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# Preface

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Brassicas are highly valuable sources of food, fodder, forage, condiments and ornamentals. They demonstrate significant genotypic and phenotypic diversity and flexibility; showing convergent evolution in the European and Asian forms of *Brassica oleracea* and *Brassica rapa*, respectively. A resultant rich array of fresh foodstuffs has evolved through selection and directed breeding developed initially by satisfying regional preferences. Since the first edition of *Vegetable Brassicas and Related Crucifers* plant breeders' hybrids have significantly amplified crop diversity, responding to changing market demands. In parallel, have come significant changes in crop science and technology. These now ensure high-quality crop production is achieved by sustainable means, which safeguard local biodiversity and conserve its environment. As a result, the use of synthetic crop protection formulations is diminishing, replaced by biostimulants, biofertilizers and active systems of biological pest and pathogen control. Regrettably, the spectrum of parasites, herbivores and microbes attacking crops is increasing, encouraged by climatic warming, moister, warmer environments and added virulence and aggressiveness. Physical change is happening in methods by which crops are monitored, measured and resource use calculated. Electronics are powering change in crop husbandry and the resultant opportunities are described and discussed. Automatic and autonomous systems are rapidly replacing muscle power for brassica production, harvesting, storage, cold-chain handling and delivery to the ultimate consumer as safe and trusted foods.

Wider arrays of brassica forms now offer higher quality fresh and more easily consumed brassicas. These trends encourage brassica use in diets that help reduce the impact of the diseases of affluence, such as cancers, coronary distress, and strokes. Evidence associating longer term brassica consumption with healthiness and greater welfare is now largely irrefutable. Rising consumption of brassica baby leaves, watercress and kale indicate public acceptance of this association. Each of these changes is supported by the vastly increased scientific literature reporting research concerning brassicas. Aspects of this research are absorbed into this revision. Massive growth in the world-wide importance of industrial brassicas, principally *Brassica napus* as oilseed

rape or canola and the associated scientific research has in turn boosted the literature relevant to vegetable brassicas. The enormous scientific importance of *Arabidopsis thaliana*, the first plant whose genome was sequenced, adds additional weight and volume into the brassica literature. The first edition of *Vegetable Brassicas and Related Crucifers* retained relevance for a generation. Hopefully, this revision will similarly provide knowledge for researchers, students, industrialists, growers, advisors, consultants and those with an intelligent general interest in these fascinating plants.

Views and interpretation expressed in the second edition of *Vegetable Brassicas and Related Crucifers* are solely those of the two authors, Geoffrey R. Dixon and Rachel Wells. We accept responsibility for all errors, omissions and unconventional thinking.

Geoffrey Dixon's roots for this book are set deep in a lifetime of scientific fascination in the biology of *Brassica* allied to the husbandry associated with commercial production. His knowledge of brassica science, technology and husbandry reflects working and travelling nationally and internationally, epitomised by the concept of '*One foot in the furrow and one hand on the laboratory bench*'. Rachel Wells is a Brassica geneticist with a keen interest in translating scientific research into commercial reality. This includes working on anything from producing biolubricants in oilseed rape to the architectural development of a cauliflower or the feeding habits of cabbage stem flea beetle. She can just as often be found in a field with farmers, agronomists and plant breeders as in a controlled environment room supporting students in their research.

Geoffrey Dixon expresses deep gratitude for decades of support and encouragement from numerous friends, students and professional colleagues. Nationally, these encompass studying at Wye College (University of London), working in the National Institute of Agricultural Botany, Cambridge, Aberdeen School of Agriculture, the Scottish Agricultural College, Strathclyde University and, most recently, the School of Agriculture, Policy and Development of Reading University.

Particular friends and mentors are Professors Paul Hadley and Helmut van Emden who have offered much valued friendships and intellectual stimulation at Reading University. Professor Paul Williams of Wisconsin University at Madison, USA is a source of abiding friendship, deep intellectual sustenance and a common view of science over many decades. Professor Stephen Strelkov, University of Alberta, Canada brought a vibrant window into the opportunities resulting from molecular science. My friends in the Vegetable Consultants Association have moulded my views on the interactions between industry and science.

My dearest wife, Kathy, continues with her unstinting and unflinching support of my life and interests aided by Lucy, Dougal, Isabella, Hector and Richard, Amanda and James.

Rachel gives thanks to all those that have worked with her as part of 'Team Brassica' at the John Innes Centre and beyond; colleagues, mentors, and students alike. Deepest thanks go to Ian Bancroft and Judith Irwin, who supported

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her during her early career and most recently Lars Ostergaard, Richard Morris and Steve Penfield as amazing research collaborators and friends.

Last, to my wonderful, unconventional, family, that have supported me in my work. My daughter Charlie, who believes so much in her mother the scientist, and my partner Gary, for bringing light to my life and whose art graces the pages of this book.

Geoffrey R. Dixon, Sherborne, UK and Rachel Wells, Norwich, UK: 2024.

## **NAMING CONVENTIONS**

Naming of plants, pests and pathogens used in this book has been very carefully assessed in an attempt to achieve consistency and conformity. There may, however, be failures and inconsistencies, since this is a complex and intricate topic, for which the authors accept responsibility.

## **SOURCE ACKNOWLEDGEMENTS**

The use of 'after' indicates that permissions were granted for use in the first edition of *Vegetable Brassicas and Related Crucifers* and this has been carried forward into this second edition. Sincere apologies are offered to any collaborators who feel this is an unwarranted action. Significant attempts have been made to trace the sources of Figures 7.24 and 8.6 without success; sincere apologies are offered to the collaborators who created these illustrations for the failure to acknowledge their excellent illustrations.



# ORIGINS AND DIVERSITY OF **1** *BRASSICA* AND ITS RELATIVES

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## Abstract

The *Brassica* genus comprises an abundance of phenotypically diverse species that have been adapted during domestication into an array of vegetable, oilseed and condiment crops. Understanding *Brassica*<sup>1</sup> vegetables involves a fascinating, biological journey through evolutionary time, witnessing wild plant populations interbreeding and forming stable hybrids. Humankind took both the wild parents and their progeny, refined them by selection and further combination, and over time produced crops that are, together with the cereals, the mainstay of world food supplies. This, in part, is down to the complex nature of *Brassica* genome evolution: ancient genome duplications, speciation, gene loss, hybridization and polyploidization events. This complexity and variation provides the flexibility for speciation, adaptation and selection that drives crop development. Modern genetic marker technologies have vastly improved the resolution of population structure and phylogenetic analyses, greatly enhancing our previous understanding of *Brassica* crop evolution. Here we discuss the origins, evolution and vast levels of diversity that are observed in today's wild, feral and cultivated *Brassica* species.

## ORIGINS AND DIVERSITY OF *BRASSICA* CROPS

Genetic diversity and flexibility are characteristic features of all members of the family Brassicaceae (previously Cruciferae). Possibly, these traits encouraged

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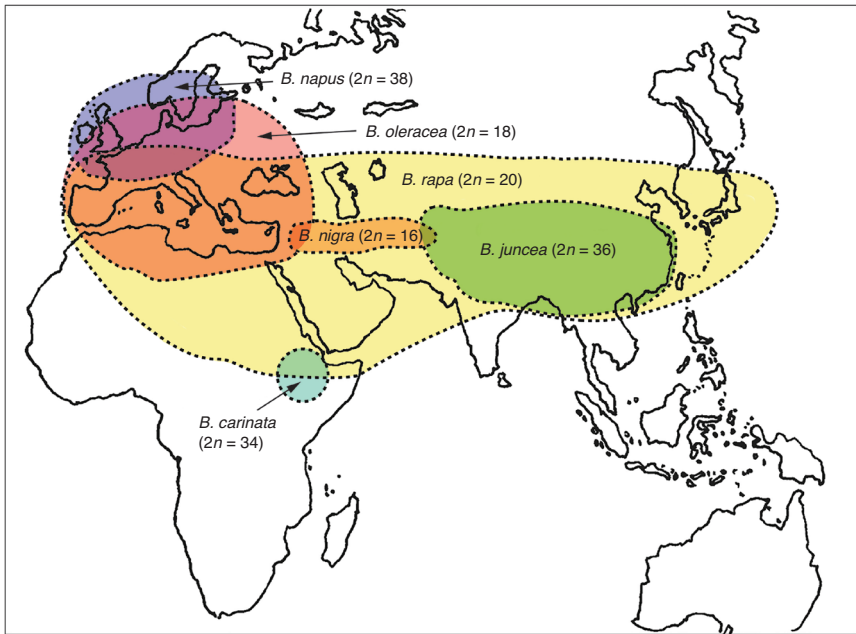
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their domestication by Neolithic people. *Brassica* crops were first described in a Chinese almanac from around 3000 BCE and ancient Indian texts from around 1500 BCE (Keng, 1974; Prakash *et al.*, 2011). Records show that the Ancient Greeks, Romans, Indians and Chinese all valued and used them greatly. The etymology of *Brassica* has been contested since Herman Boerhaave suggested in 1727 that it might come from the Greek *αποτουβραζειν*, Latin *vorare* (both meaning 'to devour') (Henslow, 1908). An alternative derivation from *Bresic* or *Bresych*, the Celtic name for cabbage, was suggested by Hegi (1919). This is a contraction of *praesecare* (to cut off early) since the leaves were harvested for autumn and early winter fodder. Another suggested origin is from the Greek *βρασσω* (crackle), coming from the sound made when the leaves are detached from the stem (Gates, 1953). A further suggestion is a Latin derivation from 'to cut off the head' and was first recorded in a comedy by Plautus in the 3rd century BCE. Aristotle (384–322 BCE), Theophrastus (371–286 BCE), Cato (234–149 BCE), Columella (1st century CE) and Pliny (23–79 CE) all mention the importance of brassicas.

Further east, the ancient Sanskrit literature *Upanishads* and *Brahmanas*, originating around 1500 BCE, mention brassicas and the Chinese *Shijing*, possibly edited by Confucius (551–479 BCE), refers to the turnip (Prakash and Hinata, 1980). European herbal and botanical treatises of the Middle Ages clearly illustrate several *Brassica* types and Dutch paintings of the 16th and 17th centuries show many examples of brassicas. In the 18th century, species of coles, cabbages, rapes and mustards were described in the genera *Brassica* and *Sinapis* in *Institutiones Rei Herbariae* (de Tournefort, 1700) and *Species Plantarum* (Linnaeus, 1735). Probably the most important early, formal classifications of *Brassica* were made by Otto Eugen Schultz (1874–1936) and published in *Das Pflanzenreich* and *Die Natürlichen Pflanzenfamilien* (Schulz, 1919 and 1936, respectively). These classifications were supported broadly by the great American botanist and horticulturist Liberty H. Bailey (1922, 1930).

Brassica crops worldwide provide the greatest diversity of products used by humans derived from a single genus. Other members of the family Brassicaceae extend this diversity. Overall, brassicas deliver: leaf, flower and root vegetables that are eaten fresh, cooked and processed; fodder and forage, contributing especially as an overwintering feed supply for meat- and milk-producing domesticated animals; sources of protein and oil used in low-fat edible products, fuel for illumination and industrial lubricants; condiments such as mustard, herbs and other flavourings; flowering and variegated ornamentals; and soil conditioners as green manure and composting crops.

Wild diploid *Brassica* and related hybrid amphidiploids (Greek: *amphi*=both; *diploos*=double; possessing the diploid genomes from both parents) evolved naturally in inhospitable places with abilities to withstand drought, heat and salt stresses (Gómez-Campo and Prakash, 1999). The Korean botanist Woo Jang-choon (known in scientific literature as Nagaharu U)



**Fig. 1.1.** Biogeography of the origins and diversity of major crop-founding *Brassica* species. (After UNFAO, courtesy Garry Breeze).

(Nagaharu, 1935) deduced that three basic diploid *Brassica* forms were probably the parents of subsequent amphidiploid crops. *Brassica nigra* (black mustard), itself the ancestor of culinary mustards, is found widely distributed as annual herbs growing in shallow soils around most rocky Mediterranean coasts. Natural populations of *Brassica oleracea* and associated types are seen historically as potential progenitors of many European cole vegetables. These populations inhabit rocky cliffs in cool damp coastal habitats. They have slow, steady growth rates and are capable of conserving water and nutrients. Domestication of *B. oleracea* occurred in a Mediterranean location, with the crop reaching the Atlantic coast through the movement of people and cultures (Maggioni, 2015). The putative ancestor of many Asian brassica vegetables, *Brassica rapa*, originates from the 'Fertile Crescent' in the high-plateau regions of today's Iran, Iraq and Turkey. Here, these plants grow rapidly in the hot, dry conditions forming copious seed. Other family members evolved as semi-xerophytes in the Saharo-Sindian regions in steppe and desert climates. Early hunter-gatherers and farmers discovered that the leaves and roots of these plants provided food and possessed medicinal and purgative properties when eaten either raw or boiled. Some types supplied lighting oil, extracted from the seed, and others were simply used for animal feed. These simple herbs have developed into a massive array of essential crops grown all around the world (see Fig. 1.1).

## BIODIVERSITY

Wild diploid *Brassica* species still cling to survival in inhospitable habitats and thus are indicative of the natural diversity of this genus. Such species can be seen in Table 1.1.

Such diversity has expanded in domestication and the service of humankind. However, wild species of our current cultivated brassicas are rare. Recent analyses by Mabry *et al.* (2021) suggest that many, previously considered wild, C genome species are feral, containing a proportion of cultivated germplasm within the genome, and therefore have escaped from previous domestication. This suggests cultivated forms may revert to a wild-like state with relative ease (Mabry *et al.*, 2021).

## Wild hybrids

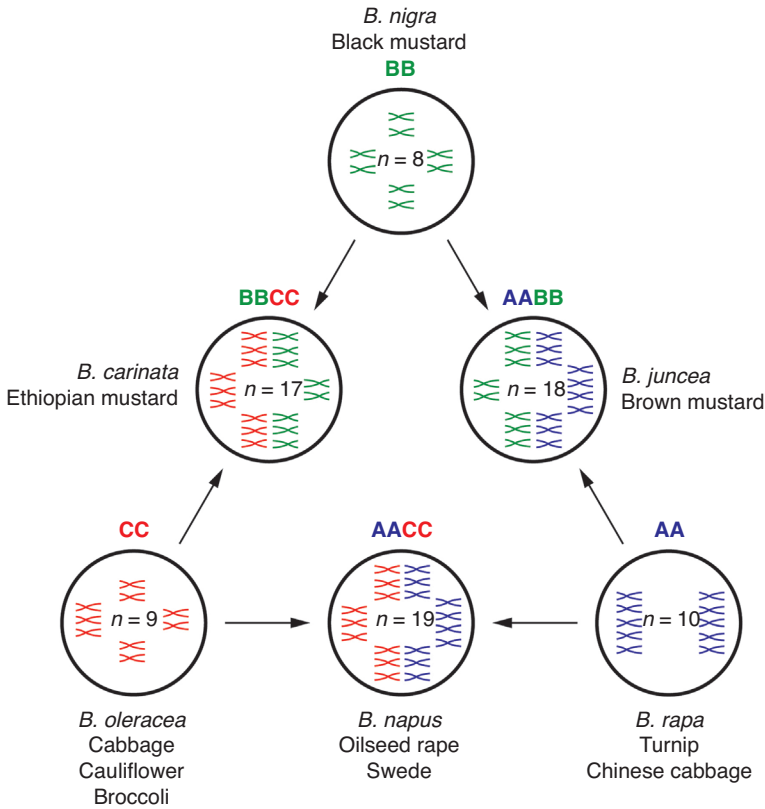
Wild *Brassica* and its close relatives hybridized naturally to form polyploids. These amphidiploids and their parental wild diploids were key building blocks from which our domesticated brassica crops have evolved. Three hybrid species are of especial interest as ancestors of the crop brassicas as described by Nagaharu (1935). The relationships between the hybrid amphidiploids and their parental species are summarized in the gene flow 'Triangle of U' (Nagaharu, 1935) (see Fig. 1.2).

*Brassica carinata* (BBCC,  $n = 17$ , genome size  $\sim 1300$  Mb) is proposed to have evolved through spontaneous hybridization between the wild kale form of *B. oleracea* (CC,  $n = 9$ , genome size  $\sim 490$  Mb) and *B. nigra* (BB,  $n = 8$ , genome size  $\sim 515$  Mb) in the adjoining regions of the highlands of Ethiopia, East Africa and the Mediterranean coast (Seepaul *et al.*, 2021). This hypothesis is supported by evidence of the presence of these progenitor species in the region during the emergence and domestication of *B. carinata* (Alemayehu and Becker, 2002) and that *B. carinata* shares the chloroplast genome with the hybridization donor, *B. nigra* (Li *et al.*, 2017). This species is characterized by the slow, steady growth of *B. oleracea* and the mustard oil content of *B. nigra*. Wild forms of *B. carinata* are not known but primitive domesticated types are cultivated in upland areas of Ethiopia and further south into Kenya. *Brassica carinata* has been traditionally cultivated as both an oilseed and leafy vegetable in the Ethiopian Highlands (Ojiewo *et al.*, 2013). Carinata crops themselves are locally referred to as *gomenzer* in the Amharic language (Hagos *et al.*, 2020), Abyssinian mustard, Ethiopian mustard or Ethiopian cabbage, though this is not necessarily synonymous with the sophisticated heads seen on today's supermarket shelves. It is one of the most drought- and heat-tolerant species within the Brassicaceae. However, both kale and carinata crops thrive in the cool environments that local farmers term 'kale gardens', typical of the Ethiopian Highlands.

*Brassica juncea* (AABB,  $n = 18$ , genome size  $\sim 930$  Mb) is a hybrid between *B. rapa* (AA,  $n = 10$ , genome size  $\sim 350$  Mb)  $\times$  *B. nigra* (BB,  $n = 8$ , genome size  $\sim 515$  Mb) and can be divided into four recognized subspecies. These

**Table 1.1.** Examples of the diversity of some wild *Brassica* species. (After Tsunoda *et al.*, 1984).

Name	Chromosome Count	Geographical Distribution	Habitat
<i>Brassica amplexicaulis</i>	$n = 11$	Intermountain area south-east of Algiers	Small plant, colonizes colluvial slopes, especially medium-sized gravel
<i>Brassica barrelieri</i>	$n = 9$	Iberian Peninsula, extending to Morocco and Algeria	Common on wastelands, especially areas of more dense vegetation
<i>Brassica elongata</i>	$n = 11$	Plateau steppe – lands of south-eastern Europe and western Asia, as far as Iran	Semi-arid areas
<i>Brassica fruticulosa</i> ssp. <i>fruticulose</i>	$n = 8$	Found around the Mediterranean coasts, especially among pine trees;	Biennial or perennial Annual
<i>Brassica fruticulosa</i> ssp. <i>cossoniana</i>	$n = 8$	the ssp. <i>cossoniana</i> extends beyond the coastal zone and is found on the Saharan side of the Middle Atlas mountains in Morocco	Both subspecies require well-drained sites; on inland sites they characteristically colonize stony mountain slopes and alluvial areas
<i>Brassica maurorum</i>	$n = 8$	Endemic to North Africa; inhabits arable land in Morocco and Algeria	Colonizes stony pastures in semi-arid areas from the coast to low mountainous zones; on arable land grows to 2 m high in dense clumps similar to <i>Brassica nigra</i>
<i>Brassica oxyrrhina</i>	$n = 9$	Southern Portugal, Spain and north-western Morocco	Coastal sandy habitats
<i>Brassica repanda</i> and <i>Brassica gravinae</i>	$n = 10$	Inland rocky areas	These species grow together in the lithosol in the crevices of rocky outcrops A polyploid ( $n = 20$ ) form has been found north of Biskra in Algeria
<i>Brassica spinescens</i>	$n = 8$	Endemic to North Africa	Coastal calcareous or siliceous cliffs Diminutive growth habit with small, thick glabrous leaves; <i>B. fruticulosa</i> , <i>B. maurorum</i> and <i>B. spinescens</i> possibly form a single cytodeme
<i>Brassica tournefortii</i>	$n = 10$	Coastal areas of the Mediterranean extending to western Asia as far as India	Capable of colonizing arid alluvial sand where other vegetation is sparse



**Fig. 1.2.** Relationships between diploid and amphidiploid crop-founding *Brassica* species. (The 'Triangle of U': Nagaharu, 1935, courtesy Garry Breeze).

include *juncea* (seed mustard) that is used as oilseed and condiment, *integrifolia* (leaf mustard) with a diverse variation of leaf morphology, *napiformis* (root mustard) with a tuberous root and *tumida* (stem mustard) with an enlarged edible stem (Kang *et al.*, 2022). Yang *et al.* (2016, 2018) demonstrated that *B. juncea* first diversified into root mustard, followed by seed mustard, leaf mustard and stem mustard. They determined a monophyletic origin for *B. juncea* based on phylogenetic analyses of the A subgenome. This was confirmed by analysis of variation within cytoplasmic DNA by Kang *et al.* (2021). *Brassica juncea* is used as a source of vegetable oil in India and throughout Asia, especially in China and Japan, while vegetable forms are of immense dietary importance. Feral forms are classed as weeds in cropping systems throughout China and Japan (Sun *et al.*, 2018). Reputedly, wild forms are still found on the Anatolian Plateau and in southern Iran.

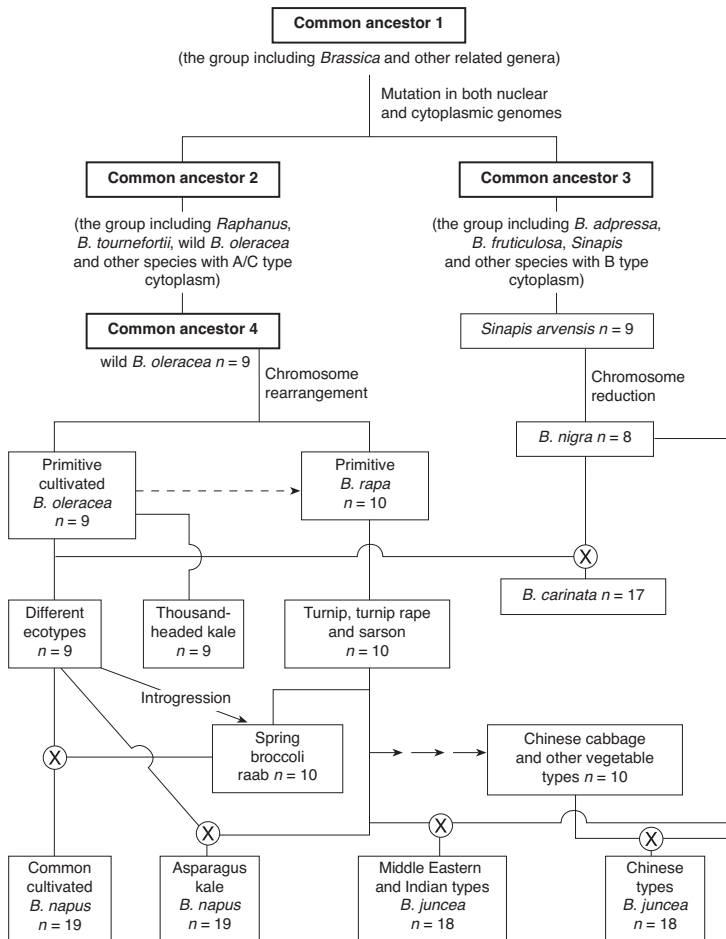
The third hybrid, *Brassica napus* (AACC,  $n = 19$ , genome size  $\sim 1130$  Mb), developed from *B. rapa* (AA,  $n = 10$ , genome size  $\sim 350$  Mb)  $\times$  *B. oleracea* (CC,  $n = 9$ , genome size  $\sim 490$  Mb). There are three recognized subspecies:

rapeseed/oilseed rape (*B. napus* ssp. *oleifera*), swede or rutabaga (*B. napus* ssp. *rapifera*) and Siberian kale or leaf rape (*B. napus* ssp. *pabularia*). Wild populations do not exist, and the true species progenitors are unknown. *Brassica napus* may have Mediterranean origins or this hybrid may have formed as *B. oleracea* types expanded into agricultural regions along the coasts of northern Europe and *B. rapa* extended from the Irano-Turanian regions. Lu *et al.* (2019) determined the *B. napus* A subgenome evolved from the ancestor of the European turnip; and hypothesized the *B. napus* C subgenome evolved from the common ancestor of kohlrabi, cauliflower, broccoli and Chinese kale. However, it is believed that within the last 1000 years, further gene flow has occurred from the two progenitor species. Feral populations of *B. napus* have acquired major scientific significance as a means of determining the potential for gene flow to and from genetically modified cultivars of oilseed rape.

## Diversity within the amphidiploids

Considerable genetic diversity is present within the three amphidiploid species. This is hypothesized to be due to two major factors: multiple hybridizations with different diploid parents and genome modifications following polyploidization. Evidence of multiple hybridizations was reported by Song *et al.* (1996) showing four cytoplasmic types were present within *B. napus* accessions that matched different parental diploid cytoplasm (see Fig. 1.3).

In more recent analysis, Li *et al.* (2017) performed *de novo* assembly of 60 complete chloroplast genomes of *Brassica* genotypes for all six species within U's triangle. Chloroplast genome sequences, which are maternally inherited and therefore only represent the maternal lineage, have been used extensively for inferring plant phylogenies. Phylogenetic analysis separated the *Brassica* species into four clades: Clade I contained *B. juncea*, *B. rapa* and *B. napus*; Clade II *B. oleracea*; Clade III *B. rapa* and *B. napus*; and Clade IV *B. nigra* and *B. carinata*. *Brassica rapa* showed evidence of two types of chloroplast genomes, with the Clade IV type specific to some Italian broccoletto accessions, while *B. oleracea* and *B. nigra* were only represented by a single clade. No amphidiploid hybrids were grouped with *B. oleracea*, suggesting that *B. oleracea* is not the maternal parent to any amphidiploid species. This fits with the observation that in interspecific crosses, *B. oleracea* can only be used as a male parent. *Brassica carinata* and *B. juncea* share their chloroplast genome with one of their hybridization donors, *B. nigra* and *B. rapa*, respectively, fitting with U's model. Chloroplast genomes of all eight *B. juncea* accessions clustered with the chloroplast genomes of *B. rapa* accessions in subclade 'I-a' (Japanese leafy types and turnips, plus one broccoletto), supporting the hypothesis of Palmer *et al.* (1983) that *B. rapa* is the ancestral maternal parent of the amphidiploid. *Brassica napus* clearly had evidence for two independent hybridization events, as accessions were either within Clade I *B. rapa* subclade 'e' (sarson-like morphotype) or *B. rapa* Clade IV (Italian broccoletto morphotype).



**Fig. 1.3.** Hypothetical scheme for genome evolution of *Brassica* species and cultivated forms. (After Song *et al.*, 1988, courtesy Garry Breeze).

Direct evidence for genome changes after polyploidization can be obtained by studying synthetic amphidiploids developed by resynthesis via interspecific hybridization of the diploid progenitor species. The production of synthetics is a recognized methodology used to increase genetic variation and introduce desired phenotypic characters. However, it is also associated with genome instability and rapid genomic change. Analysis for morphological traits, chromosome numbers and restriction fragment length polymorphisms (RFLPs) in chloroplast, mitochondrial and nuclear DNA clones in artificially synthesized analogues of *B. napus*, *B. juncea* and *B. carinata*, in comparison with the natural amphidiploids, showed the synthetic hybrids were closer to their diploid parents when compared with natural polyploids. Genome changes,

mainly involving either loss or gain of parental fragments and novel fragments, were seen in the early generations of synthetic amphidiploids (Song *et al.*, 1993). It has also been shown, that within the first generations after interspecific hybridization, *Brassica* hybrids experience altered gene expression patterns (Lloyd *et al.*, 2018), changes in transposable element activity (Sarilar *et al.*, 2013) and altered gene methylation patterns (Lukens *et al.*, 2005; Gaeta *et al.*, 2007). Samans *et al.* (2017) showed the size and number of rearrangements per generation is much lower in natural populations of *B. napus* than in resynthesized *B. napus*. This indicates that genome stability increases across evolutionary time, as many individuals with detrimental chromosomal rearrangements are lost, and suggests natural *B. napus* must have mechanisms that prevent non-homologous chromosome pairing.

The frequency of genome change, and the direction of its evolution in the synthetic hybrids, were associated with divergence between the parental diploid species. Quantitative analysis of phylogenetic trees based on RFLP data from *Brassica* by Song *et al.* (1988), and more recently by Li *et al.* (2017), suggest that:

1. *Brassica nigra* originated from one evolutionary pathway with *Sinapis arvensis*, or a close relative, as the likely progenitor, whereas *B. rapa* and *B. oleracea* came from another pathway with a possible common ancestor in wild *B. oleracea*, or a closely related species possessing nine chromosomes.
2. The estimated divergence of *B. rapa* and *B. oleracea* from *B. nigra* varies between studies – 7.9 million years ago (Mya) (Lysak *et al.*, 2005), 13.7 Mya (Li *et al.*, 2017), and 20 Mya (Arias *et al.*, 2014).
3. The estimated divergence of the A genome *B. rapa* (*B. juncea* and *B. napus*) from *B. oleracea* is between 0.12 and 1.37 Mya (Cheung *et al.*, 2009), 2.18 Mya (Li *et al.*, 2017) and 3.7 Mya (Inaba and Nishio, 2002).
4. The amphidiploid species *B. napus* and *B. juncea* have evolved through different combinations of the diploid morphotypes and thus polyphyletic origins may be a common mechanism generating the natural occurrence of amphidiploids in *Brassica*.
5. The cytoplasm has played an important role in the nuclear genome evolution of amphidiploid species when the parental diploid species contain highly differentiated cytoplasm.

## Contrasting the physiology and morphology of wild and cultivated brassicas

It will be evident to the reader by now that many of the wild and feral *Brassica* spp., and their close allies, inhabit dry coastal, arid rocky or desert habitats. These wild plants have very thick leaves containing less chlorophyll and many more cell wall components compared with cultivated plants. Typically, they have well-developed xylem vessels and small leaf areas. These characteristics

increase the efficiency of water conservation in plants. The foliage of wild xerophyllous plants has evolved high photosynthetic rates per unit leaf area (or per quantum of light received), even in dry air conditions.

Conversely, cultivated brassicas have broadly expanded, thin leaves that are well supplied with chlorophyll. These characteristics are advantageous for receiving, absorbing and utilizing solar radiation when there are ample supplies of water and nutrients available. Typically, these are mesophyllous environments found in fertile, cultivated fields.

Similar contrasts between the ecology of wild progenitors of crops and cultivated plants are found between the wild allies of wheat and artificial cultivars. Wild forms possess small, thick leaves whereas wheat cultivars have large, thin leaves. Both wild *Brassica* and *Hordeum* spp. evolved strategies for successful growth under arid conditions involving the restriction of transpiration, intensification of water movement to sites of photosynthesis, restriction of light absorption and efficient fixation of the absorbed solar radiation. Such traits became redundant in cultivation and consequently were removed by generations of artificial field selection and more latterly by directed plant breeding.

## **Other brassica relatives illustrating the biodiversity of this family**

Several other members of the Brassicaceae illustrate the diversity of this family and their evolution in cultivation. Examples are summarized in Tables 1.2 and 1.3.

## **CULTIVATED *BRASSICA* SPECIES AND FORMS**

### ***Brassica oleracea* group ( $n = 18$ ) – the European group**

The European brassica vegetables originate from *B. oleracea* and some probably closely related Mediterranean species. They can be divided into subordinate groups often at the variety (var.), subvariety (subvar.) or cultivar (cv.) levels. Much of the basis of current understanding of diversity within this group comes from the detailed studies of American horticultural botanist Bailey (1922, 1930, 1940).

### **Multiple origins and parents**

One school of thought suggests that the constituent crops within the *B. oleracea* group have multiple origins derived from cross-breeding between closely related *Brassica* species living in geographical proximity to each other. In consequence, the taxonomy of parents and progeny is confused and clouded still further by millennia of horticultural domestication. For example, the progenitors of headed cabbages and kales were postulated by Netroufal (1927)

**Table 1.2.** Genera allied to *Brassica* that form crop plants: *Eruca*, *Sinapis* and *Raphanus*. (After Tsunoda *et al.*, 1984).

*Eruca sativa* ( $n = 11$ , syn. *Eruca vesicaria* ssp. *sativa*), commonly known as 'garden or salad rocket', is a salad vegetable in southern Europe. In India it forms an oilseed (taramira) and is used for fodder. *Eruca sativa* has recently become a popular salad vegetable in western Europe. Wide distribution occurs across southern Europe, North Africa, western Asia and India. Variation within the cytodeme *Eruca* is substantial with ecotypes evolved for several habitats in relation to available water.

*Sinapis alba* ( $n = 12$ ) (white mustard) grows wild in Mediterranean areas with abundant moisture and ample soil nutrients, often coexisting with *Sinapis arvensis* ( $n = 9$ ) (charlock or wild mustard) although the latter prefers lower soil moisture levels. In dry areas, *Sinapis turgida* ( $n = 9$ ) is common. In wet habitats, *S. alba* reaches 2 m in height with a high mustard oil content. It is grown in Europe as 'white' or 'yellow' mustard. Cultivation is increasing, particularly in Canada, in combination with 'brown' mustard (*Brassica juncea*).

*Raphanus* (radish) – there are about 18 genera in the subtribe Raphininae including *Rapistrum*, *Cakile* and *Crambe*. Possibly all *Raphanus* spp. with  $n = 9$  form a single cytodeme. The genus is found along Mediterranean coasts forming the dominant plant on coastal areas of the Sea of Marmara and the Bosphorus Strait. Around field margins, *Raphanus raphanistrum* and *Raphanus rapistrum rugosum* tend to coexist. Culinary radishes (*Raphanus sativum*) possibly evolved in southern Asia and provide a wide diversity of root forms and flavours. Fodder radishes (*Raphanus sativus* var. *oleiferus*) are a source of animal fodder obtained from both roots and foliage. *Crambe* is a source of seed oil and is beginning to be used more extensively in North America.

as *Brassica montana* and of kohlrabi as *Brassica rupestris*. Later, Schiemann (1932) realised that several of the Mediterranean wild types had formed the origins for locally cultivated landraces. Schulz (1936) supported this view and identified *Brassica cretica* as a progenitor of cauliflower and broccoli.

Lizgunova (1959) grouped cultivars into five different species and proposed a multiple origin from wild forms. Helm (1963), in devising a triple origin, combined cauliflower, broccoli and sprouting broccoli into one line, thousand-headed kale and Brussels sprouts in another, and all other crop forms in a third. Further analysis was completed by Toxopeus (1974) and Toxopeus *et al.* (1984) suggested that for simplicity a horticulturally based taxonomy was preferable to attempted botanical versions.

### Potential wild species contributing to the *Brassica oleracea* group

Populations of wild relatives, which cross-fertilize with *B. oleracea* and form interbreeding groups, are found on isolated cliffs and rocky islets. They form distinct units that often display phenotypic differentiation leading to several layers of variation superimposed on each other.

**Table 1.3.** Selected examples of wild relatives of *Brassica*. (After Tsunoda *et al.*, 1984).

Name	Chromosome count	Geographical Distribution	Habitat
<i>Diplotaxis acris</i>	$n = 7$	Saharo-Sindian area	Dry, desert regions
<i>Diplotaxis harra</i>	$n = 13$		
<i>Diplotaxis tenuisiliqua</i>	$n = 9$	North Africa	Moist areas, sometimes associated with <i>Sinapis alba</i>
<i>Erucastrum cardaminoides</i>	$n = 9$	Endemic to the Canary Islands	
<i>Erucastrum laevigatum</i>	$n = 28$	Southern Italy, Sicily and North Africa	Probably an autotetraploid of <i>Erucastrum virginatum</i> ( $n = 7$ )
<i>Erucastrum leucanthum</i>	$n = 8$	Endemic to North Africa, particularly the seaward side of the Middle Atlas mountains	Coexists with <i>Hirschfeldia incana</i>
<i>Hirschfeldia incana</i>	$n = 7$	Dominant component of Mediterranean flora	Large roadside colonies especially favoured by fine textured soils
<i>Hutera</i> spp.	$n = 12$	Iberian Peninsula	Rocky outcrops and colluvial sites; <i>Hutera</i> and <i>Rhynchosinapis</i> form a cytodeme complex found in the Spanish Sierra Morena regions
<i>Sinapidendron</i> spp.	$n = 10$	Madeira	Rocky cliffs; perennial habit

Maggioni (2015) detailed the domestication of *B. oleracea*. This identified the 11 accepted wild species of the *B. oleracea* group, including three subspecies of *B. cretica*, from the National Plant Germplasm System (NGPS)/ Germplasm Resources Information Network (GRIN) taxonomy for plants (USDA, Agricultural Research Service, National Plant Germplasm System, 2023). Some separate species detailed by Maggioni (2015) can be grouped into the *Brassica rupestris-incana* complex as they demonstrate distinct regional variation. These potential progenitors of European *B. oleracea* are detailed in Table 1.4.

A detailed study into the evolutionary history of wild, domesticated and feral *B. oleracea* was published by Mabry *et al.* (2021). This provided new genetic evidence combined with knowledge of archaeology, literature and environmental niche modelling to support the hypothesis of a single eastern Mediterranean domestication origin for *B. oleracea*, agreeing with the conclusions of Maggioni *et al.* (2018). Using population structure modelling Mabry *et al.* (2021) identified *B. cretica* and *Brassica hilarionis* as likely progenitor

**Table 1.4.** Examples of potential progenitors of European (*Brassica oleracea*) brassica vegetables. (After Tsunoda *et al.*, 1984).

*Brassica cretica*: Populations occur around the Aegean, including Crete, southern Greece and in south-western Turkey. The plant has a branching, woody habit, carrying glabrous, fleshy leaves and persisting in perennial form for 5–8 years but flowering in the first year under favourable environments. The inflorescence axis elongates between buds prior to opening with light yellow to white flowers. Three subspecies are known: *Brassica cretica* ssp. *cretica*, which grows on the mountainous cliffs and gorges of the Peloponnese and Crete, and central to south Lebanon (probably introduced); *Brassica cretica* ssp. *aegaea* growing in southern Greece, south-west Turkey and Israel (Mount Carmel) (probably introduced); and *Brassica cretica* ssp. *laconica* from south Peloponnese.

The *Brassica rupestris–incana* complex: This group has developed a number of distinct regional variants. The complex is characterized by forming a strong central stem, and a large apical inflorescence succeeded by further branching. The top of each partial inflorescence forms a tight grouping of buds which may open before the axis between them elongates. Foliage consists of large petiolate leaves which are poorly structured since they shrivel when past maturity, in contrast to *B. cretica* which retains mature leaves with a recognizable morphology. Hairs are characteristically found on both seedlings and adults. Distribution includes Sicily, southern and central Italy, and parts of Croatia, Bosnia and Montenegro. Species that have been separated but which are included within the complex include: *Brassica incana* Ten., *Brassica villosa*, *Brassica rupestris* Rafin., *Brassica tinei* Lojac., *Brassica drepanensis* (Car.) Dam., *Brassica botteri* Vis., *Brassica mollis* and *Brassica cazzae* Ginzb. and Teyb.

*Brassica macrocarpa* Guss.: A species restricted to Aegadian Islands to the west of Sicily with a habit similar to *B. rupestris–incana* with which it forms fertile hybrids and characterized by possessing smooth-surfaced, thick fruits containing seeds produced in two rows within the loculus. There are questions as to whether this species should be placed in the genus *Brassica* in view of the seed capsule. Conceivably, this species is a subordinate of the *B. rupestris–incana* complex.

*Brassica insularis* Moris.: Found in Corsica, Sardinia and Tunisia, the plants are similar in low-branching habit to *B. cretica* but the stiff, glabrous leaves, with pointed lobes and large white fragrant flowers and seed glucosinolates, differ from other *Brassica* spp. Species rank has been given to the Tunisian form as *B. atlantica* (Coss.) Schultz, but the morphology and intercrossing indicate clear inclusion in *B. insularis* without subdivision.

*Brassica montana* Pourr. (syn. *B. robertiana* Gay): Found growing in north-eastern coastal areas of Spain, southern France and northern Italy, these plants are shrubby perennials with lobed green, glabrous or possibly hairy leaves. An intermediate status between the *B. rupestris–incana* complex and *B. oleracea* is suggested by biogeographical and morphological evidence.

*Continued*

**Table 1.4.** Continued

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*Brassica oleracea*: Found on coasts of northern Spain, western France and southern and south-western UK; as a stout perennial forming strong vegetative stocks which then flower and branch. The greyish coloration and glabrous nature of the leaf surfaces distinguish *B. oleracea*. Morphological differences between *B. bourgeauii* Kuntz, endemic to the Canary Islands, and *B. oleracea* are limited, therefore its status as a separate species is unclear.

*Brassica hilarionis*: Located solely in the Kyrenia Mountains of Cyprus, *B. hilarionis* has fruit reminiscent of the size and texture of *B. macrocarpa* and vegetatively a habit and leaf morphology close to *B. cretica*.

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species of *B. oleracea* cultivars. This was further refined to support *B. cretica* as the progenitor species.

### Crops developed within *Brassica oleracea* and allies

The vast array of crop types that have developed within *B. oleracea* (and also *B. rapa*) is probably unique within economic botany (Nieuwhof, 1969). This has led to acceptance at the subspecies and variety (cultivar) levels of descriptions based around the specialized morphology of the edible parts and habits of growth within the crop types (Wellington and Quartley, 1972). The nomenclature and common names of cultivated *B. oleracea* are given in Table 1.5.

### *Brassica oleracea* (the cole or cabbage brassicas)

**BRUSSELS SPROUTS: *B. OLERACEA* VAR. *GEMMIFERA*.** Brussels sprouts may have emerged in the Low Countries (coastal Rhine–Meuse–Scheldt delta) in the medieval period and risen to prominence in the 18th century around the city of Brussels. Subsequently, they became established as an important vegetable crop in north-eastern Europe, especially the northern Netherlands and parts of the UK. Local open-pollinated landraces were developed that were suited to specific forms of husbandry but usually subdivided into early, mid-season and late maturity groups. Often, they would be capable of resisting pests and pathogens common within their locality and have morphologies adapted to prevailing climatic conditions. In the 1930s, early maturing types were developed in Japan where many of the original F<sub>1</sub> hybrids were produced. These hybrids, and their derivatives, formed the basis for cultivars ideally suited to the emerging ‘quick-freeze’ vegetable processing industry. The entire worldwide crop of Brussels sprouts is now dominated by an F<sub>1</sub> germplasm derived by American, Dutch and Japanese breeders and originating from the initial crosses.

**Table 1.5.** The nomenclature and common names of cultivated *Brassica oleracea*. (After Wellington and Quartley, 1972).

<i>B. oleracea</i> L.	Common synonym	Common name
var. <i>alboglabra</i> (L.H. Bailey) Musil.	<i>Brassica alboglabra</i> L.H. Bailey	Chinese kale, Kailan
var. <i>botrytis</i> L.		Cauliflower
var. <i>capitata</i> L.		Red/white/Shetland cabbage
var. <i>costata</i>		Portuguese kale/Tronchuda kale
var. <i>gemmifera</i>		Brussels sprouts
var. <i>gongyloides</i> L.	<i>Brassica caulorapa</i> (DC.) Pasq.	Kohlrabi
var. <i>italica</i> Plenck		Broccoli
var. <i>medullulosa</i> Thell.		Marrow-stem kale
var. <i>palmifolia</i>		Palm kale/Jersey kale
var. <i>ramosa</i> CD.	ssp. <i>fruticosa</i> Metzg.	Thousand-headed kale, Branching bush kale
var. <i>sabauda</i> L.		Savoy cabbage
var. <i>sabellica</i> L.		Curly kale
var. <i>viridis</i> L.	var. <i>acephala</i> DC.	Kale, collard

In the 1990s, trials revealed that the content of the glucosinolates, sinigrin and progoitrin, was found to be correlated with bitterness ( $r^2_{\text{multiple}} = 0.67$  and 0.93, respectively) (van Doorn *et al.*, 1998). Later studies showed these traits were under strong genetic control with high heritability (van Doorn *et al.*, 1999). This knowledge was used for the selection of sweeter-tasting lines with low levels of sinigrin and progoitrin from the natural variation in historical varieties. Botanically, the plants are biennial with simple erect stems up to 1 m tall. Axillary buds develop into compact miniature cabbage heads or 'sprouts' that are up to 30 mm in diameter. At the top of the stem is a rosette of leaves; the leaves are generally petiolate and rather small, with a subcircular leaf blade (see Chapter 2 section, Floral Biology as Related to Controlled Pollination).

CAULIFLOWER: *B. OLERACEA* VAR. *BOTRYTIS*; BROCCOLI: *B. OLERACEA* VAR. *ITALICA*. A remarkable diversity of cauliflower- and broccoli-like vegetables developed in Europe, probably emanating from Italy, and possibly evolved from germplasm introduced in Roman times from the eastern Mediterranean. A classification of the colloquial names used to describe these crops was proposed by Gray (1982) and is shown in Table 1.6.

Over the past 400 years, white-headed cauliflowers (derived from the Latin *caulis* (stem) and *floris* (flower)) have spread from Italy to central and northern Europe, which became important secondary centres of diversity for

**Table 1.6.** Classification of *Brassica oleracea* var. *botrytis* and var. *italica* with associated colloquial crop names. (After Gray, 1982).

<i>Brassica oleracea</i> L. var. <i>botrytis</i> DC.	Cauliflower Heading broccoli Perennial broccoli Bouquet broccoli White-sprouting broccoli <sup>a</sup>
<i>Brassica oleracea</i> L. var. <i>italica</i> Plenck	Purple-sprouting broccoli Cape broccoli Purple cauliflower Calabrese and other green-sprouting forms (broccoli in North America) White-sprouting broccoli <sup>a</sup>

<sup>a</sup>White-sprouting broccolis are thought to have evolved independently in northern Europe. Their close affinity to winter-hardy cauliflower suggests that the late form may be more correctly regarded as a form of *B. oleracea* var. *botrytis*.

the annual and biennial cauliflowers now cultivated worldwide in temperate climates. Cauliflowers adapted to hot humid tropical conditions have evolved in India during the past 200 years from biennial cauliflowers, mainly of British origins.

Crisp (1982) proposed a taxonomic basis for grouping the various types of cauliflower found in cultivation. He admits this has limitations but at least it gives order where little previously existed (see Table 1.7).

Cauliflower is a biennial or annual herb, 50–80 cm tall at the mature vegetative stage and 90–150 cm when flowering. The root system is strongly ramified, concentrating in the top 30 cm of soil with thick laterals penetrating to deeper layers. The stem is unbranched, 20–30 cm long and thickened upwards. There is a rosette (frame) of 15–25 large, oblong, erect leaves surrounding the compact terminal flower head (curd). Usually, lateral buds do not develop in the leaf axils. The glabrous leaves are almost sessile and coated with a layer of wax; the leaf blade is grey to blue–green in colour with whitish main and lateral veins. Leaves vary in shape from short and wide (40–50 cm × 30–40 cm) with curly edges to long and narrow (70–80 cm × 20–30 cm) with smooth edges. The curd consists of a dome of proliferated floral meristems that are white to cream or yellow in colour, growing on numerous short and fleshy peduncles. The curd varies from a rather loose to a very solid structure, with a flattened to deeply globular shape from 10 to 40 cm in diameter. Young leaves may envelop the curd until a very advanced stage of development is reached. Bolting cauliflower plants often have several flower stalks (see Chapter 2 section, Floral Biology as Related to Controlled Pollination).

Broccoli is an Italian word from the Latin *brachium*, meaning an arm of a branch. In Italy, the term is used for the edible floral shoots on brassica plants,

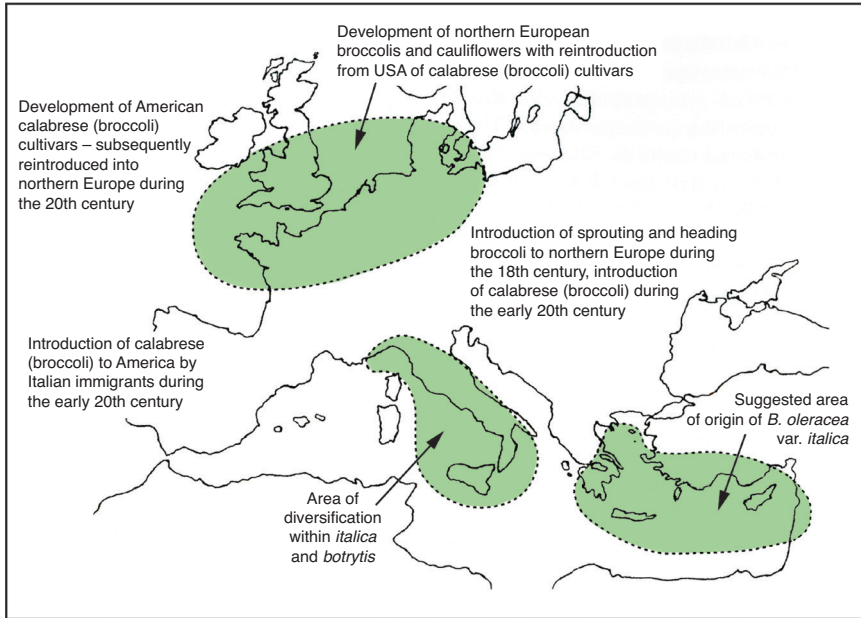
**Table 1.7.** Groups of cauliflower as determined by their phylogeny. (After Crisp, 1982).

Group name	Characteristics	Common types
Italian	Very diverse, includes annuals and biennials and types with peculiar curd conformations and colours.	Jezi Naples (= Autumn Giant) Romanesco Flora Blanca
North-west European biennials	Derived within the last 300 years from Italian material.	Old English Walcheren Roscoff Angers St Malo
Northern European Annuals	Developed in northern Europe for at least 400 years. Origin unknown, perhaps Italian or possibly eastern Mediterranean.	Le Cerf Alpha Mechelse Erfurt Danish
Asian	Recombinants of European annuals and biennials, developed within the last 250 years. Adapted to tropical climates.	Four maturity groups are recognized by Swarup and Chatterjee (1972)
Australian	Recombinants of European annuals and biennials, and perhaps Italian stocks; developed during the last 200 years.	Not yet been categorized

including cabbages and turnips, and was originally applied to sprouting forms, but now includes heading types that develop a large, single, terminal inflorescence. Broccoli with multiple green, purple or white flower heads (sprouting broccoli) became popular in northern Europe in the 18th century. Broccoli with a single, main, green head (calabrese – the name has been taken from the Calabria region of Italy) was introduced into the USA by Italian immigrants during the early 20th century (see Fig. 1.4). It has become a popular ‘convenience’ vegetable, spreading back into Europe from the USA and into Japan and other parts of the Pacific Rim over the past 50 years.

The white-heading forms are also colloquially referred to as cauliflower. Broccoli is often used to describe certain forms of cauliflower, notably in the UK where the term heading or winter broccoli is traditionally reserved for biennial types. The term broccoli, without qualification, is also generally applied in North America to the annual green-sprouting form known in the UK and Italy as calabrese. The term ‘sprouting’ as used in sprouting broccoli refers to the branching habit of this type, the young edible inflorescences often being referred to as sprouts. The term ‘Cape’ used in conjunction with broccoli, or as a noun, is traditionally reserved for certain colour-heading forms of *B. oleracea* var. *italica*. A classification of broccoli is given in Tables 1.8 and 1.9.

Green broccoli (the single-headed or calabrese type) differs from cauliflower in the following respects: the leaves are more divided and petiolate,



**Fig. 1.4.** The evolution of broccoli and cauliflower in Europe and North America. (After Gray, 1982, courtesy Garry Breeze).

**Table 1.8.** Classification of colour-heading and sprouting broccoli. (After Giles, 1941).

Coloured-heading types	
Dark purple heading	} Early, intermediate and late maturing cultivars
Copper-coloured or purplish-brown heading	
Green heading	
Sulfur-coloured or yellowish-green heading	
Sprouting types	
Green sprouting	
Purple sprouting	

and the main head consists of clusters of fully differentiated green or purple flower buds, which are less densely arranged with longer peduncles. Axillary shoots with smaller flower heads usually develop after removal of the dormant terminal shoot. The flower head is fully exposed from an early stage of development. Green broccoli plants carry inflorescences from the lateral branches as well. Sprouting forms of broccoli bear many, more-or-less uniform and relatively small flower heads instead of the single large head of the calabrese type.

**Table 1.9.** Classification of Italian sprouting broccoli by morphological types. (After Giles, 1944).

Type	Description
Green-sprouting of Naples	Small shoots produced on long stems, considered to be a counterpart to white-sprouting broccoli.
Early summer broccoli of Naples	Shows aggregation of smaller shoots with fewer larger shoots. Stems shorter than the Naples green-sprouting type.
Calabrese	Further reduction in stem length, which gives the plant a heading appearance.

CHINESE KALE: *B. OLERACEA* SSP. *ALBOGLABRA*. Chinese kale (*B. oleracea* ssp. *alboglabra*) has formed a cultivated stock since ancient times without apparent wild progenitors, but there are possible similarities to *Brassica cretica* ssp. *nivea*. Following early cultivation in the eastern Mediterranean trade centres, it could have been taken to China. The lines cultivated in Europe may have lost their identity through uncontrolled hybridization. Recently, much horticultural attention has focused on Chinese kale. Chinese kale is now a cultigen native to southern and central China. It is popular and widely cultivated throughout China and South-east Asia and is used as leaves in salads and other dishes. The flower bud, flower stalk and young leaves are consumed. A classification into five groups, which vary in flower colour from white to yellow and in depth of green coloration in the leaves and their shape, was produced by Okuda and Fujime (1996) using cultivars from Japan, Taiwan, China and Thailand as examples.

It is an annual herb, up to 0.4 m tall during the vegetative stage and reaching up to 1–2 m at the end of flowering. All the vegetative organs are glabrous and glaucous. The narrow single stem forks at the top. Leaves are alternate, thick, firm and petiolate and leaf blades ovate to orbicular–ovate in shape. The margins are irregularly dentate and often undulate and characteristically auriculate at the base or on the petiole. The basal leaves are smaller and sessile without auricles. The inflorescence is a terminal or axillary raceme 30–40 cm long, with pedicels 1–2 cm long (see Chapter 2 section, Floral Biology as Related to Controlled Pollination). The taproot is strongly branched.

OTHER KALES: *B. OLERACEA* SSP. *ACEPHALA*. Many groups are distinguished: borecole or curly kale, collard, marrow-stem kale, palm tree kale, Portuguese kale and thousand-headed kale. Kales are ancient cole crops, closely related to the wild forms of *B. oleracea*, and many distinctive types were developed in Europe. There are residual populations of the original progenitors, such as the wild kale of Crimea, variously ascribed to *B. cretica* and *B. sylvestris* but now identified as a hairy form of *B. rupestris-incana*. It is suggested that, as a consequence of trade around the Mediterranean, this form was transferred to the

Crimea and is evidence of early widespread cultivation of *B. rupestris-incana* types. A similar relic population exists in the wild kale of Lebanon, inhabiting the cliffs near Beirut, which is morphologically similar to *B. cretica* ssp. *nivea*. Both are possible evidence for widespread trade by the earliest Mediterranean civilizations that moved the botanical types around. This allowed interbreeding resulting in the widening diversity of horticultural crops that were artificially segregated from the botanical populations.

Brussels sprouts, the kales and kohlrabi are part of a similar group of polymorphous, annual or biennial erect herbs growing up to 1.5 m tall, glabrous and often much branched in the upper parts. In particular, kales are extremely variable morphologically, most closely resembling their wild cabbage progenitors. The stem is coarse, neither branched nor markedly thickened and 0.3–1 m tall. At the apex is a rosette of generally oblong, sometimes red-coloured leaves. Sometimes, the leaves are curled. This is caused by disproportionately rapid growth of leaf tissues along the margins. In borecole or curly kale, the leaves are crinkled and more-or-less finely divided. Often green or brownish-purple and they are used as vegetables. Collards have smooth leaves, usually green, and they are most important as forage in western Europe. Marrow-stem kale has a succulent stem up to 2 m tall and is used as animal forage. Palm tree kale is up to 2 m tall with a rosette of leaves at the apex – it is mainly used as an ornamental. Portuguese kale has leaves with succulent midribs that are used widely as a vegetable. Thousand-headed kale carries a whorl of young shoots at some distance above the soil. Together they are more-or-less globular in outline, and this type of kale is mainly used as forage.

KOHLRABI: *B. OLERACEA* VAR. *GONGYLODES*. Kohlrabi first appeared in the Middle Ages in central and southern Europe. The crop has become well-established in parts of Asia over the last two centuries and is economically important in China and Vietnam. Kohlrabi are biennials in which secondary thickening of the short stem produces the spherical edible portion, 5–10 cm in diameter and coloured green or purple. The leaves are glaucous with slender petioles arranged in compressed spirals on a swollen stem.

WHITE-HEADED CABBAGE: *B. OLERACEA* VAR. *CAPITATA* F. *ALBA*; RED-HEADED CABBAGE: *B. OLERACEA* VAR. *CAPITATA* F. *RUBRA*; SAVOY-HEADED CABBAGE: *B. OLERACEA* VAR. *SABAUDA*. These varieties were defined by Nieuwhof (1969). Heading cabbage are the popular definitive image of vegetable brassicas in Europe, indeed the terms 'cabbage garden' and 'vegetable garden' were synonymous in some literature.

Early civilizations used several forms of 'cabbage' and these were probably refined in domestication in the early Middle Ages in north-western Europe as important parts of the human diet and medicine and as animal fodder. It is suggested that their progenitors were the wild cabbage (*B. oleracea*)

feral forms, which are now found on the coastal margins of western Europe, especially England and France, and leafy, unbranched and thick-stemmed kales that had been disseminated by the Romans. Pliny described methods for the preservation of cabbage and sauerkraut was of major importance as a source of vitamins in winter and on long sea journeys. In most cabbages it is chiefly the leaves that are used. Selection pressure in cultivation has encouraged the development of closely overlapping leaves forming tight compact heads, the heart or centre of which is a central undeveloped shoot surrounded by young leaves. Head shape varies from spherical to flattened to conical. The leaves are either smooth, curled or savoyed (Milan type). Seed propagation of cabbage is relatively straightforward and in consequence large numbers of localized regional varieties, or landraces, were selected with traits that suited them to particular climatic and husbandry niches such as: Aubervilliers, Brunswick, de Bonneuil, Saint Denis, Strasbourg, Ulm and York. From the 16th century onwards, European colonists spread cabbages worldwide. Scandinavian and German migrants introduced cabbages to North America, especially the mid-western states such as Wisconsin. In the tropics, cultivation is usually restricted to highland areas and to cooler seasons. White-heading cabbage is especially important in Asia and India. The majority of cultivars are now  $F_1$  hybrids coming from a circumscribed group of breeders using similar parental genotypes. Forms derived originally from the Dutch White Langedijk dominated the market for storage cabbage and more recently fresh white cabbage in supermarkets. Refinement of Savoy types through breeding of  $F_1$  hybrids has expanded the range now on offer. Large-headed cabbages with ample anthocyanin pigmentation are found in Shetland, used as winter sheep fodder or part of the human diet in harsh conditions.

Cabbages are biennial herbs that are 0.4–0.6 m tall at the mature vegetative stage and 1.5–2.0 m tall when flowering in the second year. Mature plants have a ramified system of thin roots, 90% in the upper 0.2–0.3 m of the soil, but some laterals penetrate down to 1.5–2 m deep. Stems are unbranched, 20–30 cm long, gradually thickening upward. The basal leaves form in a rosette of 7–15 sessile outer leaves each 25–35 cm × 20–30 cm in size. The upper leaves form in a compact, flattened, globose to ellipsoidal head, 10–30 cm in diameter, composed of a large number of overlapping fleshy leaves around the single growing point. These leaves are grey to blue–green, glabrous and coated with a layer of wax, on the outside of the rosette, and light green to creamy white inside the head, especially with white-headed cabbage. The leaves are red–purple in red-headed cabbage and green to yellow–green and puckered in Savoy-headed cabbage. The inflorescence is a 50–100 cm bractless long raceme on the main stem and on axillary branches of bolted plants. Germination is epigeal and the seedlings have a thin taproot and cordate cotyledons; the first true leaves are ovate with a lobed petiole (see Chapter 2 section, Floral Biology as Related to Controlled Pollination).

## Novel crop types

Breeders continuously select for novel characteristics desired by consumers. These include miniature cauliflower, sprouting broccoli and cauliflower and exploit the vast variation in colour available within brassicas (Dixon, 2017). Crossing between different morphological types also offers the development of novel forms. Crosses between stable and uniform kale and Brussels sprout parent lines, resulted in the development of the kalette (also known as kale sprout or flower sprout). Varieties were selected that combine the best characters of both crop types while eliminating undesirable characters. The kalette is a tender Asian-type vegetable without the tough stalk of kale, but with improved flavour due to removing the bitterness sometimes found in both kale and Brussels sprouts. The open rosette of the kalette allows for quick cooking. Kalettes grow very much like Brussels sprouts and are particularly winter hardy without many cultivation issues.

## Hybridization between taxa

Crossings occur even between distant taxa of the Brassicaceae, giving at least semi-fertile hybrids, and this may be analogous to the means by which genetic mixing between wild forms led to the horticultural types grown commercially today. Meiotic pairing is normal and indicates close identity particularly throughout the  $2n = 18$  forms. Although pollen fertility and seed set are variable there is usually enough to provide for the survival of further generations.

These characteristics indicate that where races, varieties or species are cultivated in close proximity, crossings will occur. Self-sterility is found in many of the taxa. It is far from absolute but sufficiently robust to ensure high proportions of outbreeding. Outbreeding normally results from a high frequency of similar S genes between individuals belonging to the same population (see Chapter 2 section, Hybrid Production: Self-incompatibility). It is concluded that present day cultivars include much introgressed genetic material derived from other cultivated or wild forms. Consequently, it is important to understand and use the historical literature that describes crops derived from *B. oleracea* alongside that derived from genetical and taxonomic sources in order to interpret the status of modern forms and hybrids.

## Comparative taxonomy using ancient and medieval literature and science

Some syntheses of the literature have been attempted specifically for the Brassicaceae, notably that of Toxopeus (1974). Greek writers, especially Theophrastos (370–285 BCE), discussed cole crops. It is evident that 'branching' types were known at that date, and these may have resembled bushy kales that were also found in uncultivated ground. Possibly, this indicates the domestication of *B. cretica*. Comments are found describing bushy kales with curled

leaves, thus both forms may have been present and undergoing hybridization before spreading to other parts of Europe. The Romans (Cato, 234–149 BCE; Pliny the Elder, 23–79 CE) knew of both stem kales and heading cabbage which were cultivated together. Since seed would be produced locally, hybrids could form and the best selected for further improvement thereby developing local cultivars. Highly prized types might then have spread further as items of trade. Zeven (1996) suggested that the ‘perpetual kale’ (*B. oleracea* var. *ramosa*) was the Tritian kale of the Romans (referred to by Pliny in 70 CE), which they took throughout their empire. Some relic populations are still grown in various parts of Europe (Belgium, England, France, Ireland, Netherlands, Portugal, Scotland) and in Brazil, Ethiopia and Haiti. The crop is known as ‘Hungary Gap’ in England and ‘Cut and Come Again’ in Scotland. Plants reach up to 3 m in height, some forms appearing to have lost the capacity to flower, as in those found in the Dutch province of Limburg, resulting from long selection pressure for leafiness and multiple branching habit. The patchwork of dissemination in Europe suggests previously widespread distribution by traders. A picture of a ‘kail stock’ (cabbage stalk) by Richard Waite painted in 1732 and entitled ‘The Cromartie Fool’ (the Earl of Cromartie’s Jester) is owned by the Scottish National Portrait Gallery.

Cole and neep crops were grown throughout Europe (Sangers, 1952, 1953). Analysis of archives indicates that cole crops were well recognized in the early 14th century to the extent that the name *Coolman* or *Coelman* (cabbage-man) were common surnames while the term *coeltwn* (modern Dutch = *kooltuin*) indicated a cabbage garden. Trade was established between the Low Countries and England for the export of cabbages by the 1390s. Dodenaeus had, by 1554 (Zeven and Brandenburg, 1986), classified cole crops as white cabbage, Savoy cabbage, red cabbage and curly kale and had recognized the turnip which, in 1608, he had differentiated into flat-rooted and long-rooted forms.

Useful evidence of the forms of brassicas in cultivation comes from studies of the Dutch and Flemish painters of the 15th and 16th centuries where red and white cabbages and cauliflowers figure prominently. Only turnips (*B. rapa*) are seen in these paintings with an apparent absence of swede (*B. napus*) at this time (Toxopeus, 1974, 1979, 1993). Some evidence is available for the presence of radishes in these paintings, but unfortunately there is also conflict with similarities to turnips. However, it is probable that the French ‘icicle’ radish can be distinguished. It is likely that all subgroups of *Brassica*: kohlrabi, cauliflower and sprouting broccoli were developed by medieval times and spread westwards and northwards. While further south and south-east other *Brassica* groups were developed for cultivation but generally with the exception of *B. oleracea* ssp. *alboglabra*.

Diversification of *Brassica* crops is well demonstrated in Portugal where original cole crops were introduced by Celtic tribes over several centuries before the Common Era (CE) began and in advance of the Roman conquests. These developed into the Galega kale (*B. oleracea* ssp. *acephala*), Tronchuda cabbage

(*B. oleracea* var. *trunchuda*) and Algarve cabbage (*B. oleracea* var. *capitata*). The Trunchuda types are vigorous growing collard-type plants with a small, loose head and large, thick leaves; while the Galega types are leafy and headless plants, with large leaves having long petioles and a single indeterminate stem which can attain 2–3 m before bolting (Monteiro and Williams, 1989). These crops, together with vegetable rape (*B. napus* var. *napus*), Nabo (turnip) (*B. rapa* var. *rapa*), Nabica (turnip greens) (*B. rapa* var. *rapa*) and Grelos (turnip tops) (*B. rapa* var. *rapa*), form an essential part of the rural diet in Portugal. There are numerous landraces of these crops distributed throughout Portugal which have very low within-population uniformity due to the allogamic pollination mechanism, associated with the poor isolation used by farmers for seed production. The high levels of variability in shape, size, colour, taste, earliness and pest and pathogen resistance in these populations constitutes an immense reservoir of diversity for breeding purposes.

Comparative morphology gives further information on the origins of brassicas, an important character is the greyish surface texture of the west European *B. oleracea* found principally in headed cabbage and Brussels sprouts. The strong, dominating, central structure of stem kales is found in the *B. rupestris-incana* from which primary origin could be inferred. *Brassica cretica* is probably the origin of the bushy kales since they share common branching, shrubby habit and fleshy leaves. The presence of white flowers may have been derived from *B. oleracea* ssp. *alboglabra* and *B. cretica* or combinations between them.

### Local stocks (landraces)

Various localities still utilize old cultivars and landraces although there is great economic pressure for these to be supplanted by high-yielding, standardized and often hybrid cultivars. Information concerning the older open-pollinated types is fragmentary but of great value in understanding the history of *Brassica* in cultivation. Around the Aegean, primitive kales, similar to *B. cretica*, are still cultivated, some with branching inflorescences similar to sprouting broccoli. Even wild types may be utilized in some island villages as salad vegetables.

In Bosnia, Croatia, Montenegro and Serbia, wild type kales grow on field margins, waste areas and building sites and are still used as animal fodder. Two forms are apparent: a tall single-stem type, similar to marrow-stem kale, and a more branching type with high anthocyanin content, often with a habit similar to cabbage. Neither of these produce heads but are possibly early kale types similar to the wild progenitors.

In general, it is inferred that the west European headed-cabbage types derived from *B. oleracea* on the grounds of morphology with cross-fertilization with Roman kales. The Savoy type is possibly a result of further introgression between other coles. The branching bushy kales possibly originate from *B. cretica* with perhaps 2000 years of hybridization with other forms. Stem kales

may well originate from the *B. rupestris-incana* complex in the Adriatic or more southerly parts of Italy. Hybridization to cabbages and perhaps *B. cretica* will have added to variation and type differentiation. Origins for the inflorescence kales, cauliflower and broccoli are still unresolved. Their rapid growth and morphology may have suggested that *B. cretica* is involved but the leaf characteristics would also indicate that *B. oleracea* is a progenitor. The rapid flowering *B. oleracea* ssp. *alboglabra* possibly segregated from *B. cretica* ssp. *nivea*. Then, via cultivation and trade, it spread from ancient Greece into the eastern Mediterranean and then further eastwards.

The relationships between regional groups of Italian landrace cauliflower (*B. oleracea* var. *botrytis*) and broccoli (*B. oleracea* var. *italica*) have recently been unravelled (Massie *et al.*, 1996). A large pool of genetic diversity exists within cauliflower and broccoli grown throughout Italy following centuries of selection for local conditions and preferences. Different provinces of Italy have been associated with specific variant types, for example: Romanesco cauliflower in the Lazio region; Di Jesi, Macerata and Tardivo di Fano varieties in the Marche region; Cavolfiore Violetto di Sicilia (Sicilian purple cauliflower) in Sicily, except for the Palermo province where a green cauliflower is typical. Intermediate forms are also reported, such as between the Macerata and Sicilian purples (Gray and Crisp, 1985).

### ***Brassica rapa* group ( $n = 18$ ) – the Asian group**

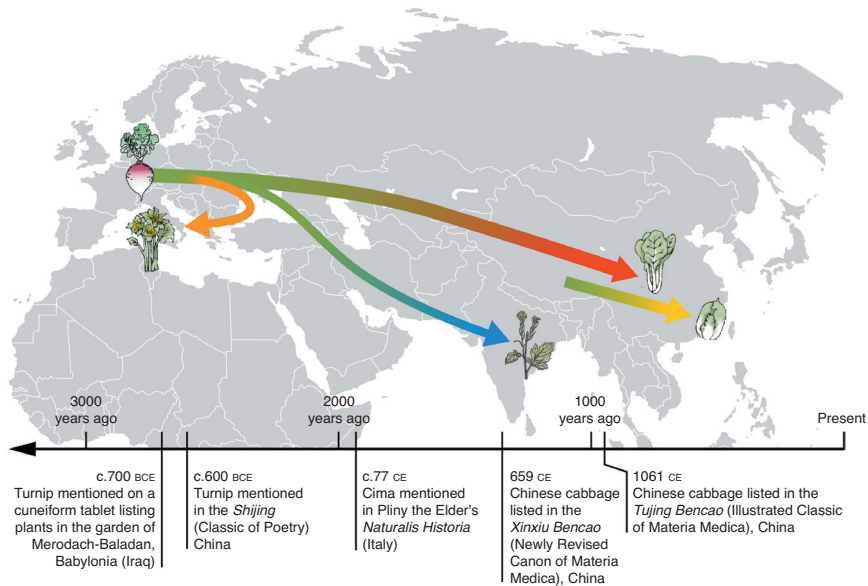
The International Code of Nomenclature for Algae, Fungi, and Plants (previously known as the International Code of Botanical Nomenclature: Gilmour *et al.*, 1969; Stafleu *et al.*, 1972) rules that the author who first combines taxa of similar rank bearing epithets of the same date chooses one of them for the combined taxon. Metzger (1833) first united *B. rapa* and *Brassica campestris* of 1753 under *B. rapa* as used in this text.

*Brassica rapa* (AA,  $n = 10$ , genome size ~350 Mb) and the amphidiploids *B. carinata* (BBCC,  $n = 17$ , genome size ~1300 Mb), *B. juncea* (AABB,  $n = 18$ , genome size ~930 Mb) and *B. napus* (AACC,  $n = 19$ , genome size ~1130 Mb), and *R. sativus* (RR,  $n = 9$ ) are grown extensively throughout Asia with a huge number of distinct varieties. Differentiation results from selection both in nature and by the forces of cultivation; this is a two-way process with great intermingling and recombination. Several distinct groupings are distinguished, especially in the headed Chinese cabbages and Japanese radishes.

Initially, the centre of origin of *B. rapa* is postulated as the Mediterranean from where it spread northwards and eastwards to Germany and into central Europe, and eventually towards Asia (Mizushima and Tsunoda, 1967). Along the way, great local variation in cultivation developed. The plant reached China via Mongolia as an agricultural crop and was introduced to Japan either via China to the western part of the country or via Siberia and into the eastern part of the country. In India, *B. rapa* and *B. rapa* var. *sarson* (derived from the

former species) are used as oil plants, with no records of wild progenitors having been found. Phylogenetic analysis by Qi *et al.* (2017), using 126 global accessions with more than 31,000 genome-wide single nucleotide polymorphism (SNP) markers, suggested five distinct genetic groups, while also supporting a European–Central Asian origin followed by an eastward expansion. Evidence suggested that pak choi, Chinese cabbage and yellow sarson are monophyletic groups while the oil-type *B. rapa* ssp. *oleifera* and brown sarson were polyphyletic (see Fig. 1.5).

Based on morphology, seven vegetable groups can be differentiated: var. *campestris*, var. *pekinensis*, var. *chinensis*, var. *parachinensis*, var. *narinosa*, var. *japonica* and var. *rapa*. The leaf vegetables are thought to have developed after they entered China, with the exception of the var. *japonica* group which has a common ancestor in the oil rapes. Parallels are frequently drawn by the development of *B. oleracea* vegetables in Europe and *B. rapa* vegetables in Asia. The headed Chinese cabbages tend to dominate the use for cultivation, but there are parts of China itself where *B. juncea* is prominent and in central China the forms var. *chinensis* and var. *narinosa* are of importance largely for climatic reasons.



**Fig. 1.5.** The eastward introduction and diversification of *Brassica rapa* as shown by the coloured arrows. The *Brassica rapa* genetic groups are represented by: European *Brassica rapa* – green (on the left side of the map); rapini (ssp. *sylvestris*) – orange; yellow sarson (ssp. *trilocularis*) – blue; pak choi (ssp. *chinensis*) – red; and Chinese cabbage (ssp. *pekinensis*) – yellow. A timescale of occurrence recorded within historical written records is shown on the arrow below. (After Qi *et al.*, 2017, courtesy Garry Breeze).

There are close parallels between the manner of differentiation and selection in cultivation of *B. oleracea* in Europe and of *B. rapa* and *B. juncea* in Asia. Species may have developed along similar lines in a single region as, for example, the trend towards entire glabrous leaves in *B. rapa*, *B. juncea* and *R. sativus*. It is possible to find atypical characters, such as thick stems, which are poorly represented in the putative parents but which have formed extensively in the progeny. Thus neither *B. rapa* (A genome) nor *B. nigra* (B genome) possess thick stems but there are forms of *B. juncea* (AB genome) which are far more developed than the parents and are similar to *B. oleracea* (C genome) (see Table 1.2).

Crop plants of *B. rapa*, *B. juncea* and *R. sativus* are used as leaf or root vegetables in Japan and China, whereas in India they are developed as oil plants and *R. sativus*, in particular, has produced very impressive siliquae. Thus, differentiation has arisen over time in the respective directions of cultivation for either vegetative or reproductive organs. In China, differentiation of headed Chinese cabbages has produced types adapted to several climatic zones. In the north, cold-tolerant forms are used in the summer with a similar but separate segregation in the south for types suited to winter culture. Distinct types have been developed separately in the two areas capable of accomplishing similar tasks.

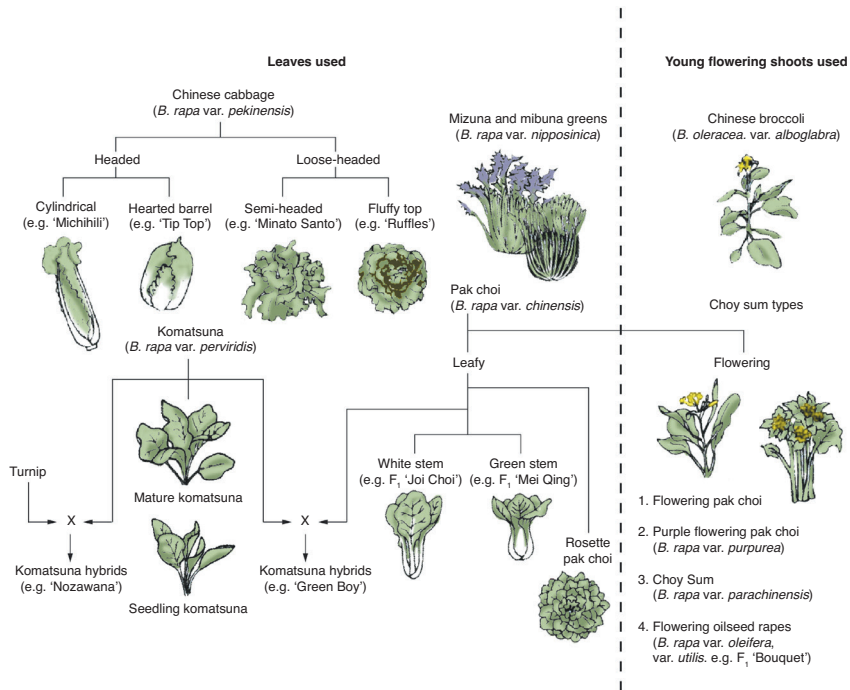
Leaf greens types for crops have been developed in the main from *B. rapa* and *B. juncea* to the exclusion of radishes and turnips, which could form the same product but with a lower level of efficacy. Vegetables which are eaten in high volume as fresh forms tend to have been differentiated into the greatest numbers of improved types, whereas those used for preserves and processing have less variation produced by segregation in cultivation. Fig. 1.6 summarizes leaf greens developed from both *B. oleracea* ssp. *alboglabra* and *B. rapa*.

### Crops developed within *Brassica rapa* and allies

CAISIN: SYN. VAR. *B. PARACHINENSIS*; *B. CHINENSIS* VAR. *PARACHINENSIS*. Caisin (also known as choy sum) is generally thought to have differentiated along with the leaf neeps (Chinese cabbage, pak choi) from oil-yielding turnip rapes, which were introduced into China from the Mediterranean area through western Asia or Mongolia. Caisin originated in middle China where it was selected and popularized for its inflorescences. It may be seen as a parallel variation in *B. rapa* comparable with Chinese kale (*B. oleracea* cv. group Chinese kale) in *B. oleracea*.

Where headed Chinese cabbage is grown, caisin and the non-heading leaf neeps (e.g. pak choi) are also indispensable vegetables. Caisin is cultivated in southern and central China, in South-east Asian countries, such as Indonesia, Malaysia, Thailand, Vietnam and in other parts of the region, and in areas of western India.

The var. *parachinensis* is probably a derivative of var. *chinensis*. Used for the flower stalk and very popular in central China, the plants will bolt readily and the time from seeding to harvest can be 40–80 days depending on the cultivar



**Fig. 1.6.** Asian leafy and flowering forms developed from *Brassica oleracea* and *Brassica rapa*. (After Larkcom, 1991, courtesy Garry Breeze).

used (Herklots, 1972). The var. *campestris* is the most primitive of vegetables, closely resembling oil rape and used for flower stalks and rosette leaves.

Caisin is an annual, taprooted herb, 0.2–0.6 m tall with a usually open, erect or sometimes prostrate growth habit. The stems are normally less than 1 cm diameter, small in comparison with other leafy cabbages, and usually profusely branched. There are few leaves in the rosette, with only one or two leaf layers. There are long petiolate, spatulate or oblong, bright green stem leaves. These may be glabrescent to glabrous, green to purple–red and finely toothed when young. Lower stem leaves are ovate to nearly orbicular and central stem leaves ovate to lanceolate to oblong, with long and narrow-grooved petioles that are sometimes obscurely winged. Upper stem leaves gradually pass into narrow bracts. Inflorescences form as a terminal raceme, elongating when in fruit.

CHINESE CABBAGE: SYN. *B. PEKINENSIS*; *B. CAMPESTRIS* SSP. *PEKINENSIS*; *B. RAPA* SSP. *PEKINENSIS*.

Chinese cabbage is a native of China. It probably evolved from the natural crossing of pak choi (non-headed Chinese cabbage), which was cultivated in southern China for more than 1600 years, and turnip, which

was grown in northern China. Much of its variety differentiation took place in China during the past 600 years. Its derivatives were introduced into Korea in the 13th century, the countries of South-east Asia in the 15th century and Japan in the 19th century. An illustration of the headed shape of Chinese cabbage with wrapping leaves was first recorded in China in 1753. Chinese cabbage is now grown worldwide.

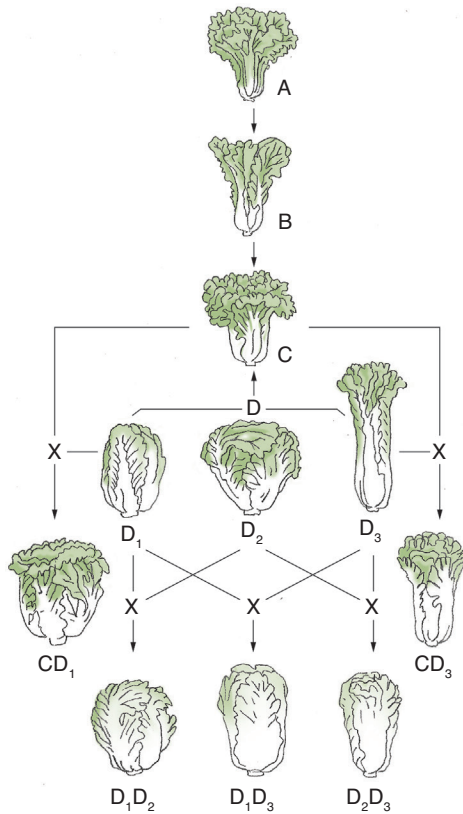
The origins of var. *pekinensis* may correlate with the oil rapes of northern China, developing first as a headed type where the lower parts of the plant were swollen and latterly where the entire plant developed a headed form. Several variants exist with head forms distinguished as either 'wrapped-over' or 'joined-up'. In the former, the leaves overlap at the top of the conical head which does not happen in the 'joined-up' or multi-leaved types. The 'wrapped-over' forms are heavy-leaved, early maturing and round-headed with an adaptation to warmer climates.

The 'joined-up' types are late maturing with firm texture and adaptation to cooler climates. It is possible that both forms originated first in the Shandong Peninsula and the 'joined-up' types spread northwards from there, while the 'wrapped-over' forms developed in a southerly direction. The latter eventually differentiated into a more 'southerly' type which has very early maturity, a small head and heat tolerance (see Fig. 1.7).

Shapes of Chinese cabbage are classified on the degree of heading, as non-, half- and completely headed types with further refinements to give long, short, tapered, round-topped, wrapped-over and joined-up forms. The Chinese largely use these cabbages in the autumn for preserving and processing. In Japan, they are freshly boiled or salt-pickled with early and late types but there is insufficient production to meet consumer demands. Consequently, crops are distributed between regions in Japan according to seasonal availability. The crop probably entered Japan from Shandong in the Meiji era (1868–1912), being well adapted to the Japanese climate.

Chinese cabbage is a biennial herb, cultivated as an annual, 0.2–0.5 m tall during the vegetative stage and reaching up to 1.5 m in the reproductive state. The taproot and lateral roots are prominent in older plants forming an extensive, fibrous, finely branched system. During vegetative stages the leaves are arranged in an enlarged rosette. This forms a short, conical, more-or-less compact head, with ill-defined nodes and internodes and alternate heading and non-heading leaves; leaves are 20–90 cm × 15–35 cm in size. Leaves vary in shape with different growth stages, the dark-green outer leaves are narrowly ovate with long with winged petioles. Inner heading leaves are broad, subcircular and whitish-green. The flowering stem carries lanceolate leaves, much smaller than heading leaves, with broad, compressed petioles and blades clasping the stem.

The origin of *B. rapa* is not known. The wide variation of neep crops evolved in different parts of the Eurasian continent. Besides Chinese cabbage, pak choi and caisin, the leafy vegetable types or leaf neeps comprise cultivar



**Fig. 1.7.** The evolution of Chinese cabbage (*Brassica rapa* ssp. *pekinensis*), where: A=var. *dissoluta*, B=var. *infarcta*, C=var. *laxa*, D=var. *cephalata*, D<sub>1</sub>=f. *ovata*, D<sub>2</sub>=f. *depressa*, D<sub>3</sub>=f. *cylindrica*, CD<sub>1</sub>=var. *laxa* x f. *ovata*, CD<sub>3</sub>=var. *laxa* x f. *cylindrica*, D<sub>1</sub>D<sub>2</sub>=f. *ovata* x f. *depressa*, D<sub>1</sub>D<sub>3</sub>=f. *ovata* x f. *cylindrica*, D<sub>2</sub>D<sub>3</sub>=f. *depressa* x f. *cylindrica*. (After Dickson, courtesy Garry Breeze).

groups Mizuna, Neep Greens and Tatsoi, developed in temperate regions of Asia.

MIZUNA: SYN. *B. JAPONICA*; *B. CAMPESTRIS* SSP. *NIPPOSINICA*; *B. RAPA* SSP. *NIPPOSINICA*. The var. *japonica* is a vegetable unique to Japan, carrying many basal branches and leaves. This plant resembles *B. juncea* since the inflorescence stalk has no leaves, the petioles and siliquae are slender, and the seeds are small (Matsumura, 1954). Possibly, this variety is derived from hybridization between *B. rapa* and *B. juncea*. Grouping of cultivars rests on the level of dissection of the leaves.

NEEP GREENS: SYN. *B. PERVIRIDIS*. See Bailey (1940) for certain forms (komatsuna).

TATSOI: SYN. *B. NARINOSA*: *B. CAMPESTRIS* SSP. *NARINOSA*; *B. RAPA* SSP. *NARINOSA*. The var. *narinosa* developed in middle China. It is very cold-tolerant with thick leaves and crisp petioles that are used as boiled vegetables.

VEGETABLE TURNIP: SYN. *B. CAMPESTRIS* SSP. *RAPA*; *B. CAMPESTRIS* SSP. *RAPIFERA*; *B. RAPA* SSP. *RAPA*. The many forms of vegetable turnip are highly regarded in Japan as well as in Europe where also fodder turnip used to be a very popular crop (root neeps). Oilseed types (seed neeps), grown for rape oil, are important in India and Canada.

The turnip is the oldest *B. rapa* crop on record. It was described in the ancient Greek times of Alexander the Great, whose empire included the Middle East and Persia, from where it may have found its way to eastern Asia. Quite independently of each other in Europe and in Japan, well-defined polymorphic groups of vegetable turnips had been created by the 18th century.

Although turnips (var. *rapa*) are grown around the world, Japan is one of the major areas of variety development, while in eastern Asia radishes have predominated. Turnips grow best in cool climates. Worldwide, turnips can be classified into: Teltou turnips, West European turnips with dissected leaves, Anatolia and Palestine turnips, Russian turnips of the Petrovskij type, Asiatic turnips with dissected leaves of the Afghan type and a subgroup of Asiatic turnips of the Afghan type with entire leaves, Japanese entire-leaved turnips with entire glabrous leaves, and European entire-leaved turnips with pubescent leaves. (Sinskaia, 1928).

The Afghan types are thought to be close to the original var. *rapa* with glabrous dissected leaves, ascending rosette and small taproots. Japanese forms possibly developed from these with entire leaves, no hairs and well-formed taproots demonstrating the effects of selection in cultivation. A further classification (Shebalina, 1968) identified Anatolia, Central Asia, Europe, Iraq and Japan types. The latter includes types derived either indigenously in Japan or developed from European types with several intermediates. Characters used to differentiate types include the form of the seed coat, which either swell (type A) or form a thick layer of epidermal cells (type B) (Shibutani and Okamura, 1954).

The cultivar groups, Mizuna, Neep Greens, Tatsoi and vegetable turnips, are annual or biennial herbs with stout taproots, often becoming fusiform to tuberous (turnips). Stems are erect, branched and up to 1.5 m tall. Leaves are very variable, depending on the cultivated type. They grow in a rosette during the vegetative phase. The basal leaves are petioled, bright green and lyrate-pinnatifid, dentate, crenate or sinuate, bearing large terminal lobes and up to five pairs of smaller lateral lobes. Lower cauline leaves are sessile, clasping and pinnatifid, and upper cauline leaves are sessile, clasping, undivided, glaucous, and entire to dentate.

Cultivar group Mizuna consists of spontaneously tillering plants with pinnate leaves (mizuna cultivars) or entire leaves (mibun cultivars). The cultivar group Neep Greens comprises essentially non-heading plants including crops such as komatsuna, zairainatane, kabuna and turnip greens. The

cultivar group Tatsoi typically grows a flat rosette of many, small dark-green leaves. The cultivar group vegetable turnip consists of forms in which the storage organ (swollen hypocotyl and root (i.e. the turnip)) is used as a vegetable as well. Turnip roots vary widely in shape, from flat through globose to ellipsoid and cylindrical, blunt or sharply pointed, flesh white, pink or yellow, apex white, green, red, pink or bronze. All these characteristics may occur in cultivars in any imaginable combination.

PAK CHOI: SYN. *B. CHINENSIS*; *B. CAMPESTRIS* SSP. *CHINENSIS*; *B. RAPA* SSP. *CHINENSIS*. Pak choi evolved in China and its cultivation was recorded as far back as the 5th century CE. It is widely grown in southern and central China, and Taiwan. This group is a relatively new introduction in Japan where it is still referred to as 'Chinese vegetable'. It was introduced into South-east Asia in the Malacca Sultanate in the 15th century. It is now widely cultivated in the Philippines and Malaysia, and to a lesser extent in Indonesia and Thailand. In recent years, it has gained popularity in North America, Australia and Europe.

The var. *chinensis* is the 'large white cabbage' of China, while var. *narinosa* and the like are 'small white cabbage' (Wu, 1957). These varieties are particularly important where headed forms are not grown and are extensively used in Malaysia and Indonesia. As with var. *pekinensis*, these forms are differentiated in China from oilseed rape with distinctions between type related to the width and cross-section of the petioles. Those with narrow, flat petioles are nearest to the parental origin forming both branching and non-branching types. Petiole colour varies from white to green, the former being used in autumn while the latter is more cold-tolerant and resistant to bolting. Frequently, the Chinese forms are larger than those grown in Japan.

Pak choi is an erect biennial herb, cultivated as an annual. In the vegetative state it is glabrous, dull green and 0.15–0.3 m tall and in the generative stage reaches 0.7 m. The leaves are arranged spirally, not forming a compact head but spreading in groups of 15–30. Petioles are enlarged, terete or flattened, 1.5–4 cm wide and 0.5–1 cm thick, growing in an upright manner forming a subcylindrical bundle. Each white, greenish-white to green leaf blade is orbicular to obovate, 7–20 cm × 7–20 cm. Stem leaves are entire, tender, smooth or blistering, shiny green to dark green and auriculate-clasping.

### *Brassica juncea*

BRASSICA JUNCEA: SYN. *SINAPIS JUNCEA*; *S. TIMORIANA*; *B. INTEGRIFOLIA*. *Brassica juncea* crops are grown worldwide, from India to North Africa, to Central Asia, to Europe and North America. The exact origin is unknown, but as an amphidiploid it seems logical that it originated in an area where the parental species *B. nigra* and *B. rapa* overlap in their distribution (e.g. Central Asia). It is generally agreed that the primary centre of diversity of *B. juncea* is north-west

India, including the Punjab and Kashmir, with secondary centres in central and western China, eastern India and Myanmar, and Anatolia (via Iran). In *B. juncea*, two types of mustards with varying uses have evolved – these are oilseed types and vegetable types. The oilseed types (oilseed mustard) are particularly important in India, Bangladesh and China. The vegetable types contain forms with edible leaves (leaf mustard), stems (stem mustard) and roots (root mustard).

The vegetable mustards are widely cultivated in Asian countries. The highest degree of variation occurs in China, which is regarded as the primary centre of varietal differentiation. The early Chinese traders might well have carried the crop into South-east Asia, whereas the appearance of *B. juncea* near European ports suggests a connection with grain imports. It has also been suggested that Indian contract labourers brought it to the Caribbean. In South-east Asia it is the leaf mustards which are the most common.

*Brassica juncea* is an erect annual to biennial herb, 0.3–1.6 m tall. Normally unbranched, sometimes with long, ascending branches in the upper parts, in appearance it is subglabrous and subglaucous. The taproot is sometimes enlarged (root mustard). Leaves are highly variable in shape and size, either pinnate or entire with petioles that are pale to dark green, smooth or pubescent, and heading or non-heading.

Oilseed mustards are grown as crops worldwide but are chiefly found in a belt from India to Europe. As vegetables, they appear mainly in Asia, and especially China, with a great diversity of types. In India, they are spice plants used in curries while the young leaves may be eaten as greens. Most of the *B. juncea* vegetables of Asia have been developed as pickles hence their use in Europe is limited.

In China, vast amounts of different types of mustard are consumed. Where leaf vegetables of *B. rapa* and *R. sativus* are difficult to grow, as in southern China, *B. juncea* is also used as a leaf vegetable. Growth is slow with tolerance to high temperatures and humidity. Long days are required to stimulate flowering with some varieties being days neutral. This is in contrast to *B. rapa* and explains the distribution of crop types. The greatest differentiation of *B. juncea* for greens is found in China, especially in Sichuan Province. Sinskaia (1928) differentiated on leaf characters in relation to geographical occurrence with an eastern Asian group with bipinnate leaves, a Central Asian Group with entire leaves and a Chinese Group with crisp leaves. Variations of stem characters were used to differentiate forms in Taiwan (Kumazawa and Akiya, 1936), some with compact stems (Kari-t'sai) and others with enlarged stems (Ta-sin-t'sai). Indian types are characterized by their content of the oil 3-butenyl isothiocyanate, which is absent from Chinese types (Narain, 1974), and with the recognition of early bolting north-eastern, late bolting north-western and intermediate types. (Singh *et al.*, 1974). In Japan, succulent leafy types were reputedly introduced in the Meiji era (1868–1912).

Seven types may be distinguished by geographical and botanical characters:

Hakarashina group (*B. juncea*) with pinnate leaves, distributed in India, Central Asia and Europe. They have course-textured, dissected leaves like those of radishes. The majority are cultivated for oil but may form greens when young.

Nekarashina group (*B. juncea* var. *napiiformis*) with enlarged roots, distributed in Mongolia, Manchuria and north China. The taproot is well-enlarged like those of turnips. The crop is absent in Japan. Variation in root character is simple as the root shape is solely conical and root colour is equally upper green and lower white. This group is acclimatized to cold unlike most *B. juncea* crops and hence is an important Chinese crop.

Hsueh li hung (*B. juncea* var. *foliosa*) and Nagan sz kaai (*B. juncea* var. *japonica*) group with glabrous leaves and many branches, distributed in middle and northern China. They are characterized by bipinnate leaves dissected in thread-like segments like those of carrots which form a cluster of rosettes. Dissection is deeper in Hsueh li hung and rosettes more vigorous in Nagan sz kaai. Cold tolerance is relatively high, the leaves are pubescent, dark green and pungent to taste.

Azamina group (*B. juncea* var. *crispifolia*), ecologically similar to Takana, but the leaves are firmly dissected, like parsley, with a general appearance of curly kale. They are used for salads and as ornamentals in the USA, possibly as progeny of the introduced cultivar Fordhook Fancy.

Takana group (*B. juncea* var. *integrifolia*) with entire succulent leaves distributed in southern and middle China, and South-east Asia towards the Himalayas (Kumazawa, 1965). They have either dissected or entire leaves, the latter being more frequent, forming vigorous large plants up to 1 m high. The leaves are soft in texture with midribs varying from narrow to wide and crescent shaped in transverse section, internodes are extended. The leaves are also glabrous or crisp and green to dark green. Cultivated as specialized regional products in Japan.

Takana group (*B. juncea* var. *rugosa*), large plants with leaves that have wide, flat, entire midribs and are extremely succulent. The Paan sum of Guangdong Province has a moderately wrapped head and the Chau chiu tai kai tsai forms a completely wrapped head. The Liu tsu chieh of Zhejiang Province bears protuberances on the midrib.

Ta hsin tsai group (*B. juncea* var. *bulbifolia*), plants with succulent stems and elongated internodes. The leaves are not eaten. Those used for Za-tsai have enlarged stems up to 6–7 cm with protuberances on the petioles; stem enlargement is encouraged by low temperature.

### ***Raphanus sativus* – radish**

Radish (*R. sativus*) is an anciently annual or biennial cultivated vegetable (Frandsen, 1943). The radish crop can be classified into five morphotypes: European small (*R. sativus* var. *sativus*), Asian or daikon (*R. sativus* var.

*longipinnatus*), black (*R. sativus* var. *niger*), rat-tail (*R. sativus* var. *mougri*) and oil (*R. sativus* var. *oleiformis*) (Yamagishi, 2017). In addition to cultivated varieties, four wild taxa are currently recognized: *R. raphanistrum*, *R. raphanistrum* ssp. *landra*, *R. raphanistrum* ssp. *raphanistrum* and *R. raphanistrum* ssp. *rostratus*.

World radish production is estimated at 7 million t/year, which is 2% of total vegetable production. They are particularly prominent in Japan, Korea and Taiwan. The mild-flavoured East Asian radish produces large roots that can be sliced, diced and cooked. The Daikon form is increasing in popularity worldwide, especially as it is reputed to be tolerant to clubroot disease caused by *Plasmodiophora brassicae*. The small-rooted European radish is used for relishes, appetizers and to add variety and colour to green leaf salads. Other forms are used as leaf greens, green manure crops and sources of oilseeds.

The origins of the culinary radish are not known since there is no immediately obvious wild progenitor. However, the zone of maximum diversity runs from the eastern Mediterranean to the Caspian Sea and eastwards to China and Japan. Radish crops were cultivated around the Mediterranean before 2000 BCE and are reported in China in 500 BCE and Japan in 700 CE. New varieties such as var. *caudatus* and var. *hortensis* probably originated during migration. These would then have been domesticated in South Asia, South-east Asia and East Asia. *Raphanus sativus* var. *hortensis* is thought to have been transported to Japan via southern China. They are now found worldwide.

Until recently, little has been known about the origin and spread of radishes. However, recent studies have demonstrated that cultivated radishes have multiple origins from their wild progenitors. Yang *et al.* (2002) hypothesized that *Raphanus* was derived from a hybridization between the *B. nigra* and *B. rapa* lineage, the latter as the female parent, with the production of *Raphanus* inferred to be about 4.7–8.8 Mya. Other studies suggest *Raphanus* diverged from *B. rapa* 13–19 Mya (Moghe *et al.*, 2014) and 16.7 Mya (Mitsui *et al.*, 2015).

Kobayashi *et al.* (2020) surveyed genome-wide SNPs in 520 radish accessions. Principle component analysis grouped the accessions into four populations and showed a strong association with their geographic distribution: (i) Japan, (ii) China and Korea, (iii) South and South-east Asia, and (iv) Europe and the eastern Mediterranean. Phylogenetic analysis identified five clades – four clades comprised cultivated radish accessions, while one clade comprised wild radish species such as *R. raphanistrum* and *R. maritimus*.

## Note

<sup>1</sup> Throughout this book 'Brassica' is used in botanical contexts and 'brassicacae' is used in horticultural contexts.

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