Compendium of Plant Genomes
*Series Editor:* Chittaranjan Kole

Nils Stein · Gary J. Muehlbauer *Editors*

# The Barley Genome

Springer

# Compendium of Plant Genomes

**Series editor**

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Whole-genome sequencing is at the cutting edge of life sciences in the new millennium. Since the first genome sequencing of the model plant Arabidopsis thaliana in 2000, whole genomes of about 70 plant species have been sequenced and genome sequences of several other plants are in the pipeline. Research publications on these genome initiatives are scattered on dedicated web sites and in journals with all too brief descriptions. The individual volumes elucidate the background history of the national and international genome initiatives; public and private partners involved; strategies and genomic resources and tools utilized; enumeration on the sequences and their assembly; repetitive sequences; gene annotation and genome duplication. In addition, synteny with other sequences, comparison of gene families and most importantly potential of the genome sequence information for gene pool characterization and genetic improvement of crop plants are described.

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# The Barley Genome

Springer

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*This book series is dedicated to*
*my wife Phullara, and our children*
*Sourav, and Devleena*

Chittaranjan Kole

*In Memory*

*Dr. Patrick Schweizer*

(1959–2018)

# Preface to the Series

Genome sequencing has emerged as the leading discipline in the plant sciences coinciding with the start of the new century. For much of the twentieth century, plant geneticists were only successful in delineating putative chromosomal location, function, and changes in genes indirectly through the use of a number of 'markers' physically linked to them. These included visible or morphological, cytological, protein, and molecular or DNA markers. Among them, the first DNA marker, the RFLPs, introduced a revolutionary change in plant genetics and breeding in the mid-1980s, mainly because of their infinite number and thus potential to cover maximum chromosomal regions, phenotypic neutrality, absence of epistasis, and codominant nature. An array of other hybridization-based markers, PCR-based markers, and markers based on both facilitated construction of genetic linkage maps, mapping of genes controlling simply inherited traits, and even gene clusters (QTLs) controlling polygenic traits in a large number of model and crop plants. During this period, a number of new mapping populations beyond F2 were utilized and a number of computer programs were developed for map construction, mapping of genes, and for mapping of polygenic clusters or QTLs. Molecular markers were also used in studies of evolution and phylogenetic relationship, genetic diversity, DNA-fingerprinting, and map-based cloning. Markers tightly linked to the genes were used in crop improvement employing the so-called marker-assisted selection. These strategies of molecular genetic mapping and molecular breeding made a spectacular impact during the last one and a half decades of the twentieth century. But still they remained 'indirect' approaches for elucidation and utilization of plant genomes since much of the chromosomes remained unknown and the complete chemical depiction of them was yet to be unraveled.

Physical mapping of genomes was the obvious consequence that facilitated development of the 'genomic resources' including BAC and YAC libraries to develop physical maps in some plant genomes. Subsequently, integrated genetic–physical maps were also developed in many plants. This led to the concept of structural genomics. Later on, emphasis was laid on EST and transcriptome analysis to decipher the function of the active gene sequences leading to another concept defined as functional genomics. The advent of techniques of bacteriophage gene and DNA sequencing in the 1970s was extended to facilitate sequencing of these genomic resources in the last decade of the twentieth century.

As expected, sequencing of chromosomal regions would have led to too much data to store, characterize, and utilize with the-then available computer software could handle. But development of information technology made the life of biologists easier by leading to a swift and sweet marriage of biology and informatics, and a new subject was born—bioinformatics.

Thus, evolution of the concepts, strategies, and tools of sequencing and bioinformatics reinforced the subject of genomics—structural and functional. Today, genome sequencing has traveled much beyond biology and involves biophysics, biochemistry, and bioinformatics!

Thanks to the efforts of both public and private agencies, genome sequencing strategies are evolving very fast, leading to cheaper, quicker, and automated techniques right from clone-by-clone and whole-genome shotgun approaches to a succession of second generation sequencing methods. Development of software of different generations facilitated this genome sequencing. At the same time, newer concepts and strategies were emerging to handle sequencing of the complex genomes, particularly the polyploids.

It became a reality to chemically—and so directly—define plant genomes, popularly called whole-genome sequencing or simply genome sequencing.

The history of plant genome sequencing will always cite the sequencing of the genome of the model plant Arabidopsis thaliana in 2000 that was followed by sequencing the genome of the crop and model plant rice in 2002. Since then, the number of sequenced genomes of higher plants has been increasing exponentially, mainly due to the development of cheaper and quicker genomic techniques and, most importantly, development of collaborative platforms such as national and international consortia involving partners from public and/or private agencies.

As I write this preface for the first volume of the new series 'Compendium of Plant Genomes,' a net search tells me that complete or nearly complete whole-genome sequencing of 45 crop plants, eight crop and model plants, eight model plants, 15 crop progenitors and relatives, and three basal plants is accomplished, the majority of which are in the public domain. This means that we nowadays know many of our model and crop plants chemically, i.e., directly, and we may depict them and utilize them precisely better than ever. Genome sequencing has covered all groups of crop plants. Hence, information on the precise depiction of plant genomes and the scope of their utilization is growing rapidly every day. However, the information is scattered in research articles and review papers in journals and dedicated Web pages of the consortia and databases. There is no compilation of plant genomes and the opportunity of using the information in sequence-assisted breeding or further genomic studies. This is the underlying rationale for starting this book series, with each volume dedicated to a particular plant.

Plant genome science has emerged as an important subject in academia, and the present compendium of plant genomes will be highly useful both to students and teaching faculties. Most importantly, research scientists involved in genomics research will have access to systematic deliberations on the plant genomes of their interest. Elucidation of plant genomes is of interest not only for the geneticists and breeders, but also for practitioners of an array of plant science disciplines, such as taxonomy, evolution, cytology,

physiology, pathology, entomology, nematology, crop production, biochemistry, and obviously bioinformatics. It must be mentioned that information regarding each plant genome is ever-growing. The contents of the volumes of this compendium are therefore focusing on the basic aspects of the genomes and their utility. They include information on the academic and/ or economic importance of the plants, description of their genomes from a molecular genetic and cytogenetic point of view, and the genomic resources developed. Detailed deliberations focus on the background history of the national and international genome initiatives, public and private partners involved, strategies and genomic resources and tools utilized, enumeration on the sequences and their assembly, repetitive sequences, gene annotation, and genome duplication. In addition, synteny with other sequences, comparison of gene families, and, most importantly, potential of the genome sequence information for gene pool characterization through genotyping by sequencing (GBS) and genetic improvement of crop plants have been described. As expected, there is a lot of variation of these topics in the volumes based on the information available on the crop, model, or reference plants.

I must confess that as the series editor, it has been a daunting task for me to work on such a huge and broad knowledge base that spans so many diverse plant species. However, pioneering scientists with lifetime experience and expertise on the particular crops did excellent jobs editing the respective volumes. I myself have been a small science worker on plant genomes since the mid-1980s and that provided me the opportunity to personally know several stalwarts of plant genomics from all over the globe. Most, if not all, of the volume editors are my longtime friends and colleagues. It has been highly comfortable and enriching for me to work with them on this book series. To be honest, while working on this series I have been and will remain a student first, a science worker second, and a series editor last. And I must express my gratitude to the volume editors and the chapter authors for providing me the opportunity to work with them on this compendium.

I also wish to mention here my thanks and gratitude to the Springer staff, Dr. Christina Eckey and Dr. Jutta Lindenborn in particular, for all their constant and cordial support right from the inception of the idea.

I always had to set aside additional hours to edit books besides my professional and personal commitments—hours I could and should have given to my wife, Phullara, and our kids, Sourav, and Devleena. I must mention that they not only allowed me the freedom to take away those hours from them but also offered their support in the editing job itself. I am really not sure whether my dedication of this compendium to them will suffice to do justice to their sacrifices for the interest of science and the science community.

Kalyani, India Chittaranjan Kole

# Preface

Barley (*Hordeum vulgare* L.) was selected by early humans in the Fertile Crescent around 10,000–12,000 years ago and is likely one of the first domesticated plants. Subsequently, barley became a foundation for early human civilization and due to its adaptability is now grown in all temperate regions of the world. Currently, it is the fourth most important cereal crop behind maize, rice, and wheat. Barley is primarily used for animal feed, and malting and brewing, with a small percentage devoted to food. Due to the economic and agronomic importance of barley as a crop, it has been the subject of numerous genetic and genomics studies.

Barley has a large and highly repetitive 5.1 Gb genome, which presented significant obstacles to developing of a high-quality genome sequence. However, in 2006, a small group of barley geneticists had the foresight to form the International Barley Sequencing Consortium (IBSC), resulting in the coordination and data sharing to develop and release of a draft sequence in 2012. Subsequent effort by the IBSC resulted in releasing a high-quality genome sequence in 2017. Thus, this book is timely in that it describes the current status of barley genetics, breeding, and biology, and sets the stage for increased genome sequence-enabled understanding and improvement of this ancient crop. This volume covers aspects of the barley genome (sequencing and assembly approaches, gene prediction, chromosomal genomics, sequence diversity and structural variation, and variation in the secondary and tertiary gene pools), taxonomy, domestication, development (vegetative and inflorescence), genome characteristics (cytogenetics, repetitive sequences,), biotic and abiotic stress responses, organellar genomes, proteomics, gene cloning and expression, and genomics-enabled improvement.

It has been a great privilege to work with members of the barley research community on this book. We are indebted to all of the authors for their expertise and time. Experts in the field reviewed each chapter, and thus we are thankful for their efforts to improve the quality of this compilation. We hope that this volume will serve as a reference for those new to barley and to experienced barley researchers.

Seeland, Germany — Nils Stein
St. Paul, USA — Gary J. Muehlbauer

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# Contents

# Economic and Academic Importance of Barley

1

Peter Langridge

**Abstract**

Barley has had an interesting history. It is thought to be the first crop domesticated and developed as the staple food for the earliest farmers. It has remained an important food in many regions but its main uses now are as an animal feed and for beer production. While production for the other major cereal crops, maize, rice and wheat, has continued to grow, barley production has stagnated over the past two decades. Nevertheless, over the last century, barley has been an important crop model for a wide range of studies on genetics, biochemistry and developmental biology, particularly for barley's close relative, wheat. Many key concepts and tools in modern crop research can be traced back to early studies on barley. As techniques for genetic and genome analysis improve, and genomic research in wheat becomes more tractable, the role of barley as a model is likely to shift. However, there are several aspects of barley that are likely to keep it as an important crop for study.

## 1.1 Background

Barley (*Hordeum vulgare*) is the fourth major cereal in terms of production after maize, rice and wheat. Barley with nonshattering rachises has been found at the oldest archaeological sites dated at just around 11,000 years ago. These are likely to represent the first plants morphologically modified by human selection and just predated the first domesticated wheats—diploid or einkorn wheat (*Triticum monococcum*) (Allard 1999). Wheat and barley are closely related, and it is possible to produce fertile hybrids between the two crops. However, barley is often seen as being an inferior food staple compared to wheat and has been described as the 'poor man's bread'. Despite this limitation, barley is usually hardier than wheat and has been an important crop in many regions where wheat might struggle to yield and this characteristic has ensured barley cultivation from domestication to the present day (Zohary and Hopf 1988).

## 1.2 World Barley Production

Barley has profited from the changes that have occurred in breeding strategies and in farming practices resulting in a steady rate of yield increases. Today, barley is grown across the temperate regions of both the northern and southern hemispheres. Figure 1.1 shows the

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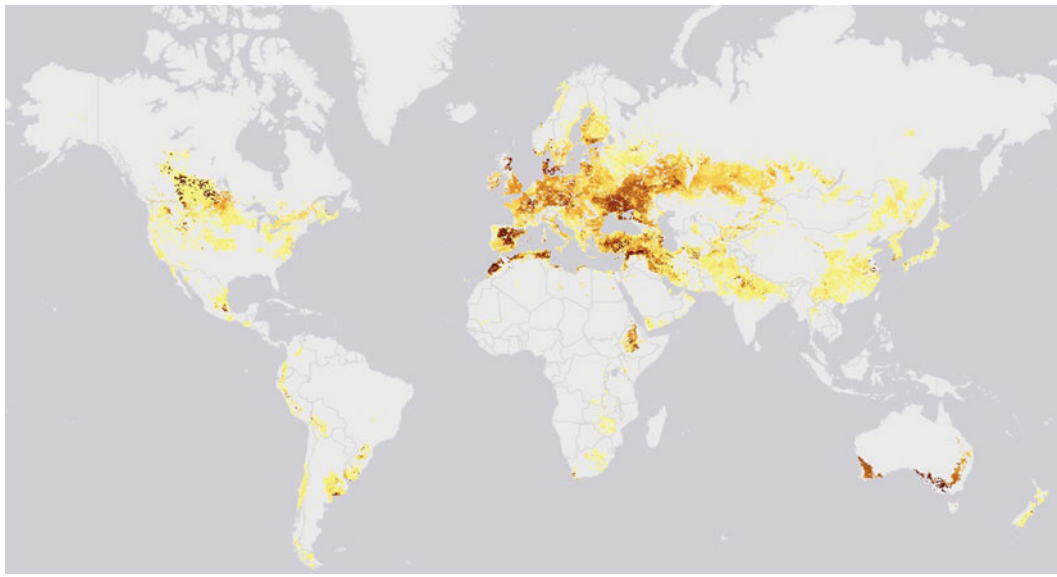

**Fig. 1.1 Distribution of barley production globally** (You et al. 2014 MapSpam). Colour intensity relates to the proportion of land devoted to barley production

distribution of barley production across the world. Europe and the Russian Federation account for around 65% of global production but barley has remained an important food crop in parts of North Africa, Asia and South America.

The ten biggest barley producers are shown in Fig. 1.2. The Russian Federation is not only the largest producer by quantity but also has the largest area sown to barley. It can also be seen from Fig. 1.2 that yields in Russia and Australia are quite low at around 2.5 tonne/ha compared to France and Germany where yields are usually well over 6 tonne/ha. In 2014, almost 150 million tonne of barley were produced on almost 50 million ha giving an average global yield of around 3 tonne/ha.

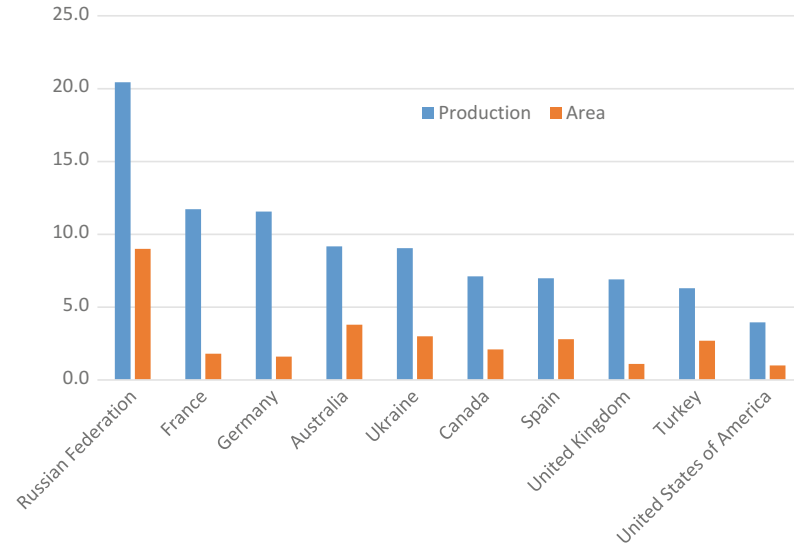


**Fig. 1.2 The world's ten major barley producers for 2014**. Data from FAOSTAT (2017)

In 2013, barley exports were valued at over US$8.5 billion (31 million tonne) with the biggest exporting countries France, Australia, Argentina, Germany and Ukraine. Conversely, the value of barley imports globally was just over US$9.4 billion with Saudi Arabia (10.5 million tonne) by far the biggest importer accounting for almost one-third of the total global barley imports.

Figure 1.3 shows the global changes that have occurred in the area sown to barley and the total production since 1961. Over this period, the yields of barley have risen from an average of 1.3 tonne/ha to over 2.5 tonne. However, it is interesting to note that since the mid-1980s the area sown to barley has been declining. This is probably related to the increasing success of new maize hybrids and soybean cultivars in the USA and to the higher value of wheat in many areas. Brassica crops have also tended to replace barley as an alternative to wheat in many regions. A second factor is the reduction of barley as a traded staple. While barley yields showed rapid increase from the early 1960s until the mid-1980s, there has been little real improvement in yields for the past 15 years. This is probably related to barley being pushed out of some of the more productive cropping regions and moving further to low rainfall, stressed environments where it can outperform wheat. It is possible that the small investment in barley improvement, relative to wheat and particularly maize, is a contributing factor to the slow yield gains.

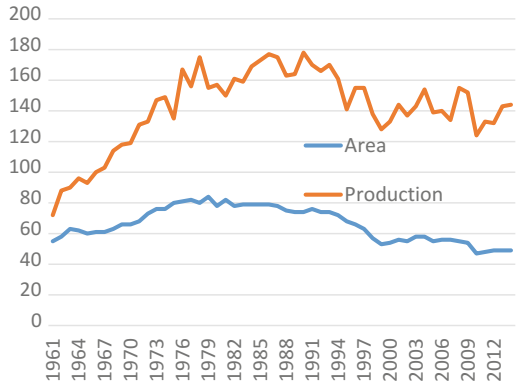


**Fig. 1.3 Global barley production and area sown**. Area (blue) is given in million hectares and production (orange) in million tonne. Data from FAOSTAT (2017)

## 1.3 Barley End Uses

Since 1960, the major use of barley is as animal feed which accounts for between 61 and 77% of barley use. However, malting represents the high-value use for barley with malting barley commanding substantial premiums compared to feed. Over the same period, between 9 and 22% of barley production goes to malting. Although barley was likely to have been originally domesticated for human food and has remained an important food source for people in many regions, currently, food consumption accounts for only around 5% of barley end use (FAOSTAT 2017). The most obvious trend in barley end use has been an increase in barley going to malting and a decrease in human consumption of barley (Fig. 1.4). In the 1960s, just over 10% of barley was used for malting and over 15% for humans. Now the situation is reversed with over 20% of barley production going to malting in some years while human consumption has remained around 5% since the 1980s (Fig. 1.4).

Barley malt is a key raw material for beer brewing and whiskey production—about 130 g of malt is used to produce a litre of beer. There are many different characteristics of barley that are important for malting. These characteristics are primarily related to the speed and consistency of germination, the breakdown of the endosperm cell walls and the degradation of starch into fermentable sugars. High protein is undesirable for malting, and efficient degradation of endogenous proteins is also important for producing high-quality malt (Fox et al. 2003). The importance of the malting process has meant that grain structure, development and germination have been intensively studied in barley and this now represents one of the best-studied cereal grains (Schulte et al. 2009).

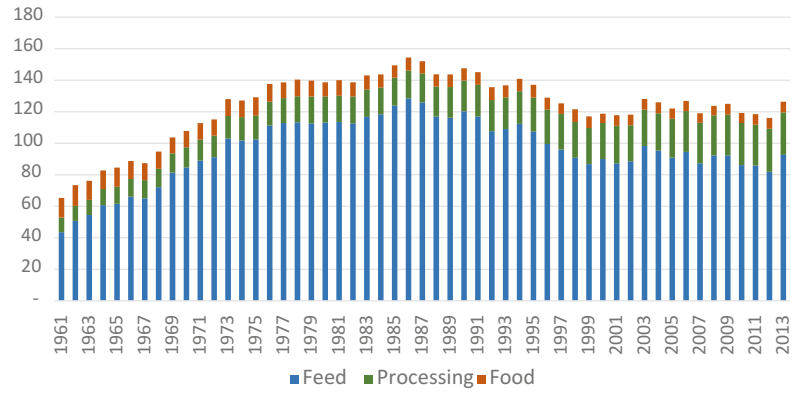


**Fig. 1.4 End uses of barley grain**. The major end uses, in million tonne, are for animal feed (blue), processing or malting (green) and human food (red). Data from FAOSTAT (2017)

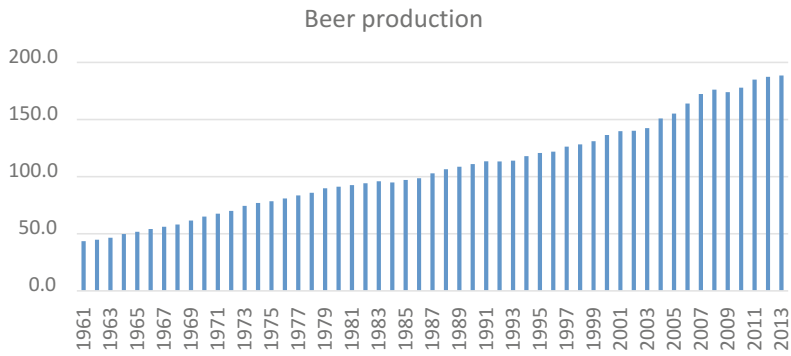


**Fig. 1.5 Beer from barley in million tonne**. Data from FAOSTAT (2017)

Despite the decline in barley production over the past three decades, beer production from barley has shown steady growth (Fig. 1.5) with worldwide beer production at well over a billion hectolitres annually. This is reflected in the rising proportion of barley that has been used for malting, ranging from around 10% prior to the mid-1980s to around 20% more recently.

Food uses have been important historically in many regions including the Middle East, North Africa and northern and eastern Europe and Asia (reviewed in Baik and Ullrich 2008). Barley flour is usually prepared from pearled barley and can be incorporated into wheat-based foods (Newman and Newman 1991). However, wheat and rice provide a better quality product and better mouthfeel than barley which led to a decline in barley consumption over the past 200 years (Newman and Newman 2006). Consequently, breeders have largely ignored food quality in barley improvement.

### 1.3.1 New Trends in Barley End Uses

In recent years, there has been a trend away from the major breweries to small or independent brewing facilities. The craft brewing industry is made up of brewpubs, microbreweries, regional craft breweries and contract brewers. It has been estimated that in 2015 there are over 10,000 craft breweries globally with the vast majority in Europe (4486) and North America (4483) (http://ag.alltech.com/en/blog/2015-craft-brewery-count). While overall beer production in the USA has remained constant or even declined, craft breweries and imported beers have been growing rapidly (up by 6.2 and 6.8% in 2016, respectively) and the craft brewing market in the US represented 12.3% of total consumption in 2016. In 2016, the craft brewing industry in the USA was valued at US$67.8 billion and employed over 456,000 people (https://www.brewersassociation.org/statistics/economic-impact-data/). Importantly,

the growth of the craft brewing industry has been accelerating with an increase in the number of craft breweries in the USA of over 16% between 2015 and 2016 (https://www.brewersassociation.org/statistics/number-of-breweries/). These numbers are significant for barley production not only because of their rapid growth in the craft brewing industry but also because they are heavy users of high-quality barley malt in contrast to many of the major breweries who use large amounts of adjunct from non-barley sources.

In addition to the rise of the craft brewing industries, opportunities also exist for increasing the use of barley for human food. Several studies indicate that barley is one of the healthiest cereals for the human diet due to high levels of some important nutrients (Table 1.1). The overall nutritional value of cereal grains varies greatly depending on how the grain is processed and consumed. There is also considerable variation between accessions (Shewry et al. 2013). However, some barley accessions have high levels of dietary fibre, particularly beta-glucans, and good levels of other bioactive compounds and minerals, such as iron and zinc (Shewry et al. 2013; HealthGrain forum https://healthgrain.org/). The high overall levels and extensive genetic variation were used to select for lines with particularly high concentration of fibre and resistant starch (https://www.thehealthygrain.com/). High fibre barleys were developed by CSIRO in Australia and have been commercialised as BARLEYmax™.

Despite the clear benefits of barley as a human food, its use for food remains low relative to other cereals and there has been no indication that its use will grow. In 2016, the global per capita food use of barley was only 1 kg/person compared to the 67 kg for wheat, 17 kg for maize and 54 kg for rice (FAO 2016). The highest per capita consumption is in North Africa, particularly Morocco (41 kg/person in 2016), Ethiopia (15 kg) and Syria (15 kg).

## 1.4 Academic Importance of Barley

Since the mid-1800s, there have been over 47,000 scientific publications on barley (based on a Scopus search using 'barley' as keyword). The number of barley and *Hordeum* publications since 1950 is shown in Fig. 1.6. The 47,000 barley publications contrast to over 150,000 publications on wheat, and around 92,000 for maize over the same period. Importantly, there were almost 14,000 publications where both wheat and barley were listed as keywords.

Barley has been an important model for wheat but as resources and technologies have advanced, wheat researchers have become increasingly independent. For the period from 1950 to around 1970, there were about twice as many

**Table 1.1** Nutritional composition of major cereals

| Nutritional value (/100 g raw) | Units | Whole grain wheat flour | Oats | Brown rice | Whole grain barley |
|---|---|---|---|---|---|
| Energy | kcal | 340 | 389 | 357 | 334 |
| Protein | g | 13.2 | 16.9 | 8.3 | 10.6 |
| Total fat | g | 2.5 | 6.9 | 2.6 | 2.1 |
| Carbohydrates | g | 61.3 | 55.7 | 73.5 | 60.8 |
| Fibre | g | 10.7 | 10.6 | 3 | 14.8 |
| Calcium | mg | 34 | 54 | 12 | 50 |
| Iron | mg | 3.6 | 4.7 | 1.3 | 6 |
| Zinc | mg | 2.6 | 4 | 0.8 | 3.3 |

Data adapted from https://ec.europa.eu/jrc/en/health-knowledge-gateway/promotion-prevention/nutrition/whole-grain#_Toc479239823

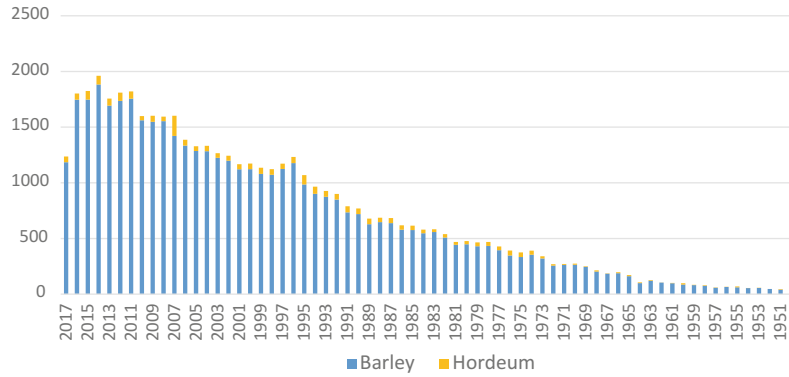


**Fig. 1.6 Numbers of publications giving 'barley' or '*Hordeum*' as keywords since 1950**. Publications listing only 'barley' as a keyword are shown in blue while those with only '*Hordeum'* are in orange. Data from Scopus

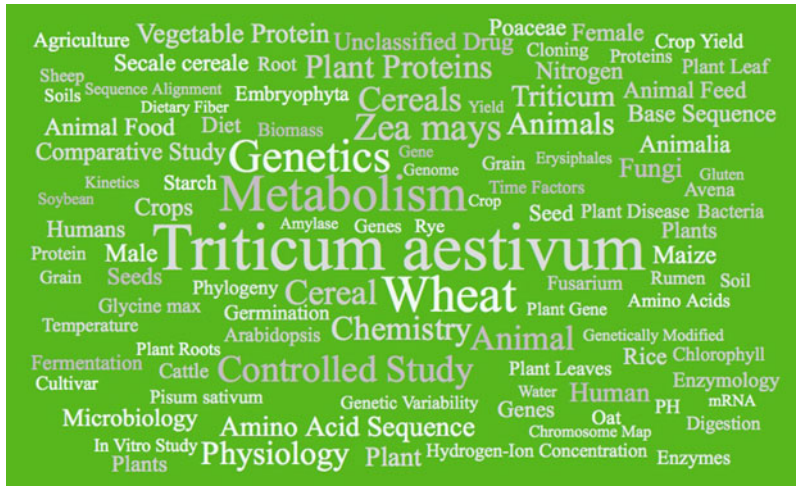


**Fig. 1.7 Word cloud based on keywords used in the 47,436 publications that also included barley as a keyword**. The size of the word in the image reflects the frequency of this word amongst the keywords. Raw data from Scopus and word cloud generated with WordItOut (https://worditout.com/)

publications on wheat compared to barley. However, since the mid-1990s, publications on wheat have exceeded barley fourfold.

The close relationship between barley and wheat research is further emphasised in the Word cloud shown in Fig. 1.7. The most frequently associated keywords are '*Triticum aestivum'* and 'wheat'. The word cloud also shows the importance of barley in research on metabolism, genetics and physiology.

## 1.4.1 Examples of the Broad Impact of Barley Research

### 1.4.1.1 Domestication

There are many aspects of barley domestication, physiology, biochemistry and developmental biology that have been critical for crop science. Many of our ideas about crop domestication have come from studies of diversity in barley, and as noted above, barley is believed to have been the

first crop domesticated. The concept of geographical centres of origin for our modern crops fits well with early ideas of barley domestication in the Fertile Crescent and in the close proximity to wild barley, *Hordeum spontaneum*. However, the more recent discovery of two different rachis mutations in barley (Pourkheirandish et al. 2015) provides strong evidence for two separate domestication events (Morrell and Clegg 2007). This diversity was reinforced with new archaeological evidence for at least two separate domestication events in the Middle East (Riehl et al. 2013). These discoveries are now raising questions about the whole concept of single origin for our major crops and have stimulated a reanalysis of diversity in other species (Allaby 2015).

#### 1.4.1.2 Disease Resistance

The *Mlo* gene was cloned from barley about 20 years ago (Büschges et al. 1997). This gene was first found in an Ethiopian landrace and became a central tool in the control of barley powdery mildew in Europe. However, powdery mildew, caused by over 650 fungal species, is a disease of around 10,000 plant species. It now seems that the *Mlo* resistance mechanism found in barley could have broad application for control of the disease in many other species. This has led to the description of *mlo* as a possible 'universal weapon to defeat powdery mildew disease' (Kusch and Panstruga 2017). This strategy was adopted to generate mutations at all three homoeoloci of *Mlo* in wheat through genome editing to provide broad-spectrum resistance to powdery mildew (Wang et al. 2014).

#### 1.4.1.3 Mutation Research

Mutation research in barley goes back to the very start of mutation work in crop plants with the early work of Stadler, Nilson-Ehle and Gustafsson (Lundqvist 2014). Indeed, barley has been used as a model for the application of mutations to the study of pathogen resistance, physiological, biochemical and developmental processes and to the production of novel commercial varieties based on specific mutations. For example, a gamma-ray-induced mutant of the cultivar 'Valticky' was produced in 1965 and released as the variety 'Diamant'. Diamant was about 15 cm shorter than its parent variety and showed about 12% higher yield. This variety resulted in over 150 new varieties in Europe, North America and Asia (Ahloowalia et al. 2004). Another gamma ray mutant, Golden Promise derived from Maythorpe, has been a mainstay of the Scottish whiskey industry. It was originally selected for its short stature, stiff straw and good malting properties but the mutant also proved to be more salt tolerant than its parent variety (Wei et al. 2003). These characteristics are likely to have been important in two Australian varieties, Hindmarsh and La Trobe, which both have Golden Promise sister lines in their pedigree.

More recently, lipoxygenase-deficient mutants have been adopted by the malting and brewing industry for their improved effects on beer stability (Skadhauge et al. 2011).

The development of genomics resources has led to a revitalisation of barley mutant research and renewal of interest in the extensive series of development mutants identified in the 1950s to 1970s. These mutants have been used to elucidate a range of developmental and metabolic pathways in plants (Druka et al. 2011). In several cases, the work on barley has provided critical starting points for equivalent work in other cereals, notably wheat. Some key examples are the work on flowering time control through the isolation of vernalisation and photoperiod response genes (Fu et al. 2005; Turner et al. 2005; Cockram et al. 2007; Beales et al. 2007) and the analysis of floral morphology with the work on floret fertility (two-row vs. six-row barley) and the hulless traits (Komatsuda et al. 2007; Taketa et al. 2008).

#### 1.4.1.4 Grain Development and Germination

Although more barley is used for animal feed than for beer production, malting is the high-value product of barley and there has been considerable work to understand the characteristics and properties of barley that have made it so important for beer production. Grain development determines the composition and

properties of the grain, while germination is critical for the malting process and providing the sugars needed for beer fermentation. Consequently, barley has provided an important model for a range of physiological and biochemical studies around grain development and germination in the cereals. For example, isolated aleurone layers of barley were used to study the effects of phytohormones gibberellic acid and abscisic acid. Enzymes secreted by the aleurone in response to hormone treatment could be readily isolated and characterised (Chrispeels and Varner 1967; Jacobsen and Varner 1967; Slakeski and Fincher 1992; Gómez-Cadenas et al. 2001). The early work on enzyme isolation and characterisation also meant that barley grain enzymes were amongst the first plant proteins to be crystallised and with solved structures (Varghese et al. 1994; Kadziola et al. 1994).

The barley aleurone was also important in early studies of the control of gene expression in response to hormonal signals (Chandler et al. 1984) and the characterisation of gene promoters (Lanahan et al. 1992; Gubler et al. 1995).

The long history of research on barley grains has made this species a valuable model for applying new techniques for studying different aspects of seed development. For example, transcript dynamics have been measured during both grain development (Zhang et al. 2016) and germination (Betts et al. 2017), and a detailed analysis and three-dimensional reconstruction of grain development has also been produced from careful histological study (Gubatz et al. 2007). These new resources will mean that barley grain remains an important system for plant research.

## 1.5 Conclusions

The recent trends suggest that barley is in decline as a crop and as a research tool. Global production of barley has been falling and publications on barley are not growing as rapidly as for wheat, maize and rice. Barley was long seen as a good diploid model for hexaploid wheat and although the genome size of barley is large, it is still only a third of the size of wheat. However, wheat has now been sequenced and other genomic resources are rapidly accumulating. Gene discovery is now far less dependent on genome size and structure than only a few years ago.

Does barley still have something to offer for crop research? There are two key features of barley that are likely to ensure its continued importance as a model species. First, it is one of the hardiest of the cereal crops. Consequently, barley has been proposed as a good model for studying adaptation to climate change (Dawson et al. 2015). The second important feature of barley is diversity. There is increasing awareness that expanding the germplasm base for our crops will be critical in continuing to advance yields in the face of a wide range of societal and environmental challenges (McCouch et al. 2013). Wild barley, *H. spontaneum*, can be directly crossed to cultivated barley (primary gene pool) and resources for accessing diversity in the secondary gene pool of barley are developing rapidly (Wendler et al. 2014). There are over 400,000 accessions of barley in gene banks (Knüpfer 2009), so the scope to use barley to develop efficient strategies for exploit genetic resources is enormous. Therefore, barley is likely to remain an important model but the prime opportunities can be expected to lie in the use of barley to understand and enhance adaptation to environmental instability and the development of tools and techniques for enhancing the utilisation of diversity in landraces and wild relatives of our crops.

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# Taxonomy of the Genus *Hordeum* and Barley (*Hordeum vulgare*)

2

Frank R. Blattner

**Abstract**

*Barley* refers to the cereal *Hordeum vulgare* subsp. *vulgare* but also more generally to the barley genus *Hordeum* that, apart from cultivated barley, comprises more than 30 wild grass species distributed in temperate and arid regions of the world. Like wheat and rye, *Hordeum* belongs to the Triticeae tribe of grasses, most conspicuously characterized by their inflorescence that is a spike instead of the panicle that occurs in most other grasses. The wild progenitor of the cereal is *H. vulgare* subsp. *spontaneum* from Southwest Asia. Together with bulbous barley (*Hordeum bulbosum*), the closest relative of the crop, and wall barley (*Hordeum murinum*) these species are grouped within subgenus *Hordeum*, while all other species belong to subgenus *Hordeastrum*. The crop is easily crossable with its wild progenitor (forming the primary gene pool of barley), while hybrids between cultivated and bulbous barley (secondary gene pool) exhibit low fertility. All other species belong to the tertiary gene pool, resulting in sterile hybrids that can only be established through embryo rescue techniques. However, barley's tertiary gene pool holds traits for pathogen resistances and adaptations to extreme environmental conditions, which are of high value if they can be transferred into cultivated barley or other cereals. Taxonomic and nomenclatural issues are discussed here in the light of recent findings in molecular systematics and gene function.

## 2.1 Taxonomic Principles

The field of taxonomy has three subareas, which in an ideal world would be integrated into a single consecutive workflow consisting of (i) the analysis of the evolutionary history of organisms (phylogenetics), (ii) circumscribing evolutionary meaningful categories (systematics), and (iii) providing names for such categories (nomenclature). Thus, taxonomic units like species, genera, families, etc. would all be defined through their unique evolutionary history and relationships among each other. However, since the advent of DNA-based phylogenetic analysis about 30 years ago, it became clear that many historically defined and still used taxonomic categories did not represent natural units, i.e., they are not monophyletic. Monophyly is defined as describing a group of organisms derived from the most recent common ancestor that is different from the ancestor of other such lineages (Fig. 2.1a). Imposing the monophyly criterion on systematics should

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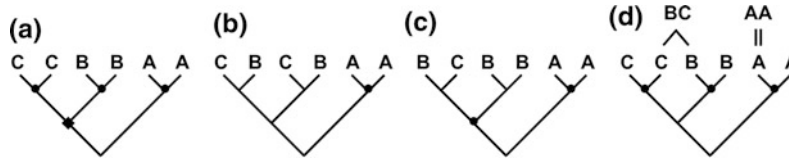


**Fig. 2.1 Explanations for terms describing phylogenetic relationships**. **a** Taxa A, B, and C are all monophyletic units, each reaches back to its own most recent common ancestor (•) and all clade members within A, B, and C share the same name. Taxa B and C could alternatively also be unified within a single taxon, as both go back to a common ancestor (♦). **b** Taxa B and C are both polyphyletic, i.e., they originated multiple times independently but share the same name. Such groups are taxonomically preposterous, as they are not defined through a common evolutionary history. **c** Taxon B is paraphyletic, as not all descendants (C) of its most recent common ancestor (•) carry the same name. This reflects ongoing evolution, i.e., a population starts to diverge clearly from other conspecific populations, and paraphyletic groups might therefore in some cases be tolerable taxonomic units—although defining monophyletic groups should, if possible, be preferred. **d** Through whole-genome duplication in A an autopolyploid originated, while BC is an example for an allopolyploid taxon, combining the genomes of its parents B and C

automatically result in natural units (clades), where members are more closely related to each other than to members of other units. Such clades are defined through phylogenetic analyses of morphological or molecular characters and most often the relationships of taxa are depicted in phylogenetic trees like in Fig. 2.1. As clades are the result of the evolutionary process, they are solidly fixed through their common history. A system based on this principle will automatically result in long-term stability of the names of organismic units, which hierarchically reflect gradual relationships, and has a certain predictive value (i.e., closely related organisms should share more traits than more distant relatives). Although this system cannot account for all mechanisms that drive evolution (for example, taxon relationships cannot always be represented by bifurcating trees but might involve also reticulations resulting in organisms belonging to two or more clades), and determination of such clades might still change with improving methods of phylogenetic analysis, taxonomists now consider the identification of clades the best way to come up with meaningful taxonomic units for the majority of higher plant taxa on Earth, although it might not always be possible or desirable (Brummitt 2006) to avoid paraphyletic groups (Fig. 2.1c). And also the circumscription of clades regarding how wide or narrow a taxon should be defined (Fig. 2.1a) could still be a matter of discussion.

To name taxonomic units, nomenclatural rules were specified, including the priority principle, meaning the oldest validly published name for a taxon has to be used, and that a description of the organism has to be given that at least defines the differences to the most similar other organism. For a long time, these descriptions had to be in Latin but recently also English descriptions became valid. For plants, the rules were fixed in different editions of the International Code of Botanical Nomenclature (ICN, last version: McNeill et al. 2012). This code determines, however, only *how* the naming has to be done and not the criteria that define systematic entities like species, genera, families, etc. Thus, depending on authors and the species and/or genus concepts they follow, different *correct* scientific names might exist in parallel for the same species. Hence, Löve (1984) split *Hordeum* into two genera resulting, for example, in the valid names *H. murinum* L. and *Critesion murinum* (L.) Á.Löve for wall barley. *H. murinum* L. means that this species was first described by Linnaeus (1753), while *C. murinum* (L.) Á.Löve refers to the older Linnean name, the authority now put into brackets, that was sorted into a new genus by Löve (1984). In cases where the meaning of a taxon name is explicit, giving the authority for a taxon can be omitted. In other cases, it might help to make clear to what organisms a name is referring by providing the

authority together with a taxon name (Barkworth and von Bothmer 2009).

## 2.2 *Hordeum* and Triticeae

*Hordeum* is a medium-sized genus within the grass tribe Triticeae. The tribe comprises about 350 species (Barkworth and von Bothmer 2009); among them the important cereals are wheat (*Triticum* spp.), rye (*Secale cereale*) and triticale (x*Triticosecale*; an artificial wheat x rye hybrid), many forage grasses (*Elymus* and *Thinopyrum*), and ecologically important taxa of temperate grasslands (*Aegilops*, *Agropyron*, *Elymus*, *Hordeum*, *Pseudoroegneria,* and others). All Triticeae have chromosome numbers based on $x = 7$, with di-, tetra-, hexa-, and octoploid taxa. Sometimes, even higher ploidy levels can be found. The Triticeae taxa are characterized by their inflorescence that is a spike, the open leaf sheath with membranous ligules, and the hairy top of the developing grain.

Among taxonomists, disagreements exist about the generic concept to be used within the tribe (Bernhardt 2015). An extreme view is that of Stebbins (1956) who argued that the weak hybridization barriers among the different taxa allow to subsume all Triticeae species within a single genus *Triticum*. Others grouped species into different genera according to similar morphological features and life history traits (Linnaeus 1753; Bentham 1882; Nevski 1934; Hitchcock 1951; Tzevelev 1976) or according to the cytogenetic data, defining different so-called genome groups through meiotic crossing-over frequencies in interspecific hybrids (Kihara 1930; Dewey 1984; Löve 1984). Thus, Löve (1984) recognized 37 genera in Triticeae, 13 of them belonging to traditional *Aegilops* (van Slageren 1994; Yen et al. 2005; Barkworth and von Bothmer 2009). As phylogenetic relationships among the genera and species in Triticeae are currently not finally resolved (Escobar et al. 2011; Bernhardt 2015; Bernhardt et al. 2017; and references therein), a rational basis for a solid generic concept of Triticeae is still missing.

## 2.3 The Genus *Hordeum* and Subgeneric Units Within

In *Hordeum*, about 33 annual and perennial species are currently recognized (Blattner 2009). As some of them are divided into several subspecies, about 45 different taxa belong to the genus. They are distributed in temperate and arid parts of all continents except Australasia. *Hordeum* originated approximately 14–10 million years ago (Mya) in an area that became today's Southwest Asia and the Mediterranean and started to diversify 9 Mya (Brassac and Blattner 2015) afterward colonizing Asia, the Americas, and South Africa involving multiple intercontinental dispersals (Blattner 2006). The highest species numbers are found in southern South America, where about 16 species evolved during the last 1.5 million years, more than one-third of them being allopolyploids. As in many Triticeae and grasses generally, allopolyploidization is an important mechanism in *Hordeum* contributing to the generation of biodiversity (Kellogg 2015, 2016). In *Hordeum*, diploid ($2n = 2\times = 14$), tetraploid ($2n = 4\times = 28$), and hexaploid ($2n = 6\times = 42$) taxa exist. Except two autopolyploid cytotypes (in *H. bulbosum* and *H. brevisubulatum*), all polyploids are allopolyploids (Jakob et al. 2004; Brassac and Blattner 2015).

Allopolyploids originate through interspecific hybridization followed by a genome duplication that stabilizes the karyotype by allowing chromosome pairing and an orderly distribution of chromosomes during meiosis. Due to the initial hybridization, allopolyploids create problems in taxonomy, as such organisms evolve from multiple parental species (within *Hordeum*) or even different genera (within Triticeae), which means they reach back to two (or more) most recent common ancestors. To account for this mechanism in the Triticeae, where the majority of species are allopolyploids, genera were defined according to the combined parental genomes/genera (Dewey 1984; Löve 1984; Barkworth and von Bothmer 2009). To name just a few examples, the allopolyploid genus *Douglasdeweya*

obtained a genome each from *Agropyron* and *Pseudoroegneria*, while *Stenostachys* is characterized by the possession of an *Australopyrum* and a *Hordeum* genome, and the combination of genomes from *Pseudoroegneria* and *Hordeum* results in *Elymus*. Although this system is artificial and not consistently used throughout the tribe (Bernhardt 2015), it is the convention that most grass taxonomists currently agree on. In *Hordeum*, taxonomic problems are less pronounced, as allopolyploids evolving from within the genus are treated as new *Hordeum* species. Although the taxonomy is still not completely consistent regarding the rank and status of *Hordeum* polyploids, this will be solved in the frame of the future monograph of the genus (Blattner, in prep.).

For *Hordeum*, different taxonomic treatments exist, regarding the genus, subgeneric entities (like subgenera, sections, and series), and species or subspecific units (like subspecies or varieties). In contrast to the genera closely related to wheat, the monophyly of the taxa belonging to *Hordeum* was nearly never disputed. No matter if unified into one genus or split into two, it was clear that all species evolved from a most recent common ancestor that was different from the ancestors of other lineages within Triticeae. This is due to the unique inflorescence structure of *Hordeum*, where the spike consists of three single-flowered spikelets at each rachis node (named triplets) making *Hordeum* taxa easily recognizable. Monophyly was later also confirmed by molecular methods (below) so that this genus seems somehow exceptional within Triticeae, as it is less burdened by multiple contradicting taxonomic treatments in comparison to many other genera of the tribe.

Still, the most important changes in the systematics of the genus were the ones proposed by Dewey (1984) and Löve (1984). Based on the analysis of pairing behavior of meiotic metaphase I chromosomes in hybrids, four different genomes were recognized in *Hordeum* (von Bothmer et al. 1995). Löve (1984) therefore split *Hordeum* into *Hordeum* L. s.str., consisting only of *H. vulgare* and *Critesion* Raf., comprising all other species of the genus. Dewey (1984) arrived at a similar solution, although he added *H. bulbosum* in his *Hordeum* s.str. instead of *Critesion*.

Few taxonomists followed this approach, probably due to the clear morphological characters unifying *Hordeum* and *Critesion*, making them easily recognizable as 'belonging together'. Later, molecular systematic analyses of nuclear loci (Petersen and Seberg 2003; Blattner 2004; Petersen et al. 2011; Brassac and Blattner 2015) showed that neither Dewey's nor Löve's treatment provides monophyletic units. As both *H. vulgare* and *H. bulbosum* are nested within the *Critesion* lineage (Fig. 2.2), *Hordeum* s.str. would indeed be in both cases monophyletic. *Critesion*, however, is a paraphyletic genus, as not all species derived from the most recent common ancestor of *Critesion* would be included in this taxon. Only the transfer of *H. murinum* from *Critesion* either into *Hordeum* or a genus of its own would make *Critesion* monophyletic. Keeping all species within a single genus named *Hordeum* provided a relatively stable and intuitive solution, and it prevents botanists from learning more than 30 new taxon names.

For a long time, the *Hordeum* species were also grouped into units below the genus level, mostly sections and series that were erected to harbor species with similar morphology or certain life history traits. *Hordeum vulgare* was placed in sect. *Crithe* Doell or sect. *Cerealia* Anders., all the other annual species in sect. *Hordeastrum* Doell, the perennials with rather long awns in sect. *Critesion* (Raf.) Nevski, the short-awned species from South America into sect. *Anisolepis* Nevski, the remaining species from North America, Asia, and Europe in sect. *Stenostachys* Nevski, and *H. bulbosum* in sect. *Bulbohordeum* Nevski (Nevski 1941). Bothmer and Jacobsen (1985) recognized only the four sections *Anisolepis*, *Critesion*, *Hordeum,* and *Stenostachys*. In a later monograph of the genus, von Bothmer et al. (1995) already expressed their doubts about these sections being natural units but deterred to erect a new classification system, as they found the evidence from then emerging molecular data not strong enough to base far-reaching taxonomic changes on. Petersen and Seberg (2003) undertook an approach toward a

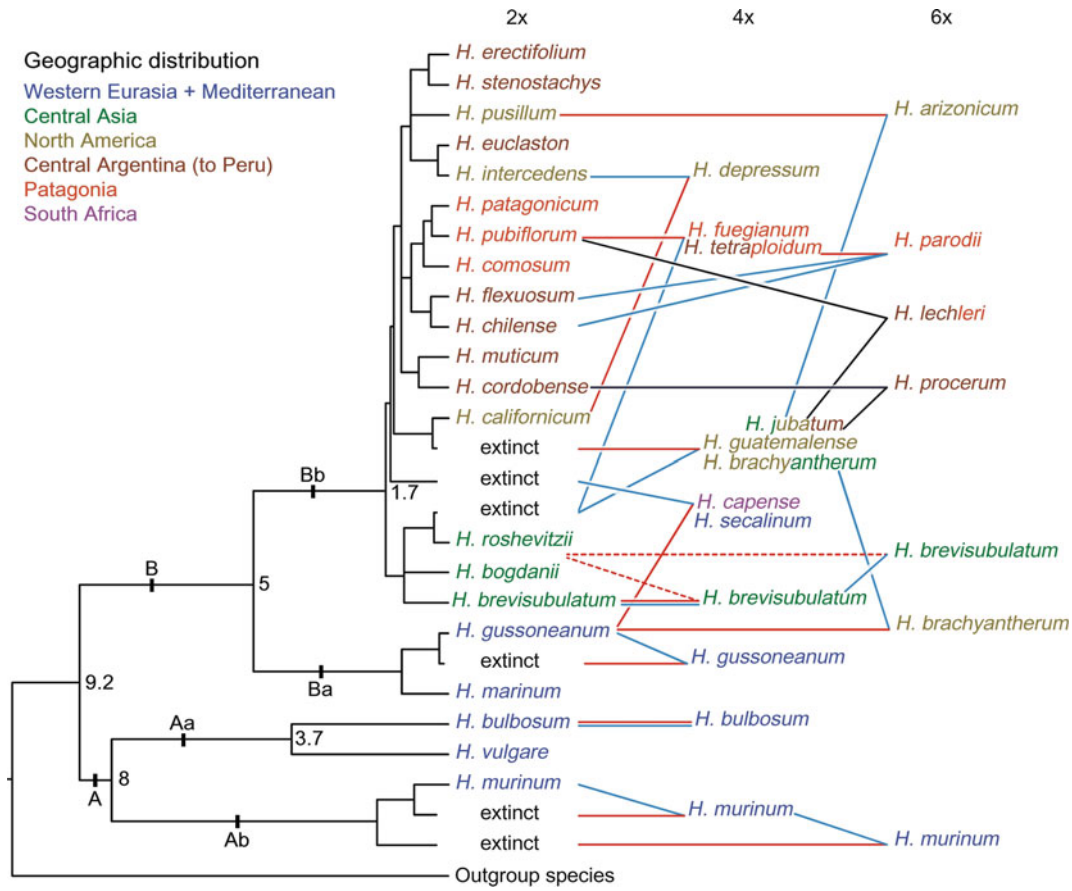


**Fig. 2.2 Phylogenetic relationships of *Hordeum* species**. The tree is based on the combined analysis of DNA sequences from one chloroplast and 12 nuclear single-copy genes. Diploid species are provided at the tips of the tree, polyploid species (4×, 6×) are connected through lines with their ancestral di- or polyploid progenitors. Extinct taxa/genotypes were inferred from the presence of gene copies (homeologs) in polyploids, which do not occur any more in extant diploid taxa. Numbers at major nodes in the tree provide clade ages (in million years). A = subg. *Hordeum*, Aa = sect. *Hordeum*, Ab = sect. *Trichostachys*, B = subg. *Hordeastrum*, Ba = sect. *Marinae*, Bb = sect. *Stenostachys*. The figure is modified from Brassac and Blattner (2015)

new system for *Hordeum,* based on phylogenetic data of sequences of two nuclear loci plus characters derived from the chloroplast genome. They proposed four sections *Hordeum*, *Critesion*, *Sibirica,* and *Stenostachys*. Through time, accumulating phylogenetic data (Komatsuda et al. 1999; Blattner 2004; Petersen et al. 2011; Wang et al. 2011; Brassac et al. 2012; Brassac and Blattner 2015) proved, however, that apart from sect. *Hordeum* the other sections were again not monophyletic when used in the sense of Petersen and Seberg (2003).

A new system (Blattner 2009), which tried to include all evidence available to be strictly based on natural units, now divides *Hordeum* in two subgenera (subg. *Hordeum* and *Hordeastrum*), each with two sections conforming the four genome groups occurring within *Hordeum* (von Bothmer et al. 1995), plus one section comprising three intersectional allopolyploid hybrid species of subg. *Hordeastrum* (for more details see Table 2.1). Blattner (2009), and Yen and Yang (2009) independently proposed to base *Hordeum* sections onto natural units or genomes

**Table 2.1** Taxa of *Hordeum* L. (modified from Blattner 2009)

| Taxon | Ploidy | Haploid genome[2] | Distribution area |
|---|---|---|---|
| **Subgenus *Hordeum*** | | | |
| **Section *Hordeum*** | | | |
| *H. vulgare* L. | | | |
| subsp. *vulgare* | 2× | **H** | Cultivated |
| subsp. *spontaneum* (K. Koch) Thell. | 2× | **H** | SW to C Asia |
| *H. bulbosum* L. | 2×, 4× | **H, HH** | Mediterranean to C Asia |
| **Section *Trichostachys* Dum.** | | | |
| *H. murinum* L. | | | |
| subsp. *glaucum* (Steud.) Tzvel. | 2× | **Xu** | Mediterranean to C Asia |
| subsp. *murinum* | 4× | **XuXu** | NW Europe to Caucasus |
| subsp. *leporinum* (Link) Arc. | 4×, 6× | **XuXu, XuXuXu** | Mediterranean to C Asia |
| **Subgenus *Hordeastrum* (Doell) Rouy** | | | |
| **Section *Marinae* (Nevski) Jaaska** | | | |
| *H. gussoneanum* Parl. | 2×, 4× | **Xa, XaXa** | Mediterranean to C Asia |
| *H. marinum* Huds. | 2× | **Xa** | Mediterranean |
| **Section *Stenostachys* Nevski** | | | |
| **Series *Sibirica* Nevski** | | | |
| *H. bogdanii* Will. | 2× | **I** | C Asia |
| *H. brevisubulatum* (Trin.) Link[1] | 2×, 4×, 6× | **I, II, III** | C Asia |
| *H. roshevitzii* Bowden | 2× | **I** | C Asia |
| **Series *Critesion* (Raf.) Blattner** | | | |
| *H. californicum* Covas & Stebb. | 2× | **I** | SW North America |
| *H. chilense* Roem. & Schult. | 2× | **I** | Chile and W Argentina |
| *H. comosum* Presl | 2× | **I** | S Argentina |
| *H. cordobense*Bothmer et al. | 2× | **I** | C Argentina |
| *H. erectifolium* Bothmer et al. | 2× | **I** | C Argentina |
| *H. euclaston* Steud. | 2× | **I** | C Argentina, Uruguay |
| *H. flexuosum* Steud. | 2× | **I** | E + C Argentina |
| *H. intercendens* Nevski | 2× | **I** | SW USA, NW Mexico |
| *H. muticum* Presl | 2× | **I** | C to N Andes |
| *H. patagonicum* (Haum.) Covas[1] | 2× | **I** | S Argentina |
| *H. pubiflorum* Hook.f.[1] | 2× | **I** | S Argentina |
| *H. pusillum* Nutt. | 2× | **I** | C + E USA |
| *H. stenostachys* Godr. | 2× | **I** | C Argentina |
| *H. depressum* (Scribn. & Sm.) Rydb. | 4× | **II** | W USA |

(continued)