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

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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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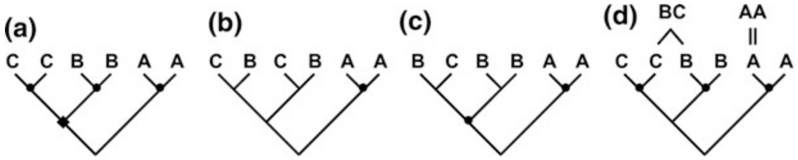

Fig. 2.1 Explanations for terms describing phylogenetic relationships. **a** Taxa A, B, and C are all monophyletic units, each reaches back to its own most recent common ancestor (•) and all clade members within A, B, and C share the same name. Taxa B and C could alternatively also be unified within 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, allopolyp loidization 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

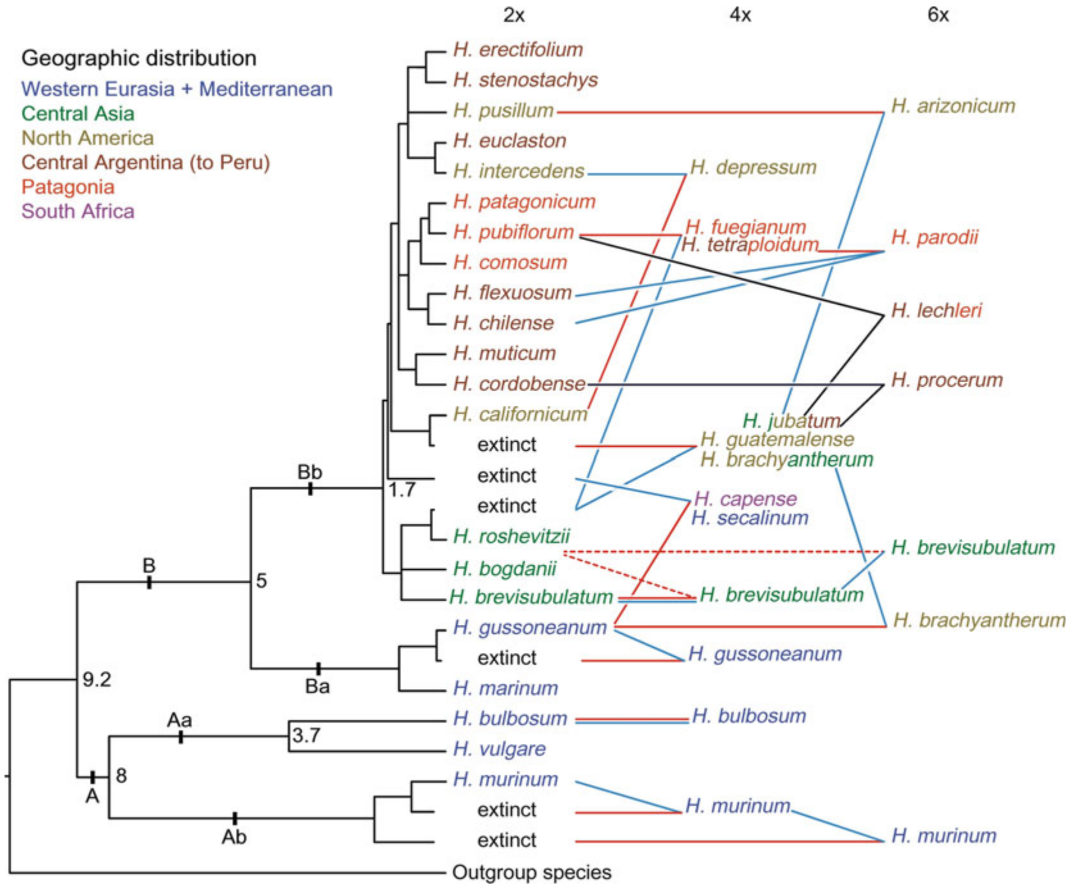

Fig. 2.2 Phylogenetic relationships of *Hordeum* species. The tree is based on the combined analysis of DNA sequences from one chloroplast and 12 nuclear single-copy genes. Diploid species are provided at the tips of the tree, polyploid species (4×, 6×) are connected through lines with their ancestral 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)

Table 2.1 (continued)

Taxon	Ploidy	Haploid genome[2]	Distribution area
Interserial allopolyploids of series *Critesion* (all combining genomes of an American species with an extinct relative of *H. roshevitzii*)			
H. brachyantherum Nevski	4×	**II**	W North America, Kamchatka, Newfoundland
H. fuegianum Bothmer et al.	4×	**II**	S Argentina, S Chile
H. guatemalense Bothmer et al.	4×	**II**	Guatemala, S Mexico
H. jubatum L.	4×	**II**	NE Asia, W North America, C Argentina
H. tetraploidum Covas	4×	**II**	C Argentina
H. arizonicum Covas	6×	**III**	SW USA
H. lechleri (Steud.) Schenk	6×	**III**	C + S Argentina
H. parodii Covas	6×	**III**	C Argentina
H. procerum Nevski	6×	**III**	S Argentina
Section *Nodosa* (Nevski) Blattner			
H. brachyantherum Nevski	6×	**IIXa**	C California
H. capense Thunb.	4×	**IXa**	S Africa
H. secalinum Schreb.	4×	**IXa**	Mediterranean, C Europe

[1] Species with subspecies not further detailed here; [2] for details regarding *Hordeum* genomes, see Blattner (2009)

but unfortunately came up with partly different names for their sections. It will be a matter of time to see which system finally reaches wider acceptance within the community of grass and *Hordeum* researchers.

2.4 The Gene Pool Concept in Barley

Based on the possibility to use related species for utilization in crop breeding, the gene pool concept was introduced by Harlan and de Wet (1971), classifying crop wild relatives into three levels depending on the absence or presence and strength of crossing barriers with the crop species. For barley breeding, the primary gene pool refers to plants where no crossing barrier toward barley is present, i.e., the wild progenitor of cultivated barley *H. vulgare* subsp. *spontaneum* (see Schmid et al., Chap. 17). The secondary gene pool consists of *H. bulbosum* where crossing with barley is possible, although either fertility of the hybrid is strongly reduced or the *H. bulbosum* chromosomes are completely eliminated at very early developmental stages resulting in haploid plants (see Wendler, Chap. 18). All other species of *Hordeum* belong to the tertiary gene pool of barley, which means that crossing is only possible if embryo rescue techniques are employed and the resulting hybrids are sterile. While the transfer of favorable traits from the primary and secondary gene pool into barley can be achieved relatively easy, often characters are cotransferred that are non-desirable and have to be eliminated through series of backcrosses to the cultivar. The transfer of genes from the tertiary gene pool by traditional breeding methods is nearly impossible. New methods of genome editing might provide an easy and fast way for crop improvement when the genetic basis of certain traits of the wild species will finally be understood.

In *Hordeum,* interbreeding and the definition of gene pools are very closely correlated with the ages of the different groups. The populations of the primary gene pool are still seen as belonging to the same species as cultivated barley, which diverged under human influence only during the last 20,000 years (Weiss et al. 2008) from its wild progenitor and, even in nature, is still interbreeding when wild and cultivated stands are in close proximity (Russell et al. 2011; Jakob et al. 2014; Mascher et al. 2016). The *H. bulbosum* and the *H. vulgare* lineages split approximately 3.7 Mya (Fig. 2.2), which is still young enough for a certain amount of interfertility. In contrast, *H. murinum*, the sister species of *H. vulgare* and *H. bulbosum*, separated from them by 8 Mya, all other *Hordeum* species groups diverged 9.2 Mya (Brassac and Blattner 2015), which is well beyond the time frame where crossing is possible. These ages are much higher than the divergence ages found in, for example, *Aegilops*/*Triticum* (Bernhardt et al. 2017) and might explain why it is easier to utilize wild species in the wheat group in comparison to the wild *Hordeum* species. Another element is that the cultivated barley is a diploid taxon that seems to be much more sensitive toward introgression of foreign genomic material than the polyploid wheat species, where redundancy through homeologous loci might buffer against the detrimental genomic effects of hybridization (von Bothmer et al. 1995).

2.5 The Taxonomy of Barley in the Light of Its Evolution

Linnaeus (1753) in his *Species Plantarum* listed eight species belonging to his genus *Hordeum*, five of them referring to cultivated barley types (*H. vulgare*), two to bulbous barley (*H. bulbosum*), plus wall barley (*H. murinum*). These species are the most common *Hordeum* taxa of Central and Northern Europe, and therefore were easily accessible for the Swedish botanist at that time. The example of the five names Linné created for what we today understand to be a single species illustrates two major pitfalls for the taxonomy of cultivated plants. (i) Cultivars often have a much more diverse appearance than wild plants due to the breeding process that tries to generate diversity, and in addition humans select conspicuously mutated forms and propagate mutants if they might possess an advantage to them or rise their curiosity. In natural populations, these mutants would only very rarely reach a noticeable frequency or become fixed. (ii) The economic importance of crops ensures them the attention of many taxonomists, which naturally have diverse perceptions of how to classify and name the taxa in a most favorable way. For barley that has a close mutualistic relationship with humans for more than 10,000 years, both processes contributed to generate diverse systems and a plethora of taxonomic names. Here, I will provide a suitable way to taxonomically harness the diversity that is present in the crop and its wild progenitor. My conclusions are very much in accord with the treatment of *H. vulgare* by von Bothmer et al. (1995) in the last monograph of *Hordeum*, which became more and more widely accepted during the last decades.

It is important to note the difference in the objective between the taxonomy of wild and cultivated taxa in general. While for wild taxa the aim of botanists is to put names on natural units so that the meaningful names exist for comparable categories throughout the plant kingdom, in cultivated plants this is not equally straightforward, as cultivar taxonomy should fulfill different requirements. These depend very much on the users of the taxonomic system. Breeders and seed bank managers might need fine categories, which describe their plant stock quite precisely (Mansfeld 1950), but as soon as it comes to marketing of a certain variety, easy and catchy names are needed. This results in rather different taxonomic approaches. So, on the one hand there is a name like *Hordeum vulgare* L. subsp. *vulgare* convar. *distichon* (L.) Alef. var. *nutans* (Rode) Alef. The other kind of naming could be *Hordeum vulgare* ‘Golden Promise’ or even barley ‘Golden Promise’, both providing valid names for barley cultivars under the Code of Nomenclature for Cultivated Plants (CNCP; Brickell et al. 2009). The first example describes that we deal with a cultivated two-rowed, naked barley variety. The second example is a hulled spring barley cultivar of the UK breeding company Miln Marsters from the mid-1960s. It is a mutant originating through X-ray treatment from the cultivar ‘Maythorpe’ and was widely used in Scotland to produce ale and whisky, as it had excellent malting quality. Only the last property might be deduced from the cultivar name, if at all, every other information has to be obtained from the descriptions of the breeder. Although the first example looks like a real taxonomic name, it is without any meaning regarding monophyly of the two-rowed and naked barleys appointed with this name. Many of the morphological traits important in cultivated cereals are based on single or very few genes, which means that the specific phenotypes might originate over and over again. For example, six-rowed barley evolved several times independently through loss of the function of the *Vrs1* gene that, if functional, results in the normally two-rowed *Hordeum* spike type (Komatsuda et al. 2007). This makes the six-rowed type polyphyletic and the two-rowed type paraphyletic. Therefore, these are not taxonomically valid units no matter if referring to the assumed wild six-rowed [convar. *agriochriton* (Åberg) Bowd.] or cultivated six-rowed materials [var. *hexastichon* (L.) Aschers.]. It has to be understood that this highly scientifically looking nomenclature of cultivars is completely artificial. Taking this into account, I consider naming a cultivar *Hordeum vulgare* ‘Golden Promise’ or barley ‘Morex’ more appropriate than the system above, as it does not feign to be based on scientifically defined taxonomic categories. With its reference to *H. vulgare* or even barley, the cultivars are connected to a botanical species and therefore rooted in the botanical nomenclatural system (ICN). The cultivar name, provided in single quotation marks (CNCP), then refers to a certain entity produced by a breeder. However, as landraces and many ancient cultivars have no trademark name, both systems of naming cultivated barley will still be used in parallel for a long time depending on context.

In the scientific naming system for barley, the crop and its wild progenitor are assumed to be conspecific and subsumed under the species name *Hordeum vulgare* L. (von Bothmer et al. 1995). All cultivated types are placed in *H. vulgare* subsp. *vulgare* and the wild form in *H. vulgare* subsp. *spontaneum* (K. Koch) Thell. This treatment reflects the current knowledge that all cultivated barleys are domesticated types derived from wild barley and still group within the wild barley clade in phylogenetic analyses. There is some weak evidence that the crop could be derived from a gene pool that is different from extant wild barley and is no longer present in the wild (Jakob et al. 2014). If this should be proven, it would be valid to treat both forms as two different species: *H. vulgare* L. for the cultivars and *H. spontaneum* K. Koch for the wild populations. However, I think it requires stronger evidence than currently available to decide about the presence of one or two species. The often encountered name *H. spontaneum* in scientific publications of the last years (Dai et al. 2012, 2014 but also many others) is most probably not a statement of the authors regarding this being an independent species from cultivated barley but seems due to the effort to keep articles within the word limits of journals. Correct would, however, be to mention first the correct taxonomic name and only afterward use the abbreviated forms *H. spontaneum* or subsp. *spontaneum*.

The most important morphological character that is consistently different between both types is the brittle rachis in the wild plants versus the tough rachis in the cultivars. At maturity, the spike disarticulates in the wild type at each rachis node, releasing the triplets as dispersal units (Sakuma et al. 2011). In contrast, in cultivated forms, the tough rachis does not disarticulate and the spike can be harvested as an entire unit. This trait, as most other traits referred to as domestication syndrome (Hammer 1984), is under very strong selection in cultivated plants, as shattering immediately results in the exclusion of the respective seeds/genotypes from next year’s sowing. Vice versa it is also under selection in the wild populations (Zohary 1959), as a tough rachis reduces the dispersal ability for the grains. Natural selection here is, however, much less severe than the human-enforced selection in cultivated stands. Thus, tough rachis types occur sometimes in the wild, which initially allowed their selection during the domestication process.

The rachis type is controlled by two adjacent genes (*Btr1*, *Btr2*), which both can induce the loss of the brittle rachis by recessive mutations (Pourkheirandish et al. 2015). The geographical distribution of the respective alleles indicates that two independent domestications of barley occurred (Azhaguvel and Komatsuda 2007; Dai et al. 2012; Pourkheirandish et al. 2015), one initially based on the mutated *Btr1* (that is *btr1*) in the Southern Levant, and a second one that resulted from selecting the *Btr2* mutation (that is *btr2*) in today's northern Syria and adjacent Turkey (Pourkheirandish et al. 2015). Cultivars with the mutated *Btr1* gene are today mostly distributed in Southwest Asia and Europe (from where they were introduced into American and Australian cultivars), while the *Btr2* mutants occur mainly between northern Africa and the Central Mediterranean in the West, and Central and East Asia in the East. Pourkheirandish et al. (2015) explain this distribution either with differences in ecological conditions between the two areas, favoring one or the other genotype, or that early trade or migration of farming could have resulted in the preferential distribution of the respective ancient stocks of extant cultivars. Taxonomically, it would be correct to provide different names for the independently domesticated variants of subsp. *vulgare*. However, as they cannot be distinguished without a still time-consuming screening of sequence differences at the *Btr* loci, this might provide practical obstacles for the use of such taxonomic entities.

There are regular claims of Tibet as an additional and independent domestication center for East Asian barley (Dai et al. 2012, 2014; Wang et al. 2015; and references therein) that then would also earn the status of a separate taxon. However, currently I am not finally convinced by this hypothesis. My uncertainty is caused by two not very well explained matters regarding (i) wild barley occurring under very diverse ecological conditions and (ii) the interpretation of the phylogenetic data that, to me, does not really support an independent domestication of barley in Tibet.

'Tibetan wild barley' is ecologically clearly distinct from the populations occurring in the Fertile Crescent, as they occur under much harsher conditions at elevations of 3500–4500 m on the Tibetan Plateau in comparison to the Southwest Asian stands that normally are found well below 1500 m elevation (von Bothmer et al. 1995; Zohary and Hopf 2000). It is not easy, at least to me, to envision a scenario for the Tibetan Plateau that was glaciated till 8400 years ago and influenced by a minor glaciation cycle about 4400 years ago (Kuhle 2005), to be (re-)colonized by wild barley, (re-)colonized by Neolithic humans, them starting immediately the domestication of local wild barley, and afterward spread their local high-elevation crop through trade to the vast areas in East Asia, where barley is cultivated at much lower elevation and with a very different temperature regime. Although not impossible, this seems a rather elaborate hypothesis.

How the new findings regarding the origin and domestication of the *Btr* types can contribute to the discussion about Tibetan barley has yet to be evaluated. The preferential presence of *btr2* in East Asian cultivated barley (Azhaguvel and Komatsuda 2007) was used to argue for an independent domestication of Asian barley in Tibet or China, as six-rowed brittle rachis barleys occur in Tibet and are more closely related to East Asian barley cultivars than to barley from western Eurasia (Dai et al. 2012; Wang et al. 2015). However, the resolution of this topic completely hinges around the identity of wild barley on the Tibetan Plateau. If Tibetan barley really would represent an autochthonous wild population, then Tibet has to be acknowledged as an independent domestication area. If wild barley there is merely a feral and weedy population derived from the locally adapted cultivated forms, a completely different interpretation results. von Bothmer et al. (1990) linked the observation of the locally high frequency of brittle rachis types to the specific cultivation praxis in the Tibetan highland. Due to in some years rather short vegetation periods at elevations above 3500 m, barley is often harvested in a premature, sometimes even green stage and dried in the homes of the farmers afterward. If harvesting is done before disarticulation of the spike starts, the purifying selection against brittle rachis types is no longer severe and reversals to the dominant wild-type genotypes can spread in the population. These weedy types might then accumulate in disturbed habitats in the farmed areas during long summers, when the brittle spikes disarticulate already in the field before harvesting. Classifying such secondary 'wild barley' as native wild barley would, of course, result afterward in a close relationship between them and their local cultivated progenitors when analyzed for genetic similarity. With the recent discovery of function and structure of *Btr* (Pourkheirandish et al. 2015), a route to clarifying the nature of Tibetan wild barley is opening. Thus, it would be helpful to see if Tibetan cultivated barley possesses a *btr2* allele identical to the Southwest Asian one or if a different mutation rendered *Btr2* nonfunctional. While true wild barley of Tibet should have the *Btr2* allele, feral brittle rachis types must be characterized either by a compensatory mutation reversing *btr2* of cultivated Asian material back into a functional *Btr2* in feral plants or by recombination between *Btr1*/*btr2* and *btr1*/*Btr2* types recreating a *Btr1*/*Btr2* brittle rachis type. The analysis of the respective gene regions in Tibetan wild barley and comparison with the materials from Southwest Asia could show if they share the Southwest Asian wild-type allele or if there are indications for a reversal to a secondary-functional brittle rachis *Btr2*. This most probably should be different, as it is unlikely that the same frameshift mutation happened twice in Southwest Asia and Tibet or was compensated by an identical reversal mutation from Tibetan cultivar's *btr2* toward the Southwest Asian-derived *Btr2* allele. Producing *Btr1*/*Btr2* brittle rachis barley by hybridization of *Btr1*/*btr2* and *btr1*/*Btr2* domestic barleys followed by recombination between the two loci is possible, as demonstrated experimentally (Pourkheirandish et al. 2015).

2.6 Conclusions

During the last decades, taxonomists agreed more and more that monophyletic groups (= clades) should be the principle units for nomenclatural categories, as they would—through time—result in long-term stable systematics. Although there are inherent problems in some organism groups, where monophyly is not always a useful criterion (hybrids, allopolyploids, asexual organisms, etc.) and paraphyletic groups also reflect the course of evolution, for the majority of organisms this clade-based nomenclature works satisfactorily. All species of *Hordeum* form a clade and can therefore be unified in a single genus. Earlier proposals to split *Hordeum* into two genera (*Hordeum* and *Critesion*) were mostly not accepted by the Triticeae research community, as all *Hordeum* species are easily recognized as forming one unit.

Cultivated barley and its progenitor wild barley are thought to still belong to a single species, as they are freely interbreeding and form a clade in phylogenetic analyses. To account for both forms, they are differentiated at the subspecies level with *H. vulgare* subsp. *vulgare* denoting the cultivar and *H. vulgare* subsp. *spontaneum,* the wild progenitor. While this treatment is unambiguous, within the subspecies different naming approaches exist. According to the Code of Nomenclature for Cultivated Plants, cultivar names are given in single quotation marks after a taxon name (*Hordeum* 'Morex'). However, there was and still partly is also an artificial system of naming in place that looks very much like valid taxonomic categories, although these categories do mostly not depict monophyletic units. Thus, six-rowed barley was/is named *H. agriocrithon*, implying that this is a species of its own, different from *H. vulgare*. But it could be also found as *H. vulgare* subsp. *agriocrithon* or *H. vulgare* subsp. *vulgare* convar. *agriocrithon*, assuming that it is either a subspecies equal to subsp. *vulgare* and subsp. *spontaneum* or a convariety within the cultivated barleys. As six-rowed barley originated multiple times, this character does not qualify as a valid taxonomic unit (as it does not describe a clade) but names a morphological type of barley. Using this kind of names might be useful in certain fields of agronomy or for seed bank management. When using them it should just be understood that such categories are completely artificial and very different from real taxonomic groups defined through their evolutionary history.

Recent research in barley domestication shows that assuming monophyly for cultivated barley might also not describe the history and groups completely correct. There are strong indications that the cultivated barley was domesticated at least twice from slightly different stocks of the Southwest Asian subsp. *spontaneum* population. This means that cultivated barley is polyphyletic and the two independently domesticated lineages rightfully should have two different names. However, as it is only possible to discern these lineages through analysis of the tough rachis genes and interbreeding partly merges the two gene pools, labeling these units with different scientific names seems currently impractical and essentially not necessary. Everyone working with these plants should have in mind that there are at least two cryptic lineages within cultivated barley germplasm going back to the slightly different genotypes that were initially selected by Neolithic humans during the domestication process from the same (meta) population of wild barley.

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