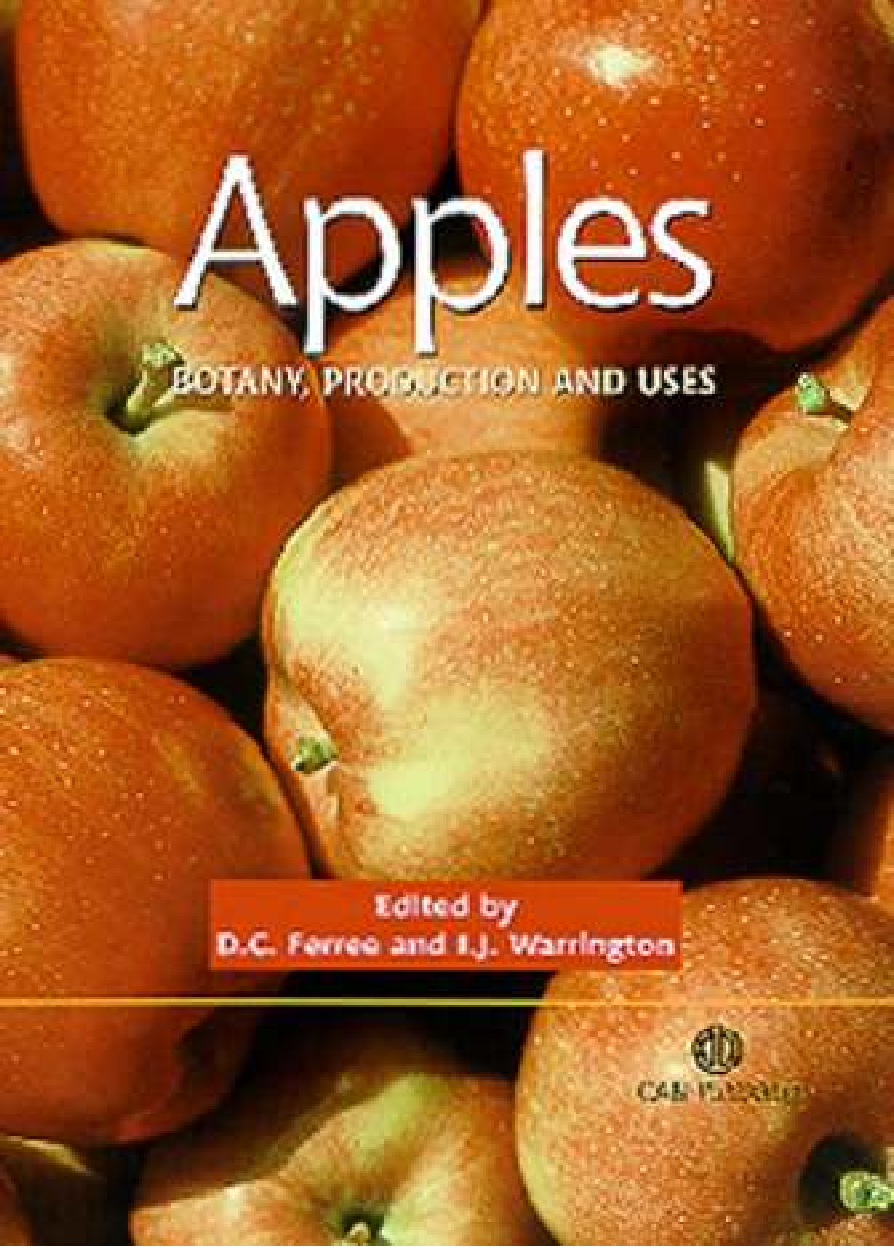
Apples
BOTANY, PRODUCTION AND USES
Edited by
D.C. Ferree and I.J. Warrington

Apples

Botany, Production and Uses

The editors dedicate this book to all the professors, teachers, extension personnel, commercial growers and other professionals who willingly shared their knowledge, inspired their students and contributed to the extensive knowledge that is represented in this book.

Apples

Botany, Production and Uses

Edited by

D.C. Ferree

Department of Horticulture and Crop Science, Ohio State University, USA

and

I.J. Warrington

Department of Horticultural Science, Massey University, Palmerston North, New Zealand

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Contents

Contributors

J. LaMar Anderson, *Plants, Soils, and Biometeorology Department, Utah State University, Logan, UT 84322, USA.*

Jesús Avilla, *Centro UdL-IRTA de R+D de Lleida, University of Lleida, Rovira Roure 177, 25198 Lleida, Spain.*

John A. Barden, *Department of Horticulture, Virginia Polytechnic Institute and State University, Blacksburg, VA 24061, USA.*

Elizabeth H. Beers, *Washington State University, Tree Fruit Research and Extension Center, 1100 N. Western Avenue, Wenatchee, WA 98801, USA.*

Susan K. Brown, *Department of Horticultural Sciences, Cornell University, New York State Agricultural Experiment Station, Geneva, NY 14456, USA.*

Ross E. Byers, *Department of Horticulture, Virginia Polytechnic Institute and State University, Winchester, VA 22602, USA.*

Luca Corelli Grappadelli, *Dipartimento di Colture Arboree, University of Bologna, Via Fillippo Re. 6, 40126 Bologna, Italy.*

Robert M. Crassweller, *The Pennsylvania State University, Department of Horticulture, Fruit Research and Extension Center, PO Box 330, Biglerville, PA 17307, USA.*

Frank Dennis, Jr, *Department of Horticulture, Michigan State University, East Lansing, MI 48824, USA.*

Kenneth C. Eastwell, *Irrigated Agriculture Research and Extension Center, Washington State University, Prosser, WA 99350, USA.*

David C. Ferree, *Department of Horticulture and Crop Science, Ohio Agricultural Research and Development Center, Ohio State University, Wooster, OH 44691, USA.*

Duane W. Greene, *Department of Plant and Soil Sciences, University of Massachusetts, Box 30910, Amherst, MA 01003, USA.*

George M. Greene, II, *The Pennsylvania State University, Department of Horticulture, Fruit Research and Extension Center, PO Box 330, Biglerville, PA 17307, USA.*

Gary G. Grove, *Irrigated Agriculture Research and Extension Center, Washington State University, Prosser, WA 99350, USA.*

Cheryl R. Hampson, *Pacific Agri-Food Research Center, Agriculture and Agri-Food Canada, Summerland, BC V0H 1Z0, Canada.*

Andreas Häseli, *Research Institute of Organic Agriculture (Forschungsinstitut für biologischen Landbau (FiBL)), Ackerstrasse, Postfach, CH-5070 Frick, Switzerland.*

Alan L. Jones, *Department of Botany and Plant Pathology, Michigan State University, East Lansing, MI 48824, USA.*

Henk Kemp, *Applied Plant Research, Fruit Section, Lingewal 1, 6668 LA Randwijk, The Netherlands.*

Alan N. Lakso, *Fruit Crop Physiology Program, Cornell University, Department of Horticultural Sciences, New York State Agricultural Experiment Station, Geneva, NY 14456, USA.*

James J. Luby, *Department of Horticultural Sciences, University of Minnesota, 342 Alderman Hall, 1970 Folwell Avenue, St Paul, MN 55108, USA.*

Kevin E. Maloney, *Department of Horticultural Sciences, Cornell University, New York State Agricultural Experiment Station, Geneva, NY 14456, USA.*

Ian A. Merwin, *Department of Horticulture, Cornell University, Ithaca, NY 14853, USA.*

Denise Neilsen, *Agriculture and Agri-Food Canada, Pacific Agri-Food Research Centre, Summerland, British Columbia, V0H 1Z0, Canada.*

Gerry H. Neilsen, *Agriculture and Agri-Food Canada, Pacific Agri-Food Research Centre, Summerland, British Columbia, V0H 1Z0, Canada.*

Desmond O'Rourke, *Belrose Inc., 1045 NE Creston Lane, Pullman, WA 99163, USA.*

John W. Palmer, *The Horticulture and Food Research Institute of New Zealand Ltd, Nelson Research Centre, PO Box 220, Motueka, New Zealand.*

Jean P. Privé, *Agriculture and Agri-Food Canada, PO Box 667, Boutouche, New Brunswick, Canada.*

Ronald J. Prokopy, *Department of Entomology, University of Massachusetts, Fernald Hall, Box 30910, Amherst, MA 01003, USA.*

Helmut Riedl, *Mid-Columbia Agricultural Research and Extension Center, Oregon State University, 3005 Experiment Station Drive, Hood River, OR 97031, USA.*

Terence L. Robinson, *Department of Horticultural Sciences, New York State Agricultural Experiment Station, Cornell University, Geneva, NY 14456, USA.*

James R. Schupp, *Department of Horticultural Sciences, Cornell University, New York State Agricultural Experiment Station, Hudson Valley Laboratory, Highland, NY 12528, USA.*

Schuyler D. Seeley, *Plants, Soils, and Biometeorology Department, Utah State University, Logan, UT 84322, USA.*

D. Max Suckling, *The Horticulture and Food Research Institute of New Zealand Ltd, Gerald Street, PO Box 51, Lincoln, Canterbury, New Zealand.*

Turner B. Sutton, *Department of Plant Pathology, North Carolina State University, Raleigh, NC 27695, USA.*

D. Stuart Tustin, *The Horticulture and Food Research Institute of New Zealand Ltd, Hawke's Bay Research Centre, Private Bag 1401, Havelock North, New Zealand.*

Ian J. Warrington, *Department of Horticultural Science, Massey University, Private Bag 11222, Palmerston North, New Zealand.*

Christopher B. Watkins, *Department of Horticulture, Cornell University, Ithaca, NY 14853, USA.*

Anthony D. Webster, *Crop Science Department, Horticulture Research International, East Malling, West Malling, Kent ME19 6BJ, UK.*

Franco Weibel, *Research Institute of Organic Agriculture (Forschungsinstitut für biologischen Landbau (FiBL)), Ackerstrasse, Postfach, CH-5070 Frick, Switzerland.*

S.J. Wertheim, *Fruit Research Station, Lingewal 1, 6668 Randwijk, The Netherlands.*

Preface

> There is no fruit in temperate climates so universally esteemed, and so extensively cultivated, nor is there any which is so closely identified with the social habits of the human species as the apple.
>
> (Dr Robert Hogg, *The Apple*, 1851)

Although the precise origin of today's apple is not entirely clear, it probably evolved from extensive forests of apples in central Asia, particularly in Kazakhstan. Due to its unique qualities, people collected and spread the most desirable types. Remains of apple have been reported in historic sites dated to 6500 BC. Long-distance trade routes between the Mediterranean area and various areas of Asia developed as early as 3500 BC and fostered the spread of both fresh and dried apples. Theophrastus (around 320 BC) studied apples brought back to Greece from conquests of Alexander the Great. He described grafting and general tree care and also dwarf types that later were used as rootstocks. Followers of both the Christian and Islam religions were instrumental in the spread of apples throughout Europe, Africa and the New World. By 1826, the Royal Horticultural Society of England had identified 1200 apple cultivars.

Commercial production of apples started as complements in gardens, as field borders or as overstorey trees in pastures. Apples are produced commercially in most countries in the temperate region of the world and also in some tropical areas with high altitude. In the last 100 years production has become increasingly intensified, with the use of dwarfing rootstocks and training systems designed to improve orchard efficiency. Apple is unique among fruit plants in having a range of rootstocks that permit development of a 'designer tree size' appropriate to the training system and management skills of modern orchardists.

In the last 50 years the development of herbicides, insecticides and fungicides has permitted the production of high-quality fruit in many areas where production was previously difficult. Currently, as more information is gained through research, the trend is to reduce pesticide inputs through integrated production systems or organic production. Apple breeders are assisting by developing high-quality cultivars with resistances to the most serious pests, through both conventional breeding and genetic engineering. Research in storage and postharvest handling techniques have dramatically improved fruit quality and currently apples are a quality product available throughout the year. Many of these current cultural practices are based on research results of detailed studies of the effects of various aspects of the environment on apple growth and development.

This book is an effort by 39 research scientists from eight countries to summarize the current research information on apples in a comprehensive treatise. Authors attempted to provide the information and physiology behind current cultural practices as well as future trends. The objective was to provide horticultural students, research and extension personnel, professional fruit growers and others with a comprehensive textbook on apples and their culture.

David C. Ferree
Ian J. Warrington

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1 Taxonomic Classification and Brief History

James J. Luby
Department of Horticultural Sciences, University of Minnesota, St Paul, Minnesota, USA

1.1 The Origin and Spread of the Domesticated Apple

The common domesticated apple is putatively an interspecific hybrid complex, usually designated *Malus* × *domestica* Borkh. (Korban and Skirvin, 1984) or *M. domestica* Borkh. (Phipps *et al*., 1990). Other synonyms, now considered illegitimate, have been applied, including *Pyrus malus* L., *Malus malus* Britt., *Malus pumila* Mill. and *Malus sylvestris* Mill. *M.* × *domestica* is now cultivated widely in temperate latitudes or at high elevations in the tropics on all continents except Antarctica. The fruits are eaten fresh, dried or tinned or processed into juice, preserves or alcoholic beverages. Besides *M.* × *domestica*, fruits of several other species are consumed fresh or processed or are used for medicinal purposes and the plants are used as rootstocks (Table 1.1). Many species and interspecific hybrids are used as ornamental plants.

The origin and ancestry of the *M.* × *domestica* complex remain unknown. Borkhausen, when first describing *M.* × *domestica* in 1803, believed it originated as a hybrid derived from *M. sylvestris* Mill., *Malus dasyphyllus* Borkh. (a synonym for *M. pumila*) and *Malus praecox* Borkh. (a synonym for *M. sylvestris* var. *praecox* (Pall.) Ponomar.) (Korban and Skirvin, 1984). Currently, however, *Malus sieversii* (Ledeb.) Roem. is hypothesized as the key species in its origin (Ponomarenko, 1983; Vavilov, 1987; Roach, 1988; Way *et al*., 1990; Hokanson *et al*., 1997; Juniper *et al*., 1998). *M. sieversii* is widespread in the mountains of central Asia at elevations between approximately 1200 and 1800 m. The forests are extensive and *M. sieversii* is the dominant overstorey species in many areas (Plate 1.1). The fruit of *M. sieversii* is highly variable (Plate 1.2) and individual trees resembling *M.* × *domestica* are commonly found in the forests of this region but their precise history is difficult to ascertain. Humans have inhabited and practised nomadic agriculture in this region for thousands of years. People of this region today will save desirable trees when the forest is cleared for agriculture (Ponomarenko, 1983)

Table 1.1. *Malus* species, synonyms and infraspecific classifications, from the taxonomy database of the US Department of Agriculture Germplasm Resource Information Network (USDA, ARS, National Genetic Resources Program. Germplasm Resources Information Network (GRIN), 2000) and their chromosome number, presence of apomixis, distribution and uses (from GRIN and also Phipps *et al.*, 1990; Way *et al.*, 1990; Zhang *et al.*, 1993; Deng *et al.*, 1995; Schuste and Büttner 1995; Zhou, 1999).

Species	Chromosome number and apomixis (A)	Synonyms and infraspecific classifications and [putative origin of secondary species]	Distribution	Uses
Primary species				
M. angustifolia (Aiton) Michx.	34		Eastern USA	Ornamental, preserves
M. baccata (L.) Borkh.	34, A	*M. baccata* var. *baccata* *M. rockii* Rehder *M. sibirica* (Maxim.) Kom., nom. illeg. *M. baccata* f. *gracilis* Rehder *M. baccata* f. *jackii* Rehder *M. baccata* subsp. *himalaica* (Maxim.) Likhonos *M. baccata* var. *himalaica* (Maxim.) C.K. Schneid. *M. baccata* var. *sibirica* C.K. Schneid.	North-eastern China, eastern Siberia, Mongolia, northern India, Bhutan, Nepal	Ornamental, rootstock
M. baoshanensis G.T. Deng	–		South-central China	Rootstock
M. brevipes (Rehder) Rehder	34		Only known in cultivation	Ornamental
M. coronaria (L.) Mill.	51, 68, A	*M. coronaria* var. *dasycalyx* Rehder *M. fragrans* Rehder *M. glabrata* Rehder *M. glaucescens* Rehder *M. lancifolia* Rehder *M. bracteata* Rehder	Eastern USA and Canada	Ornamental, fruit, preser
M. daochengensis C.L. Li	–		South-central China	
M. × *domestica* Borkh.	34, 51, 68, A	*M. malus* (L.) Britton, nom. inval. *M. pumila* auct. *M. sylvestris* auct. *M. sylvestris* var. *domestica* (Borkh.) Mansf.	Cultivated and naturalized in temperate regions	Fruit, preserves, bevera base, medicinal
M. doumeri (Bois) A. Chev	–	*M. formosana* Kawak. & Koidz. *M. laosensis* (Cardot) A. Chev.	South-east China, Taiwan, South-east Asia	Preserves
M. florentina (Zuccagni) C.K. Schneid.	34	*M. crataegifolia* (Savi) Koehne	Turkey, Greece, Italy and Balkans	Ornamental

M. floribunda Siebold ex Van Houtte	34		Only known in cultivation	Ornamental
M. fusca (Raf.) C.K. Schneid.	34	*M. fusca* var. *diversifolia* (Bong.) C.K. Schneid. *M. rivularis* Douglas ex Hook. *M. diversifolia* (Bong.) M. Roem.	Western USA and Canada	
M. halliana Koehne	34, 51		Central and eastern China, Japan	Ornamental, rootstock
M. honanensis Rehder	–		North-central China	
M. hupehensis (Pamp.) Rehder	34, 51, 68, A	*M. theifera* Rehder	Central and south-east China	Ornamental, rootstock, f beverage base, medicin
M. ioensis (A.W. Wood) Britton	34, 51	*M. ioensis* var. *texana* Rehder	Central USA	Ornamental, fruit
M. jinxianensis J.Q. Deng & J.Y. Hong	–		Northern China	
M. kansuensis (Batalin) C.K. Schneid.	34		Central China	
M. komarovii (Sarg.) Rehder	–		North-east China	
M. leiocalyca S.Z. Huang	–		South-east China	
M. maerkangensis M.H. Cheng *et al.*	–		Central China	
M. mandshurica (Maxim.) Kom.	34	*M. sachalinensis* Juz. *M. baccata* var. *cerasifera* (Spach) Koidz. *M. baccata* var. *mandshurica* (Maxim.) C.K. Schneid. *M. cerasifera* Spach *M. mandshurica* var.*sachalinensis* (Juz.) Ponomar.	Central and north-east China, far-eastern Russian, Japan	Rootstock
M. melliana (Hand.-Mazz.) Rehder	–		South-east China	Fruit, beverage base
M. micromalus Makino	34, 51		Central and eastern China, Japan	Rootstock, fruit, medicin
M. muliensis T.C. Ku	–		Central China	
M. ombrophila Hand.-Mazz	–		South-central China	
M. orientalis Uglitzk.	–	*M. sylvestris* subsp. *orientalis* (Uglitzk.) Browicz	Caucasus, Iran	
M. orthocarpa Lavallee ex anon.	–	An uncertain taxon	Only known in cultivation	Ornamental
M. prattii (Hemsl.) C.K. Schneid.	34	*M. kaido* Dippel	Central China	Fruit

Contin

Table 1.1. *Continued.*

Species	Chromosome number and apomixis (A)	Synonyms and infraspecific classifications and [putative origin of secondary species]	Distribution	Uses
M. prunifolia (Willd.) Borkh.	34		Central and eastern China	Ornamental, rootstock
M. pumila Mill.	34	*M. pumila* var.*niedzwetzkyana* (Dieck) C.K. Schneid. *M. sylvestris* var. *niedzwetzkyana* (Dieck) L.H. Bailey *M. niedzwetzkyana* Dieck *M. paradisiaca* (L.) Medik. *M. dasyphylla* Borkh. *M. pumila* var.*paradisiaca* (L.) C.K. Schneid.	Eastern Europe	Ornamental, rootstock
M. sargentii Rehder,	34, 51, 68, A		Only known in cultivation	Ornamental
M. sieversii (Ledeb.) M. Roem.	–	*M. sieversii* subsp. *turkmenorum* (Juz. & Popov) Likhonos *M. sieversii* var. *turkmenorum* (Juz. & Popov) Ponomar. *M. sieversii* var. *kirghisorum* (Al. Fed. & Fed.) Ponomar. *M. kirghisorum* Al. Fed. & Fed. *M. turkmenorum* Juz. & Popov	Central Asia	Rootstock, fruit, preserve
M. sikkimensis (Wenz.) Koehne ex C.K. Schneid.	51, A		South-central China, northern India, Bhutan	Rootstock, ornamental
M. spectabilis (Aiton) Borkh.	34, 51		Eastern China	Ornamental
M. sylvestris Mill.	–	*M. praecox* (Pall.) Borkh. *M. sylvestris* var. *praecox* (Pall.) Ponomar.	Europe	Ornamental, fruit, preser
M. toringo (Siebold) Siebold ex de Vriese	34, 51, A	*M. sieboldii* (Regel) Rehder *M. sieboldii* var. *arborescens* Rehder	Eastern China, Japan, Korea	Ornamental, rootstock
M. toringoides (Rehder) Hughes	51, 68, A	*M. transitoria* var. *toringoides* Rehder	Central China	Rootstock
M. transitoria (Batalin) C.K. Schneid.	34, 51		North central China	Rootstock
M. tschonoskii (Maxim.) C.K. Schneid.	34		Japan	

M. xiaojinensis M.H. Cheng & N.G. Jiang	–		Central China	Rootstock
M. yunnanensis (Franch.) C.K. Schneid.	34	*M. yunnanensis* var. *veitchii* (Veitch) Rehder *M. yunnanensis* var. *yunnanensis*	South-central China	Ornamental, rootstock
M. zumi (Matsum.) Rehder	34	*M. zumi* var. *calocarpa* (Rehder) Rehder *M. sieboldii* var. *calocarpa* Rehder	Japan	
Docynia indica (Wall.) Decne.	–	*M. docynioides* C.K. Schneid.	Eastern Himalayas, south-east Asia	
Eriolobus trilobata (Poir.) M. Roem.	34	*M. trilobata* (Poir.) C.K. Schneid.	Eastern Mediterranean	
Secondary species				
M. × *adstringens* Zabel	34, 51	[= *M. baccata* × *M. pumila*]	Only cultivated	Ornamental
M. × *arnoldiana* (Rehder) Sarg. ex Rehder	34	[= *M. baccata* × *M. floribunda*] *M. floribunda* var. *arnoldiana* Rehder	Only cultivated	Ornamental
M. × *asiatica* Nakai	–	[= *M. prunifolia* × *M. sieversii*] *M. prunifolia* var. *rinkii* (Koidz.) Rehder *M. ringo* Siebold ex Carriere	Cultivated in east Asia	Rootstock, fruit, preserve
M. × *astracanica* hort. ex Dum. Cours.	–	[= *M. prunifolia* × *M. pumila*]	Only cultivated	Ornamental
M. × *atrosanguinea* (Spath) C.K. Schneid.	–	[= *M. halliana* × *M. toringo*]	Only cultivated	Ornamental
M. × *dawsoniana* Rehder	34	[= *M. domestica* × *M. fusca*]	Only cultivated	Ornamental
M. × *hartwigii* Koehne	34	[= *M. baccata* × *M. halliana*]	Only cultivated	Ornamental
M. × *magdeburgensis* Hartwig	–	[= *M. pumila* × *M. spectabilis*]	Only cultivated	Ornamental
M. × *moerlandsii* Door.	34	[= *M.* × *purpurea* 'Lemoinei' × *M. toringo*]	Only cultivated	Ornamental
M. × *platycarpa* Rehder	51, 68, A	[= *M. domestica* × *M. coronaria*]	Eastern North America	
M. × *purpurea* (E. Barbier) Rehder	34	[= *M. astrosanguinea* × *M. pumila* 'Niedzwetzkyana'] *M.* × *purpurea* f. *eleyi* (Bean) Rehder [= M. × *purpurea* 'Eleyi' (*M. astrosanguinea* × *M. pumila* 'Niedzwetzkyana'] *M. floribunda* var. *lemoinei* E. Lemoine [= *M.* × *purpurea* 'Lemoinei'] *M.* × *purpurea* f. *lemoinei* (E. Lemoine) Rehder [= *M.* × *purpurea* 'Lemoinei'] *M.* × *purpurea* var. *aldenhamensis* Rehder [= *M.* × *purpurea* 'Aldenhamensis']	Only cultivated	Ornamental

Contin

Table 1.1. *Continued.*

Species	Chromosome number and apomixis (A)	Synonyms and infraspecific classifications and [putative origin of secondary species]	Distribution	Uses
M. × *robusta* (Carriere) Rehder	34	[= *M. baccata* × *M. prunifolia*]	China, cultivated	Ornamental, rootstock
M. × *scheideckeri* Spath ex Zabel	–	[= *M. floribunda* × *M. prunifolia*]	Only cultivated	Ornamental
M. × *soulardii* (L.H. Bailey) Britton	34	[= *M. ioensis* × *M. pumila*]	Central USA, naturalized and cultivated	Fruit, ornamental
M. × *sublobata* (Dippel) Rehder	–	[= *M. prunifolia* × *M. toringo*]	Only cultivated	Ornamental

and will commonly graft and plant desirable *M. sieversii* from the forest in their gardens. Planting desirable trees from root suckers may also have been a common practice prior to, or in addition to, grafting, as *M. sieversii* trees sucker freely. Conversely, people may have cloned and moved some of their horticulturally desirable trees to areas where they seasonally grazed their animals. These trees or their open-pollinated descendants may be among the horticulturally elite specimens observed in some of the forests today.

The passage of trade routes from China to the Middle East and Europe through Central Asia probably facilitated repeated short- and long-distance dispersal to the east and west, either intentionally or unintentionally, of *M. sieversii* and its hybrid derivatives. The *M.* × *domestica* complex may then have arisen through hybridization to the east with species native to China, including *Malus prunifolia* (Willd.) Borkh., *Malus baccata* (L.) Borkh., *Malus mandshurica* (Maxim.) Kom. and *Malus sieboldii* (Regel) Rehder. To the west, hybridization with the local species *M. sylvestris* and *Malus orientalis* Uglitzk. is conjectured (Ponomarenko, 1983; Morgan and Richards, 1993; Hokanson *et al.*, 1997; Juniper *et al.*, 1998).

During the late 19th and 20th centuries, *M.* × *domestica* cultivars found or bred in Europe, Russia, North America, New Zealand, Japan and Australia were introduced throughout the world and form the basis for most current commercial apple production (Way *et al.*, 1990; Janick *et al.*, 1996). Several species are known to have contributed to the *M.* × *domestica* complex in modern breeding programmes including *Malus floribunda* Siebold ex Van Houtte, *Malus micromalus* Makino, *Malus* × *atrosanguinea* (Spath) C.K. Schneid., *M. baccata*, *Malus zumi* (Matsum.) Rehder and *Malus sargentii* Rehder (Ponomarenko, 1983; Way *et al.*, 1990; Janick *et al.*, 1996).

In southern and eastern Asia, nai or the Chinese soft apple, *Malus asiatica* Nakai, was the primary cultivated apple in China and surrounding areas for over 2000 years until *M.* × *domestica* was introduced in the late 19th and early 20th centuries (Morgan and Richards, 1993; Zhang *et al.*, 1993; Watkins, 1995; Zhou, 1999). *Malus* × *asiatica* is probably a hybrid complex derived primarily from *M. sieversii* with *M. prunifolia* and perhaps other species.

Prehistoric remains and historical records, reviewed by Morgan and Richards (1993), provide evidence of the cultivation, dispersal and human use of the apple in Asia and Europe over the last several thousand years. Archaeological remains of apple that dated to about 6500 BC were found in Anatolia, though it is impossible to know the source of this fruit or whether it was cultivated. Historical evidence referring to apple cultivation dates to the second millennium BC from Anatolia and northern Mesopotamia. By 500 BC, the apple was probably cultivated widely throughout the Persian Empire, as fruit orchards feature prominently in writings from the period. When Alexander the Great conquered the Persians around 300 BC, the cultivation of fruits was dispersed through the Greek world. By this time, the Greek philosopher, Theophrastus, had distinguished the sweet cultivated apple from astringent wild forms.

The ascendance of the Roman Empire spread cultivation of the domesticated apple north and west through Europe, where it supplanted and probably hybridized with the native crab apple, *M. sylvestris*. Multiple varieties were recorded by the Roman writer Pliny, and they had attained an important place in Roman cuisine, medicine and aesthetics by the 1st century AD. The Roman goddess Pomona was revered as the deity associated with apple and other fruits. With the rise and spread of Christianity and Islam over the next several centuries, apples were carefully maintained, even through wars and difficult times, in the abbey gardens throughout Europe and the orchards of Iberia. These apparently replaced the native crab apples, which had a place in the diet of early Celts, Gauls, Franks, Scandinavians and other peoples of northern Europe in fermented, dried or cooked forms. Maintenance of fruit gardens was encouraged as a basic monastic skill and many abbeys developed large orchards with many *M.* × *domestica* cultivars. Likewise in the Muslim world of the eastern Mediterranean and Iberia, fruit growing was revered in keeping with Koranic teachings and skills of grafting, training and pruning became highly developed.

From the 13th century, apples became more and more widely planted throughout Europe in gardens of royalty and commoners. Raw apples were occasionally consumed, but they were more greatly prized when cooked and sometimes blended with spices and sugar or honey. Fermented juice, or cider, like beer, was preferred to the sometimes questionable local water-supply. By the 17th century there were at least 120 cultivars described in western Europe. The rise and spread of Protestantism, which saw the apple as the special fruit of God, is credited with expanding apple cultivation across northern and eastern Europe after beginning in Germany in the early 17th century. By the end of the 18th century, many hundreds of cultivars were recognized throughout Europe. The Royal Horticultural Society of England acknowledged at least 1200 in 1826. The 18th and 19th centuries saw apple cultivars recognized and classified based on their suitability for their end uses (Plate 1.3). Aromatic dessert apples were more widely appreciated by this time, while good cooking types were still appreciated for puddings and pastries (Plate 1.4). Flavourful cultivars with moderate acid and tannin levels were prized for cider production. The late 19th and early 20th centuries represented the maximum of diversity in apple cultivation in Europe, with hundreds of locally popular cultivars being grown in thousands of small orchards (Plates 1.5 and 1.6). In the 20th century, the rise of imported fruit from the Americas, New Zealand (Plate 1.7), Australia and South Africa (Plate 1.8) forced European orchards to increase in size and decrease in number and, to a large extent, to adopt the very same cultivars that were developed in and imported from the New World.

Apples were established in the 1650s near Cape Town in South Africa to sustain settlers and to supply the ships of the Dutch East India Company. The commercial apple orchard district in the Western Cape was started by Cecil Rhodes and his associates in the late 19th and early 20th century to replace a faltering wine industry.

Apples were introduced to Australia, on the island of Tasmania and at the present site of Sydney, in 1788. Orchards were established by settlers in Tasmania and New South Wales by the early 1800s. Significant production areas were eventually developed in Tasmania and the south-eastern mainland. In 1814, English missionaries brought apples from Australia to New Zealand, where two large apple-production districts became established in the districts of Hawke's Bay and Nelson during the 19th and 20th centuries.

Beginning in the 16th and 17th centuries, European colonists brought apples to the Americas. Spanish priests introduced them to their missions in Chile and California. Spanish and Portuguese settlers introduced apples to their settlements in suitable temperate climate zones of South America. European settlers brought apple seeds to establish orchards in the eastern USA and Canada. Apples grew well from northern Georgia to eastern Canada and, as in Europe, were soon highly prized for food and drink and as a source of sugar and alcohol. The first orchards in New England were recorded in the 1620s and 1630s and became important components of the New England farmstead (Plate 1.9). Likewise, they became important on the large plantations of the mid-Atlantic colonies by the mid-1700s, including those of the early US presidents George Washington and Thomas Jefferson. Jefferson, an astute horticulturist, acquired and carefully tested dozens of cultivars for his Monticello gardens in Virginia.

In Canada, French colonists established orchards in the 17th century along the St Lawrence valley. Settlers also established orchards around Lake Ontario and in the milder valleys of Nova Scotia and New Brunswick.

As settlers moved westward in the USA, apple orchards were a requirement of homesteading throughout the territories of the Ohio River valley. Jonathan Chapman, known as Johnny Appleseed (Fig. 1.1), devoted his later life, from 1806 to 1847, to helping settlers establish thousands of apple trees on their new farms in the Ohio River drainage. The Great Lakes region of the USA,

Fig. 1.1. Only known drawing of Jonathan Chapman, 'Johnny Appleseed', supplied by Johnny Appleseed Heritage Center, Inc.

especially the states of New York, Michigan and Ohio, continues to be a major apple-production area.

In 1847, as settlers moved into the productive valleys of western Oregon, Washington and northern California, Henderson Llewelling brought 700 trees with his family on the Oregon Trail and eventually established the first fruit nursery in the Pacific Northwest. As irrigation schemes were eventually developed, the Pacific Northwest, especially including the basin of the Columbia River and its tributaries west of the Cascade Mountains and extending to the Okanagon River valley in British Columbia, eventually became one of the pre-eminent apple-production areas of the world (Plate 1.10).

By the early 20th century, the USA and Canada were the two largest apple-producing nations. Later in the century, the USSR also became important. By the beginning of the 21st century, China has become the largest apple producer, with a large proportion of the crop being exported as concentrated juice (Plate 1.11). Major southern-hemisphere production, much of it for export to northern-hemisphere countries during their spring and summer, occurs in South Africa, Chile, Argentina, New Zealand and Australia. Production is currently dominated by strains of just a few cultivars: 'Delicious', 'Golden Delicious', 'McIntosh' and 'Jonagold' developed in North America; 'Braeburn' and 'Gala' from New Zealand; 'Granny Smith' from Australia; and 'Fuji' from Japan. Though many other cultivars remain locally important, these dominate current production and are also widely used in breeding programmes around the world.

From its origins among the millions of wild *M. sieversii* trees in the mountains of central Asia and from the early development of thousands of local cultivars in Europe and America, the domesticated apple, as cultivated in the 21st century, has shrunk drastically in diversity.

1.2 Taxonomy and Evolution

1.2.1 Apples in the family *Rosaceae*

Apples are members of the genus *Malus* Miller, which is placed in the subfamily *Maloideae* of the family *Rosaceae* (Fig. 1.2). Other members of the *Maloideae* that are cultivated for their fruit include pears (*Pyrus* L. spp.), quinces (*Cydonia oblonga* Mill.), loquats (*Eriobotrya japonica* (Thunb.) Mill.), medlars (*Mespilus germanica* L.) and species of *Amelanchier*, *Aronia*, *Crataegus* and *Sorbus*. The subfamily *Maloideae* is one of four in the family *Rosaceae*. The other subfamilies are *Rosoideae*, *Spiroideae* and *Amygdaloideae*. The circumscription of these subfamilies has defied general agreement among systematists, depending on whether classification schemes emphasize morphological traits, chromosome numbers, intergeneric crossability or molecular polymorphisms (Rohrer *et al.*, 1991, 1994; Morgan *et al.*, 1994). The *Maloideae*

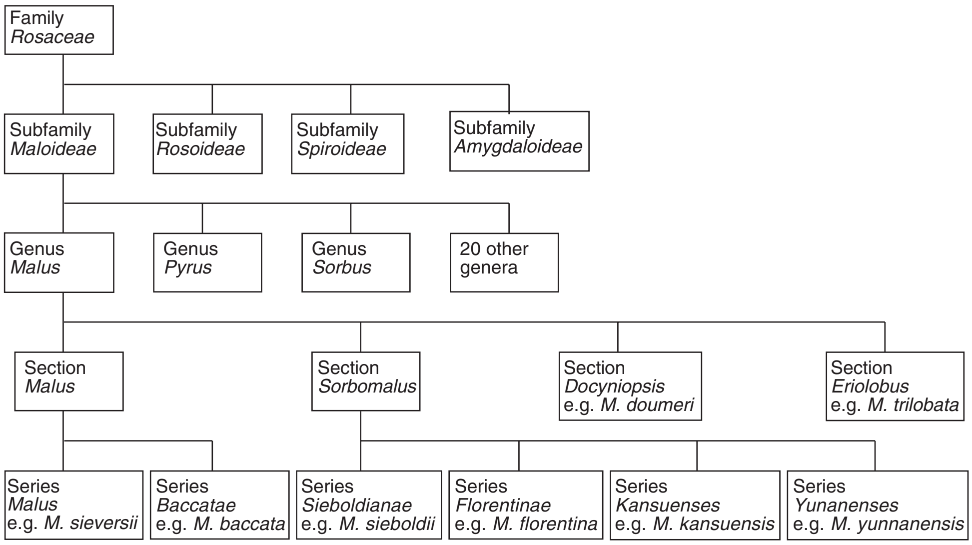

Fig. 1.2. Taxonomy of *Malus* (adapted from Phipps *et al.*, 1991).

are characterized by a hypanthium and gynoecium that remain fused to form an inferior ovary that develops into a fleshy, indehiscent fruit, or pome. Some genera with capsules or follicles, however, are apparently more closely related to genera in the *Maloideae* than to genera in other subfamilies, based on DNA sequence variation (Morgan *et al.*, 1994).

The subfamily *Maloideae* has a high haploid base chromosome number of x = 17 and is generally considered to be monophyletic when morphological traits, chromosome number (Kalkman, 1988; Phipps *et al.*, 1991) and DNA sequence variation from the chloroplast *rbcL* gene (Morgan *et al.*, 1994) and S-RNase (self-incompatibility) gene (Ushijima *et al.*, 1998) are considered. Data from nuclear ribosomal DNA sequences, however, support a single phylogeny for most of the genera, including *Malus*, but a separate phylogeny for the genera *Eriobotrya*, *Rhaphiolepis* and *Vauquelinia* (sometimes placed in the *Spiroideae*) (Campbell *et al.*, 1995).

Based on cytology and analysis of morphological characters, the *Maloideae* probably have a polyploid origin (Phipps *et al.*, 1991). Isozyme studies in *Malus* support an allopolyploid origin, based on the presence of duplicated gene systems, allele segregations and fixed heterozygosities (Chevreau *et al.*, 1985; Weeden and Lamb, 1987; Dickson *et al.*, 1991). An allotetraploid origin involving ancestral *Spiroideae* (mostly x = 9) and *Amygdaloideae* (x = 7) was proposed by Sax (1931, 1933) and is supported by flavonoid chemistry (Challice, 1974; Challice and Kovanda, 1981) and morphological traits (Phipps *et al.*, 1991). DNA sequence variation in the *rbcL* chloroplast gene suggests that *Amygdaloideae* and *Maloideae* are both advanced groups that arose from x = 9 spiraeoid-like ancestors (Morgan *et al.*, 1994). Data from internal transcribed spacer regions of nuclear ribosomal DNA genes are less comprehensive but support *Spiraea* as a closer relative to the *Maloideae* than *Rosa* or *Prunus* (Campbell *et al.*, 1995).

The taxonomic treatment of genera within *Maloideae* has varied from five cited in Linnaeus's original treatment up to 33 (Robertson *et al.*, 1991). Varying morphology and numerous instances of intergeneric hybridization complicate delimitation of genera. Robertson *et al.* (1991) describe 28 genera, including *Malus*. Species currently included in *Malus* were included in *Pyrus* by Linnaeus and others until the mid- to late 19th century. Campbell *et al.* (1995) considered molecular, morphological and wood anatomical data in determining relationships among genera.

Parsimony analyses of nuclear ribosomal DNA sequence variation placed *Malus* close to *Heteromeles*, *Chaenomeles*, *Photinia*, *Cydonia* and *Pyrus*. A numerical taxonomic treatment of morphological and wood anatomical studies placed *Malus* in a cluster that includes *Crataegus*, *Mespilus*, *Amelanchier*, *Peraphyllum* and *Rhaphiolepis*. A parsimony analysis, with both morphological and molecular data pooled, placed *Malus* close to *Chaenomeles*, *Pyrus* and *Aria*.

1.2.2 Species in the genus *Malus*

The delimitation of species within *Malus* has been problematic, with various treatments recognizing from as few as eight to as many as 78 primary species (Ponomarenko, 1986; Phipps *et al*., 1990). Many hybrid species, derived naturally or artificially, are recognized (Phipps *et al*., 1990; Way *et al*., 1990). Many of the commonly described primary species and hybrid derivatives are listed in Table 1.1. The classification and species retained here are consistent with the taxonomy database of the US Department of Agriculture Germplasm Resources Information Network (USDA, ARS, National Genetic Resources Program. Germplasm Resources Information Network (GRIN), 2000) at http://www.ars-grin.gov on the World Wide Web. A primary centre of species richness and diversity is in south-west China, with several species ranging east to Manchuria and Japan and others extending to western Europe. A secondary centre exists in North America, with four native species.

The species of *Malus* have been arranged in varying numbers of sections or subgenera, some of which are, in turn, divided into series (Fig. 1.2). Most recent authors modify the treatment of Rehder (1940) and assign *Malus* species to five sections of the genus based on morphological traits and flavonoid similarities (Phipps *et al*., 1990):

1. Section *Malus*, consisting of series *Malus*, including many European and Asian species (including *M. sieversii* and *M.* × *domestica*), with fruit having five carpels and mostly persistent calyces on the fruit, and series *Baccatae*, containing several Asian species, with fruit consisting of three to five carpels and deciduous calyces.
2. Section *Sorbomalus*, including series *Sieboldianae*, with species native to Japan, series *Florentinae*, with *Malus florentina* (Zuccagni) C.K. Schneid. from south-east Europe, series *Kansuenses*, containing small-fruited Chinese species (and the North American *Malus fusca* (Raf.) C.K. Schneid.), with deciduous calyces and persistent fruit, and series *Yunnanenses*, species from China with persistent calyces and generally persistent fruit.
3. Section *Eriolobus*, containing only *Malus eriolobus* (Poir.) C.K. Schneid. from the eastern Mediterranean.
4. Section *Choromeles*, containing exclusively North American species.
5. Section *Docyniopsis*, containing the species *Malus tschonoskii* (Maxim.) C.K. Schneid., *Malus doumeri* (Bois) A. Chev., *Malus melliana* (Hand.-Mazz.) Rehder and *Malus formosana* Kawak. & Koidz. of Japan, Taiwan and South-East Asia.

Robertson *et al*. (1991) revised the genera in *Maloideae* based primarily on a comprehensive numerical taxonomic treatment of 115 morphological traits, including foliage, inflorescence and fruit by Phipps *et al*. (1991). In the genus *Malus*, they retained three subgenera: (i) *Malus*; (ii) *Sorbomalus*; and (iii) *Chloromeles*. Several former *Malus* species are placed in other genera: *Eriolobus* includes *E. trilobata* (Poir.) M. Roem. (= *Malus trilobata*) and *Docyniopsis* includes *D. tschonoskii* (Wall.) Decne. (= *M. tschonoskii*) and presumably would include *M. doumeri*, *M. formosana* and *M. melliana*. They suggested that further work may support inclusion of the genus *Docyniopsis* as part of the genus *Docynia* and elevation of subgenus *Chloromeles* to genus.

The difficulty in species delimitation in *Malus* arises from the great diversity, potential for hybridization and polyploidy and presence of apomixis in the genus (Campbell *et al*., 1991). These phenomena may be indicative of a fairly recently derived genus in which species have developed rapidly through adaptive radiation and are primarily