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Raffaele Testolin
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Allan Ross Ferguson *Editors*

The Kiwifruit Genome

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Preface

The kiwifruit (*Actinidia chinensis* var. *chinensis*/*A. chinensis* var. *deliciosa* complex, with diploid, tetraploid and hexaploid races) is one of the most recently domesticated fruit crops. Native to China, like most taxa of the genus *Actinidia*, the kiwifruit was introduced to New Zealand as seed in 1904. By the 1930s small orchards were established and in the 1960s its fruit became known to western consumers. Growers of the world's temperate regions introduced its cultivation to their own countries leading to a rapid expansion of this crop that currently accounts for ca. 200,000 hectares with nearly 3 million tons of fruits produced annually. Kiwifruit is now cultivated also in its homeland, China: indeed, China produces more kiwifruits than any other country.

The genome of a *A. chinensis* var. *chinensis* genotype was sequenced in 2013 by a Chinese team (Huang et al. Nature Communications 4:2640), following the classical procedures that brought analogous achievements in other crops: development of markers and genetic maps, large EST collections, and finally whole-genome sequencing based on Next Generation Sequencing platforms.

The draft sequence has a total length of 616.1 MB and contains 39,040 annotated genes, an unusually high number that indicates repeated polyploidization of this species. Analysis of the genome structure has indeed revealed ancient polyploidization events shared by core eudicots and two more recent whole-genome duplications, which occurred after the divergence of kiwifruit from tomato and potato. The assembly of the diploid ($x = 29$) kiwifruit genome was challenging not only because of the multiple chromosomal copies but also because of the dioecy of the species that implies high genome heterozygosity. In the absence of haploids, seemingly never described in this species, the production of well-saturated genetic maps based on genotype-by-sequencing protocols together with resequencing of a number of genotypes are improving the genome assembly.

This book starts with a description of the basic botanical features of kiwifruit and its wild relatives, then reports on the steps that led to the genome sequencing and discusses the results obtained with the assembly and annotation. The book has been planned and is intended as a tool for taxonomists, biologists, horticulturists, geneticists, and especially for breeders. For this reason, the core chapters are dedicated to a description of the main gene families that characterize this species as a crop, including genes

controlling sugar and starch metabolism, pigment biosynthesis and degradation, the ascorbic acid pathway, fruit softening and postharvest metabolism, and allergens.

Being a book specially intended as a guide for kiwifruit breeders, the last chapters are dedicated to gene introgression from wild relatives and genome-based breeding, in the belief that information from the genome sequence may be an extraordinarily useful tool for the evaluation of the breeding value of individuals based on whole-genome scans.

Raffaele Testolin
Hong-Wen Huang
Allan Ross Ferguson

Contents

Abbreviations

1-MCP	1-methylcyclopropene
2C-value	Holoploid (total) genome size
2*n*	Holoploid (zygotic) number of chromosomes
4CL	4-coumaryl CoA:ligase
AAT	Alcohol acyl transferase
ACC	Aminocyclopropane-1-carboxylic acid
ACD1/2	Accelerated cell death 1/2
ACO	ACC oxidase
Act	*Actinidia*
ADH	Alcohol dehydrogenase
ADP	Adenosine diphosphate
AFLP	Amplified fragment length polymorphism
AGPase	ADP-glucose pyrophosphorylase
AL	Aldonolactonase
AMR1	Ascorbic acid mannose pathway regulator 1 (F box protein)
AMY	α-amylase
ANR	Anthocyanidin reductase
ANS	Anthocyanidin synthase
asl	Above sea level
AtERF98	Ethylene response factor subfamily b-3 of ERF/AP2 transcription factor family
ATP	Adenosine triphosphate
ATPHT4;4	Anion transporter 2
BAC	Bacterial artificial chromosome
BAHD	BEAT, AHCT, HCBT, and DAT acyltransferase family
BAM	β-amylase
BBCH	Biologische Bundesanstalt Bundessortenamt und Chemische Industrie
Bet v	*Betula verrucosa* (European white birch)
bHLH	Basic helix-loop-helix
BLAST	Basic local alignment search tool
BLASTn	Nucleotide-nucleotide BLAST
BLAT	BLAST-like alignment tool
BLUP	Best linear unbiased prediction
BSA	Bulk segregant analysis

C3H	*p*-coumarate 3'-hydroxylase
C4H	Coumarate 4-hydroxylyase
CBR	Chlorophyll *b* reductase
CCD	Carotenoid cleavage dioxygenase cross-reactive carbohydrate determinant
CCS	Circularized consensus sequencing
CDK	Cyclin-dependent kinase
cDNA	Complementary DNA
CDS	Carotene desaturase Coding sequence Protein-coding regions
CDTA	Cyclohexane-*trans*-1,2-diaminetetra-acetate
CEG	Core eukaryotic gene
CEGMA	Core eukaryotic gene analysis
CF	5(6)-carboxyfluorescein
CHI	Chalcone isomerase
CHO	Carbohydrate
CHS	Chalcone synthase
CLH1/2	Chlorophyllase 1/2
Cp	Chloroplastic
CPPU	N-(2-chloro-4-pyridyl)-N'-phenylurea
CRTISO	Carotenoid isomerase
CSN5B	Cop9-signalosome 5b
CSN8	Constitutive photomorphogenic 9
CSO	Centro Servizi Ortofrutticoltuta (Italy)
CWI	Acid cell wall-bound invertase
Cyt	Cytoplasmic
D	Days
Daa	Days after anthesis
DAFB	Days after full bloom
DAHP	Deoxy-D-arabino-heptulosonate 7-phosphate
DdRADseq	Double digest restriction associated DNA sequencing
DFR	Dihydroflavonol 4-reductase
DHAR	Dehydroascorbate reductase
DHase	Dehydrogenase
DHQ	Dehydroquinate
DHQS	Dehydroquinate synthase
DMADP	Dimethylallyl diphosphate
DMHF	2,5-dimethyl-4-hydroxy-3(2H)-furanone
DMMF	2,5-dimethyl-4-methoxy-3(2H)-furanone
DMS	Dimethyl sulfide
DNA	Deoxyribonucleic acid
DOXP	1-deoxy-D-xylulose 5-phosphate
DW	Dry weight
DXS	1-deoxy-D-xylulose 5-phosphate synthase
EIN3	Ethylene insensitive 3 transcription factor
EST	Expressed sequence tag
F3H	Flavanone 3-hydroxylase
F3'H	Flavonoid 3'-hydroxylase

F3’5’H	Flavonoid 3'5'-hydroxylase
FaOMT	*Fragaria* x *ananassa* S-adenosyl-L-methionine dependent O-methyltransferase
FAOSTAT	Statistics Division of the Food and Agriculture Organization of the United Nations
FaQR	*Fragaria* x *ananassa* quinone reductase
FDR	First division restitution (meiosis)
FISH	Fluorescence *in situ* hybridization
FK	Fructokinase
FLS	Flavonol synthase
FW	Fresh weight
GalA	α-(1,4)-galacturonic acid
GalDH	L-galactose dehydrogenase
GalLDH	L-galactono-1,4-lactone dehydrogenase
GalPP	Galacturonate-1-phosphate phosphatase
GalR	D-galacturonic acid reductase
GalUT	Galacturonate-1-phosphate uridylyltransferase
GBLUP	Genomic best linear unbiased prediction
GBS	Genotyping-by-sequencing
GC	Gas chromatography
GC-O	GC-olfactometry
GDP	Geranyl diphosphate
GEBV	Genomic breeding value
GER	GDP-L-fucose synthase/GDP-4-keto-6-deoxy-D-mannose-3, 5-epimerase-4-reductase
GGP	GDP-L-galactose phosphorylase
GGPP	Geranylgeranyl pyrophosphate
GluPP	D-glucurono-1-phosphate phosphatase
GluPU	Glucuronate-1-phosphate uridylyltransferase
GluR	Glucuronate reductase
GME	GDP-mannose-3′,5′-epimerase
GMP	GDP-mannose pyrophosphorylase
GPP	L-galactose-1-phosphate phosphatase
GS	Genomic selection
GT1	Anthocyanidin 3-O-glucosyltransferase 1
GT2	Anthocyanidin 3-O-glucosyltransferase 2
GuL	Gulonolactonase
GuLO	L-gulono-1,4-lactone oxidase/D-arabinino-1,4-lactone oxidase
H	Hour
Ha	Hectare
HG	Homogalacturonan
HK	Hexokinase
HPL	Hydroperoxide lyase
HPLC	High-performance liquid chromatography
HQT	Hydroxycinnamoyl-CoA quinate transferase
HXK	Hexokinase
ICDH	Isocitrate dehydrogenase

IDP	Isopentenyl diphosphate
IGA	Istituto di Genomica Applicata, Udine, Italy
IgE	Immunoglobulin E
IKO	International Kiwifruit Organization
INV	Invertase
IR	Inverted repeat
IUIs	International Union of Immunological Societies
LAR	Leucoanthocyanidin 4-reductase
LASSO	Least absolute shrinkage and selection operator
LCYβ	Lycopene β-cyclase
LCYε	Lycopene ε-cyclase
LD	Linkage disequilibrium
LDOX	Leucoanthocyanidin dioxygenase
LGM	Last Glacial Maximum
LHCB	Light-harvesting chlorophyll binding [protein]
LINE	Long interspersed nuclear element
LOD score	Logarithm (base 10) of odds
LOX	Lysyl oxidase Lipoxygenase
LSC	Large-single-copy region
LTR	Long terminal repeat retroelement
LTR-RT	Long terminal repeat retrotransposon
LYCβ	Lycopene β-cyclase
LYCε	Lycopene ε-cyclase
MAN	Endomannanase
MAS	Marker-assisted selection
Mb	Million bases
Mbp	Million base pairs
MBW	MYB–bHLH–WDR protein complex
MCS	Metal-chelating substance
MDAR	Monodehydroascorbate reductase
MEH	Mannan endohydrolase
MEP	2-C-methyl-D-erythritol 4-phosphate
MeS	Methylsulfanyl
MET	Mannan transglcosylase
MIOX	*myo*-inositol oxygenase
MIPS	L-*myo*-inositol 1-phosphate synthase
MITE	Miniature inverted-repeat transposable elements
MLP	Major latex protein
MS	Mass spectrometry
Mt	Mitochondrial
MTH	Mannan endotransglycoylase/hydrolase
MUR	GDP-D-mannose-4,6-dehydratase
MYA	Million years ago
MYB	Myeloblastosis family [transcription factor]
N	NewtonNorth
N	Haploid number of chromosomes
NAC	NAM (no apical meristem), ATAF1/2, CUC2 (cup-shaped cotyledons 2) transcription factor
NAD	Nicotinamide-adenine dinucleotide

NADP	Nicotinamide-adenine dinucleotide phosphate
NCBI	National Center for Biotechnology Information
NCC	Non-fluorescent chlorophyll catabolite
NGS	Next generation sequencing
NI	Neutral (cytoplasmic) invertase
NOL	NYC1-like
NsLTP	Non-specific lipid transfer proteins
NXS	Neoxanthin synthase
NYC1	Non-yellow colouring 1
OAS	Oral allergy syndrome
PAL	Phenylalanine ammonia lyase
PAO	Pheophorbide α oxygenase
PCD	Programmed cell death
PCR	Polymerase chain reaction
PDC	Pyruvate decarboxylase
PDH	Pyruvate dehydrogenase
PDS	Phytoene desaturase
PEP	Phosphoenolpyruvate
PEPC	Phosphoenolpyruvate carboxylase
PEPCK	Phosphoenolpyruvate carboxykinase
Pfcc	Fluorescent chlorophyll catabolite
PFR	The New Zealand Institute for Plant & Food Research Limited
PG	Polygalacturonase
PGI	Phosphoglucoisomerase
PGM	Phosphoglucomutase
PGT	Polygalacturonate 4-α-galacturonosyltransferase
Ph-CNL	*Petunia hybrida* cinnamate:CoA ligase
Pi	Phosphate
PL	Pectin lyase
PME	Pectin methylesterase
PMEi	Gglycoprotein inhibitor of PME
PMI	Phosphomannose isomerase
PMM	Phosphomannomutase
PPH	Pheophorbide pheophytin hydrolase
PPi	Pyrophosphate
Ppm	Parts per million
PR-10	Pathogenesis-related protein family 10
Psa	Bacterial canker of kiwifruit caused by *Pseudomonas syringae* pv. *actinidiae*
PSII	Photosystem II
PSY	Phytoene synthase
PUFA	Polyunsaturated fatty acid
pv.	Pathovar
QTL	Quantitative trait locus
RAD	Restriction-associated DNA [sequencing]
RAPD	Random amplified polymorphic DNA
RCCR	Red chlorophyll catabolite reductase
RCP1	Reduced carotenoid pigmentation1

RE	Restriction enzyme
REML	Restricted maximum likelihood
RFLP	Restriction fragment length polymorphism
RG-I	Rhamnogalacturonan-I [pectin]
RGase	Rhamnogalacturonase
RIN	Ripening inhibitor
RNA	Ribonucleic acid
RNA-seq	High-throughput messenger RNA sequencing
RR-BLUP	Ridge-regression BLUP
RRP	Ripening-related protein
SAM	*S*-adenosyl methionine
SDC	Sex-determining chromosome
SDH	Shikimate dehydrogenase
SDR	Second division restitution (meiosis)
SDS-PAGE	Sodium dodecyl sulphate-polyacrylamide gel electrophoresis
SGR	Stay-green protein
SINE	Short interspersed nuclear element
SMRT	Single-nucleotide real-time sequencing
SNP	Single-nucleotide polymorphism
SPA	Sugar partitioning-affecting
spp.	Species [plural]
SPS	Sucrose-phosphate synthase
SSC	Soluble solids content
SSC region	Small-single-copy region
SSR	Simple sequence repeat
STP	Hexose transporter
STS	Sequence-tagged site
SUC	Sucrose transporter
SUS	Sucrose synthase
T	Metric tonne
TA	Titratable acidity
TAIR10	The Arabidopsis Information Resource 10th Annotation Release
TBG	Tomato β-galactosidase
TC	Tentative consensus [sequences]
TE	Transposable element
TF	Transcription factor
TLP	Thaumatin-like protein
TPS	Terpene synthase
TUNEL	Terminal deoxynucleotidyl transferase dUTP nick end labeling
UDP	Uridine 5'-diphosphate
UFGT	UDP-glucoside:flavonoid glucosyltransferase
UGalE/UGluE/GAE	UDP-glucuronate epimerase/ UDP-galacturonate epimerase
UGD	UDP-glucose dehydrogenase
UGP	UDP-glucose-pyrophosphorylase
Uorf	Upstream open reading frame

USRDI	United States reference daily intake
UTR	untranslated region
var.	Botanical variety
V-ATPase	Vacuolar adenosine triphosphatase
VDE	Violaxanthin de-epoxidase
VI	Acid vacuolar invertase
VOC	Volatile organic compound
V-PPase	Vacuolar pyrophosphorylase
VTC3	Protein kinase/protein phosphatase
WDR	WD40 repeat protein
WGD	Whole genome duplication
WHO	World Health Organization
X	Monoploid number of chromosomes
XEH	Xyloglucan endohydrolase
XET	Xyloglucan endotransglycosylae
XTH	Xyloglucan endotransglycosylase/hydrolase
XyEH	Xylan endohydrolase
XyET	Xylan endotransglycosylase
XyTH	Xylan endotransglycosylase/hydrolase
ZEP	Zeaxanthin epoxidase
β-gal	β-galactosidase
βOH	β-ring carotene hydroxylase
εOH	ε-ring carotene hydroxylase
ζCDS	ζ-carotene desaturase

Botanical Description

1

Allan Ross Ferguson

Abstract

Kiwifruit belong to *Actinidia*, a genus comprising more than 50 species found mainly in southern China. All members of the genus are climbing plants and are functionally dioecious. The fruit are berries with seed embedded in a fleshy pericarp. The kiwifruit of commerce are large-fruited selections of two varieties of the species, *A. chinensis* Planch.: *A. chinensis* var. *chinensis* and *A. chinensis* var. *deliciosa* (A. Chev.) A. Chev., formerly known as *A. deliciosa* (A. Chev.) C.F. Liang et A.R Ferguson. Other *Actinidia* species are grown on a small scale or have limited commercial potential: *A. arguta* (Sieb. et Zucc.) Planch. ex Miq., *A. eriantha* Benth. and *A. kolomikta* (Maxim. et Rupr.) Maxim. Commercial cultivation techniques must take into account the biological characteristics such as the growth habit, flowering and dioecism. Diversity in fruit characteristics, such as flesh colour and flavour, potential health benefits and responses to storage are important commercially.

1.1 The Name Kiwifruit

The name 'kiwifruit', or regrettably 'kiwi', is often used to refer to any member of the genus *Actinidia* Lindl. The closest Chinese equivalent is 'mihoutao' (monkey peach), widely used for any *Actinidia* species but particularly for fruit of *A. chinensis* Planch. var. *chinensis* and *A. chinensis* var. *deliciosa* (A. Chev.) A. Chev. Similarly, 'kiwifruit' is commonly restricted to large-fruited selections of *A. chinensis* var. *chinensis* and *A. chinensis* var. *deliciosa* (United Nations Commission for Europe Standard FFV-46). The older names of Chinese gooseberry or the equivalents in other languages are now of historic interest only. Even in China the name kiwifruit is widely used.

Some small-fruited *Actinidia* species, such as *A. arguta*, are distinguished by the common names: 'hardy kiwifruit', 'baby kiwifruit' or 'kiwiberry', the last of which is becoming the most widely used.

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1.2 The Family Actinidiaceae

Actinidia is placed in the small family Actinidiaceae (Ericales) together with the genera *Clematoclethra* (Franch.) Maxim. and *Saurauia* [Saurauja] Willdenow. *Saurauia* has sometimes been separated into its own family and the genus *Sladenia* Kurz, previously included in the Actinidiaceae, is now generally placed in a separate family, the Sladeniaceae. Embryological characteristics, floral features and molecular analyses indicate that the Actinidiaceae are most closely related to the Sarraceniaceae, a family of pitcher plants with three genera, and the Roridulaceae, an even smaller family of only one genus, *Roridula,* with two species.

Saurauia is a genus of nearly 300 species of trees and shrubs in both Asia and Central and South America, mainly in tropical regions. The South American species are considered to be functionally dioecious (Soejarto 1969), as are possibly all *Saurauia* species. The flowers have three to five fused carpels with the styles partially free, and with the anthers usually falling together with the petals as a unit.

Actinidia and *Clematoclethra* are deciduous woody vines. *Clematoclethra* is distinguished from *Actinidia* and *Saurauia* by having ten stamens rather than numerous stamens and a five-loculed ovary with the styles fused to form a hollow tube, sometimes fluted. The flowers are variously described as 'bisexual' (Li et al. 2007a) or 'hermaphroditic or unisexual' (Dressler and Bayer 2004). The number of species of *Clematoclethra* is debatable: more than 20 have been described, but Tang and Xiang (1989) reduced all these to one very variable species with four subspecies, a treatment accepted in the recent Flora of China (Li et al. 2007a). *Clematoclethra* is endemic to China.

1.3 The Genus *Actinidia*

Actinidia is a genus of climbing or scrambling perennial, usually deciduous plants. They are stem or branch climbers ascending without special organs such as spines or tendrils to assist climbing (Fig. 1.1). The stems are either hairless

Fig. 1.1 *Actinidia* vines, in this case *A. chinensis* var. *deliciosa*, are climbers (Photograph: Plant & Food Research)

or have simple hairs. Their pith is solid or lamellate, and this feature has often been used to subdivide the genus. The bark usually has small lenticels. Growth occurs from axillary buds enclosed to varying extents in the swollen bases of the petioles. The leaves are alternate, usually dentate and have long petioles; the leaf blade ranges from membranous to leathery. Leaf hairs are most common on the lower leaf surfaces. Hairs range from occasional simple hairs to abundant stellate hairs. In at least some species, raphide cells (containing calcium oxalate needles) occur in most parts of the plant.

All *Actinidia* species appear to be dioecious (Fig. 1.2), although rare, gender-inconstant variants do occur. Within a species, staminate flowers are usually smaller than pistillate flowers.

Fig. 1.2 *Actinidia* species (here *A. chinensis* var. *deliciosa*) are dioecious (Photograph: Plant & Food Research)

Flowers are axial, sometimes solitary, usually in small cymes (determinate inflorescences) but in some species in large pseudoumbels. The sepals, usually 5, are free, distinct or sometimes fused at the base, with or without hairs. The petals, usually 5, are white or greenish (fading to dirty yellow as they age), pale yellow to pink to red, sometimes with only part of the petals coloured. The flowers contain large numbers of hypogynous stamens with slender filaments and yellow, brown, purple or black, versatile anthers, pivoting freely, dehiscing lengthwise. The filaments of pistillate flowers are usually shorter than those of staminate plants, the anthers are smaller, and the pollen released is sterile. The ovary is free and superior, ovoid, cylindrical or bottle-shaped with or without hairs. It is formed by the fusion of many carpels but leaving free the radiating styles (Fig. 1.3). The locules contain many ovules, which are anatropous (inverted on the ovule stalk) and unitegmic (with a single protective cell layer). In staminate flowers, the ovary is poorly developed, very small, with an abbreviated tuft of minute, rudimentary styles and lacks ovules.

The fruit is a globose to cylindrical berry (Fig. 1.4). The skin of the fruit can be with or without hairs and is sometimes spotted with obvious lenticels. The internal flesh consists of an outer pericarp, an inner pericarp and a central core or columella (Schmid 1978; Ferguson 1984; Beever and Hopkirk 1990). The locules of the inner pericarp contain two radial rows of seeds within a mucilaginous matrix. The seed albumen is copious; the embryo is comparatively large. The central core consists of large parenchyma cells, although at the stem-end there may be a hard woody spike of sclerified tissue.

There are detailed photographs of the leaves, flowers and fruit of most *Actinidia* species in Huang et al. (2014).

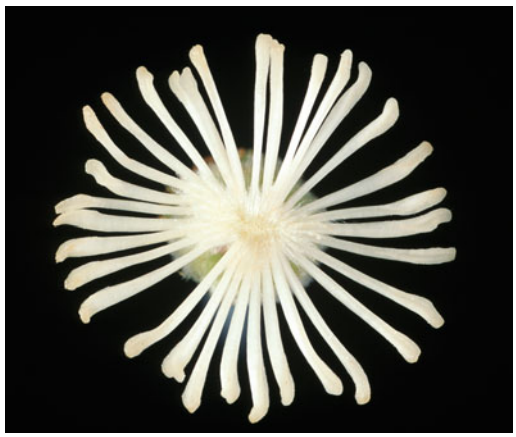

Fig. 1.3 The radiating styles of the female flowers of all *Actinidia* species are characteristic of the genus (Photograph: Plant & Food Research)

Fig. 1.4 *Actinidia* fruit (here *A. eriantha*) are berries with seed embedded in a fleshy pericarp (Photograph: Plant & Food Research)

1.3.1 *Actinidia* Species

Circumscription of *Actinidia* species is often difficult because, like many other climbing plants, members of the genus are very variable in vegetative morphology. Furthermore, hybridisation between species is common.

There can be vegetative differences between pistillate and staminate plants, even if usually small, and the leaves produced at different stages of growth on different shoots of the one plant can vary considerably in size, shape and hairiness (Dunn 1911). Flower colour and fruit characteristics can also vary. In those species that are geographically widespread, morphologically distinct varieties occupying discrete geographic areas have been identified, but the differences are not always consistent or correlated.

Molecular evidence indicates that many *Actinidia* species are polyphyletic and that there has been frequent hybridisation in the wild (Chat et al. 2004), with reticulate evolution being influenced by geographic patterns of distribution. There can be considerable gene flow between *Actinidia* species in the same geographic locality (Liu et al. 2008, 2010) (see Chaps. 2 and 5). At times, a single tree can support two different species (MA McNeilage personal communication). This would account for the many rather ill-defined *Actinidia* taxa, often lacking discrete taxonomic boundaries and the intermingling of characters, both morphological and molecular (Hsieh et al. 2011).

Taxonomists vary in the broadness of the taxonomic concepts they use. The early taxonomic treatments of the genus are described in Dunn (1911) and Li (1952). Liang (1984), in his revision of *Actinidia*, the first for more than 30 years, described many new species, varieties and forms, and by 2007 at least 76 species and 50 infraspecific taxa had been described (Huang and Ferguson 2007). Li et al. (2007a, b), in their more recent revision, combined or synonomised many of these to accept only 52 species and 16 varieties within China and two species in adjoining countries, not describing any forms. Further changes are likely: some taxa are described from only a few collections, while others are poorly understood and may be yet combined. For example, Li et al. (2009) discuss the problems of distinguishing between pairs of species such as *A. arguta* and *A. melanandra* Franch.

1.3.2 Subdivisions Within the Genus

Much effort has gone into subdividing the genus *Actinidia* into sections and series (see Huang and Ferguson 2007) based on morphological features such as the degree of pubescence, the structure of the leaf hairs, ovary shape, the presence or the absence of lenticels on the fruit surface (spotted or maculate vs. non-spotted or immaculate) and whether the pith of the stem is lamellate or solid. Liang (1984) modified previous subdivisions and divided the genus into four sections: the *Leiocarpae*, further divided into series, *Lamellatae* and *Solidae*, based on whether the stem pith was solid or lamellate, the *Maculatae*, the *Strigosae* and the *Stellatae*, further divided into the series *Perfectae* and *Imperfectae* on whether the stellate hairs on the undersides of the leaves were perfect and persistent or imperfect and deciduous. Some subdivisions seemed to be justified, e.g. the *Leiocarpae*, a largely monophyletic group of species which have smooth-skinned, hairless fruit, containing well-known species such as *A. arguta* and *A. polygama* (Sieb. et Zucc.) Maxim. However, the characters used to separate the other sections were inconsistent, e.g. the nature of the stellate hairs, and molecular evidence indicated that many of the sections were polyphyletic (see Chap. 4). It seems preferable for the infrageneric subdivisions of *Actinidia* to take into account the geographic distributions of the species (Huang and Ferguson 2007; Huang et al. 2014). The most recent revision of the genus (Li et al. 2007a, b) does not, probably wisely, attempt to subdivide the genus into sections.

1.3.3 Distribution of *Actinidia* Species

The centre of the geographic distribution of *Actinidia*, and the probable centre of current evolution of the genus, is between the Yangzi (Chang Jiang) and Pearl (Zhu Jiang) rivers, China, in a zone between approximately 25° and 30° north (Liang 1983). The broken topography of this part of China, the diverse soil conditions and the very variable microclimates influenced by mountain ranges have probably encouraged increased rates of speciation (Huang and Ferguson 2007). Recurrent polyploidisation and frequent hybridisation between sympatric species would also have favoured speciation. Outside this zone, the genus extends from about 50° north (in Siberia) to just south of the Equator (in Indonesia). Most *Actinidia* species are endemic to China and only a few also extend to the neighbouring countries, and only two species are not found in China. The vertical distribution of an individual species varies according to the climatic requirements of the species as affected by latitude. Thus, in different parts of their

extensive geographic ranges, *A. arguta*, *A. kolomikta* (Maxim. et Rupr.) Maxim. and *A. polygama* (Sieb. et Zucc.) Maxim. can be found almost at sea level in Heilongjiang Province or Siberia (50° north), but in south-western China, in subtropical areas at the other extreme of their geographic range (25°N), they may be restricted to higher altitudes at 3000 m above sea level (asl) or even higher. In contrast to these widespread species, those restricted to relatively limited areas in south China have much more restricted altitudinal distributions.

1.4 *Actinidia* Species in Cultivation

Only a small number of *Actinidia* species are currently in cultivation and the most promising potential use of the other species is as a possible source of genetic diversity rather than in providing prospective commercial cultivars.

1.4.1 Actinidia chinensis *Species Complex*

Nearly all cultivated kiwifruit belong to this complex, and the fruit are those most readily available commercially and generally recognised as 'kiwifruit'. The relationships between these taxa and others in *Actinidia* are discussed in Gui (1981), Liang and Ferguson (1984, 1986), Xiong (1991), Hirsch et al. (2002), Huang et al. (2002), Li et al. (2003), Chat et al. (2004), Huang and Ferguson (2007), Li et al. (2007a, b, 2009), Datson and Ferguson (2011), Hsieh et al. (2011) and Huang et al. (2014). *A. chinensis* var. *setosa* is restricted to Taiwan; *A. chinensis* var. *chinensis* occurs mainly in the warmer, lowland areas of eastern China and along the coast, south of the Huai He (Huai River) in eastern Henan, Anhui, Hubei, Hunan, Jiangxi, Fujian, Zhejiang, Jiangsu, south Shaanxi as well as some areas of Guangdong, Guangxi and Yunnan; and *A. chinensis* var. *deliciosa* grows more inland in colder regions as far north as the Qinling Mountains and to the west in Chonqing, Sichuan, Shaanxi, western Henan, western Hubei, western Hunan, Gansu, Guizhou, Guangxi and Yunnan. Where the two varieties overlap, they are usually separated vertically, with *A. chinensis* var. *deliciosa* being found at higher, colder altitudes. Thus, *A. chinensis* var. *chinensis* occurs mostly at altitudes between 200 and 900 m asl, but can be found as high as 1200 m asl (Li et al. 1985); *A. chinensis* var. *deliciosa* is usually at 800–1400 m asl sometimes up to 1950 m asl. The two varieties at the geographic extremes are readily distinguished, but the existence of clines between the clear extremes of *A. chinensis* var. *chinensis* and *A. chinensis* var. *deliciosa,* and the extensive introgressive hybridisation where the two taxa coexist (Liang 1982a, b; Zhang et al. 2007; Li et al. 2010; Liu et al. 2010, 2015; Huang et al. 2014), suggest that the taxa are better treated as varieties of the one species rather than as distinct species. This was the conclusion of Li et al. (2007a, b) in their revision of the genus. However, they also reduced *A. setosa* to a variety of *A. chinensis,* whereas Hsieh et al. (2011) in a treatment of the *Actinidia* taxa in Taiwan retained it as a separate species. *A. chengkouensis* C.Y. Chang should probably be included in the complex (Li et al. 2009), as should a number of other taxa which are possibly natural hybrids involving *A. chinensis* var. *chinensis* or *A. chinensis* var. *deliciosa* (Huang and Ferguson 2007).

Most of the publications considered in the different chapters in this book have treated *A. chinensis* and *A. deliciosa* as distinct species, but for consistency the nomenclature has been updated to follow that of Li et al. (2007a, b):

A. chinensis Planch. becomes *A. chinensis* Planch. var. *chinensis*

A. deliciosa (A. Chev.) C.F. Liang et A.R. Ferguson becomes *A. chinensis* var. *deliciosa* (A. Chev.) A. Chev.

1.4.2 Actinidia arguta *(Sieb. et Zucc.) Planch. ex Miq. Species Complex*

This is amongst the most widespread of all *Actinidia* species, being found in Siberia, Korea and Japan as well as throughout much of China. Like other species that are geographically widely distributed, it shows considerable morphological variation, particularly in leaf shape, the presence or absence of leaf hairs, and in fruit shape and colour when ripe. Liang (1984) recognised five varieties in China, but Li et al. (2007a, b) reduced these to two varieties and considered that fruit colour was not a useful diagnostic character as it did not correlate with variation in leaf morphology. They therefore merged what had been described as *A. purpurea* Rehder or subsequently as *A. arguta* var. *purpurea* (Rehder) C.F. Liang with *A. arguta* var. *arguta*. The Japanese species *A. hypoleuca* Nakai is also sometimes treated as a variety of *A. arguta*: *A. arguta* var. *hypoleuca* (Nakai) Kitam.

Vines of *A. arguta* are large and vigorous. The fruit are small, averaging 5–7.5 g, with smooth, hairless skins. Mostly, the external appearance and the fruit flesh are bright green, but ripe fruit can be light green to pink to bright dark red or purple, sometimes changing during storage. Fruit of the closely related *A. hypoleuca* and *A. melanandra* can also be red to purple when ripe. These are the only *Actinidia* species in which both the outer appearance and the internal flesh can be red-purple. The fruit are globose to cylindrical ellipsoid. They have a good flavour and can be eaten whole as they are small and the skin is edible, even if sometimes bitter.

1.4.3 Actinidia kolomikta *(Maxim. et Rupr.) Maxim.*

This is the hardiest of all *Actinidia* species, being able to withstand winter temperatures as low as −35 °C. The vines are usually compact growers and the fruit mature very early in the season, little more than a couple of months after flowering. The fruit can be very sweet and have a fine flavour, with a remarkably high vitamin C content of up to 1 % fresh weight (Chesoniene et al. 2004), but they are small, being only 2–5 g. The small size of the fruit, their mixed on-vine maturity, their short storage life and the relatively low yields per plant generally limit interest in this species to regions such as Eastern Europe and Russia that have very cold winters and a limited range of alternative fruiting plants. Strikingly variegated male plants of *A. kolomikta* are popular as ornamental climbers.

1.4.4 Actinidia eriantha *Benth.*

This is a species from south-eastern China and has the largest fruit in the genus after those of *A. chinensis* var. *chinensis* and *A. chinensis* var. *deliciosa*. Fruit from most plants of *A. eriantha* growing in the wild have a poor flavour and are too small for commercialisation. Recently, however, several selections with larger and better flavoured fruit have been released: ‘Bidan’ has sweet fruit, although small with an average fruit weight of 25 g (Jo et al. 2007), whilst ‘White’ has an average fruit weight of 94 g (Wu et al. 2009). The main attributes of interest of *A. eriantha* are the fruit with very high content of vitamin C, up to 1.1 % fresh weight, and the comparatively ready peelability of the fruit (Harker et al. 2011).

1.5 Kiwifruit Cultivars

The kiwifruit that are grown in commercial orchards are selections which have been vegetatively propagated by tissue culture, by cuttings or by grafting scions onto rootstocks, often *A. chinensis* var. *deliciosa* ‘Bruno’ seedlings. Pistillate (fruiting vines) are accompanied by complementary staminate (polleniser) selections.

Kiwifruit are unusual amongst fruit crops in that they have been domesticated for little more than a century and most of the cultivars grown commercially are only one or two generations removed from the wild: budwood was collected from plants that were identified as having commercial promise, propagated, evaluated and eventually released. This is the case with most of

the important kiwifruit cultivars grown in China (Huang and Ferguson 2001; Cui et al. 2002; Zhen et al. 2004; Ferguson et al. 2012). Good examples would be the two *A. chinensis* var. *deliciosa* cultivars 'Qinmei' and 'Miliang No. 1' or the cultivar *A. eriantha* 'White'. In other cases, seed was collected from the wild and the more promising of the seedlings were selected, or seedlings themselves were collected from the wild. Most of the early *A. chinensis* var. *deliciosa* cultivars developed in New Zealand, such as 'Bruno' and 'Hayward', are also seedling selections, but at least one generation removed from the original introduction of seed to New Zealand (Ferguson 1997). Some cultivars have arisen as selections from open-pollinated seedlings of named cultivars, e.g. 'Jinkui'. Many of the current *A. arguta* cultivars are likewise open-pollinated seedlings of material introduced from the wild.

Variation has arisen within cultivars of *A. chinensis* var. *deliciosa*: the more obviously distinguishable of these have been named as distinct cultivars, e.g. 'Wilkins' Super'; others have been named as selections, e.g. the Kramer strain of 'Hayward'.

Until recently, very few *Actinidia* cultivars were the results of deliberate crossing programmes. Some of Michurin's selections of *A. arguta* may have resulted from planned crosses (Michurin 1949). The *A. arguta*/*A. melanandra* hybrid released by MA McNeilage and colleagues (Williams et al. 2003) came from a planned cross, but has been cultivated only on a limited scale. The first widely grown cultivar to have resulted from controlled, planned crosses was *A. chinensis* var. *chinensis* 'Hort16A' (Muggleston et al. 1998), as did its replacement, *A. chinensis* var. *chinensis* 'Zesy002' (commonly known as Gold3). The first interspecific *Actinidia* hybrid widely grown is 'Jinyan', reportedly a hybrid between *A. chinensis* var. *chinensis* and *A. eriantha* (Zhong et al. 2012).

Except in China and New Zealand, there is little diversity in the kiwifruit cultivars grown. *A. chinensis* var. *deliciosa* 'Hayward' accounts for about two-thirds of all the fruiting kiwifruit grown throughout the world (see Chap. 3).

1.5.1 Actinidia chinensis var. chinensis *'Hongyang'*

The cultivar 'Hongyang' [Red Sun] chosen for genome sequencing by Huang et al. (2013) is the most widely cultivated diploid cultivar of *A. chinensis* var. *chinensis*. It is therefore an important cultivar and diploid genomes are obviously much easier to sequence than tetraploid genomes or the even more widely planted hexaploids such as *A. chinensis* var. *deliciosa* 'Hayward'. 'Hongyang' was originally classified as belonging to *A. chinensis* var. *rufopulpa* (C.F. Liang et R.H. Huang) C.F. Liang et A.R. Ferguson but this taxon is now included in *A. chinensis* var. *chinensis* (Li et al. 2007a). The most striking characteristic of 'Hongyang' is its brilliant red inner pericarp (for illustration see Wang et al. 2003). Such red-fleshed genotypes of *A. chinensis* var. *chinensis* and *A. chinensis* var. *deliciosa* are scattered sporadically throughout the natural range of these two varieties in China, particularly in Henan, Hunan, Jiangxi and Sichuan provinces (Sui et al. 2013).

'Hongyang' was selected by the Sichuan Provincial Natural Resources Research Institute, Chengdu, Sichuan, China and the Agriculture Bureau, Cangxi County, Sichuan, China, from open-pollinated seed collected from the wild in Henan Province, China (Wu and Li 1993; Wang et al. 2003): 3213 seedlings were planted out in 1984 and by 1989, 921 female plants were fruiting. Three seedlings bore fruit in which red pigment was mainly distributed in the locules around the core. These seedlings were propagated by topworking and evaluated and the best clone was selected in 1994 and was called 'Hongyang'. It remained true to type through successive asexually propagated generations by grafting at Chengdu and other locations in China. The obovoid fruit have a deeply depressed stylar end, thin, dark green or brownish skin, depending on exposure to the sun, with fine, downy hairs which are readily shed, a mean fruit weight of 50—60 g, yellow-green flesh with deep red locules in the inner pericarp around the core and excellent eating qualities. The ripe fruit are sweet, 16°–20° Brix and have a high vitamin C

content, 136 mg/100 g fresh weight. 'Hongyang' was registered in 1997 by the Sichuan Provincial Crop Cultivar Registration Committee and the US Plant Patent, US 20080155721 P1, was published in 2008.

The vine is precocious and productivity is high with high flower production and fruit set, and the fruit receive exceptionally high prices in Chinese markets. However, the vine is vulnerable to heat and drought and is readily infected by Psa (*Pseudomonas syringae* pv. *actinidiae*). As with many other red-fleshed kiwifruit selections, expression of the red pigmentation can be affected by climatic conditions (Jiang 2011; Wang 2010).

1.6 Implications of Some Distinctive Features of *Actinidia* Species for Commercial Cultivation

1.6.1 Growth Habit

All *Actinidia* species are long-lived, perennial climbers but their vigour varies with species, altitude and latitude (Huang and Ferguson 2007). Some species are weak growers, whereas others are very vigorous and can climb to the tops of tall trees, smothering them in rampant growth, although at their altitudinal or latitudinal limits such strong growers can be reduced to scramblers.

Actinidia species that are cultivated can live for 50 years or more and require strong, expensive and permanent structures, as the vines are not self-supporting. Newly established plants may take three to five years to develop a full canopy. They have to be rigorously trained and pruned so that the canopy of leaves allows efficient interception of light yet is not so dense that fungal diseases are favoured; allows sufficient light penetration for fruit quality and flower evocation; allows ready access for bees during pollination; and makes vine management, such as spraying and harvesting, easier. Removal of excessive vegetative growth in summer and winter pruning is a major expense and, apart from the trunk and the main leaders, much of the above-ground parts of vines are replaced each year.

Vine management, based mainly on research with *A. chinensis* var. *chinensis* and *A. chinensis* var. *deliciosa*, needs to take into account the growth habit of the vines:

- flowers are produced only on lateral shoots of the current growing season;
- these lateral shoots are normally those growing from buds in leaf axils of canes produced the previous growing season, i.e. one-year-old canes. Some lateral shoots are vegetative, whilst others develop into flowering shoots;
- shoots coming from older wood when it is pruned seldom produce flowers in their first growing season;
- shoots should be carried on canes of the previous season originating as close as possible to the leaders (the main branches coming from the trunk);
- shoots from canes that were heavily shaded during the previous season carry fewer flowers than those exposed to the sun;
- the choice of canes is important—in general, stronger canes are more floriferous but excessively vigorous shoots seldom produce fruit;
- inflorescences are carried towards the base of flowering shoots and consist of a terminal flower and, potentially, successive lateral flowers. Usually, inflorescences of staminate vines contain a number of flowers, those of pistillate vines a smaller number, sometimes a single flower. Selection of fruiting cultivars has favoured those genotypes that carry single flowers since single flowers produce fruit, which are more consistent in size, are often larger and are less prone to proximity damage;
- crop load is determined by the number of flowers carried, as normally most flowers that open and are pollinated set fruit which

survive until maturity. Kiwifruit are therefore very different to many other fruit crops in which only a small proportion of the flowers that are initiated set fruit which develop to maturity.

The first step in controlling crop load therefore is managing the number of canes that will carry flowering shoots. Flower evocation occurs in late summer/early autumn but the potential flowering shoot enters dormancy with undeveloped floral meristems which differentiate in spring. Budbreak is affected by winter temperatures and flower development by temperatures in spring.

The aim in pruning is to retain sufficient one-year-old wood to provide more than enough flowers for the target crop load and, depending on the extent of budbreak and flower abortion, it may be necessary to remove excess flowers before and after flower set. The aim of crop load management was to achieve the most profitable compromise between fruit number, size and dry matter content (Paterson and Currie 2011). Insufficient winter chilling in warmer climates can lead to commercially inadequate crop yields and differences amongst cultivars in winter-chilling requirements are important. The fruit contain many seed, up to 1000 or more, and fruit size is proportional to the number of seed. Efficient pollination is therefore essential for commercial crop production.

Individual cultivars may respond differently to management practices and to the particular climatic conditions in different regions.

1.6.2 Dioecism

All *Actinidia* species are apparently dioecious but functional dioecy has been confirmed in only a few species (Kawagoe and Suzuki 2004). Pistillate plants not only have flowers with well-developed ovaries and styles but also have stamens. Pistillate flowers therefore appear 'perfect', having both stamens and carpels: they appear to be bisexual or hermaphroditic but the pollen they produce is sterile (pseudopollen). It has been proposed that stamens of pistillate flowers aid reproduction by attracting pollinating insects (Kawagoe and Suzuki 2004). *Actinidia* species can be considered morphologically as appearing to be androdioecious but functionally as cryptically dioecious (Schmid 1978; Kawagoe and Suzuki 2004; Mizugami et al. 2007).

Dioecism is not absolute and gender inconstancy has been detected through the identification in commercial *A. chinensis* var. *deliciosa* orchards of 'fruiting male' plants which produce both staminate flowers and flowers which are, to varying extents, bisexual (McNeilage 1991a, b). Such vines have been used for the breeding of hermaphrodite plants.

Gender inconstancy has also been observed in *A. arguta* (Hirsch et al. 1990), *A. chinensis* var. chinensis (Tang and Jiang 1995), *A. eriantha* (Cui et al. 2002), and an unidentified *Actinidia* taxon from southern Japan (Matsumoto et al. 2013) probably closely related to *A. callosa* Lindl. (I Kataoka personal communication); it probably occurs in other *Actinidia* species as well.

Parthenocarpy has been observed in one heptaploid (7*x*) clone but not in other clones of *A. arguta* 'Issai', a generic term used in Japan denoting a number of clones characterised by precocious flowering (Mizugami et al. 2007). Parthenocarpy can be induced in *A. chinensis* var. *deliciosa* by the application of plant growth substances such as N-(2-chloro-4-pyridyl)-N′-phenylurea (CPPU) (Iwahori et al. 1988).

Dioecy imposes commercial constraints. At present, about 10 % of the canopy in commercial orchards is occupied by non-fruiting staminate pollenisers. Orchards need to be managed so that bees brought in remain active and effective in transferring pollen from the polleniser plants to the fruiting plants. The distribution of pollenisers within the orchard is therefore important (Testolin 1991). An alternative is to apply mechanically pollen collected from polleniser vines.

A good polleniser vine needs to coincide in flowering with the particular fruiting cultivar grown, should be floriferous, should have inflorescences with lateral flowers to extend the flowering time and should produce large

quantities of viable pollen which can set seed and size fruit. The spent flowers should drop cleanly.

1.6.3 Fruit Diversity

Morphologically, *Actinidia* fruit are defined as berries, i.e. they are fleshy fruit produced from a single flower containing a single ovary, the entire ovary wall ripening into an edible pericarp with the seed embedded in the fleshy interior of the ovary. They are therefore different from many of the fruits known horticulturally as berryfruit, e.g. strawberries, raspberries or mulberries, which are aggregate fruits.

There is great variation between and within *Actinidia* species in fruit characteristics (Fig. 1.5) such as size, shape, skin hairiness, colour (both internal and external), flesh texture, flesh flavour, flesh composition (especially of health-promoting constituents such as vitamin C), time of maturity, time of ripening and responses to prolonged storage (Li 1952; Huang et al. 1983; Liang 1984; Li et al. 1985; Ferguson 1990; Cui et al. 2002; Huang et al. 2003, 2004, 2014; Huang and Ferguson 2007; Nishiyama 2007). Such variation is important horticulturally and for the handling, storage and marketing of the fruit. This variation is fully discussed in Chap. 2.

The first kiwifruit available in international markets were green-fleshed owing to the retention of chlorophyll. This is unusual as most fleshy fruit lose their chlorophyll during development and ripening. Although green-fleshed kiwifruit still predominate in the market, some kiwifruit cultivars, mainly of *A. chinensis* var. *chinensis*, lose some or all of their chlorophyll as they ripen or during storage, revealing yellow flesh owing to the presence of carotenoids. In other species, the loss of chlorophyll exposes the presence of anthocyanins. Pigmentation in kiwifruit is discussed further in Chap. 12.

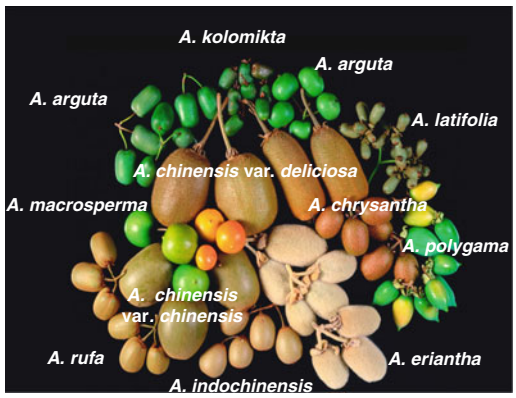

Fig. 1.5 Diversity in *Actinidia* fruit (Photograph: Plant & Food Research)

Other constituents in the flesh can also affect the appeal of kiwifruit to consumers. The vitamin C content is amongst the highest in readily available fruit. One standard green-fleshed 'Hayward' kiwifruit can satisfy the human daily requirements for vitamin C. The fruit of other *A. chinensis* var. *deliciosa* cultivars or other *Actinidia* species can contain even more vitamin C (Huang and Ferguson 2007). This is discussed further in Chap. 13. However, not all constituents are an advantage: allergens in kiwifruit can present a serious problem to some consumers (Chap. 17).

One of the most valuable characteristics of the fruit of *A. chinensis* var. *deliciosa* 'Hayward' is its remarkably long storage life, which allowed the successful export of the fruit produced in New Zealand to overseas markets (Hewett et al. 1999). 'Hayward' fruit are particularly tolerant of low temperatures and can be stored close to 0 °C, thereby prolonging storage life (Burdon and Lallu 2011). Fruit of other kiwifruit cultivars may be prone to chilling injury when stored at such low temperatures; they have initially to be stored at higher temperatures, and this reduces their potential storage life. The response of the fruit of different *Actinidia* genotypes to storage conditions is of great commercial importance: the behaviour of 'Hayward' fruit is exceptional (see also Chap. 16).

1.7 Scientific Studies on Kiwifruit Cultivars

Only a few genotypes of individual *Actinidia* species have been studied in any detail and it is hence unwise to generalise about any species as a

whole. Many species, especially those with wide geographic distributions, can be very variable. The plants that have been studied may well be atypical. Most of the scientific literature on kiwifruit refers to the cultivar 'Hayward', but it is just one pistillate cultivar of one variety (var. *deliciosa*) of one species (*Actinidia chinensis*). Furthermore, 'Hayward' is hexaploid and most genome-sequencing studies have used diploid selections of *A. chinensis* var. *chinensis*, such as 'Hongyang'. It is important not to extrapolate unquestioningly what is known about current kiwifruit cultivars to any new cultivars that may be released in the future.

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