molinari NCP 1647	Venezuela (1993)	0.239	White	Black	4 / 2	9 - 1
<i>cuneata</i> 'Miguel Molinari' Vanderpl (1998)	J. Vanderplank NCP 1044	Cultivated UK	0.252	White	Black	4 / 2	9 - 1
<i>cuprea</i> L. (1753)	J. Vanderplank NCP 1592	Bahamas (1997)	0.234	White	Black	7	9 - 1
<i>x decaisneana</i> Planchon. (1853)	J. Vanderplank NCP 1064	Cultivated UK (1997)	3.931	Pale yellow	Yellow		1 - 1
<i>x decaisneana</i> Planchon. (1853)	J. Vanderplank NCP 1064	Cultivated UK (1998)	4.193	Pale yellow	Yellow		1 - 1
<i>discoreifolia</i> Killip (1924)	J.M. MacDougal	Costa Rica		Orange	Red	4 / 12	2
<i>discophora</i> Jorg. & Law. (1987)	Jorgen	Brazil	6.210			4 / 4	11
<i>edulis</i> Sims (1818)	J. Vanderplank NCP 1582	Cultivated UK	1.993	Yellow	Purple	15 / 11	5 - 2
<i>edulis</i> var 'Norfolk'	J. Vanderplank NCP 1613	Cultivated UK (1997)	1.702	Yellow	Purple	15 / 11	5 - 2
<i>edulis</i> forma <i>flavicarpa</i> Degner.	J. Vanderplank NCP 1068	Surinam	1.832	Yellow	Yellow or red	15 / 11	5 - 2
<i>edulis</i> forma <i>flavicarpa</i> var 'Golen Star'	Axel Frank	Brazil	2.445	Yellow	Yellow	15 / 11	5 - 2
<i>edulis</i> forma <i>flavicarpa</i> Degner	J. Vanderplank NCP 1340	French Guyana Cultivated	2.354	Yellow	Pale yellow	15 / 11	5 - 2
<i>eichleriana</i> Mast. (1872)	M. Feather	Belize	1.478	Yellow	Mustard yellow	15 / 5	5 - 1

Species, authority & date	Collector and collection no.	Origin of seed	Mass 100 seed (g)	Colour of arils (when ripe)	Colour of fruit (when ripe)	Subgenus /section	New seed group no.
<i>eichleriana</i> Mast. (1872)	James Compton	Argentina (2000)	1.030	Yellow	Mustard yellow	15 / 5	5 - 1
<i>elegans</i> Mast. (1872)	J. Vanderplank NCP 1410	Cultivated UK (2003)	1.281	Yellow	Deep yellow	15 / 5	5 - 2
<i>x exoniensis</i> Mast. (1872)	J. Vanderplank NCP 1066	Cultivated UK	2.501	Yellow	Yellow		8
<i>exsudans</i> Zuccarini (1837)	J.M. MacDougal 3015	Mexico		Orange	Black	4 / 12	2
<i>exura</i> Feuillet (1994)	P. Pomie NCP 1573	French Guyana	1.424			15 / 5	5 - 1
<i>fanchonae</i> Feuillet (1986)	P. Pomie NCP 1571	French Guyana	0.883		Red	4 / 2	9 - 1
<i>ferruginea</i> Mast. (1872)	P. Pomie	French Guyana	0.506			4 / 2	9 - 1
<i>fieldiana</i> sp nov. ined. Tillett.	S. Tillett	Venezuela		White	Orange		
<i>flexipes</i> Triana & Planch. (1873)	L.E. Escobar	Colombia				11 / 4	8
<i>foetida</i> L. (1753)	J. M. MacDougal 6181 NCP 1633	Cultivated USA	0.592	White	Yellow	17	1 - 4
<i>foetida</i> (Anguilla)	J. Baker 1663 NCP 1587	Anguilla, West Indies	0.946	White	Yellow	17	1 - 4
<i>foetida</i> var. <i>galapagensis</i> Killip (1938)	J. Vanderplank NCP1388	Cultivated UK (2000)	0.990	Pale yellow	Yellow	17	1 - 4
<i>foetida</i> var. <i>gossypifolia</i> (Desv.) Mast. (1871)	Chelsea Physic Gard. NCP 1585	UK	1.523	White	Yellow	17	1 - 4

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<i>foetida</i> var. <i>hibiscifolia</i> (Lam.) Killip (1938)	J. Vanderplank NCP 1087	Cultivated UK (1995)	1.064	White	Deep Red	17	1 - 4
<i>foetida</i> var. <i>hispida</i> (D.C.) Killip (1931)	J. Daniels	Australia	0.916	White	Orange	17	1 - 4
<i>foetida</i> var. <i>hispida</i> (D.C.) Killip (1931)	J. Vanderplank NCP 1337	French Guyana	0.854	White	Orange	17	1 - 4
<i>foetida</i> var. <i>hispida</i> (D.C.) Killip (1931)	J. Vanderplank NCP 1623	Thailand (2002)	0.939	White	Yellow	17	1 - 4
<i>foetida</i> var. <i>hirsutissima</i> Killip (1936)	J. Vanderplank NCP 1078	Cultivated UK (1994)	1.850	White	Pink	17	1 - 4
<i>foetida</i> var. <i>hirsuta</i> Killip (1936)	J. Vanderplank NCP 1556	Thailand (2002)	0.890	White	Yellow	17	1 - 4
<i>foetida</i> var. <i>hirsuta</i> Killip (1936)	J. Vanderplank NCP 1084	Cultivated UK (1997)	1.402	White	Yellow	17	1 - 4
<i>foetida</i> var. <i>lanuginosa</i> Killip (1936)	J.M. MacDougal NCP 1635	Cultivated Missouri Bot. Gard.	1.572	White	Blood Red	17	1 - 4
<i>foetida</i> var. <i>maxoni</i> Killip (1936)	C. Feuillet CF 0096 NCP 1584	Guadeloupe	0.740	White		17	1 - 4
<i>foetida</i> var. <i>monitziana</i> (Planch.) Killip (1937)	C. Feuillet, CF 0113 NCP 1586	French Guyana	0.985	White	Yellow	17	1 - 4
<i>foetida</i> var. <i>orinocensis</i> Killip (1930)	M. Molinari NCP 1580	Venezuela	1.152	White	Red	17	1 - 4
<i>foetida</i> var. <i>parvifolia</i> Killip (1938)	M. Cooper NCP 1426	Mexico (2000)	1.410	White	Deep red	17	1 - 4

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<i>foetida</i> var. <i>riparia</i> (C. Wright) Killip (1938)	J. Vanderplank NCP 1294	Bahamas	1.609	White	Red	17	1 - 4
<i>foetida</i> var. <i>subpalmata</i> Killip (1936)	J. Vanderplank NCP 1293	Mexico	1.043	White	Red	17	1 - 4
<i>foetida</i> var. <i>vitacea</i> Mast. (1872)	J. Compton NCP 1385	Argentina (2000)	0.770	White	Scarlet	17	1 - 4
<i>gabrielliana</i> sp. nov. ined. (Vanderpl.)	J. Vanderplank NCP 1434	French Guyana (2001)	1.620	Clear white	Orange and deep orange		1 - 3
<i>garckeii</i> Mast. (1872)	J. Vanderplank NCP 1655	French Guyana (2001)	3.220	Clear white	Yellow/green	4 / 2	7
<i>garckeii</i> Mast. (1872)	C. Feuillet CF 0113 NCP 1626	French Guyana	2.103	Clear white	Yellow/green	15 / 5	7
<i>gibertii</i> Brown (1896)	M. Molinari	Venezuela	1.938	Yellow	Yellow	15 / 5	1 - 3
<i>gibertii</i> Brown (1896)	J. Vanderplank NCP 1092	Cultivated UK	1.604	Yellow	Mustard yellow	15 / 5	1 - 3
<i>gilbertiana</i> MacDougal (1989)	J. Vanderplank NCP 1089	Costa Rica	0.190	White	Black	4 / 2	9 - 1
<i>glandulosa</i> Cav. (1790)	P. Pomie	French Guyana (1998)	1.641	White	Yellow brown	13	4
<i>glandulosa</i> Cav. (1790)	J. Vanderplank NCP 1227	French Guyana (1999)	1.548	White	Yellow brown	13	4
<i>glandulosa</i> Cav. (1790)	J. Vanderplank NCP 1556	French Guyana (2001)	1.215	Pale yellow	Green	13	4

Species, authority & date	Collector and collection no.	Origin of seed	Mass 100 seed (g)	Colour of arils (when ripe)	Colour of fruit (when ripe)	Subgenus /section	New seed group no.
<i>gracilis</i> Jacq. & Link. (1822)	S. Tillett 8011-331	Venezuela	0.8033	Orange	Red	4 / 1	2
<i>gracilis</i> Jacq. & Link. (1822)	Royal Bot.Gard., Kew 1993-28 NCP 1606		0.941	Orange	Red	4 / 1	2
<i>gracilis</i> Jacq. & Link. (1822)	J. Vanderplank NCP 1094	Cultivated UK	0.856	Orange	Red	4 / 1	2
<i>gracillima</i> Killip (1924)	J. Vanderplank NCP 1097	Cultivated UK (2000)	2.010	Clear white	Deep orange	23	5 - 3
<i>gritensis</i> Karst (1859)	M. Molinari NCP 1576	Venezuela	0.982			15 / 5	7
<i>guatemalensis</i> Wats. (1887)	T. Fox	Belize	1.323			4 / 7	3
<i>guatemalensis</i> Wats. (1887)	M. Molinari NCP 1099	Venezuela	1.405			4 / 7	3
<i>guatemalensis</i> Wats. (1887)	L. Gilbert 9016 NCP 1654	Cultivated USA	0.852			4 / 7	3
<i>guazumaefolia</i> Juss. (1805)	M. Molinari	Venezuela	1.303			15 / 4	7
<i>hahnii</i> Mast. (1872)	L. Gilbert NCP 1593		1.165			4 / 7	3
<i>helleri</i> Peyr. (1859)	J. Vanderplank NCP 1105	Cultivated UK	0.286	White	Black	4 / 2	9 - 1
<i>herbertiana</i> Ker-Gawl. (1823)	J. Vanderplank NCP 1104	Cultivated UK	0.358	White	Green	4 / 5	6
<i>herbertiana</i> Ker-Gawl. (1823)	Royal Bot. Gard., Kew (1989) 53501	Australia	0.289	White	Green	4 / 5	6

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<i>herbertiana</i> ssp. <i>Howinsula</i> P.S. Green (1972)	Royal Bot. Gard., Kew.(1989) 1651 NCP 1607	Lord Howe Island	0.819	White	Green	4 / 5	6
<i>holosericea</i> L. (1753)	J. M. MacDougal NCP 1617		0.259	Pale yellow	Deep purple	4 / 1	9 - 1
<i>holosericea</i> L. (1753)	J. Vanderplank NCP 1106	Cultivated UK	0.378	White	Purple/brown	4 / 1	9 - 1
<i>hollrungii</i> Sch (1888)	J. J. O. de Wilde	Malaysia				4 / 8	3
<i>incarnata</i> L. (1753)	J. Vanderplank NCP 1113	Cultivated UK	3.278	White	Green	15 / 11	5 - 2
<i>incarnata</i> L. (1753)	H. Heilman (1997)	Cultivated Tennessee USA	3.818	White	Green	15 / 11	5 - 2
<i>incarnata</i> L. (1753)	S. Vanderplank NCP 1562	Mississippi USA	2.689	White	Green	15 / 11	5 - 2
<i>incarnata</i> L. (1753)	J. Vanderplank	Cultivated UK	3.657	White	Green	15 / 11	5 - 2
Incense Winters & Knight(1975)	J. Vanderplank NCP 1111	Cultivated UK	2.902	White	Green / yellow		5 - 1
<i>jurullensis</i> Kunth (1818)	J. Vanderplank NCP 1119	Cultivated UK	0.297	White	Black	4 / 2	9 - 1
<i>juliana</i> MacDougal (1992)	J.M. MacDougal 492	Mexico		White	Black	4 / 1	3
<i>juliana</i> MacDougal (1992)	J. Vanderplank NCP 1116	Cultivated UK	0.605	White	Black	4 / 1	3
<i>kalbreyeri</i> Mast. (1883)	M. Molinari NCP 1603	Venezuela	0.278		Black	4 / 11	9 - 1

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<i>x kewensis</i> Nicholson (1901)	J. Vanderplank NCP 1611	Cultivated UK	1.189	White	Green		5 - 1
<i>karwinskii</i> Mast. (1872)	J.M. MacDougal	Mexico		Clear white	Pale green	4 / 12	5 - 2
<i>karwinskii</i> Mast. (1872)	J. Vanderplank NCP1120	Cultivated UK (2000)	0.850	Clear white	Pale green	4 / 12	5 - 2
<i>kermesina</i> Link. & Otto. (1826)	A. Frank NCP 1568	Brazil (2001)				15 / 5	7
<i>lancearia</i> Mast. (1885)	J. Vanderplank NCP 1485	Costa Rica	2.821	Purple	Purple	4 / 2	9 - 1
<i>lancetillensis</i> sp nov ined.	C. Laurens NCP 1653	Belize	4.192	White	Green		1 - 1
<i>lancetillensis</i> sp nov ined.	L. Gilbert 9305 NCP 1567	Cultivated USA (2000)	3.988	White	Green		1 - 1
<i>lancetillensis</i> sp nov ined.	J. Meerman NCP 1567	Belize	4.235	White	Green		1 - 1
<i>laurifolia</i> L. (1753)	E. Chen NCP 1135	Singapore	1.876	Yellow	Orange	15 / 4	5 - 2
<i>laurifolia</i> L. (1753)	P. Pomie (1997)	French Guyana	1.776	Yellow	Orange	15 / 4	5 - 2
<i>laurifolia</i> L. (1753)	M. Molinari (1994)	Venezuela	1.436	Yellow	Orange	15 / 4	5 - 2
<i>laurifolia</i> L. (1753)	J. Vanderplank NCP 1127	Cultivated UK	1.972	Yellow	Orange	15 / 4	5 - 2
<i>laurifolia</i> L. (1753)	J. Vanderplank NCP 1646	Cultivated UK	1.973	Yellow	Orange	15 / 4	5 - 2

Species, authority & date	Collector and collection no.	Origin of seed	Mass 100 seed (g)	Colour of arils (when ripe)	Colour of fruit (when ripe)	Subgenus /section	New seed group no.
<i>ligularis</i> Juss (1805)	J. Vanderplank NCP 1133	Colombia	2.957	Yellow	Orange	15 / 17	1 - 1
<i>ligularis</i> Juss (1805)	M. Molinari	Venezuela	3.048	Yellow	Orange	15 / 17	1 - 1
<i>lindeniana</i> Tr. & Planch. (1873)	M. Molinari NCP 1336	Venezuela	1.526	White	Green	20 / 3	5 - 4
<i>lobata</i> (Killip) Hutch (1967)	J.M. MacDougal NCP 1563	Costa Rica		Orange	Red	4 / 12	2
<i>loefgrenii</i> Vitta (1997)	J. Vanderplank NCP 1637	Cultivated UK (2003)	1.229	Clear white	Yellow/green		5 - 3
<i>luismanvelii</i> sp. nov. ined.	M. Molinari NCP 1622	Venezuela	0.945				9 - 3
<i>lutea</i> L. (1753)	S. Vanderplank NCP 1652	Mississippi USA	1.116	White	Black	4 / 2	9 - 1
<i>lutea</i> L. (1753)	J.M. MacDougal NCP 1137	Missouri USA	1.147	White	Black	4 / 2	9 - 1
<i>macrophylla</i> Spruce ex Mast. (1883)	R. Boender (1995) NCP 1138	Florida USA	1.188			20 / 3	13
<i>macropoda</i> Killip (1960)	P. Pomie NCP 1572	Bolivia (1997)	1.561			10	5 - 2
<i>magnifica</i> Escobar (1990)	C. Howell NCP 1598	Colombia	1.809			15 / 17	1 - 3
<i>malletii</i> MacDougal (1989c)	J.M. MacDougal	Panama			Black	4 / 2	9 - 1
<i>maliformis</i> L. (1753)	M. Molinari (1994)	Venezuela	1.531	White	Yellow	15 / 17	5 - 3

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<i>maliformis</i> L. (1753)	J. Vanderplank NCP1143	Venezuela Cultivated	1.463	Pale yellow	Greeny-yellow	15 / 17	5 - 3
<i>maliformis</i> L. (1753)	J. Vanderplank NCP1283	Ecuador Cultivated	1.640	Pale yellow	Greeny-yellow	15 / 17	5 - 3
<i>manicata</i> (Juss) Pers. (1807)	R. McCain	Cultivated USA	1.533	White	Green	12	5 - 1
<i>manicata</i> (Juss) Pers. (1807)	J. Vanderplank NCP 1157	Cultivated UK (1997)	1.935	White	Green	12	5 - 1
<i>manicata</i> (Juss) Pers. (1807)	J. Vanderplank NCP 1621	Cultivated UK (1996)	2,064	White	Green	12	5 - 1
<i>manicata</i> Juss) Pers. (1807)	M. Molinari (1994)	Venezuela	1.889	White	Green	12	5 - 1
Mary Jane R. Boender (2001)	J. Vanderplank NCP1511	Cultivated UK (2002)	0.672	Clear white	Green		4
<i>matthewsii</i> (Mast.) Killip (1927)	P. Pomie	Ecuador	0.492	Yellow	Yellow	11 / 8	5 - 2
<i>matthewsii</i> (Mast.) Killip (1927)	J. Vanderplank NCP1390	Peru Cultivated	1.130	Pale yellow	Yellow	11 / 8	5 - 2
<i>mayarum</i> MacDougal (1989)	C. Laurens (2000) NCP 1566	Belize	4.241	White	Yellow	15 / 11	1 - 3
<i>membranacea</i> Benth (1841)	R. McCain NCP 1601	Cultivated USA	0.680			4 / 7	5 - 2
<i>membranacea</i> Benth. (1841)	M. Cooper	Guatemala (2001)	2.571			4 / 7	5 - 2
<i>menispermifolia</i> Kunth (1817)	C. Howell	USA	1.406	Clear white	Yellow/green	15 / 8	7

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<i>menispermifolia</i> Kunth (1817)	J. Vanderplank NCP 1151	Cultivated UK (2000)	1.250	Clear white	Yellow/green	15 / 8	7
<i>microstipula</i> sp. nov. ined.	L. Gilbert 9271 NCP 1564	Cultivated USA (2000)	8.043				1 - 1
<i>misera</i> Kunth (1817)	J. Vanderplank NCP 1150	Cultivated UK (2002)	0.483	Clear white	Black	4 / 2	9 - 1
<i>mixta</i> L. (1781)	M. Molinari NCP 1644	Venezuela	3.129	Yellow	Yellow	11 / 8	5 - 2
<i>mixta</i> var. <i>pinanga</i>	K. Kingma	Venezuela	3.452	Yellow	Yellow	11 / 8	5 - 2
<i>mixta</i> var. <i>mixta</i>	M. Molinari	Venezuela	3.652	Yellow	Yellow	11 / 8	5 - 2
<i>mooreana</i> Hook (1840)	J. Vanderplank NCP1308	Cultivated UK (2000)	1.430	Blood red	Orange	15 / 5	3
<i>mooreana</i> Hook (1840)	J. Compton NCP 1386	Argentina (2000)	2.233	Blood red	Orange	15 / 5	5 - 1
<i>morifolia</i> Mast. (1872)	J. Vanderplank NCP 1148	Cultivated	1.838	Orange	Black	4 / 12	2
<i>morifolia</i> Mast. (1872)	M. Molinari NCP 1147	Venezuela	1.259	Orange	Black	4 / 12	2
<i>mucronata</i> Lam (1789)	L. Gilbert 9253 NCP 1458	Cultivated USA	0.983			15 / 16	5 - 3
<i>multiflora</i> L. (1753)	J. Vanderplank NCP 1142	Florida USA			Black	1	9 - 1
<i>murucuja</i> L. (1753)	J. Vanderplank NCP 1153	Cultivated UK	0.362	White	Black	6	3
<i>naviculata</i> Griseb. (1874)	J. Vanderplank NCP 1161	Cultivated UK	1.013	Clear White	Pale Yellow	15 / 5	5 - 1

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<i>naviculata</i> Griseb. (1874)	C. Schulz	Bolivia	1.341	Clear White	Yellow	15 / 5	5 - 1
<i>nephrodes</i> Mast. (1890)	C. Laurens NCP 1159	Brazil	1.428	Clear White	Green	15 / 8	7
<i>nephrodes</i> Mast. (1890)	J. Vanderplank NCP 1290	Cultivated UK (2000)	0.866	Clear white	Pale yellow	15 / 8	7
<i>nigradenia</i> Rusby (1927)	M. Molinari NCP 1628	Venezuela	3.308			15 / 4	1 - 2
<i>nitida</i> Kunth (1817)	M. Molinari	Venezuela	2.544	White	Orange	15 / 4	1 - 2
<i>nitida</i> Kunth (1817)	J. Vanderplank NCP 1336	French Guyana	3.413	White	Orange	15 / 4	1 - 2
<i>nubicola</i> MacDougal (1989)	C. Laurens NCP 1559	Costa Rica	1.257	White	Black	4 / 2	9 - 1
<i>oaxacensis</i> MacDougal (1992)	J.M. MacDougal	Mexico		Orange	Black	4 / 12	2
<i>obtusifolia</i> Sesse. & Moc. (1887)	J.M. MacDougal 4687	Mexico		White	Black	4 / 1	3
<i>obtusifolia</i> Sesse & Moc. (1887)	J. Vanderplank NCP 1171	Cultivated UK (2000)	1.410	White	Black	4 / 1	3
<i>oerstedii</i> Mast. (1872)	M. Molinari	Venezuela	1.543	Yellow	Yellow/green	15 / 16	7
<i>oerstedii</i> Mast. (1872)	T. Fox	Costa Rica (2001)	0.908	Pale yellow	Dull green	15 / 16	7
<i>oerstedii</i> var <i>choconiana</i> (Wats) Killip (1936)	M. Feather NCP 1167	Belize	1.483	Yellow	Purplish Green	15 / 16	7

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<i>organensis</i> Gardn. (1845)	J. Vanderplank NCP 1169	Cultivated UK	0.745	Yellow	Black	4 / 2	9 - 1
<i>ornithoura</i> Mast. (1891)	M. Cooper NCP 1624	Honduras (2001)	0.302	Clear white	Black	4 / 2	9 - 1
<i>ovalis</i> Vell. (1827)	P. Pomie NCP 1573	Brazil	6.832			22	14
<i>ovata</i> Martin (1828)	S. Hall NCP 1575	Brazil	5.630			19 / 3	14
<i>ovata</i> Martin (1828)	C. Laurens	Brazil	3.865			19 / 3	14
<i>palenquensis</i> Holm-Niel. & Law. (1987)	W. Betty	Colombia	2.081			15 / 17	1 - 1
<i>pallens</i> Poepp (1872)	R. Boender NCP 1176	Cultivated Florida USA	1.145	White	Yellow	15 / 5	1 - 3
<i>pallida</i> L. (1753)	J. Vanderplank NCP 1245	USA	0.308	White	Black	4 / 1	9 - 1
<i>palmeri</i> var. <i>sublanceolate</i> Killip (1936)	C. Laurens	Belize	1.730	White	Deep red	17	1 - 4
<i>palmeri</i> var. <i>sublanceolate</i> Killip (1936)	J. Vanderplank NCP 1287	Cultivated (2001)	2.289	White	Deep red	17	1 - 4
<i>pardifolia</i> sp. nov. ined.	J. Vanderplank NCP 1499	Cultivated UK (2002)	0.261	Clear white	Purple/black		9 - 1
<i>parritae</i> (Mast.) Bailey (1916)	L.E. Escobar	Colombia				11 / 6	8

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<i>penduliflora</i> Bert. (1828)	J. Vanderplank NCP1173	Cultivated UK (2000)	0.410	Clear white	Purple/black	2	9 - 1
<i>pendens</i> MacDougal (1994)	J.M. MacDougal	Mexico		Yellow	Black	4 / 12	2
<i>perfoliata</i> L. (1753)	J. Vanderplank NCP 1180	Cultivated UK (2000)	0.420	Pale yellow	Black	7	9 - 1
<i>pergrandis</i> Holm-Niel. & Law. (1988)	R. Boender 1304 NCP 1599	Cultivated USA	5.624	Pale yellow	Yellow	15 / 4	1 - 2
<i>phoenicea</i> Lindl. (1833)	J. Vanderplank NCP 1175	Cultivated UK	3.266	White	Orange	15 / 13	1 - 1
<i>pilosa</i> Ruiz & Pavon (1828)	J.M. MacDougal	Mexico		White	Whitey green	4 / 12	5 - 2
<i>pilosicorona</i> Sacco. (1973)	P. Worley	Bolivia	1.639	Orange	Yellow	11 / 7	5 - 2
<i>pilosicorona</i> Sacco (1973)	J. Vanderplank NCP 1185	Cultivated UK (2000)	1.690	Orange	Pale yellow	11 / 7	5 - 2
Pink Jewel Vanderpl. (2003)	J. Vanderplank NCP 1496	Cultivated UK (2001)	1.791	Yellow	Pinky red		1 - 4
<i>pinnatistipula</i> Cav. (1799)	R. Stepansky (1998) NCP 1263	Bolivia	3.489	Orange	Yellow	11 / 7	5 - 2
<i>pinnatistipula</i> Cav. (1799)	G. Farr NCP 1643	Peru (2001)	4.095	Pale yellow	Olive brown	11 / 7	5 - 2
x <i>piresae</i> Vanderpl. (1997)	J. Vanderplank NCP 1181	Cultivar UK	1.396	White	Brown		4
<i>pitteri</i> Mast. (1897)	R. Boender NCP 1561	Belize	13.668	White	Yellow	19 / 2	12

Species, authority & date	Collector and collection no.	Origin of seed	Mass 100 seed (g)	Colour of arils (when ripe)	Colour of fruit (when ripe)	Subgenus /section	New seed group no.
<i>pitteri</i> Mast. (1897)	R. Boender	Costa Rica	9.234	White	Yellow	19 / 2	12
<i>platyloba</i> Killip (1922)	J. Vanderplank NCP 1177	Cultivated UK	1.846	White	Yellow	15 / 17	5 - 3
<i>podadenia</i> Killip (1924)	J. M. MacDougal	Mexico		White	Green	4 / 12	5 - 2
<i>pterocarpa</i> MacDougal (1994)	J. M. MacDougal (1994)	Mexico		Orange	Purple	4 / 12	2
<i>punctata</i> L. (1753)	M. Molinari	Venezuela	0.207	Clear white	Black	4 / 2	9 - 1
<i>punctata</i> L. (1753)	J. Vanderplank NCP 1178	Cultivated UK	0.588	Clear white	Black	4 / 2	9 - 1
Pura Vida 1 Vanderpl. (1996a)	J. Vanderplank NCP 1179	Cultivated UK (2001)	0.963	Yellow	Yellow		7
Purple Haze Vanderpl. (1996a)	J. Vanderplank NCP	Cultivated	1.860	Yellow/orange	Orange		7
<i>quadrangularis</i> L. (1759)	M. Molinari	Venezuela	4.154	White/pale yellow	Pale green	15 / 13	1 - 1
<i>quadrangularis</i> L. (1759)	M. Molinari	Venezuela	4.789	White/pale yellow	Pale green	15 / 13	1 - 1
<i>quadrangularis</i> L. (1759)	S. Segalen	Cultivated Reunion Island	4.013	White/pale yellow	Pale green	15 / 13	1 - 1
<i>quadrangularis</i> L. (1759)	J. Vanderplank NCP 1193	Cultivated UK	5.408	White/pale yellow	Pale green	15 / 13	1 - 1
<i>quadrangularis</i> L. (1759)	J. Vanderplank NCP 1339	Cultivated French Guyana	4.629	White/pale yellow	Pale green	15 / 13	1 - 1

Species, authority & date	Collector and collection no.	Origin of seed	Mass 100 seed (g)	Colour of arils (when ripe)	Colour of fruit (when ripe)	Subgenus /section	New seed group no.
<i>quadrangularis</i> var <i>macrocarpa</i> L. (1759)	H. Annonay	Martinique	4.312	White/pale yellow	Pale green	15 / 13	1 - 1
<i>quadrifaria</i> Vanderpl. (1996b)	Royal Bot. Gard., Kew (1989) 283 NCP 1694	Brazil	0.698	White	Light brown	13	4
<i>quadrifaria</i> Vanderpl. (1996b)	J. Vanderplank NCP 1192	Cultivated UK	0.614	White	Brown	13	4
<i>quadriglandulosa</i> Rodschied (1796)	R.E.D. Baker 14583	Trinidad	1.140			13	4
<i>quercetorum</i> Killip (1938)	J.M. MacDougal	Mexico		Yellow	Green	4 / 12	5 - 2
<i>quinquangularis</i> Calderon	J. Vanderplank NCP 1189	Mexico				4 / 13	
<i>racemosa</i> Brot. (1818)	Royal Bot. Gard., Kew (1987) 283	Brazil	1.772	Clear white	Green	16	5 - 1
<i>racemosa</i> Brot. (1818)	J. Vanderplank NCP 1197	Cultivated UK	1.768	Clear white	Green	16	5 - 1
<i>reflexiflora</i> Cav (1899)	R. Boender	Ecuador	1.445	Clear white	Yellow/green	14	5 - 3
<i>reflexiflora</i> Cav. (1899)	J. Vanderplank NCP 1369	Cultivated UK (2000)	1.060	Clear white	Yellow/green	14	5 - 3
<i>resticulata</i> Mast. & Andre (1883)	M. Molinari	Venezuela	1.443	White	Yellow	15 / 5	7
<i>resticulata</i> Mast. & Andre (1883)	J. Vanderplank NCP 1202	Cultivated UK	1.714	White	Yellow	15 / 5	7

Species, authority & date	Collector and collection no.	Origin of seed	Mass 100 seed (g)	Colour of arils (when ripe)	Colour of fruit (when ripe)	Subgenus /section	New seed group no.
<i>retipetala</i> Mast. (1893)	J. Vanderplank NCP 1203	Cultivated UK (2003)	1.119	Pale yellow	Yellow/green	15 / 5	7
<i>riparia</i> Mart. ex Mast. (1872)	P. Pomie	French Guyana	2.911			15 / 4	1 - 1
<i>rovirosae</i> Killip (1922)	M. Feather	Mexico				14 / 3	
<i>rubra</i> L. (1753)(Capsule fruit)	J. Vanderplank NCP 1332	Trinidad	0.286	White	Pink	4 / 13	9 - 1
<i>rubra</i> L. (1753) (Round fruit)	J. Vanderplank NCP 1194	Cultivated UK	0.355	White	Pink	4 / 13	9 - 1
<i>rubra</i> L. (1753) (Capsule fruit)	J. Vanderplank NCP 1196	Cultivated UK	0.270	White	Dark Red	4 / 13	9 - 2
<i>rubra</i> L. (1753) (Capsule fruit)	J. Vanderplank NCP 1195	Cultivated UK	0.213	White	Dark Red	4 / 13	9 - 2
<i>rubra</i> L. (1753) (Capsule fruit)	T. Fox NCP 1379	Cultivated UK	0.356	White	Yellow-Green	4 / 13	9 - 2
<i>rufa</i> ined. (Feuillet)	P. Pomie	French Guyana	0.751	Clear white	Black	4 / 2	9 - 3
<i>rufa</i> ined. (Feuillet)	J. Vanderplank NCP 1359	French Guyana (2001)	0.881	Clear white	Black	4 / 2	9 - 3
<i>sanctae-mariae</i> MacDougal (1989)	J.M. MacDougal	Mexico			Black	4 / 2	
<i>sanguinolenta</i> Mast. (1868)	J. Vanderplank NCP1288	Cultivated UK	0.396	White	Yellow	4 / 13	9 - 2
<i>sanguinolenta</i> Mast. (1868)	J. Vanderplank NCP1213	Cultivated UK	0.339	White	Brick Red	4 / 13	9 - 2

Species, authority & date	Collector and collection no.	Origin of seed	Mass 100 seed (g)	Colour of arils (when ripe)	Colour of fruit (when ripe)	Subgenus /section	New seed group no.
<i>seemannii</i> Griseb. (1858)	M. Molinari NCP 1595	Venezuela	1.187			15 / 17	1 - 4
<i>seemannii</i> Griseb. (1858)	Royal Bot. Gard., Kew 1992- 3554 NCP 1608		0.941			15 / 17	1 - 4
<i>serratifolia</i> L. (1753)	J. Vanderplank NCP 1225	Cultivated UK	4.374	White	Yellow	15 / 14	1 - 3
<i>serratifolia</i> L. (1753)	J. J. Segalen	Reunion	3.715	White	Yellow	15 / 14	1 - 3
<i>serratifolia</i> L. (1753)	J. Vanderplank NCP 1227	Cultivated UK	3.359	White	Yellow	15 / 14	1 - 3
<i>serratodigitata</i> L. (1753)	P. Romer NCP 1625	Surinam	2.487	White	Yellow	15 / 1	5 - 1
<i>serratodigitata</i> L. (1753)	C. Laurens	Belize	1.730	White	Yellow	15 / 1	5 - 1
<i>serrulata</i> Jacq. (1767)	M. Molinari	Venezuela	1.606	White	Yellow	15 / 17	5 - 3
<i>serrulata</i> Jacq. (1767)	J. Vanderplank NCP 1221	Cultivated UK	0.792	White	Yellow	15 / 17	5 - 3
<i>sexflora</i> Juss. (1805)	R. Boender NCP 1214	Florida USA	0.162		Black	4 / 2	9 - 1
<i>sicyoides</i> Schle & Cham. (1830)	J.M. MacDougal 3031	Mexico		Orange	Black	4 / 12	2
'Simply Red' Vanderplank (2000a)	J. Vanderplank NCP 1350	Cultivated UK (2000)	1.100	Orange	Orange/yellow		7
<i>x smythiana</i> Mast. (1891)	J. Vanderplank NCP 1222	Cultivated UK (2001)	2.383	Yellow	Yellow		5 - 2

Species, authority & date	Collector and collection no.	Origin of seed	Mass 100 seed (g)	Colour of arils (when ripe)	Colour of fruit (when ripe)	Subgenus /section	New seed group no.
<i>sprucei</i> Mast. (1872)	J. Vanderplank NCP 1376	Cultivated UK (2000)	1.210	Clear yellow	Pale yellow	15 / 5	1 - 3
<i>standleyi</i> Killip (1924)	C. Laurens	Cultivated	0.334	Yellow	Black	4 / 2	9 - 1
<i>standleyi</i> Killip (1924)	J. Vanderplank NCP 1589	Cultivated UK	0.279	Yellow	Black	4 / 2	9 - 1
<i>stipulata</i> Aubl. (1775)	P. Pomie	Madagascar	1.944			15 / 5	5 - 2
<i>stipulata</i> Aubl. (1775)	J. Moser NCP 1578	Venezuela	1.941			15 / 5	7
'Star of Bristol' Vanderpl. (1987)	J. Vanderplank NCP 1219	Cultivated UK	0.082	Yellow	Orange		5 - 1
St. Rule J.H. Wilson (1900)	J. Vanderplank NCP 1224	Cultivated UK (1998)	2.741	Yellow	Yellow		1 - 3
<i>suberosa</i> L. (1753)	J. Vanderplank NCP 1208	Cultivated UK	0.559	White	Black	4 / 1	3
<i>suberosa</i> L. (1753)	Leiden Bot. Gard. NCP 1207	Cultivated	0.479	White	Black	4 / 1	3
<i>suberosa</i> L. (1753)	J. Vanderplank NCP 1206	Key Largo, Florida USA	0.329	White	Black	4 / 1	3
<i>subpeltata</i> Ortega (1798)	J. Vanderplank NCP 1223	Cultivated UK	1.243	Yellow	Yellow	15 / 5	5 - 1
'Sunburst' (P. Worley) Vanderpl. (1991)	J. Vanderplank NCP 1211	Cultivated UK	0.278	White	Black		9 - 1
<i>talamancensis</i> Killip (1922)	J. Vanderplank (2003) NCP 1286	Cultivated UK	0.249	Clear white	Black	4 / 12	

Species, authority & date	Collector and collection no.	Origin of seed	Mass 100 seed (g)	Colour of arils (when ripe)	Colour of fruit (when ripe)	Subgenus /section	New seed group no.
<i>tarminiana</i> Jorgensen & MacDougal (2001)	J. Vanderplank NCP 1341	Cultivated UK	2.203	Yellow	Yellow	11 / 3	5 - 2
<i>tarminiana</i> Jorgensen & MacDougal (2001)	J. Vanderplank NCP 1140	Cultivated Colombia	3.102	Yellow	Yellow	11 / 3	5 - 2
<i>tarminiana</i> Jorgensen & MacDougal (2001)	N. Atherton	Hawaii	2.676	Yellow	Yellow	11 / 3	5 - 2
<i>tenerifensis</i> Escobar (1988b)	L.E. Escobar	Colombia				11 / 4	5 - 2
<i>tenuifila</i> Killip (1927)	J. Vanderplank NCP 1504	Cultivated UK (2002)	1.179	Yellow	Orange	15 / 5	5 - 1
<i>tetranda</i> Banks & Sol. (1828)	C. Laurens NCP 1619	New Zealand	3.670		Orange	20	10
<i>tikilili</i> sp. nov. ined. (Vanderpl.)	J. Vanderplank NCP 1435	French Guyana (2001)	1.420	Clear white	Pinky orange		
<i>tiliifolia</i> L. (1753)	M. Molinari	Venezuela	2.052			15 / 17	1 - 3
<i>trialata</i> Feuillet & MacDougal (1996)	P. Pomie	French Guyana	1.801	White/pale yellow	Greeny yellow	15 / 13	1 - 2
<i>trialata</i> Feuillet & MacDougal (1996)	J. Vanderplank NCP 1333	French Guyana (2001)	1.895	White	Greeny yellow	15 / 13	1 - 2

Species, authority & date	Collector and collection no.	Origin of seed	Mass 100 seed (g)	Colour of arils (when ripe)	Colour of fruit (when ripe)	Subgenus /section	New seed group no.
<i>triana</i> Killip (1938)	L.E. Escobar	Colombia				11 / 4	8
<i>tricuspis</i> Mast. (1872)	C. Schulz	Bolivia	0.422	White	Black	4 / 2	9 - 1
<i>tricuspis</i> Mast. (1872)	J. Vanderplank NCP 1229	Cultivated	0.811	White	Black	4 / 2	9 - 1
<i>trifasciata</i> Lemaire (1868)	L. Gilbert NCP 1459	Cultivated USA	0.501	White or pale yellow	Black	4 / 2	9 - 1
<i>trifasciata</i> Lemaire (1868)	J. Vanderplank NCP 1656	Cultivated UK (2001)	0.522	Pale yellow	Black	4 / 2	9 - 1
<i>triloba</i> R. & P. (1828)	Andrew Adair	Bolivia (2001)	1.410	Pale Yellow	Yellow	15 / 17	1 - 3
<i>triloba</i> R. & P. (1828)	J. Vanderplank NCP 1657	Cultivated UK (2002)	0.862	Pale yellow	Yellow	15 / 17	1 - 3
<i>trisecta</i> Mast. (1872)	J. Vanderplank NCP 1244	Cultivated UK	1.402	Clear white	Yellow/green	10	5 - 2
<i>truxillensis</i> Planch. & Lind. (1873)	M. Molinari NCP 1600	Venezuela	7.080	Yellow	Yellow	11 / 4	8
<i>tryphostemmatoides</i> Harms (1894)		Ecuador				23	
<i>tuberosa</i> Jacq. (1804)	J. Vanderplank NCP 1243	Cultivated UK	0.292	Yellow	Black	4 / 2	9 - 1
<i>tuberosa</i> Jacq. (1804)	J. Vanderplank NCP 1243	Cultivated UK (1993)	0.308	Yellow	Black	4 / 2	9 - 1
<i>tuberosa</i> Jacq. (1804)	J. Vanderplank NCP 1330	Trinidad	0.225	Yellow	Black	4 / 2	9 - 1
<i>tulae</i>	J. Vanderplank	Puerto Rica	0.344	White	Black	6	9 - 1

Urban (1899)	NCP 1238						
<i>tulae</i> Urban (1899)	J. Vanderplank NCP 1239	Cultivated	0.229	White	Black	6	9 - 1
<i>umbilicata</i> Griseb. Harms (1893)	Van Herck NCP 1503	Cultivated	2.444			14	5 - 2
<i>urbaniana</i> Killip (1927)	J. Vanderplank NCP 1248	Cultivated UK (1995)	1.255	White	Dark red	17	1 - 4
<i>urnaefolia</i> Rusby (1896)	Peterson & H. Jerling 698	Argentina		Yellow	Black	4 / 2	9 - 1
<i>variolata</i> Poepp. & Endl. (1838)	P. Pomie NCP 1264	French Guyana	1.677			13	4
<i>vespertilio</i> L. (1753)	M. Molinari	Venezuela	0.416	Pale Yellow	Dark brown	4 / 2	9 - 1
<i>vespertilio</i> L. (1753)	J. Vanderplank NCP 1557	French Guyana	0.351	Pale Yellow	Dark brown	4 / 2	9 - 1
<i>vespertilio</i> L. (1753)	C. Feuillet CF 0430 NCP 1327	French Guyana	0.278	Pale Yellow	Dark brown	4 / 2	9 - 1
<i>viridiflora</i> Cav. (1799)	J. Soe NCP 1338	Ecuador	0.541	Yellow	Black	5	3
<i>vitifolia</i> Kunth (1817)	J. Vanderplank NCP 1251	Brazil	1.929	Yellow	Variegated green	13	4
<i>vitifolia</i> 'Scarlet Flame'	J. Vanderplank NCP 1252	Cultivated UK	1.729	Yellow	Variegated Green	13	4
<i>xiikzodz</i> MacDougal (1992)	J. Vanderplank NCP 1254	Cultivated UK	0.632	White	Black	4 / 1	3
<i>yucatanensis</i> Killip (1930)	J.M. MacDougal MD 4680	Mexico	0.603	Yellow/orange	Black	4 / 2	9 - 1
<i>yucatanensis</i> Killip (1930)	J. Vanderplank NCP 1255	Cultivated UK	0.657	Yellow/orange	Black	4 / 2	9 - 1

Species, authority & date	Collector and collection no.	Origin of seed	Mass 100 seed (g)	Colour of arils (when ripe)	Colour of fruit (when ripe)	Subgenus /section	New seed group no.
<i>zamorana</i> Killip & Cuatrecasas (1960)	B. Bowden 5155	Colombia	1.120	Yellow	Yellow	11 / 3	5 - 2
<i>zamorana</i> Killip & Cuatrecasas (1960)	C. Laurens	New Zealand	2.203	Yellow	Yellow	11 / 3	5 - 2

Adenia Forssk (1775) and *Hollrungia* K. Schumann (1888)

Species, authority & date.	Collector & collection no.	Origin of seed.	Mass per 100 seed (g).	New seed group number.
<i>Adenia bequaertii</i> spp. <i>occidentalis</i> W.J.J.O. de Wilde (1968)	W. J. J. O. de Wilde Liben (2384)	Central & West Africa		2
<i>Adenia firingalavenis</i> Harms (1925)	T. Fix	Madagascar	2.477	1 - 1
<i>Adenia globosa</i> ssp. <i>globosa</i> Engl. (1891)	W. J. J. O. de Wilde Drummond & Hemsley (4053)	East Africa		5 - 3
<i>Adenia hondala</i> (Gaertn.) de Wilde (1970)	W. J. J. O. de Wilde Ritchie 1763	India, Asia		5 - 4
<i>Adenia isaloensis</i> (Perr) de Wilde (1970)	J. J. Segalen	Reunion	1.865	5 - 2
<i>Adenia mannii</i> (Mast.) Engl. (1891)	W. J. J. O. de Wilde Louis (3125)	Central to West Africa		3
<i>Adenia monadelpha</i> Perr (1945)	J. J. Segalen	Reunion	2.791	11
<i>Adenia penangiana</i> (Wall ex G. Don) de Wilde (1967)	W. J. J. O. de Wilde Corner SFN 37889	Malesia		12
<i>Adenia repanda</i> (Burch) Engl. (1891)	W. J. J. O. de Wilde Anon.	Central & South West Africa		12
<i>Adenia staudtii</i> Harms (1899)	W. J. J. O. de Wilde Gerard (5764)	West Africa		5 - 3
<i>Hollrungia aurantiodes</i> K. Sch. (1888)	W. J. J. O. de Wilde Kajewski (1913)	Malasia		10

5.3 Methods

5.3.1 Morphological and mass variations in the seed of *Passiflora* species produced by interspecific pollination compared with seed of species produced by self-pollination.

Hypothesis: Interspecific cross-pollination does not influence the morphology of the resultant seed.

Over 200 species of *Passiflora* were cultivated and brought into flower over a ten-year period. Interspecific cross-pollination was attempted with every species but this was only successful in a very few species. Mature seed produced by interspecific pollination were collected, cleaned and dried, and where possible seed from the same species or taxon produced by self-pollination were also harvested. In twelve species fertile seed produced both by self-pollination and by interspecific pollination were obtained, weighed and their seed coat morphology was visually examined and compared.

5.3.2 Classification of *Passiflora* into groups and subgroups using seed morphology only and comparison with the traditional classification of *Passiflora* based on the morphology of flowers and vegetative parts. Comparison with the seed of *Adenia* and *Hollrungia* is also made with special reference to the origination and inter-relationships of these genera.

Hypothesis: Traditional classification of *Passiflora* species into subgenera, sections and series would be more meaningful and the phylogeny more accurate if greater significance had been attached to the morphology of their seed.

Seed of *Passiflora*, *Adenia* and *Hollrungia* were collected for this investigation over a long period of time by personal collection from the wild, glasshouse cultivation in the UK, botanical gardens and herbarium collection in the UK, USA, South America and Australia and private collections from many countries. Some illustrations of seed in publications by W. J. J. O. de Wilde (1972), L. Escobar (1990) and J. M. MacDougal (1994) show sufficient detail to be included in this study when live seed were unobtainable. Details of seed sources are given in Table 1 (*Passiflora* accessions in this study). Seed from each taxon were examined morphologically and placed into rough groupings without any reference to traditional taxonomy. They were examined again more closely with 11 major morphological features (Appendix V) being considered before their groups and subgroups were confirmed. After this was completed the few examples of *Adenia* and *Hollrungia* seed were examined morphologically and grouped alongside the *Passiflora* seed. *Passiflora* seed from each taxon were later re-examined using a dissecting microscope or images from a scanning electron microscope. Forty-five individual morphological features were recorded (Appendix V) in a binary code compatible with the computer program PAUP, which was later used to give a cladistical analysis of the morphology data.

5.3.3 The morphology of seed produced by interspecific hybrids

Hypothesis: The morphology of the seed of an interspecific hybrid closely resembles the seed of its maternal parent.

Many interspecific hybrids, such as *P.* ‘Allardii’, *P.* ‘Sapphire’ and *P.* ‘Byron Beauty’, are sterile and although they often produce ripe fruit, these are hollow and void of either mature or immature seed. Some interspecific hybrids, including *P.* ‘Amethyst’ and *P.* ‘Adularia’, will produce fertile fruit unaided but most require hand-pollination. The success rate for hand pollination and fertile fruit production is generally less than 10% and in many cases zero. The difficulty of producing ripe fruit and fertile seed of interspecific hybrids is reflected by the few taxa in this study. Seed of hybrids and of both maternal and paternal parents were washed, cleaned, dried, weighed and comparisons of their seed coat morphology were conducted using the 11 major morphological features described in Appendix V.

5.3.4 Moisture reduction in *Passiflora* seed

Seed that were extracted from fruit harvested on the same day were given a batch number (B). After seed had been cleaned and dried they were divided into smaller units of 10, 50, 100 or 200 seed, depending on the species, the availability of seed and the purpose for which they were to be used. These smaller samples were given a sample number (N). Each sample of seed therefore had a two-part code, the B number specifying the species and date of collection and the N number specifying the individual sample.

5.3.4.1 Development of a reliable and repeatable method for reducing the moisture content of *Passiflora* seed.

A reliable and repeatable method was required for reducing the moisture content of *Passiflora* seed to a predetermined percentage for each of the five primary taxa in this study. Dehydration procedures were considered and three were tested:

1. Gentle heat at 30⁰C
2. Silica gel
3. Di-phosphorus pentaoxide

5.3.4.1.1 Gentle heat.

100 weighed, clean, dry seed were spread evenly over double filter papers on the base of a 50 mm Petri dish and placed in an incubator maintained at 30⁰C. Seed were removed and weighed daily for the first five days and subsequently every second or third day for 27 days. This weighing process took approximately 30 seconds. The frequent disturbance to the seed was considered beneficial to promote even mass reduction. This procedure was repeated for all five taxa: *P. vitifolia* (B14 N8), *P. morifolia* (B17 N6), *P. incarnata* (B13 N4), *P. x decaisneana* (B1 N5) and *P. subpeltata* (B7 N5). All seed were weighed until a constant mass was achieved.

5.3.4.1.2 Silica gel

This method followed the technique described by Seaton and Pritchard (1990) for dehydrating orchid pollen. 100 weighed, clean, dry, fresh seed were spread thinly over the base of a 50 mm Petri dish which was fixed using Blu-tac to the base of an upturned 50 ml plastic specimen jar which was in turn fixed using Blu-tac inside a

600 ml storage jar. 20 g of silica gel were spread evenly around the top of the upturned specimen jar and the storage jar was sealed with an airtight lid. This procedure was repeated for all five taxa. Seed were removed and weighed twice a day for three days and then every two days for twelve days. Seed were so treated until they reached 'constant mass'. The time taken to remove, weigh and replace the seed in each sample was approximately 30 seconds. At the end of each dehydration procedure all the silica gel was blue. All seed were treated until they reached a constant mass.

5.3.4.1.3 Di-phosphorus pentaoxide

The method for dehydration with di-phosphorus pentaoxide was the same as that for silica gel, using 20 g per Petri dish. The procedure was repeated for all five taxa. At the end of each dehydration procedure 50% of the di-phosphorus pentaoxide was still in unspent powder form. All seed were treated until they reached a constant mass.

Graphs of mass loss over time were drawn from the data collected and used to establish the most suitable and repeatable method for dehydrating *Passiflora* seed to a predetermined percentage.

The mass reduction of the seed sample is expressed on a fresh mass basis:

$$\text{Mass reduction} = \frac{\text{fresh mass of seed} - \text{dry mass of seed}}{\text{fresh mass of seed}} \times 100$$

(Bewley & Black, 1994)

5.3.4.2 Moisture content of *Passiflora* seed

The total moisture content of freshly harvested clean dry seed of the five primary taxa in this study was determined.

Test samples of 100 clean dry seed were taken from batches of seed that had been harvested on the same day. This was done for each of the five primary taxa and repeated with successive batches of seed. Each sample was weighed and the seed spread thinly over the base of a 50 ml pyrex beaker. This was placed in an incubator maintained at 102⁰C. Each sample was removed from the incubator and the seed weighed every 15 minutes for the first two hours, then every 30 minutes for the next 11 hours and less frequently for the subsequent 11 days. The percentage moisture content of each sample is expressed on a fresh mass basis.

5.3.5 Germination of *Passiflora* seed

Samples of ten seed were used in all germination tests in this work except where otherwise stated. The best procedure to be used as the standard germination test for *Passiflora* seed was determined as follows.

5.3.5.1 The effects of differing temperature regimes on *Passiflora* seed germination.

Hypothesis: The successful germination of *Passiflora* seed is dependent on the temperature maintained during the germination period.

The recommendations of the Handbook of Seed Technology for Genebanks No. 3 (Ellis, Hong & Roberts, 1985a) were followed and a seed germination procedure using water-saturated filter papers in sealed Petri dishes was used. Samples of ten seed (clean, dry and weighed) were placed and spaced on two sheets of filter paper within the base of a plastic Petri dish (55 mm diameter). 2.5 ml of pure distilled water at 20⁰C was poured onto the filter papers. The Petri dish was covered with its lid and sealed using Parawax film. The quantity of water used created a saturated environment while the double filter papers prevented the seed from lying partly submerged in water. Three temperature regimes were investigated to evaluate the effect of temperature on the germination of *Passiflora* seed:

Constant germination temperature of 40⁰C

Constant germination temperature of 20⁰C

Dual temperature technique (Teng, 1977) – alternating 8 hours at 30⁰C and 16 hours at 20⁰C.

Three taxa were used for this trial: *P. morifolia* (B26), *P. subpeltata* (B27) and *P. vitifolia* (B28). Each seed sample was examined daily for the first 20 days after sowing. For the next 30 days samples were examined every two or three days and for the remaining 30 days samples were examined twice weekly. Condensation on the inside of the lid of the Petri dish was cleared by gently rubbing the outer surface of the lid. This caused the small droplets to fuse into large droplets, which could then be

encouraged to drip by gentle side-to-side shaking. Where visibility through the lid was too poor for seed examination, the lid was removed, the seed examined and the lid replaced and resealed with Parawax film. Seed were considered to have germinated when the epidermis had split open at the radicle end revealing a well developed radicle of 1 mm or greater in length (Plate 24).

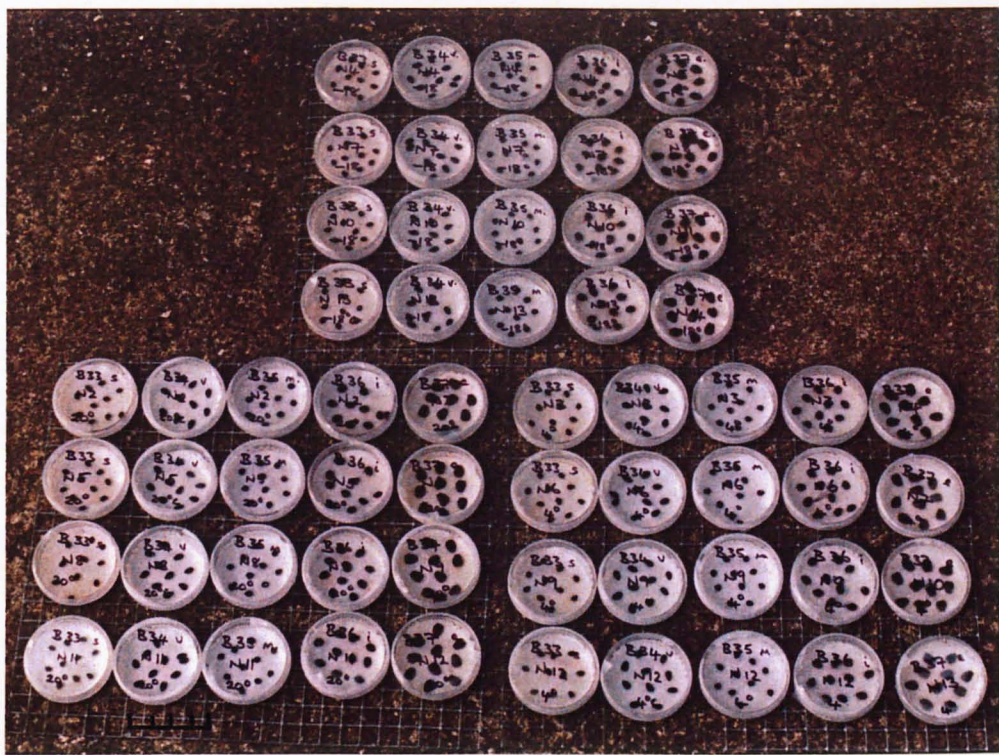
5.3.5.2 The effects of variations in the germination medium on the germination of *Passiflora* seed.

Three species were used for these tests: *P. vitifolia* (B35 N24), *P. subpeltata* (B33 NL5) and *P. morifolia* (B35 LM5). The seed had all been subjected to germination tests ten days after fruit harvest. Seed were spread on newspaper for 28 days at 20°C to dry and were then stored at 4°C. Three temperature regimes were used for germination as stated in 5.3.5.1. The control group in each case followed the methods previously described using distilled water at pH 6.5. The other five regimes followed the same procedure but included variations to the germination medium as follows:

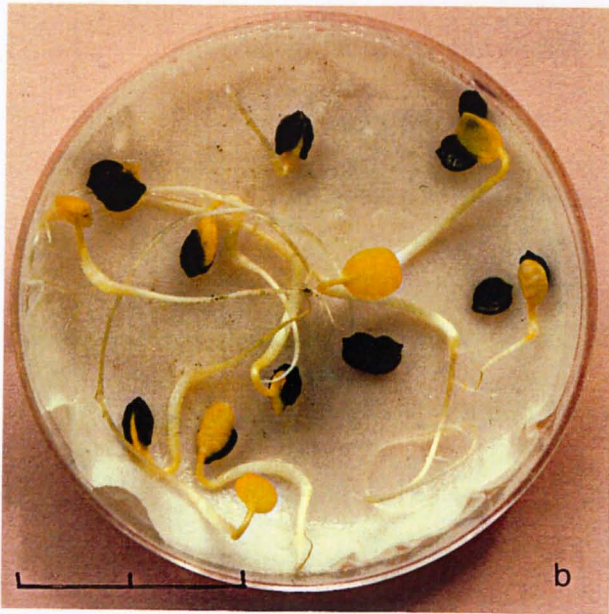
Group 1	Control	Distilled water pH 6.5
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Group 2	Cold tea	pH 4.5
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This was prepared using five teabags in 500 ml of boiling distilled water. The tea was stirred and then allowed to cool for 24 hours, after which time it was stirred again before the spent teabags were strained of excess water and discarded.



a



b



c



d

a. Seed samples of five taxa stored in three environments at the start of the germination test; b. 100% germination of *P. morifolia* B35 seed after eight days; c. *P. morifolia* B35 seed, (i) and (ii) radicle 1mm long, germination considered positive, (iii) 24 hours after germination, (iv) 72 hours after germination; d. *P. vitifolia* B34, (i) radicle 0.5mm, germination considered positive, (ii) 36 hours after germination, (iii) 72 hours after germination.

Scale bar in cm

Group 3 Agar gel (Agar-Agar) pH 7.0

A standard solution was prepared using distilled water. 10 ml of solution was poured into the base section of each Petri dish and allowed to cool and set.

Group 4 Ammonia pH 9

A 35% solution of ammonia was diluted to pH 9 using distilled water.

Group 5 Calcium carbonate pH 8

10 g of horticultural grade garden lime were added to 250 ml of distilled water and stirred intermittently during a 24 hour period. The undissolved material was allowed to settle and 100 ml of the remaining fluid poured off for use.

Group 6 Gibberellic acid $C_{19}H_{22}O_6$ GA_3

A 2×10^{-4} M solution was prepared using distilled water.

All six environments were tested at each of the temperature regimes. An extended time period of 80 days was allowed for all test samples to germinate but was primarily necessary for samples at the lower temperature of $20^{\circ}C$ only. All seed samples were prepared and introduced to their germination environments on the same day. Ten seeds were used for each test sample.

5.3.5.3 Viability of *Passiflora* seed with pale colouration compared with their siblings with dark colouration.

Hypothesis: The seed of *Passiflora* species with pale colouration have reduced viability compared with their sibling seed.

Some fruit of many species, particularly those from the subgenus *Passiflora*, and especially those harvested towards the end of the fruiting season, contain seed of variable colouration. Colours may range from dark brown to pale yellow brown in seed that otherwise appear quite healthy, both externally and internally. No variation in seed size was discernable between pale and dark seed but in *P. subpeltata* and *P. incarnata* paler seed showed a reduction in mass (up to 15.96% in *P. incarnata*). The moisture content of pale seed samples compared with dark seed samples varied by less than 0.5% in *P. incarnata* but by up to 8.62% in *P. subpeltata*. The pale seed discussed here should not be confused with 'albino seed' (MacDougal, 1994) that are often found in ripe fruit of all species. These are much smaller than mature seed, white or cream in colour and are the unfertile or immature seed in which the testa is soft and not fully developed, and the embryo is only partially developed within the testa cavity.

Seed of three species were investigated: *P. vitifolia* B28, *P. subpeltata* B27 and *P. incarnata* B29. Seed of *P. vitifolia* B27 were divided into two groups: pale brown seed (B28 N1) and dark brown seed (B28 N2). Any intermediate seed were not included in either group. Seed of *P. subpeltata* B27 were also divided in to two groups: dull pale grey-brown seed (B27 N1) and glaucous dark grey-brown seed

(B27 N2). Again, any intermediate seed were not included in either group. Seed of *P. incarnata* B29 were divided into three groups: very dark brown (B29 N3), mid-brown (B29 N2) and pale yellow-brown (B29 N1). Any seed intermediate between these categories were not included. Seed from each species group were counted, weighed and a sample of each was dehydrated at 102⁰C for 48 hours as described in

5.3.4.2. Samples of ten seed were also subjected to the standard germination test.

5.3.5.4 Germination of *Passiflora* seed stored at 20⁰C and then cooled to 4⁰C for 30 days prior to sowing.

Hypothesis: Germination rates in *Passiflora* seed stored at 20⁰C are improved by cooling to 4⁰C for 30 days prior to sowing.

Samples of 10 seed each of *P. subpeltata* B23 N2-N5-N8-N11 were dehydrated to four predetermined moisture percentages and stored at 20⁰C for nine months. One group of samples was removed and stored at 4⁰C for 30 days prior to sowing while the other was stored continuously at 20⁰C (control group). Samples of ten seed were also taken from *P. subpeltata* B33 N3-N6-N9-N12, which had been stored continuously at 4⁰C since harvest dehydration, and from B33 N4-N7-N10-N13 that had been stored at -18⁰C since harvest dehydration. All samples were prepared as described in 5.3.5.1 for the standard germination test using the bithermal rhythm technique and dehydrated using silica gel as described in 5.3.4.1. Each sample was examined every two or three days and results recorded for 37 days.

5.3.6 Seed coat-imposed dormancy in *Passiflora* seed.

Hypothesis: *Passiflora* seed that fail to germinate readily when subjected to ideal germination conditions are being influenced by seed coat-imposed dormancy.

5.3.6.1 Investigation into seed coat-imposed dormancy in *Passiflora* seed.

5.3.6.1.1 Comparison of the germination percentage of seed from *P. subpeltata* B25 and *P. lutea* B42, which are thought to be influenced by seed coat-imposed dormancy, with that of seed considered to be resting or quiescent (Bewley & Black, 1994) from *P. subpeltata* B27.

5.3.6.1.2 Comparison of the germination percentage of embryos taken from seed thought to be influenced by seed coat-imposed dormancy with embryos taken from seed considered to be quiescent.

5.3.6.1.3 The effect on embryo germination of infusions of powdered testa taken from seed coat-imposed dormant seed and seed considered to be quiescent.

Fresh seed taken from *P. subpeltata* B25 and *P. lutea* B42 failed to germinate within 60 days when subjected to the standard germination test. The tests were repeated with

the same negative results. *P. subpeltata* B27 fruit harvested ten weeks after *P. subpeltata* B25 showed 100% germination after seven days.

Embryos were removed from their protective testa (seed coat) by cracking the two halves of the seed apart using small electrical pliers. Each seed was placed between the jaws of the pliers with their side-seams nesting on the inside jaws and the chalazal beak end of the seed towards the centre of the pliers. This was to ensure that the radical end of the embryo was given the best chance of not becoming damaged in the process (the radical end of the embryo is at the opposite end to the chalazal beak). Sufficient pressure was exerted on the handles of the pliers to cause the testa to fracture along the equatorial seam. Care was taken to ensure that the jaws of the pliers could not close more than 1mm at each attempt, preventing sudden crushing of the seed and embryo. In spite of these precautions, many embryos were badly damaged and considered unusable. The crudeness of this method and the limited number of seed available for this experiment were the prime reason for the small numbers of embryos available for this trial. Even minor damage to an embryo rendered it virtually useless as it was then very susceptible to immediate fungal attack. The testas from all embryos were saved and kept isolated from other samples. Testa samples were crushed to a fine powder using a pestle and mortar. 100 mg of powder was added to 10 ml of pure distilled water. The infusion was sealed in a 50 ml test tube, which was kept at 30⁰C and shaken occasionally over a 24-hour period. This infusion rapidly became a blackish colour. The embryos were subjected to the standard germination test as used for seed but with a reduction in the quantity of water or infusion used for each test (2 ml instead of 2.5 ml). Germination of embryos was considered positive when the radicle was developed and elongated by 2 mm. Samples

under test were examined daily. Germination or deterioration of embryos was often very rapid particularly when embryos were injured during extraction.

I and II: Germination tests were repeated on samples of *P. subpeltata* B25 using both the standard germination test and with the addition of giberellic acid ($C_{19}H_{22}O_6$) GA₃ in 200 mM solution.

III: Embryos of *P. subpeltata* B25 and B27 were tested for germination using the standard germination technique.

IV: Embryos of *P. subpeltata* B27 were tested for germination using an infusion of B25 testa at different dilutions. *P. subpeltata* B25 embryos were tested using an infusion of B27 testa.

V: Embryos of *P. lutea* B42 were tested for germination using either distilled water, infusions of B42 testa and with infusions of *P. subpeltata* B25 testa.

VI: Embryos of *P. incarnata* B32 and *P. morifolia* B30 were also tested for germination with either water or infusions of *P. subpeltata* B25 testa.

5.3.6.2 The effect of high temperatures during fruit maturation on seed coat-imposed dormancy in *P. subpeltata* seed.

The taxon *P. subpeltata* NCP 1223 was propagated by vegetative cuttings and a number of additional plants were raised. Two or more rooted cuttings were potted together in several 10-20 litre pots and cultivated in three distinct environments:

Two pots of *P. subpeltata* plants were cultivated in an unheated, well-ventilated glasshouse (glasshouse no. 5) that was maintained at 3⁰C above the outside air temperature (Appendix 2) during the night and up to 5⁰C above the outside air temperature during daylight hours.

Two pots of *P. subpeltata* plants were cultivated in a heated glasshouse (glasshouse no. 6) under more humid conditions with a minimum temperature of 8⁰C and never more than 10⁰C above the outdoor temperature.

A final pot of two or three plants of *P. subpeltata* was cultivated under stove house conditions of very high humidity and high temperatures. The minimum night temperature was 12⁰C and during daylight hours the temperature rose to up to 35⁰C (glasshouse no. 7).

Plants were cultivated as described for *P. subpeltata* in 5.2.2. Fruit harvest was by natural fruit fall 45-65 days after anthesis. Seed were dried and harvested as described for *P. subpeltata* in 5.2.2. Daily thermograph records were kept of glasshouses no. 6 and 7 during this period. Maximum/minimum temperature records were recorded for glasshouse no. 5 and in the open in close proximity to all three glasshouses. Glasshouse temperature readings may be found in Appendix 2.

Individual fruit were harvested from late August 1998 to late October 1998 from plants cultivated in each of the three glasshouse environments described. The seed from each fruit were given a batch number (B) and code letters (N) when necessary for individual samples. Seed were cleaned, dried and counted. A sample of 100 seed was weighed and a germination test conducted using 10 seed from each sample.

As the germination test results from each fruit for fruits B44 to B59 were recorded it was evident that either the temperatures during fruit maturation were not sufficiently high to induce seed coat-imposed dormancy or the hypothesis that high environmental temperatures during fruit maturation induce seed coat-imposed dormancy in *P. subpeltata* must be rejected. Fruit harvested after B59 were carefully cut from the vine with the entire peduncle still attached using sharp scissors. This was performed as the fruit ripened and changed colour to mustard yellow but before natural fruit fall. Fruit were supported on the rim of a 50 ml beaker filled with water with their peduncle immersed in water. Fruit and beaker were then placed in an incubator for 8 to 27 days at 39°C and the water topped up as necessary. During this time the fruit remained turgid with the peduncle still attached. Seed were then extracted in the standard way, washed, dried and subjected to a germination test.

5.3.6.3 Dormancy breaking treatment for *Passiflora* seed identified as being in a state of seed coat-imposed dormancy.

Hypothesis: Seed coat-imposed dormancy in *Passiflora* seed can be broken by washing the seed prior to sowing.

At the time of this experiment seed of *P. subpeltata* were 48 months old and probably had greatly reduced viability, as demonstrated by other trials with *P. subpeltata* B33 seed in this study. Two other taxa, *P. lutea* and *P. cinnabariana*, had been identified as producing seed which were influenced by seed coat-imposed dormancy. Seed of *P. cinnabariana* were available in sufficient quantities to test this hypothesis. The standard germination test was conducted on *P. cinnabariana* B71 seed, which were wild collected in Australia and were less than six months old. No seed germinated within 60 days. The test was repeated, again with negative results. 100 seed of *P. cinnabariana* B71 were placed in a 60 mm diameter plastic sieve and supported under running tap water at 18⁰C for up to 175 hours. An unwashed sample of 20 seed was taken for a germination test as the control group. Samples of 10 seed were taken for germination tests at intervals during the 175-hour washing period. The same procedure was followed with seed of *P. subpeltata* B25 seed (four years old), which was subjected to washing for up to 288 hours. Seed of *P. lutea* (five months old) harvested in (Camden Delaware) USA were divided into two major samples labelled N5 and N6. N5 seed were washed in one litre of tap water maintained at 30⁰C in an incubator for up to 36 days. The water was discarded and replaced each day with clean pre-warmed tap water. N6 seed were washed in running tap water as described for *P. cinnabariana* seed at 18⁰C for up to 36 days. At the start of the trial a sample of 10 seed was taken unwashed as the control group and subjected to the standard

germination test. Samples of 10 seed were taken from N5 and N6 undergoing washing procedures at the same times at intervals during the subsequent 36 days and subjected to the standard germination test.

5.3.7 Storage of *Passiflora* seed.

5.3.7.1 Storage of *Passiflora* seed within their fruit or with their arils still attached.

Hypothesis: *Passiflora* seed are best stored within their fruit or with their arils still attached.

Fruit of three *Passiflora* species, *P. morifolia* B38, *P. vitifolia* B39 and *P. subpeltata* B40, were harvested and stored as whole fruit in a bithermal incubator at 20⁰C for 16 hours and 30⁰C for 8 hours alternately. Germination tests were conducted on seed from a single fruit of each species for each test after the following periods of time:

P. morifolia B38 10 months, 19 months and 4 years

P. vitifolia B39 9 months, 18 months and 3 years 11 months

P. subpeltata B40 10 months, 19 months and 3 years 3 months

Fruit of three *Passiflora* species, *P. vitifolia* B19, *P. subpeltata* B20 and *P. morifolia* B21, were harvested and the seed, with surrounding arils, carefully removed and

stored without further disruption in three temperature environments at 20⁰C, 4⁰C and -18⁰C. The samples stored at -18⁰C were in danger of becoming frozen together and so were stored in individual containers of approximately 15 seed each so that they could be removed for germination tests directly from the freezer without disturbance to the other samples. Germination tests were conducted on the freshly harvested seed and repeated after one year and again after two years and one month.

5.3.7.2 Viability of *Passiflora* seed after storage at different temperatures.

Hypothesis: *Passiflora* seed should be treated as recalcitrant or unorthodox for seed storage purposes as they are very short-lived and cannot survive prolonged storage periods at sub-zero temperatures. Recalcitrant or unorthodox seed are not capable of withstanding water loss of magnitude; even when stored under moist conditions their lifespan is frequently brief and low temperature storage is usually inappropriate (Bewley & Black, 1994 and Lane, 1984).

Samples of fresh, clean, dry seed of the five primary taxa in this study (*P. subpeltata*, *P. vitifolia*, *P. morifolia*, *P. incarnata* and *P. x decaisneana*) were given the standard germination test. Others were then stored at the following temperatures for up to 33 months:

20⁰C in a closed container

20⁰C in an open container (45% relative humidity of storage room)

4⁰C refrigerated

-18⁰C refrigerated

-196⁰C in liquid nitrogen

Samples of 100 seed from each taxon were stored both in 50 ml plastic specimen tubes and in airtight sealed 50 ml plastic specimen tubes at a constant 20⁰C. Other samples were stored in airtight sealed 50 ml specimen tubes at 4⁰C and -18⁰C in refrigerated units.

A prestored (12 week-old) sample of *P. subpeltata* B2 N8 seed was dehydrated using silica gel, with a mass reduction of 6.19% (100 seed - 1.211g, reduced to 1.136g). 10 seed were subjected to storage in liquid nitrogen at -196⁰C for three hours (in a container). The standard germination test was conducted on the sample five days later.

A prestored (ten week-old) sample of *P. vitifolia* B14 N10 seed were dehydrated using silica gel, with a mass reduction of 4.25% (100 seed - 1.811g, reduced to 1.730g). 10 seed were subjected to the same procedure as *P. subpeltata* B2 N8 in liquid nitrogen for three hours and tested for germination five days later.

A prestored (ten week-old) sample of *P. morifolia* B18 N12 seed were dehydrated using silica gel, with a mass reduction of 4.45% (100 seed - 1.933g, reduced to 1.847g). 10 seed were subjected to the same procedure as *P. subpeltata* B2 N8 in liquid nitrogen for three hours and tested for germination five days later.

All seed samples were subjected to the standard germination test procedure as described in 5.3.5.1 using the bithermal rhythm technique (Teng, 1977).

5.3.7.3 Long-term storage of dehydrated *Passiflora* seed.

Hypothesis: *Passiflora* seed should be treated as orthodox for seed storage purposes as their viability and longevity is extended by dehydration and storage at sub-zero temperatures.

Seed of the five primary taxa were harvested, washed, cleaned and dried as described in 5.2.2. They were then dehydrated using silica gel to three predetermined moisture levels as described in 5.3.4.1. The control group in these tests were seed that had not been subjected to any artificial dehydration procedures. Four groups from each taxon were then divided into three samples of 100 seed each for storage at three different temperatures: 20⁰C, 40⁰C and -18⁰C. Ten seed were used for each germination test and each sample was tested twice each year at approximately six-monthly intervals for the first three and a half years and then each year for the following two years. For these tests, dehydration is expressed as a percentage mass reduction of the original fresh seed mass and is calculated using the same formula as for the total moisture content (see 5.3.4.2).

Samples that have not been subjected to any artificial reduction in moisture content for germination tests and storage will therefore be given a value of 0% mass reduction and samples that have been dehydrated will be given a positive value for % mass reduction.

P. vitifolia

Samples B34 N2-N3-N4 were not subjected to any artificial dehydration procedures and are recorded as having 0% mass reduction.

Samples B34 N5-N6-N7 were dehydrated using silica gel for 12 hours and showed a 3.57% mass reduction.

Samples B34 N8-N9-N10 were dehydrated using silica gel for 36 hours and showed a 4.71% mass reduction.

Samples B34 N11-N12-N13 were dehydrated using silica gel for 72 hours and showed a 6.29% mass reduction.

Samples B34 N2-N5-N8-N11 were stored at 20⁰C.

Samples B34 N3-N6-N9-N12 were stored at 4⁰C.

Samples B34 N4-N7-N10-N13 were stored at -18⁰C.

Total moisture content % of the test sample from B34 was 9.44% moisture.

P. subpeltata

Samples B33 N2-N3-N4 were not subjected to any artificial dehydration procedures and are recorded as having 0% mass reduction.

Samples B33 N5-N6-N7 were dehydrated using silica gel for 4 hours and showed a 1.62% mass reduction.

Samples B33 N8-N9-N10 were dehydrated using silica gel for 12 hours and showed a 4.2% mass reduction.

Samples B33 N11-N12-N13 were dehydrated using silica gel for 72 hours and showed a 6.24% mass reduction.

Samples B33 N2-N5-N8-N11 were stored at 20⁰C.

Samples B33 N3-N6-N9-N12 were stored at 4⁰C.

Samples B33 N4-N7-N10-N13 were stored at -18⁰C.

Total moisture content % of the test sample from B33 was 9.96% moisture.

P.morifolia

Samples B35 N2-N3-N4 were not subjected to any artificial dehydration procedures and are recorded as having 0% mass reduction.

Samples B35 N5-N6-N7 were dehydrated using silica gel for 12 hours and showed a 6.15% mass reduction.

Samples B35 N8-N9-N10 were dehydrated using silica gel for 36 hours and showed a 7.81% mass reduction.

Samples B34 N11-N12-N13 were dehydrated using silica gel for 96 hours and showed a 10.06% mass reduction.

Samples B35 N2-N5-N8-N11 were stored at 20⁰C.

Samples B35 N3-N6-N9-N12 were stored at 4⁰C.

Samples B35 N4-N7-N10-N13 were stored at -18⁰C.

Total moisture content % of the test sample from B35 was 13.0% moisture.

P. incarnata

Samples B36 N2-N3-N4 were not subjected to any artificial dehydration procedures and are recorded as having 0% mass reduction.

Samples B36 N5-N6-N7 were dehydrated using silica gel for 20 hours and showed a 3.52% mass reduction.

Samples B36 N8-N9-N10 were dehydrated using silica gel for 52 hours and showed a 5.15% mass reduction.

Samples B36 N11-N12-N13 were dehydrated using silica gel for 96 hours and showed a 6.4% mass reduction.

Samples B36 N2-N5-N8-N11 were stored at 20⁰C.

Samples B36 N3-N6-N9-N12 were stored at 4⁰C.

Samples B36 N4-N7-N10-N13 were stored at -18⁰C.

Total moisture content % of the test sample from B36 was 9.9% moisture.

P. x decaisneana

Samples B37 N3-N4-N5 were not subjected to any artificial dehydration procedures and are recorded as having 0% mass reduction.

Samples B37 N6-N7-N8 were dehydrated using silica gel for 12 hours and showed a 5.63% mass reduction.

Samples B37 N9-N10-N11 were dehydrated using silica gel for 35 hours and showed a 6.64% mass reduction.

Samples B37 N12-N13-N14 were dehydrated using silica gel for 72 hours and showed a 7.82% mass reduction.

Samples B37 N3-N6-N9-N12 were stored at 20⁰C.

Samples B37 N4-N7-N10-N13 were stored at 4⁰C.

Samples B37 N5-N8-N11-N14 were stored at -18⁰C.

Total moisture content of the test sample from B37 was 14.16%.

6 Results

6.1 Morphology of *Passiflora* seed.

6.1.1 Morphological and mass changes in the seed of *Passiflora* species produced by interspecific pollination compared with seed of species produced by self-pollination.

Seed of 12 species were produced by both self-pollination and interspecific cross-pollination. Seed were washed and dried and samples weighed. The morphological features of the seed coat were recorded and the two groups compared. The difference between the mass of 100 seed collected from fruit produced by self-pollination and those produced by interspecific hybridisation was up to 16.8% (*P. tarminiana*) (Table 2). Although this is appreciable and may be due in part to hybridisation, it is still in keeping with the variation recorded in seed collected in different seasons and from different locations, as can be observed in other species in this study (Table 2). The variations in the morphology of the testa between seed produced by self-pollination and interspecific hybridisation were within the minute range of differences that would normally be observed within the seed from a single fruit, or fruits of a single species, in seed production by either method of pollination and no difference in seed was therefore recorded (Table 2).

Table 2. Comparison of the masses of *Passiflora* seed produced by hybridisation.

Mass in grams of samples of 100 seed produced by self-pollination and interspecific pollination in *Passiflora* species.

Ovule species	NCP no.	Pollinator species and NCP no.	Mass of 100 seed (g)
<i>P. alata</i>	1031	<i>P. alata</i> 1017	2.814
<i>P. alata</i>	1031	<i>P. actinia</i> 1003	2.851 ↑
<i>P. alata</i>	1031	<i>P. x decaisneana</i> 1064	2.639 ↓
<i>P. 'Amethyst'</i>	1012	Self-pollinated	0.818
<i>P. 'Amethyst'</i>	1012	<i>P. caerulea</i> 1035	0.863 ↑
<i>P. capsularis</i>	1045	Self-pollinated	0.367
<i>P. capsularis</i>	1045	<i>P. rubra</i> 1196	0.385 ↑
<i>P. citrina</i>	4636	<i>P. citrina</i> 4638	0.345
<i>P. citrina</i>	1058	<i>P. sanguinolenta</i> 1213	0.395 ↑
<i>P. cincinnata</i>	1059	Self-pollinated	3.099
<i>P. cincinnata</i>	1059	<i>P. alata</i> 1013	3.066 ↓
<i>P. incarnata</i>	1113	Self-pollinated	3.855
<i>P. incarnata</i>	1113	<i>P. x decaisneana</i> 1064	3.374 ↓
<i>P. incarnata</i>	1113	<i>P. caerulea</i> 1034	3.733 ↓
<i>P. laurifolia</i>	1128	Self-pollinated	1.932
<i>P. laurifolia</i>	1128	<i>P. alata</i> 1031	1.768 ↓
<i>P. quadrangularis</i>	1193	Self-pollinated	5.821
<i>P. quadrangularis</i>	1193	<i>P. alata</i> 1031	5.281 ↓
<i>P. quadrifaria</i>	1989-283	Self-pollinated	0.698
<i>P. quadrifaria</i>	1191	<i>P. vitifolia</i> 1251	0.592 ↓
<i>P. tarminiana</i>	1346	Self-pollinated	2.648
<i>P. tarminiana</i>	1341	<i>P. manicata</i> 1157	2.203 ↓
<i>P. sanguinolenta</i>	1288	<i>P. sanguinolenta</i> 1213	0.396
<i>P. sanguinolenta</i>	1213	<i>P. citrina</i> 1058	0.347 ↓
<i>P. vitifolia</i>	1250	<i>P. vitifolia</i> 1251	1.621
<i>P. vitifolia</i>	1251	<i>P. quadrifaria</i> 1191	1.914 ↑