The Origin of Cultivated Barleys: A Discussion[1]

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Introduction

Two hypotheses were considered by De Candolle (1883) for the origin of the cultivated six-rowed tough-rachis barleys (*Hordeum vulgare*): first, that the six-rowed barleys arose in early prehistoric agriculture from the two-rowed *Hordeum distichon,* in which the wild brittle-rachis *H. spontaneum* was included; and second, that the six-rowed barleys may have been derived from a wild six-rowed form. It is obvious that De Candolle was in favor of the former hypothesis because a wild six-rowed barley was then unknown. This would mean that *H. spontaneum,* which had been described by Koch (1848), was considered as the ancestor of all cultivated barleys. The term six-rowed is applied in this paper to all barleys with fertile lateral spikelets irrespective of density of the spike. Another term often used in the same sense is many-rowed.

Since De Candolle, different students of the phylogeny of the cultivated barleys have supported each of these hypotheses, although with slight variations (cf. Åberg, 1940). From the morphological point of view, Schiemann (1932) concluded that the two-rowed barleys were reduced forms and formulated the hypothesis that a wild six-rowed brittle-rachis type should be considered as the ancestor of the cultivated six-rowed barleys and the wild two-rowed brittle-rachis *H. spontaneum* as well. This view was elaborated by Åberg (1940), who stated that phylogeny not only in the genus *Hordeum* but also in the whole tribe TRITICEAE Dumort. (=HORDEAE) has probably progressed by reduction within the inflorescence.

The discovery of a six-rowed brittle-rachis barley by Åberg (1938) in material collected by H. Smith in southwestern China was welcomed as proof for the proposed hypothesis. This barley was described by Åberg as *Hordeum agriocrithon.* Evolution of the six-rowed cultivated barleys could now be easily explained, but different hypotheses have been proposed for subsequent development of other barleys, especially the two-rowed types. Discussions and diagrams of various possible evolutionary steps are given by Åberg (1940) and Schiemann (1951). It has been the opinion of most investigators during the past 20 years that the general outline of the phylogeny of cultivated barleys was well understood (Åberg 1940, Brücher and Åberg 1940, Freisleben 1940a, Hoffman 1956, Schiemann 1948, 1951, Takahashi 1955, Zukovsky 1950). In recent years, however, several papers have been published which cast doubt on the almost universally accepted theory of the origin of cultivated barleys from a six-rowed brittle-rachis ancestor. Criticism of this theory has evolved from different points of view which reflect the various disciplines employed in research on the history and evolution of cultivated plants. Bakhteyev (1947) was the first to oppose the theory. He doubted the wild character of *H. agriocrithon* because of the lack of any differences between *H. agriocrithon*

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and certain plants which he found in offspring of artificial crosses between *H. spontaneum* and six-rowed *H. vulgare*. He also found a six-rowed brittle-rachis barley plant in an experimental plot of *H. spontaneum* and concluded that this occurrence could be explained only by spontaneous hybridization with six-rowed *H. vulgare*. Zohary (1959) doubted the spontaneity of six-rowed brittle-rachis barleys from Israel which were described by Kamm (1954) and by himself. Further he gave some arguments, based on the biology of seed dispersal, against the spontaneity of such plants. Arguments based on comparative morphology were presented by Bowden (1959). Helbaek's (1953, 1959) arguments were founded on his investigations of archaeological material of barleys from prehistoric sites of Jarmo, Iraq. The radiation experiments of Gustafsson (1957), Nybom (1953), Scholz and Lehmann (1958), and Stubbe and Bandlow (1946/1947) have shown that fully fertile six-rowed mutants can be obtained from two-rowed barleys.

Altogether these investigations demonstrate the possibility that the two-rowed *H. spontaneum* has been the starting point for evolution of cultivated barleys. It should be mentioned that this is the opinion also of Bakhteyev (1957), Bowden (1959), Helbaek (1959), and Zohary (1959). Since we are faced with two diametrically opposed hypotheses, it seems worthwhile to discuss the various papers in more detail.

Discussion

According to investigations of Åberg (1940) and of Brücher and Åberg (1950), *H. spontaneum* and *H. agriocrithon* can be crossed without any difficulty with each other and with all other taxa of section HORDEUM (= CRITHE Döll = CEREALIA Anders.). The F_1 hybrids are always fully fertile. From all published data concerning hybridization and also from results of cytological investigations (Morrison, personal comm., Staudt, 1960) it may be concluded that all taxa of section HORDEUM are very closely related. Some of these, however, have been described as distinct species. There is no question that all these taxa should be combined in one species *Hordeum vulgare* L. emend. as has been done by Bowden (1959). The final infraspecific classification needs to be revised in view of new information on the relationship of *H. spontaneum*, *H. agriocrithon*, and *H. vulgare* (Bowden, 1960). Therefore, no rank is attributed to *H. spontaneum* and *H. agriocrithon* in this paper.

In addition to the typical section (sect. HORDEUM), Nevski (1941) established five other sections. The species belonging to these are morphologically quite different from those of section HORDEUM. They are also genetically and cytologically distinct from *H. vulgare* emend. (Morrison, 1959, Morrison *et al.*, 1959, Morrison and Ràjháthy, 1959). Their karyotypes are different, and the species can be crossed with *H. vulgare* only with difficulty. There is very little chromosome pairing in F_1 hybrids, which are usually sterile. According to Nevski (1941), all these undoubtedly wild species are of the two-rowed type (heterospiculate), i.e., the central spikelets of each triplet are fertile and the lateral spikelets are reduced, male, and without seeds. There are only occasional exceptions: in *H. bulbosum*, for example, seeds rarely form in the lateral spikelets.

Within section HORDEUM the two-rowed *H. spontaneum* is undoubtedly wild. From the wide geographical distribution of wild taxa, all of which are two-rowed, it may be concluded that the two-rowed type is a very old one. Considering the two-rowed character and morphology of all living *Hordeum* species it seems quite unrealistic to regard the six-rowed *H. agriocrithon* as an ancestral type. Bowden (1959) therefore considered *H. agriocrithon* as a mutant which arose in the eastern part of the range of *H. spontaneum.* He does not object to the hypothesis of a phylogenetic trend in the TRITICEAE toward reduction within the inflorescence. However, this reduction is believed to have occurred much earlier in evolution, and now no primitive six-rowed plants exist.

In considering the recent arguments against the hypothesis that *H. agriocrithon* is a primitive wild form and is the ancestor of the cultivated barleys, we should first discuss the question whether or not *H. agriocrithon* is actually a wild entity.

Anyone inspecting a plot of *H. agriocrithon* before harvest would believe that these are cultivated plants because of their vigorous growth and great spikes closely resembling cultivated barley. In contrast, when the plants mature and dry, the spikes break spontaneously, and no one would claim that *H. agriocrithon* is a very efficient cultivated plant from the standpoint of seed harvest.

Three of the collections of *H. agriocrithon* from Tibet and the bordering province (Sikang) of southwestern China (Åberg 1938, Brücher and Åberg, 1950, Schiemann 1951) were discovered as solitary grains in samples of wheat and six-rowed naked barleys respectively. Two plants grown from samples from Taofu, Sikang were described by Aberg as the varieties *euagriocrithon* and *dawoense* of *H. agriocrithon.* Progenies of these plants showed a delayed germination, the grains were narrow and thin, and the weight per 1000 grains was 27.8 and 29.8 g respectively (the weight of 1000 grains cultivated varieties varies from 30-50 g). It was believed that these and other characters indicated the wild nature of the plants. Other samples of *H. agriocrithon,* described by Freisleben (1943) from Lhasa, Tibet, require a different explanation. The weight of the original five samples varied from 11-77 g. These samples, which consisted almost exclusively of kernels of *H. agriocrithon,* must have been purchased in markets or storage houses because the expedition of Schäfer reached and stayed in Lhasa only during winter. The relatively high weight of each sample, the purity of each, and also the fact that the weights per 1000 grains were a little higher than those of Åberg's strains led Freisleben to think of them as a primitive, possibly semi-wild form which had been under cultivation as a forage crop. Members of the expedition noted that, in the higher parts of Tibet, barleys were cultivated as forage crops and that seed, therefore, had to be introduced every year from lower regions. In this regard the observations of Korshinsky (cited by Regel, 1917) may be of interest. In Transcaucasia, *H. spontaneum* occurred frequently in dense natural stands which were mowed and threshed by country people. The quality of the grains, however, was not high enough to justify its further use as a grain (or cereal?) crop. "But in its green state it is easily mowed and it gives then a forage crop of good quality and agreeable taste." *Hordeum agriocrithon* may have been used in a similar way by the inhabitants of the Tibetan plateau, a possibility already pointed out by Freisleben (1943) and by Hoffmann (1956), but rejected by Schiemann (1951). Because of the broad leaves and consequently high forage yield, cultivation of *H. agriocrithon* as a forage crop should be worthwhile. Hence it seems quite possible that *H. agriocrithon* occurs both as a primitive cultivated plant and as a weed. No final decision can be made because we lack field observations.

Six-rowed brittle-rachis barleys are not known exclusively from Tibet and southwestern China. In a sample of six-rowed barley collected by A. Scheibe in northern Afghanistan, a single plant with two-rowed brittle spikes was found. This plant produced offspring which included, among other types, six-rowed brittle-rachis plants (Freisleben 1940b). The original plant was considered to be a spontaneous hybrid, six-rowed *H. vulgare* × *H. spontaneum;* plants of *H. spontaneum* occurred in that area frequently as a weed in cereal crop fields. Additional six-rowed brittle-rachis barleys have been described from Israel by Kamm (1954) and Zohary (1959), from Iran by Kuckuck (1956), and from Turkmenistan (USSR) by Bakhteyev (1959). All these collections are located within the range of the wild *H. spontaneum* and are in areas in which six-rowed barleys are cultivated. A thorough study of the *H. agriocrithon* types in Israel was made by Kamm (1954). In several places, Mt. Tabor, the Esdraelon and Beisan valleys and the Negev Mountains, six-rowed brittle-rachis barleys, some of them distinguished as *H. agriocrithon* var. *euagriocrithon* and *H. agriocrithon* var. *dawoense* Åberg, have been discovered growing together with *H. spontaneum* and various kinds of intermediates. *Hordeum proskowetzii,* which was described by Nábělek (1929) and later transferred by Nevski (1941) as a variety to *H. spontaneum,* may be explained as such an intermediate form. These plants have two-rowed brittle-rachis spikes, but in contrast to the typical *H. spontaneum* they have awns 2-5 cm long in their lateral spikelets. They were found in Turkish Kurdistan and southwestern Iran.

Different types of the six-rowed plants were cultivated by Kamm (1954); some proved to be constant in their offspring whereas others manifested their hybrid nature by segregating. Among the wild collections, Kamm found a six-rowed brittle-rachis type comparable with Körnicke's *H. intermedium,* which he believed was of hybrid origin. Similar types had already been described by Schiemann (1951) from Tsela Dzong, Tibet. The lateral spikelets of the plants grown from the collected seeds were awnless to awn-tipped. It was possible to isolate a true breeding line of the former type, but offspring of other plants showed segregation. Length of awns on the lateral spikelets of some plants approached that of var *dawoense* of *H. agriocrithon.* The name *H. paradoxon* was proposed by Schiemann for this brittle-rachis, hulled *H. intermedium* type. This name was used by Takahashi (1955) and Hoffmann (1956) although it was not validly published.

Zohary (1959) reported more than 30 hybrid swarms between *H. spontaneum* and six-rowed *H. vulgare* from eastern Galilee and from the foothills of the Judaean Mountains. These hybrid swarms grew usually in abandoned fields, along roadsides, and in other disturbed places. All intermediates between parental types were observed, as were plants that could not be distinguished from *H. agriocrithon.* Although the brittle-rachis character suggests the wild nature of these six-rowed plants, the plants have never been found in natural habitats, but similar forms may have arisen many times in the past by hybridization. Zohary attributed the inability of six-rowed brittle-rachis barleys to establish wild populations to the inefficient function of a six-rowed barley triplet as a dispersal unit. The spreading lateral spikelets somewhat prevent the unit from entering the soil and becoming anchored. The spikelets of the two-rowed brittle-rachis barleys seem well adapted to soil penetration. Zohary, therefore, did not agree that *H. agriocrithon* is a relic prototype of the barleys and considered it as a product of hybridization.

A similar origin may be proposed for the six-rowed brittle-rachis *H. laguncliforme* (nom. invalid.), which was reported by Bakhteyev (1959) from Turkmenistan. This taxon and *H. spontaneum* as well were found in fields or edges of fields in areas in which six-rowed barleys are cultivated. It is of great interest to note that *H. lagunculiforme* was described by Bakhteyev (1957) from archaeological excavations of carbonized grains from the

Crimea, Armenia, and Azerbaijan; the Azerbaijan collection has been dated between 3000 and 2000 B.C. The lateral spikelets of this form are pedicellate, as in *H. spontaneum* and in some two-rowed tough-rachis barleys (*H. distichon*). It has been shown by Åberg (1957) that six-rowed barleys with pedicellate lateral spikelets have been found in progenies after hybridization between two-rowed and six-rowed types.

The origin of all recently described six-rowed brittle-rachis barleys from western Asia can be explained by hybridization, but it may be questioned whether the original discoveries from southwestern China can also be explained in this way.

According to Freisleben (1940a) and Nevski (1941), *H. spontaneum* extends eastward only to the Hindukush and Bokhara; according to Vavilov (in Regel 1917) it also occurs in the Pamir region. East of the Hindukush in the oases of eastern Sinkiang (Chinese Turkestan) Vavilov (1931) found neither *H. spontaneum* nor other species normally associated with crop fields in western Asia. He considered the Pamir and Hindukush region to be an efficient barrier to west-east plant migration. But Sinkiang and Tibet are still botanically little known and *H. spontaneum* may perhaps be found there. Consequently, at the moment we cannot attribute the eastern Asiatic *H. agriocrithon* to hybridization that occurred in the Tibetan area. If it can be shown that *H. spontaneum* does not and has never occurred in this area, it may be assumed that these *H. agriocrithon* forms have been introduced from west of the Hindukush and are also of hybrid origin. As Hu (1958) has pointed out, some puzzling modern plant distributions are due to introductions or migrations along ancient trade routes between China and the cultural centers of western Asia and Europe. For example, a great many of central Asiatic, Mediterranean and European genera of the Compositae occurring in China today have been found in Tibet. This is not because of chance, but rather because Tibet lay on the main southern trade route from central Asia and the Orient to China (Hu 1958). Accordingly, for at least the past 2000 years there existed a direct connection between the area of possible origin of *H. agriocrithon* and the places of recent discovery in southwestern China. Grains of *H. agriocrithon* could have been easily introduced among other cereals and selected by the inhabitants for a special purpose, probably as a forage grass.

Because of its adaptability to very harsh climates barley is able to survive in cultivation under the severe conditions found in Tibet. It therefore has become the main food plant of the Tibetans who use barley flour to prepare their national food, tsamba. No doubt they have selected naked barleys in preference to hulled barleys, since the former can be milled more easily. Naked barleys therefore are grown almost exclusively in this area, and the hulled *H. agriocrithon* has not been able to compete as a food plant.

From the genetic point of view, there are no difficulties in deriving the six-rowed from the two-rowed barleys. The radiation experiments of Gustafsson, Stubbe and Bandlow, Nybom, and Scholz and Lehmann showed that fully fertile six-rowed types can originate by a single gene mutation. Two of these artificial mutants have been shown to be monogenic recessive (Scholz and Lehmann, 1958). It has not been investigated whether these genes are identical with the series of multiple alleles $V^t \rightarrow v$ which govern the development and fertility of the lateral spikelets. The gene V^t (*deficiens*) dominates incompletely over V, V^d (two-rowed) and v (six-rowed) (Woodward, 1949). It is well known that dominant mutations are much less frequent than recessive ones. There is therefore a much higher probability for a mutation from two-rowedness to six-rowedness than in the reverse direction.

A valuable contribution to the solution of the problem of the evolution of cultivated barleys has been provided by archaeological investigations. The hypothesis of Schiemann and Åberg was in no small measure influenced by the findings of six-rowed barleys in prehistoric material from settlements of the Lake Dwellers in Switzerland and from Egyptian tombs. On the other hand, two-rowed barleys were known at that time only from later-dated findings which supported the idea of most students of barley evolution that the two-rowed barleys were derived forms. This idea has been changed in recent years. In the excavations at Jarmo in the uplands of Iraq-Kurdistan, Helbaek (1953, 1959) found only a two-rowed barley, which is similar to *H. spontaneum* but may have had a less brittle rachis and bigger grains. Helbaek interpreted the material as a transition stage from the wild *H. spontaneum* to the cultivated form. The prehistoric site at Jarmo is the earliest known village-farming community (Braidwood, 1958) and was probably built very near the beginning of the era of plant and animal domestication. By radio-carbon methods, the Jarmo site has been dated as most probably about 7000 B.C. When agriculture reached the lowlands of Mesopotamia and Egypt 2000 years later, the two-rowed barleys were replaced by a lax-eared form of six-rowed barley (Helbaek, 1959). Archaeological investigations cannot prove whether the step from two-rowed to six-rowed barley occurred first under cultivation or in nature, but it is probable that the former was the case.

Summary

For the past 20 years, it was thought that the six-rowed brittle-rachis *Hordeum agriocrithon* was the ancestral form of the cultivated six-rowed barleys and also the two-rowed brittle-rachis *H. spontaneum*. In recent years new data have provided ample evidence for revising this widely accepted theory.

A number of reasons are given for concluding that a type similar to the modern *H. spontaneum* was the ancestor of both the two-rowed and six-rowed cultivated barleys. The earliest proof of cultivation of a primitive two-rowed barley was found at Jarmo (7000 B.C.), a village situated within the present range of *H. spontaneum*. Six-rowed barley may have originated by a single gene mutation from cultivated two-rowed barley. Six-rowed barley first occurred in archaeological sites from the lowlands of Mesopotamia about 5000 B.C.

Hordeum agriocrithon does not seem to be a primitive form although it has a brittle rachis. In western Asia *H. agriocrithon* has been found only in areas where *H. spontaneum* occurs wild and six-rowed barleys also are cultivated. Nowhere has it been found growing in truly natural habits. The taxa described as *H. agriocrithon* Åberg, *H. lagunculiforme* Bakhteyev, and *H. proskowetzii* Nábělek are considered to be of hybrid origin. Hybridization of the six-rowed cultivated barleys with the ancestral *H. spontaneum* could have taken place many times in the past and undoubtedly still occurs where they grow together. The occurrence of *H. agriocrithon* in Tibet and Sikang is regarded as the results of introduction from western Asia, possibly in historic times.

Naked barleys may have arisen in several areas by gene mutation. Their present distribution is a result of human use and customs and does not necessarily designate the place of origin.

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