

# **Plant Chimeras**

Richard A. E. Tilney-Bassett

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# Preface

In recent years exciting developments in the improvement of vegetatively propagated plants by mutation breeding, and their multiplication by tissue culture, has spawned a fresh interest in plant chimeras. The newer research is often specialized, and so the authors are unable to present the significance of their findings within the broader context of chimeras in general. Indeed, the interconnecting paths between different areas of chimera studies, and of various types of chimera, are seldom trodden. It is hardly surprising, therefore, in the absence of suitable sources of information, to find that students of the plant sciences are often ignorant even of the existence of chimeras. In endeavouring to overcome this deficiency, and to bridge the gaps between one researcher and another, and between researcher and teacher, my prime purpose in writing this book is to increase the awareness of chimeras, and to show through the descriptions of the main types how much they have in common and yet how varied and fascinating they are. By carefully explaining the essential terms as they arise, and by keeping the use of an unfamiliar vocabulary to the minimum, the reader need have no more than an elementary knowledge of plant biology plus an interest in cultivated plants.

A book on chimeras would not be complete without a liberal use of illustrations, and I am indebted to the publishers for their sympathetic reaction to this essential need. I should like to thank the editors of *Heredity* for their permission to republish some illustrations from my early articles, and similarly Elsevier/North-Holland Biomedical Press, and Dr J. T. O. Kirk, for granting permission to publish a few illustrations from the second edition of *The Plastids*. The many new illustrations are the work of my daughter Amanda Tilney-Bassett, with advice from my wife Elisabeth, to both of whom I am very grateful. Many of the drawings are loosely adapted from published work as acknowledged in the legends. Some of the authors of the published work are now deceased, but to the others I should like to convey my sincere appreciation. Often the illustrations, adapted to my specific requirements, are samples of many more in the original paper and I urge the reader to seek out the original publications for a full appreciation of the authors' intentions. The photographs were donated by Dr F. A. L. Clowes and Dr A. Roberts, or were developed from my negatives by Mrs C. Fisher, to all of whom I am very grateful. I should also like to thank Mr J. K. Burras who permitted me to photograph examples of the very fine collection of variegated-leaf chimeras that he has maintained over many years at the Botanic Garden of the University of Oxford.

I should like to express my appreciation to the authors, and particularly

Dr F. Pohlheim, who have so kindly sent me copies of their papers, and especially to Professor Dr F. Bergann and Mrs L. Bergann who have fed my interest in chimeras for over twenty years. My thanks are also due to my research students – Paramjit, Osman, Ali, Ayad, Riadh and Baset, who have listened so patiently and responded so enthusiastically to my sporadic outbursts on the subject. Finally, I should like to thank all the family for their great forbearance during the many months of preparation.

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1986

# Contents

Preface	v
<b>1 The Chimera Concept</b>	<b>1</b>
The graft-hybrid hypothesis	1
The chimera hypothesis	4
Graft chimeras	10
<b>2 Meristems</b>	<b>19</b>
The apical meristem	19
Leaf, bud and floral meristems	25
<b>3 Sectorial and Mericlinal Chimeras</b>	<b>29</b>
Origin and appearance	29
Mutation induction	31
Apical initials	33
Development of periclinal chimeras	39
<b>4 Classification of Periclinal Chimeras</b>	<b>42</b>
Major groupings	42
Apical structure	43
Popular names	49
<b>5 Analysis of Periclinal Chimeras</b>	<b>51</b>
Morphology and anatomy	51
Adventitious buds	54
Tissue culture	57
Seedlings	59
Irradiation	60
<b>6 Cytochimeras</b>	<b>63</b>
Colchiploidy	63
Induction and recognition of cytochimeras	66
Polyploid cytochimeras	70
Haploid-diploid cytochimeras	74
Histogenesis	77

<b>7</b>	<b>Variegated-leaf Chimeras</b>	<b>80</b>
	Problems and solutions	80
	Thin-skinned chimeras, <i>GWW</i> and <i>WGG</i>	90
	Thick-skinned chimeras, <i>GGW</i> and <i>WWG</i>	95
	Sandwich chimeras, <i>GWG</i> and <i>WGW</i>	101
	Eversporting conifers, <i>WG</i>	108
<b>8</b>	<b>Potato Chimeras</b>	<b>111</b>
	Potato shoots	111
	Methods of investigation	112
	Potato tubers	113
	Leaf mutants	118
	Bolters, wildings and feathery wildings	120
	Production of non-chimeral mutants	121
<b>9</b>	<b>Flower Chimeras</b>	<b>122</b>
	Early flower sports	122
	Striped flowers	124
	Mutation breeding	128
	Readily sporting flowers	129
	Flower form	135
<b>10</b>	<b>Fruit Chimeras</b>	<b>137</b>
	Mericlinal sports	137
	Periclinal sports	139
<b>11</b>	<b>Other Chimeras</b>	<b>148</b>
	Mutant skins	148
	Mutant cores	150
<b>12</b>	<b>Lessons and Prospects</b>	<b>151</b>
	References	157
	Index to Subjects	
	Index to Taxa	
	Index to Authors	

# 1 The Chimera Concept

## The graft-hybrid hypothesis

In the wake of the great explorers a wealth of new species was brought to Europe by plant collectors from around the world. New trees, shrubs and herbs came into our country estates, parks, botanic and private gardens (Fisher, 1982). Trading in plants became a profitable enterprise, and many nurserymen became breeders anxious to improve their stocks. This they did by the raising of new hybrids through crosses between species, and by the selection of promising new types among the progeny recombining the most favourable characters of their parents. These were skilled men, who knew their plants well, and who had a keen eye for any new sports. A sport was a spontaneous change, or mutation, in a part of the plant that created a feature not previously known within the species, their hybrids and descendants. Sports were gratuitous, valuable sources of new variation, much prized by the ambitious breeder. Charles Darwin (1868) collated an extensive list, which he classified into sports of fruit, flowers, leaves and shoots, and suckers, tubers and bulbs. At the beginning of the century de Vries (1901–03) published his famous treatise on mutation, and Cramer (1907) his account of the known cases of bud variation.

True sports are collectively quite common but individually rare, so the repetition of a seemingly identical sport was unusual. Consequently, a variation that was so frequent as to be predictable attracted attention. The 'Bizzarria' orange was such a case. This strange plant was first described in 1674 by Nati (Strasburger, 1907). Apparently, in 1644, a Florentine gardener grafted a scion of sour orange on to a seedling stock of citron. The scion did not take successfully, but a bud arising out of the callus developing on the stock grew up into a bizarre tree. On the same plant, there were leaves, flowers, and fruit, identical with the orange or with the citron, and there were compound fruit with the two kinds blended together or sectored in various ways (Penzig, 1887; Sarastano and Parrazzani, 1911). The same fruit was sometimes half orange, half citron, or three-quarters of one kind and one-quarter of the other, and when propagated by cuttings, the tree retained its peculiar character.

A second plant, that behaved in a similar way to the 'Bizzarria', originated in 1825 at Vitry, near Paris, in the garden of Adam the nurseryman. He had inserted a shield from the bark of a broom into a stock of common laburnum. The bud lay dormant for a year, and then grew with a flourish of buds and shoots, one of which grew more upright and vigorous, and with larger leaves than the usual broom; so it was selected for further



## 2 The Chimera Concept

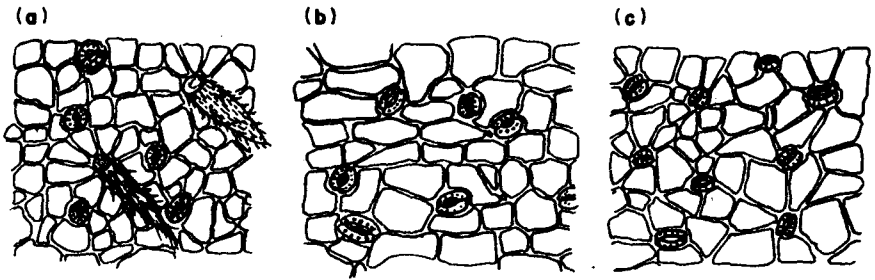
propagation, and was subsequently distributed throughout Europe as + *Laburnocytisus adamii*. (The + sign is a taxonomic convention to indicate that the plant mentioned is a graft hybrid: the × sign is a similar convention to indicate a sexual hybrid.) The tree proved to be somewhat unstable, and branches spontaneously reverted to both parental species in their flowers and leaves. The tree was often described (Poiteau, 1830; Prevost, 1830; Hénou, 1839; Braun, 1849, 1873; Caspary, 1865; Darwin, 1868; Morren, 1871; Beijerinck, 1900), but probably never better than by Darwin:

'To behold mingled in the same tree tufts of dingy-red, bright yellow and purple flowers, borne on branches having widely different leaves and manner of growth, is a surprising sight. The same raceme sometimes bears two kinds of flowers, and I have seen a single flower exactly divided into halves, one side being bright yellow and the other purple; so that one half of the standard-petal was yellow and of larger size, and the other half purple and smaller. In another flower the whole corolla was bright yellow, but exactly half the calyx was purple. In another, one of the dingy-red wing petals had a bright yellow narrow stripe on it; and lastly, in another flower, one of the stamens, which had become slightly foliaceous, was half yellow and half purple; so that the tendency to segregation of characters or reversion affects even single parts and organs. The most remarkable fact about this tree is that in its intermediate state, even when growing near both parent species, it is quite sterile; but when the flowers become pure yellow or purple they yield seed.'

When Darwin examined branches with yellow flowers they appeared to have completely recovered their laburnum character, whereas branches with purple flowers were not always exactly like the broom:

'The branches with purple flowers appear at first sight exactly to resemble those of *C. purpureus*; but on careful comparison I found that they differed from the pure species in the shoots being thicker, the leaves a little broader, and the flowers slightly shorter, with the corolla and calyx less brightly purple: the basal part of the standard petal also plainly showed a trace of the yellow stain. So that the flowers, at least in this instance, had not perfectly recovered their true character; and in accordance with this, they were not perfectly fertile, for many of the pods contained no seed, some produced one, and very few contained as many as two seeds; whilst numerous pods on a tree of the pure *C. purpureus* in my garden contained three, four and five seeds.'

One view was that these trees were just sexual hybrids (de Vries, 1901-03; Strasburger, 1906, 1907) with differences in the fruits of the 'Bizzarria' caused by vegetative segregation (Cramer, 1907). Another view was that, as a result of grafting, the two species had actually formed a hybrid through the union of their vegetative tissues (Braun, 1849; Caspary, 1865; Darwin, 1868). The idea, that vegetative nuclei of stock and scion could fuse to produce a graft-hybrid with a homogeneous hybrid growing-point, and that bud variations could arise by a somatic segregation, analogous to the segregation of different seedling characters from sexual hybrids, was not to be ignored. Proponents of the graft-hybrid hypothesis regarded a sexual hybrid as unlikely because nobody had succeeded in deliberately obtaining a hybrid between the laburnum and broom, even though both had produced hybrids with other species, whereas they were readily grafted together. The reversion to the parental types was also inexplicable from a sexual hybrid.



**Fig. 1.1** Illustrations of the surface view of the lower epidermis from leaves of the graft hybrid + *Laburnocytisus adamii* and its constituent species. (a) *Laburnum anagyroides* with hairs; (b) + *Laburnocytisus adamii* without hairs; (c) *Cytisus purpureus* without hairs. (Adapted from Macfarlane, 1892.)

Additional support for the graft-hybrid hypothesis came with the discovery of a new example. A hundred-year-old tree had been discovered in a garden in Bronvaux, near Metz, in which a medlar scion had been grafted on to a hawthorn stock. Two branches had developed from the graft union between stock and scion and these were both intermediate in character, although not identical (Jouin, 1899; Koehne, 1901; Bornmüller, 1932; Guillaumin, 1949). One branch, called + *Crataegomespilus asnieresii*, more nearly resembled hawthorn, and the other, called + *Crataegomespilus dardari*, more nearly resembled medlar. The correlation between grafting and the development of shoots with an intermediate type of growth seemed to confirm the graft-hybrid hypothesis, but increasingly evidence was accumulating against it.

Macfarlane (1892) carefully examined the anatomical structure of + *L. adamii* and its parents and found the comparison between the epidermis of broom and the graft-hybrid of particular interest:

'But the very striking resemblance which the epidermis of the hybrid portion has to that of *C. purpureus*, not only in the general structure of the cells, but in the size and structure of the cell nucleus, the distribution of the stomata, and specially of hairs (Fig. 1.1), would seem at first sight to prove that the hybrid portion was wrapped round, so to speak, by an epidermis of *C. purpureus*.'

Fuchs (1898), Laubert (1901) and Noll (1907) extended the anatomical investigations without doubting the graft-hybrid interpretation either, yet adding to the evidence that made quite a different explanation possible.

The general habit of + *L. adamii* was of a small tree more like the common laburnum than the bushy broom, and the leaves and flowers were closer to laburnum than to broom. The reversion to pure broom was less common than to laburnum (Beijerinck, 1901; Laubert, 1901), wounding enhanced the frequency of laburnum shoots, and when resting buds were induced to sprout, they frequently developed into laburnum (Beijerinck, 1908). The graft-hybrid had fairly well formed pollen grains but the embryo sac usually degenerated (Tischler, 1903), even so, rare seeds were obtained and these germinated solely into laburnum seedlings (Noll, 1907; Hildebrand, 1908). It therefore began to appear that + *L. adamii* was not

## 4 The Chimera Concept

so much a hybrid as a mixture predominantly laburnum in character but with an epidermis typically broom. Still further doubt was raised by Strasburger (1907, 1909), who examined the nuclei of + *L. adamii* and its two parents and found that all three had the same chromosome number,  $2n = 48$ ; if cell fusion had taken place cells of the hybrid would have been expected to have double the chromosome complement. With little support for the sexual hybrid hypothesis, and decreasing confidence in the graft-hybrid hypothesis for + *L. adamii*, the time was right for a better alternative, yet the breakthrough came from a different quarter.

### The chimera hypothesis

An experimental approach to testing the graft-hybrid hypothesis was begun by Winkler (1907), who made saddle grafts between the tomato and the black nightshade, using each species as stock or scion. After union, the scion was removed by a transverse cut at the junction of stock and scion. A callus soon grew across the exposed surfaces out of which adventitious buds arose. Some buds developed into shoots resembling tomato or nightshade, but one graft resulted in a plant in which the shoot was divided longitudinally into two halves – one half was composed of tomato and the other of nightshade. Recalling the Chimaera of Greek mythology, which was a fire-breathing monster, the foreparts of whose body were those of a lion, the middle parts those of a goat, and the hind parts those of a dragon, Winkler called his new plant, which was composed of two genetically distinct tissues, a chimera (Fig. 1.2).

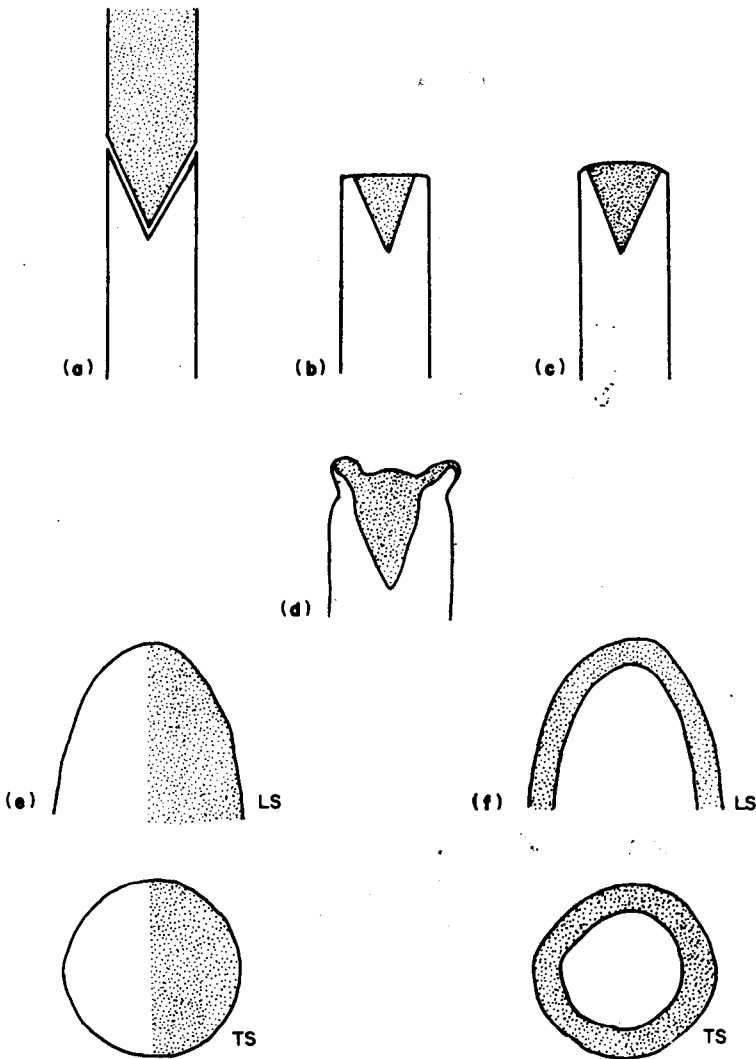
Five other grafts between tomato and nightshade developed shoots with intermediate structures, which Winkler initially believed to be the sought after graft-hybrids and to which he gave specific names (Winkler, 1908, 1909). It did not seem to have struck him as odd that fusion between identical nuclei could develop into several hybrids of varying structure, but he was soon to modify his view.

Confirmation of Winkler's chimera concept came shortly afterwards with quite unrelated experiments on white-margined, variegated-leaf, zonal pelargoniums (Fig. 1.3). After crossing green and variegated plants, Baur (1909a) obtained a mixture of green, white, and variegated progeny. Some of the variegated seedlings were divided longitudinally such that one half of the axis had green leaves and the other white leaves, and leaves which were half green, half white were occasionally produced on the border between the two. These plants were like Winkler's tomato-nightshade chimera and Baur concluded that:

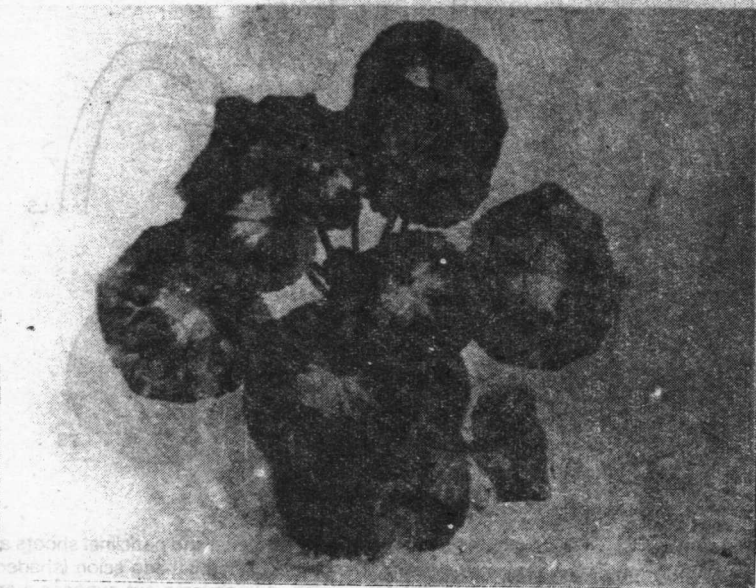
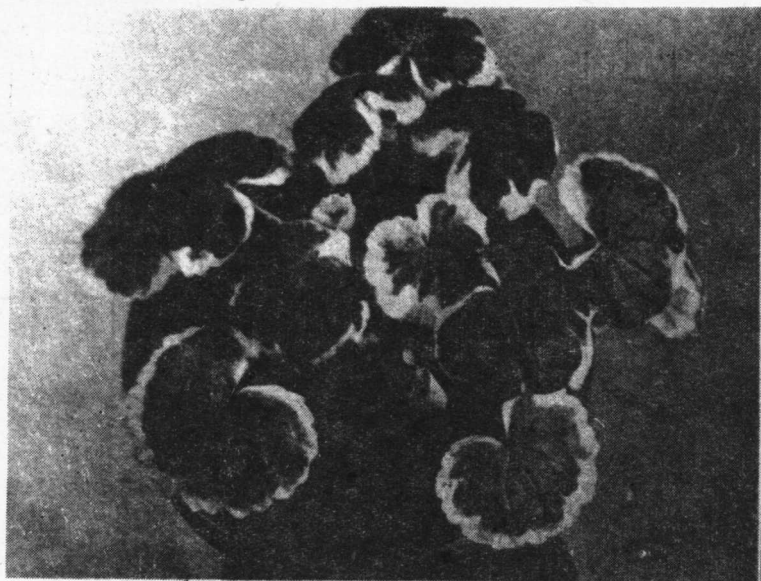
'The plants have, therefore, quite evidently a sectorially divided growing-point just as in the well known chimeras of Winkler.'

These plants Baur called sectorial chimeras.

Baur also made sections through the leaves of white-margined pelargoniums and found that a layer of colourless palisade or spongy mesophyll cells formed an unbroken skin completely enclosing the inner core of green cells. No colourless skin occurred in green plants. When he



**Fig. 1.2** Diagrams illustrating stages in the formation of sectorial and periclinal shoots after grafting a scion of one species onto a stock of another. (a) A nightshade scion (shaded) is grafted onto a tomato stock (unshaded). (b) After union, a transverse cut exposes a small wedge of scion tissue embedded in the stock. (c) Cell division leads to the growth of callus across the exposed surface of stock and scion. (d) Adventitious bud development in the callus shows the nightshade growing alongside the tomato (left) and over the tomato (right). (e) The left hand bud has developed into a sectorial chimera with nightshade and tomato tissue growing alongside each other, as seen in longitudinal section (LS) and transverse section (TS). (f) The right hand bud has developed into a periclinal chimera with a skin of nightshade enveloping a core of tomato, as seen in longitudinal section (LS) and transverse section (TS).



**Fig. 1.3** Two examples of variegated-leaf, zonal pelargonium seedlings. In both plants there is differentiation of the leaves into a margin of one colour and a centre of another. The upper plant has leaves with a green margin and white centre. The lower plant exhibits a reciprocal arrangement with a white margin and green centre. (From Tilney-Bassett (1963b), with the permission of the editors of *Heredity*.)

selfed his plants, green cultivars and occasional green shoots arising on the variegated cultivars gave green seedlings. Similarly, white-margined cultivars and occasional white shoots arising on these gave white seedlings. It thus became clear to Baur that the colour of the seedlings corresponded with the colour of the tissue forming the skin, and so the white skin and the green core of the white-margined plants must occupy distinct layers of the shoot. This relationship was only altered when the white skin replaced the green core, or the green core displaced the white skin, to form wholly white or green shoots respectively. Normally, Baur argued, the white layer must be continuous from the leaves back into the apical growing-point and into the flowers where it formed the germ layer (Fig. 1.4). Moreover, the same structural relationship of the white and green tissues could be obtained whenever variegated seedlings developed shoots with white-margined leaves just like the parental cultivars; these confirmed Baur's second conclusion:

'With that is indeed the nature of white-margined plants clear, they are likewise chimeras, not chimeras with sectorially divided growing-point but chimeras with periclinally divided growing-point, in short they may be called Periclinal Chimeras.'

The significance of Baur's hypothesis was immediately recognized because it agreed so well with the findings of the late nineteenth century anatomists. They had found that the cells at the tip of higher plant shoots were frequently organized into two or more layers, which were



**Fig. 1.4** Diagram to illustrate Baur's concept of the periclinal chimera. The leaf margin, on the left, traces back to a skin within the layered growing-point, which includes both epidermal and subepidermal layers, and is continuous with the margins and tips of the floral parts, including the germ tissues. The skin completely encloses the underlying core. In a variegated-leaf chimera, the leaf margin is white and the central tissues green. But there is no colour differentiation between skin and core in either the growing-point or the floral parts as the genes determining the contrasts in pigmentation are not expressed in these organs.

## 8 The Chimera Concept

superimposed one above the other like a series of cones from which the body structure of the plant was derived. Thus Baur was able to explain the structure of white-margined leaves by assuming that the pattern found in the leaf was a lateral and flattened extension of the layered structure already present at the growing-point (Fig. 1.4).

After Winkler had demonstrated that graft-hybrids between tomato and nightshade could be obtained experimentally, Strasburger (1909) rejected his former belief that the graft-hybrids were really sexual hybrids. But he could not accept the simplicity of Baur's periclinal theory. Instead, he assumed that there had been a more intimate and irregular arrangement of the tissues from stock and scion to produce a hyperchimera, comparing it more to a lichen than to a seed plant. Baur (1909a, 1909b, 1910, 1911) was not put off, and promptly suggested that all Winkler's tomato-nightshade grafts were periclinal chimeras too. By comparing four of these with each other and with their parental species, Baur was able to work out their probable chimeral structure. For each plant, the character was determined for the epidermis by matching the surface hairs to those of the appropriate parent, for the germ layer by the seedlings obtained after self-pollination, and for the innermost tissue by the shapes of the leaves (Table 1.1). Winkler (1910a) accepted Baur's interpretation for these four plants, yet still retained his belief in the concept of graft-hybrids.

Baur (1910) also suggested that + *L. adamii* was a periclinal chimera with an epidermis of broom over a core of laburnum. Similarly, after the comparison between the graft-hybrids of + *Crataegomespilus* and their parents by Noll (1905), Baur was able to interpret these as periclinal chimeras too – with a skin of medlar over a core of hawthorn. The anatomical investigations of Buder (1910, 1911) soon led to confirmation of the periclinal structure for + *L. adamii*. Buder was able to trace the general distribution of broom and laburnum tissue in young and old shoots, petioles and leaves by precipitating tannins with potassium bichromate. As broom is rich in tannins and laburnum has none, this made an excellent marker, which clearly revealed the periclinal structure. Moreover, it showed up patches where the epidermis from broom had thickened, or a sector of laburnum had thrust through the skin. The reversions to broom originated in periclinal divisions within the young epidermal cells of the shoot apex, which normally grew by anticlinal divisions. The more frequent reversions to laburnum probably arose because division of these cells always replaced the epidermis whenever it was damaged.

Two further, and very elegant, demonstrations of the periclinal structure were found in the development of the cork and the petals. The formation of cork in young branches arose in the epidermis in broom, below the epidermis in laburnum, and in both positions in + *L. adamii*. The petals were pigmented in the epidermal cells by purple anthocyanins in broom, by yellow plastids in laburnum, and by purple anthocyanins in + *L. adamii*. In addition, laburnum and the graft-hybrid, but not broom, contained dark brown cells forming the honey guides two cells deep below the epidermis. These observations, together with the earlier records of Macfarlane, were fully consistent with the periclinal interpretation of the graft-hybrid, which

**Table 1.1** The four distinct graft chimeras between tomato and nightshade as synthesized by Winkler, their origin, three characteristic features of each, and the interpretation of their periclinal chimera structure by Baur.

Name	Origin		Features			Structure		
	Stock	Scion	Leaf surface	Seedlings	Leaf form	Epidermis	Germ layer	Core
<i>Solanum tuberosum</i>	<i>S. nigrum</i>	<i>L. esculentum</i>	esc	nig	nig	esc	nig	nig
<i>Solanum proteus</i>	<i>S. nigrum</i>	<i>L. esculentum</i>	esc	esc	nig/esc	esc	esc	nig
<i>Solanum koelerioides</i>	<i>L. esculentum</i>	<i>S. nigrum</i>	nig	none	esc	nig	esc	esc
<i>Solanum gaerthnerianum</i>	<i>L. esculentum</i>	<i>S. nigrum</i>	nig	nig	esc/nig	nig	nig	esc



## 10 The Chimera Concept

was therefore not a hybrid at all, but a graft chimera or species chimera.

The acceptance that + *L. adamii* and four of Winkler's experimental graft-hybrids were actually periclinal chimeras did not lead to a complete abandonment of the graft-hybrid hypothesis. Daniel (1904, 1909, 1914, 1915) attributed several cases to this origin including the still inadequately resolved + *Pyrocydonia* types, derived from grafts of pear and quince, and the + *Amygdalopersica* types, derived from grafts of almond and peach (Daniel and Delpon, 1913). These cases were not unambiguous. Daniel was supported by Weiss (1930) in regarding + *Pyrocydonia* as a graft-hybrid, even though Weiss accepted the chimeral explanation for several other graft-hybrids, nor was Swingle (1927) opposed to the theoretical possibility, although he regarded proof as lacking; Krenke (1933) was more sceptical. After further experimental grafting in the Solanaceae family, Winkler (1934, 1935, 1938) was convinced that he had obtained true graft-hybrids. Cramer (1954) seemed to concur but Brabec (1949, 1954) declared that Winkler's observations could still be explained by the occurrence of chromosome abnormalities arising naturally, or by chromosome loss or gain during callus formation. Fortunately, the pursuit of these elusive hybrids, which may now be achieved in some species by the quite different technique of protoplast fusion, did not stop progress in the understanding of graft chimeras.

### Graft chimeras

Following the general acceptance of the chimera concept, interest in graft chimeras continued, partly owing to the search for the elusive graft-hybrid, and partly to investigate further properties of individual cases (Table 1.2). As detailed discussions are covered in reviews (Swingle, 1927; Weiss, 1930; Rudloff, 1931; Krenke, 1933; Neilson-Jones, 1934, 1937, 1969; Guillaumin, 1949; Cramer, 1954; Brabec, 1965) I shall keep my remarks brief.

A fresh look at 'Bizzarria' convinced Tanaka (1927a, 1927b) that the plant was a periclinal chimera with an epidermal skin of sour orange over a core of citron. In his opinion the earlier emphasis on its more bizarre features has been misleading; reversions to orange or citron, and breaches of the orange skin by the underlying citron tissue (Fig. 1.5), certainly occurred, but not so often as to completely break down its essential periclinal structure.

A further confirmation of the epidermal species of + *L. adamii* came from a biochemical observation by Keeble and Armstrong (1912). They showed that the epidermal cells of the petals of + *L. adamii* and of broom contained an oxydase enzyme that responded directly with benzidine to produce a colour reaction, whereas there was no corresponding response with the epidermal cells of laburnum unless hydrogen peroxide was added. A similar test in the petal veins showed that the tissue beneath the epidermis of + *L. adamii* was of laburnum origin. Together with the many anatomical observations, there could be no doubt that the graft chimera had a skin of broom over a core of laburnum.