Amblyopyrum (Jaub. and Spach) Eig

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8.1 Separation of *Amblyopyrum* from *Aegilops*

Amblyopyrum is a monotypic genus of the sub-tribe Triticineae represented by the species *A. muticum* (Jaub. and Spach) Eig that was separated from *Aegilops* by Eig (1929b). The name *Amblyopyrum* is derived from the Greek 'amblyos' (=blunt) and 'pyros' (=wheat) (Van Slageren 1994). The taxonomic rank of this taxon is controversial. While describing and designating this species as *Aegilops mutica,* Boissier (1844a, b) assumed it resembles *Ae. Aucheri* Boiss. (a synonym of *Ae. speltoides* ssp. *speltoides* Tausch) in morphology, and therefore, regarded it as a primitive species of *Aegilops.* Yet, Boissier (1844a, b) considered it to be an intermediate between *Aegilops* and several species of *Agropyron* (currently *Elymus* species). Eig (1929a) in his detailed and comprehensive monograph on the genus *Aegilops*, placed *Ae. mutica* too within the genus *Aegilops* but very distant from the rest of the species; he classified it as subgenus *Amblyopyrum*, whereas all the other species were placed under subgenus *Eu-Aegilops*. The inclusion of *Ae. mutica* within the genus *Aegilops* was accepted by taxonomists such as Zhukovsky (1928), Hammer (1980), and Clayton and Renvoize (1986). However, later, after studying species of *Elymus* (formerly *Agropyron*), particularly *E. elongatus,* and realizing that *Aegilops mutica* is an intermediate in several basic morphological features between *Aegilops* and several species of *Elymus,* Eig (1929b) decided to separate it from *Aegilops* as a monotypic genus, *Amblyopyrum,* that includes the species *A. muticum.* This decision was based on the following morphological traits of *A. muticum*: long (up to 30 cm) linear awnless spikes with many multi-floret spikelets, without any rudimentary spikelets. Glumes widest at apex with divergent venation. The rachis is fragile and after ripening disarticulates into single spikelets that fall with the rachis internode below the spikelets (wedge type disarticulation), and fragile rachillae (the axis of the spikelet) that disarticulate into f1orets that fall separately especially in the upper part of each spikelet (floret type disarticulation). These morphological features of *A. muticum*, particularly the floret type of disarticulation, are characteristics of the older Arctic-temperate group and especially to species of *Elymus*, thus corroborating its intermediate position between *Elymus* and *Aegilops*. It is assumed that *A. muticum* is morphologically similar to the putative ancestor of the wheat group while maintaining several features of *Elymus*. By separating this taxon, Eig (1929b) emphasized its intermediate position between *Aegilops* and *Elymus*. Numerical analysis (Baum 1977, 1978a, b; Schultze-Motel and Meyer 1981) indicated the close relationship of *Amblyopyrum* with *Aegilops* and *Triticum*, while, especially in Baum's work, confirming the morphological differences at the same time.

The morphological contrast between *Amblyopyrum muticum* and all other *Aegilops* species brought taxonomists, e.g., Bor (1968), Baum (1978a, b), Schultze-Motel and Meyer (1981), Löve (1982) Watson et al. 1985; Davis et al. 1988; Tzvelev (1989), and van Slageren (1994), to agree with Eig's (1929b) separation. Van Slageren (1994) pointed out that not only the morphological differences but also the early separation of *Amblyopyrum* from the *Aegilops* lineage requires an independent generic status.

8.2 Morphological and Geographical Notes

Amblyopyrum muticum (Jaub. and Spach) Eig (Syn.: *Aegilops mutica* Boiss.; *Triticum muticum* (Boiss.) Hack. in Fraser.; *Aegilops tripsacoides* Jaub. and Spach.; *Triticum tripsacoides* Bowden) is annual, 50–80 cm high (excluding spikes), culms usually few, mostly upright, and are sparsely foliated. Leaves glaucous-green, 8–25 cm long; Ligule short, membranous, up to 1 mm long. Spikes 15–35 (sometimes up to 45) cm long, thin, cylindrical, one-rowed, with many spikelets (15–20, sometimes more), awnless. Rachis fragile and disarticulates at maturity into individual spikelets each with a rachis segment below it (wedge type dispersal unit), and fragile rachillae (the axis of the spikelet)

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that disarticulate into f1orets that fall separately especially in the upper part of each spikelet (floret type disarticulation). Spikelets 8–15 mm long, linear to linear-elliptical, equally large or slowly decreasing in size to the tip of the spike, usually shorter than the adjacent rachis segment and diverging from it. The apical spikelet is at right angle to the lateral spikelets. Florets 5–9, the lowest 2–3 fertile. Glumes 7–10 mm long, trapezoid with the upper edge being larger than the base. Upper margin with 2–4 short blunt teeth separated by notches. Lemmas 7–10 mm long, leathery, about the same length as the glumes. Anthers 4–5 mm long. Caryopsis 4 mm long, adherent to lemma and palea (Fig. 8.1).

A variable species, however, only awnless forms are known. Variation exists in the length and width of the spike and in number of spikelets. Glumes are either hairy or glabrous, and floral parts and rachis segregates for red, black and colorless as well as for width. Different morphological forms grow in mixed stands and interbreed freely.

Amblyopyrum muticum contains two varieties: var. *muticum* and var. *loliaceum*. In var. *muticum.* the glumes and apical parts of the lemmas are covered with short, stiff hairs while in var. *loliaceum* glumes and lemmas are glabrous.

Amblyopyrum muticum is native to west Asia (Anatolian Plateau, southeastern Turkey, Turkish Armenia, Caucasus, western Iran and north-east Syria). It may also occur in northern Iraq. Grows on sandy, stony or steppical-grey soils in abandoned fields, edges of wheat fields or roadsides. In the center of its distribution (Anatolian Plateau) it forms dense stands, but in other sites it occurs more sporadically in wadis and lower slopes. Alt: 700–1200 m asl. Its distribution in this area is considered as the probable center of origin of the group, and may indicate its primitive status (Hammer 1980).

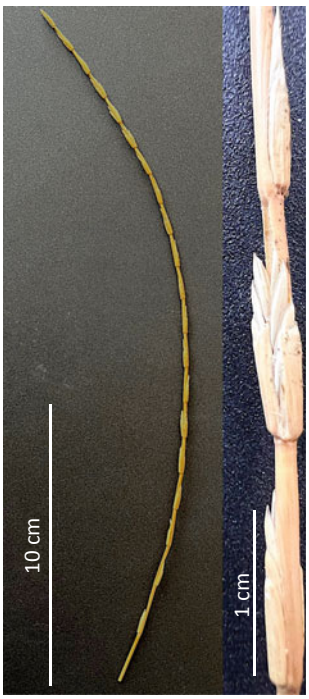

Fig. 8.1 A spike and part of a spike of *Amblyopyrum muticum* (Jaub. and Spach) Eig

Amblyopyrum muticum has a relatively limited distribution in the central region of the distribution of the wheat group (the genera *Amblyopyrum, Aegilops* and *Triticum*). It is a sub-steppical (Irano-Turanian) element; restricted mainly to steppical areas with 300 mm annual rainfall. It grows in many secondary, disturbed habitats. Sympatric with the following species: *Ae. speltoides*, *Ae. caudata*, *Ae. umbellulata*, *T. monococcum* ssp. *aegilopoides*, *T. urartu*, *Ae. geniculata Ae. biuncialis*, *Ae. neglecta*, *Ae. columnaris*, *Ae. triuncialis,* and *Ae. cylindrica*. Allopatric with *Ae. tauschii*, *T. timopheevii* ssp. *armeniacum* and. *T. turgidum* ssp. *dicoccoides.*

Othmemi et al. (2019) reviewed information showing that *A. muticum* carries several useful genes that, upon transfer to bread wheat, may improve its performance. It has been reported that this species tolerates environmental stresses (Iefimenko et al. 2015) and is resistant to powdery mildew (Eser 1998), and leaf rust (Dundas et al. 2015). In recent years, attempts are made to transfer some of these useful genes to bread wheat (King et al. 2017).

8.3 Cytology, Cytogenetics and Evolution

Amblyopyrum muticum is a diploid species (2n = 2x = 14) whose genome is designated T (Kimber and Tsunewaki 1988; Dvorak 1998) (formerly Mt; Kihara and Lilienfeld 1935). Its nuclear DNA amount is relatively small, i.e., 1C DNA is 5.82 pg (Eilam et al. 2007), similar to that of diploid *Elymus elongatus, Aegilops speltoides* and *Ae. uniaristata,* but significantly smaller than that of the other Sitopsis species and larger than that of *Ae. tauschii*, *Ae. caudata*, *Ae. umbellulata*, and *Ae. comosa* (Eilam et al. 2007). *A. muticum* has a symmetric karyotype with large metacentric or submetacentric chromosomes with two large satellites (Chennaveeraiah 1960). By means of in situ hybridization with pTa71 (18S-26S rDNA) and pTa794 (5S rDNA) DNA probes from *T. aestivum*, Badaeva et al. (1996a, b) determined the distribution of the 18S-5.8S-26S (18S-26S) and 5S ribosomal DNA gene families on chromosomes of *A. muticum.* It was found that *A. muticum* has major NOR loci, having the 18S-26S rDNA gene family on the short arm of chromosomes of groups 1 and 6 T, and a moderate-sized NOR locus was observed on the long arm of chromosome 7 T. Two 5S rDNA loci were observed, one on the short arm distal to the NOR locus of chromosome 1 T and a small locus on the short arm of chromosome 5 T. The distribution of the major NORs in *A. muticum* is as in *Ae. speltoides* and that of the 5S rDNA is similar to that of *Ae. bicornis.*

Both, *A. muticum* and *Aegilops speltoides are* allogamous species; *A. muticum* is obligatory allogamous, namely, self-incompatible (Ohta 1990), whereas *Ae. speltoides* is facultative allogamous and, at least several accessions, produce seeds upon bagging (Feldman M, unpublished). Both species have genes that promote pairing between homoeologous chromosomes in hybrids with allopolyploid wheat by counteracting the effect of the homoeologous-pairing suppressor of wheat, *Ph1* (Riley 1960, 1966; Dover and Riley 1972a). There is high pairing at meiosis in hybrids between *A. muticum* and tetraploid wheat (Kihara and Lilienfeld 1935), and hexaploid wheat (Riley 1966). The high pairing is presumably due to the occurrence of homoeologous pairing through the suppression of the activity of *Ph1* of allopolyploid wheats.

Dover and Riley (1972a) found that there is genetic variation in *Ae. mutica* affecting homoeologous chromosomal pairing at meiosis. From their study of hybrids between *T. aestivum* and different accessions of *Ae. mutica*, they concluded that *A. muticum* has two loci with alternative alleles that affect homoeologous pairing in hybrids with *T. aestivum*. Both the low pairing alleles, when together, condition little or no homoeologous pairing. The high pairing alleles are *epistatic* to the low-pairing ones at the other locus.

Two such genes inducing homoeologous pairing in hybrids with allopolyploid wheat containing the *Ph1* gene, were also found in *Ae. speltoides* (Dvorak 1972). In *Ae. speltoides* they were allocated to chromosomes 3S and 7S (Dvorak et al. 2006). In addition, a QTL with a minor effect was allocated to the short arm of chromosome 5S (Dvorak et al. 2006). The *speltoides* genes did not affect the level of pairing in the inter-specific diploid hybrids *Ae. speltoides* x *Ae. tauschii* and *Ae. speltoides* x *Ae. caudata* (Chen and Dvorak 1984). In contrast, studies of meiotic chromosomal paring in hybrids between *A. muticum* and diploid species of *Aegilops* and *Triticum* show relatively high paring with almost each of them, presumably due to the promotion of pairing by the *muticum* genes (Ohta 1990, 1991).

Kihara and Lilienfeld (1935) reported a mode of 7 bivalents (a range of 3 to 7 bivalents of which 3 to 4 were ring bivalents; mean bivalents 5.86) in F_1 hybrids of *Ae. comosa* x *Ae. mutica*. These data indicated to Kihara and Lilienfeld that *Ae. mutica* had close genomic homology with *Ae. comosa* and other M-genome diploids. Consequently, they assigned the symbol Mt to the genome of *Ae. mutica* to distinguish this species from others having M or M-derivatives (M°, M^{t}, M^{u}, M^{cr}, M^{v}, M^{b}, and M^{c}), because *Ae. mutica* has a distinctive spike morphology (Kihara 1947, 1954; Lilienfeld 1951). However, Chennaveeraiah (1960) found that the karyotype of *A. muticum* is very similar to that of *Ae. speltoides* and differ from the karyotypes of the M-genome species. In this regard, Jones and Majisu (1968) reported that chromosome pairing in *Ae. tauschii* x *A. muticum* hybrids was almost regular and exceeded the pairing in hybrids between *A. muticum* and Sitopsis species of *Aegilops* as well as between *A. muticum* and diploid *Triticum* species. They assumed that the chromosomes of *A. muticum* appear to have considerable homoeology with the D genome of *Ae. tauschii.*

Riley (1966) crossed *Ae. speltoides*, *Ae. longissima*, *Ae. caudata* and the wild and domesticated forms of *T. monococcum* with *A. muticum* and found high chromosome pairing in meiosis of all the F_1 hybrids. He suggested that *A. muticum* is cytogenetically close to *Ae. speltoides,* not only because of the high pairing, but also for the reasons that no chromosomal rearrangements were found between the two species and the similarity existing in the two species in pairing control as well as in their karyotypes (Chennaveeraiah 1960). Riley (1966) pointed out that the absence of any translocation difference between *Ae. speltoides* and *A. muticum* confirms the phylogenetic proximity that is indicated by their similarities in karyotype and pairing control of the two species. However, pairing in the *Ae. speltoides* x *A. muticum* hybrids is not so high as that in hybrids between *Ae. speltoides* and other members of the Sitopsis section of *Aegilops* (Kimber 1961).

Ohta (1990, 1991) performed a very detailed study on the cytogenetic relationships of *A. muticum* and diploids of the wheat group. He crossed *A. muticum* with 11 diploid species of the genera *Aegilops* and *Triticum*. The crossability was good and F_1 seeds were successfully obtained in all reciprocal cross combinations. However, in combinations where *A. muticum* was the female parent the seeds did not germinate. The cross *Ae. tauschii* x *A. muticum* yielded shriveled seeds while those of the reciprocal combination germinated regularly. In the cross *Ae. searsii* x *A. muticum*, the F_1 seeds did not germinate in the two reciprocal combinations. Previously, Jones and Majisu (1968) obtained similar results, i.e., shriveled seeds which did not germinate in the cross *Ae. tauschii* x *A. muticum* when *Ae. tauschii* was the female parent and normal size seeds that germinated in the reciprocal cross. They concluded that the difference in germination between the reciprocal crosses involving *Ae. tauschii* and *A. muticum* was not attributed to cytoplasmic difference between the parental species. Dhaliwal (1977) suggested that the difference in germination between reciprocal crosses might be attributed to different ratios of the parental genes in the triploid endosperm.

Most of the F_1 plants obtained by Ohta (1990) from the inter-generic crosses involving *A. muticum* and diploids of the wheat group grew normally and vigorously. From morphological features of the hybrid spikes, Ohta (1990) concluded that *A. muticum* is most similar to *Ae. speltoides*. In contrast to the F_1 hybrids between *A. muticum* and the diploid species of the wheat group that were completely sterile (except plants that formed unreduced gametes),

partially fertile F_1 hybrids were obtained from the crosses between *Ae. speltoides* and *A. muticum* (Ohta 1990). The fact that several functional male and female gametes with seven chromosomes were produced, in spite of a high frequency of inter-genomic recombination, clearly indicates that the two parental species, *Ae. speltoides* and *A. muticum*, are very closely related to each other. In the Anatolian Plateau these two species sometimes grow sympatrically. However, no natural hybrids between these two species were reported though they are out-crossing species (Ohta 1990).

Although they exhibit a high level of chromosome pairing at meiosis, the complete or partial sterility of the F_1 hybrids can result from cryptic structural hybridity (chromosomal sterility) or from genes that cause hybrid incompatibility (genic sterility). The fact that po1len grains containing unreduced chromosome complements are viable and functional, suggests that the sterility of the F_1 hybrids is not genic but chromosomal.

In most F_1 hybrids Ohta (1990, 1991) reported very high meiotic pairing (Table 8.1). Only in hybrids from the crosses of *Ae. caudata, Ae. uniaristata* and *Ae. umbellulata* x *A. muticum* there was a lower level of chromosome pairing than in the other hybrids. The relatively high pairing in most hybrids does not indicate very close relationship between the genome of *A. muticum* and the genomes of the different diploid species of *Aegilops* and *Triticum* that have diverged considerably from one another (Kihara 1954). In accord with the above, Kimber (1982), based on his numerical analysis of chromosome pairing in meiosis of F_1 hybrids between five allopolyploid *Aegilops* species and *A. muticum*, decided that the genome of *A. muticum* is non-homologous to the A, B, and D subgenomes of hexaploid wheat nor with U genomes of *Ae. umbellulata* and with the M-genome species, i.e., *Ae. comosa and Ae. uniaristata*. Consequently, Kimber and Tsunewaki (1988) while changing the two letter designations of the genome symbols in some *Aegilops* species to single capital letters, proposed the genome symbol T for *A. muticum* to distinguish it from the M-genome group and from the other diploids of the wheat group.

Amblyopyrum muticum and *Ae. speltoides* are the only species that contain B-chromosomes [Mochizuki (1957, 1960) in *muticum* and Simchen et al. (1971) in *speltoides*]. The Bs in *A. muticum* are euchromatic, metacentric and smaller than the A chromosomes, and their number in different individuals ranged from one to five (Mochizuki 1960). The Bs, in both *A. muticum* and *Ae. speltoides*, were stably found in the shoot apices and PMCs, while they were almost entirely absent from the seminal and adventitious roots (Ohta 1995).

The B-chromosomes of *A. muticum* do not affect homologous pairing but suppress homoeologous one in interspecific hybrids (Mochizuki 1964; Dover and Riley 1972b; Vardi and Dover 1972; Ohta and Tanaka 1982; Table 8.2). Studies on meiotic chromosomal pairing in F_1 hybrids between *A. muticum* and most of the diploid species of *Aegilops* and *Triticum,* containing B- chromosomes of *A. muticum,* showed much reduced chromosomal pairing, i.e., 14 univalents or 12 univalents with a rod-shaped bivalent of A-chromosomes (Vardi and Dover 1972; Ohta and Tanaka 1983; Ohta 1990, 1991; Table 8.1). Only the F_1 hybrids *Ae. speltoides* x *A. muticum* and *Ae. tauschii* x *A. muticum* exhibited somewhat higher pairing (Ohta 1990). However, in hybrids between autotetraploid *Ae. tauschii* and *A. muticum* only seven bivalents were observed, presumably between the *tauschii* chromosomes, indicating that the genomes of *muticum* and *tauschii* are not closely related (Ohta 1990).

Genome analysis in F_1 hybrids between *A. muticum* and ten different species of the wheat group, having zero or two B chromosomes of *A. muticum,* enabled Ohta (1990) to classify the various species of *Aegilops* and *Triticum* into the following three groups, based on their cytogenetic relationships to the genome of *A. muticum*: (i) the genomes of *Ae. caudata, Ae. uniaristata* and *Ae. umbellulata* are distantly related to that of *A. muticum;* (ii) the genomes of *Ae. bicornis*, *Ae. longissima*, *Ae. sharonensis*, *Ae. comosa,* and *T. monococcum* are homoeologous with that of *Ae. mutica*; and (iii) the genomes of *Ae. speltoides* and *Ae. tauschii* are closely related to that of *A. muticum*. Yet, based on plant morphology, chromosome pairing and fertility of the F_1 hybrids, Ohta (1990, 1991) concluded that the genome of *Ae. speltoides* is closer to that of *A. muticum* than the genome of *Ae. tauschii*, and that *A. muticum* and *Ae. speltoides* are the basal species in the group from which all other species have diverged.

Maan (1977) produced alloplasmic lines of bread wheat, *T. aestivum* ssp. *aestivum,* and *T. turgidum* ssp. *durum* in which their nuclear genomes were substituted into the cytoplasm of the diploid species, *Amblyopyrum muticum*, *Ae. comosa* ssp. *heldreichii*. (genome MM), *Ae. uniaristata* (genome NN), and allotetraploid *Ae. geniculata* (genome M^oM^oUU), to identify the M-genome diploid cytoplasm donor of *Ae. geniculata*. Substitution of the ssp. *durum* genome into *Ae. uniaristata* cytoplasm resulted in a large proportion of shriveled inviable seeds. A few plump viable seeds were obtained all of which produced male-sterile plants. The ssp. *aestivum* plants having *Ae. uniaristata* or *A. muticum* cytoplasms were fertile. *A. muticum* was similar to *Ae. geniculata* in the induction of delayed maturity and tall robust growth habit to the ssp. *durum* and ssp. *aestivum* plants. Cytoplasms of the other U- and M-genome diploids, *Ae. umbellulata* and ssp. *heldreichii* had been shown to differ from that of *Ae. geniculata*. Therefore, Maan (1977) concluded that *A. muticum* is the most likely cytoplasm donor to *Ae. geniculata* and its plasma type was designated "T". Panayotov and Gotsov (1973) and Panayotov (1983) found some variation in the effect of the cytoplasm of *A. muticum* on the phenotype of bread wheat and therefore, designated the *muticum* cytoplasm T^2. Thus, *Ae mutica,*

Table 8.1 Mean chromosomal pairing at first meiotic metaphase of F_1 hybrids between *Amblyopyrum muticum* (without B chromosomes) and species of *Triticum* and *Aegilops*

Hybrid combination	Genome	Univalents	Bivalents			Multivalents			Reference
			Rod	Ring	Total	III	IV	V	
Ssp. *monococcum* x *A. muticum*	A^mT	2.52	–	–	4.96	0.28	0.18	–	Riley (1966)
Ssp. *aegilopoides* x *A. muticum*	A^mT	3.70	–	–	4.88	0.10	0.06	–	
Ssp. *monococcum* x *A. muticum*	A^mT	0.63	2.70	2.83	5.53	0.10	0.50	–	Ohta (1990)
Ssp. *monococcum* x *A. muticum*	A^mT	1.20	2.58	2.48	5.06	0.28	0.46	–	
Ssp. *monococcum* x *A. muticum*	A^mT	2.03	2.80	2.23	5.03	0.23	0.30	–	
Ssp. *dicoccoides* x *A. muticum*	ABT	6.52	–	–	4.30	1.88	0.06	–	Riley (1966)
Ssp. *durum* x *A. muticum*	ABT	6.38	–	–	4.68	1.70	0.04	–	
Ssp. *aestivum* x A. muticum	ABDT	5.32	–	–	5.14	2.06	1.52	–	
Ae. speltoides x *A. muticum*	ST	2.84	–	–	5.58	–	–	–	
Ae. speltoides x *A. muticum*	ST	0.35	1.94	4.88	6.82	0.005	–	–	Ohta (1990)
Ae. speltoides x *A. muticum*	ST	1.12	2.99	3.43	6.43	0.003	0.003	–	
Ae. speltoides x *A. muticum*	ST	1.99	3.27	2.64	5.91	0.04	0.02	–	
Ae. bicornis x *A. muticum*	S^bT	0.20	1.50	5.40	6.90	–	–	–	
Ae. bicornis x *A. muticum*	S^bT	0.80	2.73	3.87	6.60	–	–	–	
Ae. sharonensis x *A. muticum*	$S^{sh}T$	0.96	2.04	4.48	6.52	–	–	–	
Ae. sharonensis x *A. muticum*	$S^{sh}T$	1.42	3.06	3.16	6.22	0.02	0.02	–	
Ae. longissima x *A. muticum*	S^lT	3.52	–	–	5.06	0.12	–	–	Riley (1966)
Ae. longissima x *A. muticum*	S^lT	1.83	3.96	1.30	5.26	0.40	0.07	–	Ohta (1990)
Ae. longissima x *A. muticum*	S^lT	0.67	1.77	3.67	5.44	0.33	0.37	–	
Ae. tauschii x *A. muticum*	DT	0.16	1.78	4.11	5.89	0.02	0.59	–	
Ae. tauschii x *A. muticum*	DT	1.09	2.62	3.78	6.40	0.01	0.02	–	
Ae. caudata x A. muticum	CT	3.53	–	–	3.33	1.27	–	–	
Ae. caudata x *A. muticum*	CT	3.03	2.83	0.70	3.53	1.30	–	–	
Ae. comosa x *A. muticum*	MT	0.33	2.87	3.97	6.84	–	–	–	
Ae. comosa x *A. muticum*	MT	1.93	3.37	2.67	6.04	–	–	–	
Ae. uniaristata x *A. muticum*	NT	4.44	3.54	0.34	3.88	0.60	–	–	
Ae. uniaristata x *A. muticum*	NT	4.48	4.10	0.13	4.23	0.35	–	–	
Ae. umbellulata x *A. muticum*	UT	2.60	2.15	0.06	2.21	2.02	0.04	0.15	
Ae. umbellulata x *A. muticum*	UT	4.00	2.52	0.08	2.60	1.54	0.02	0.02	
Ae. crassa 6x x *A. muticum*	D^cX^cDT	11.14	4.22	2.24	6.46	1.30	0.60	0.04	Melnyk and McGinnis (1962)
Ae. juvenalis x *A. muticum*	D^cX^cUT	14.21	4.66	0.08	4.74	1.08	0.25	0.02	

Table 8.2 Mean chromosomal pairing in F_1 hybrids between species of *Aegilops* or *Triticum* and *Amblyopyrum muticum* with and without B chromosomes (calculated from the data of Ohta and Tanaka 1983)

A. Pairing in hybrids lacking B- chromosomes						
Hybrid combination	Hybrid genome	Bivalents		Multivalents		Mean arm-pairing/cell
		Rod	Ring	III	IV	
Ae. speltoides x A. muticum	ST	2.75	3.06	0.03	0.04	0.65
Ae. bicornis x A. muticum	S^bT	2.80	4.00	–	–	0.77
Ae. longissima x A. muticum	S^lT	3.33	1.87	0.37	0.30	0.59
Ae. comosa x A. muticum	MT	2.79	3.93	–	–	0.77
Ae. caudata x A. muticum	CT	2.83	0.70	1.30	–	0.44
T. monococcum ssp. aegilopoides x A. muticum	A^mT	2.69	2.58	0.23	0.36	0.68
B. Pairing in hybrids containing B chromosomes						
Ae. speltoides x A. muticum	ST	3.05	0.85	0.06	0.01	0.35
Ae. bicornis x A. muticum	S^bT	0.04	–	–	–	0.003
Ae. longissima x A. muticum	S^lT	0.40	–	–	–	0.03
Ae. comosa x A. muticum	MT	0.50	–	–	–	0.04
Ae. caudata x A. muticum	CT	0.70	–	–	–	0.05
T. monococcum ssp. aegilopoides x A. muticum	A^mT	0.58	0.06	0.01	–	0.05

being an obligatory allogamous species, comprises intraspecific plasmon differentiation (Tsunewaki 2009). The plasmon of the allotetraploid *Ae. geniculata*, designated M^0, did not have any close relatives in the diploids, although their phenotypic effects to wheat characters were close to those of the T^2 plasmon of *A. muticum* (Tsunewaki 2009). Therefore, Ogihara and Tsunewaki (1988) and Tsunewaki (2009) concluded that the plasmon type of *Ae. geniculata* closely resembles plasmon types of *Ae. umbellulata* and *A. muticum*, and, therefore, either of those diploids or an unknown species related to them seems to be the cytoplasm donor of *Ae. geniculata*.

8.4 Phylogenetic Relationships of *A. muticum to Aegilops* and *Triticum*

Amblyopyrum muticum and *Aegilops speltoides* are the only allogamous species in the wheat group. Allogamy is considered a primitive character since most perennial species in the tribe Triticeae are allogamous. Stebbins (1957) pointed out that in many plant-groups autogamy derived from allogamy and therefore, autogamy may be considered as a more advanced trait. Hammer (1980) assumed that allogamous self-incompatible plants, resembling *Amblyopyrum muticum* and facultative allogamous like *Aegilops speltoides,* were ancestral types to the other genera of the wheat group, i.e., *Aegilops* and *Triticum*. He based this assumption on the combination of anther length and amount of pollen produced, with reductions in anther size and/or amount of pollen pointing at increasing autogamy, for which he found strong positive correlations. Long anthers that produce substantial amount of pollen are an indication of allogamy or transitional state to autogamy. On this, Hammer (1980) produced an evolutionary model explaining the sequence of origin of the various species.

Hammer (1980) assumed that the origin of the ancestral genera of the wheat group was in Transcaucasia. Awing to increase drought in the Pleistocene (1.8–0.01 MYA), many grass species, including the ancestral stocks of *Amblyopyrum–Aegilops*, started spreading in western and southwestern directions. The areas of the distribution of the diploids can thus be explained: the more primitive the closer to the center of origin. Thus, *A. muticum* and *Ae. speltoides*, the former restricted to Turkey, the latter in Turkey, reaching Bulgaria and along the Fertile Crescent might be considered as the most primitive species of the group. Speciation of the Sitopsis group apparently happened mainly on the western arc of the Fertile Crescent, with the species with the smallest anthers (*Ae. bicornis*) reaching the furthest (the Coast of Cyrenaica, Libya). Other diploids reached the eastern Mediterranean (*Ae. uniaristata* and *Ae. comosa*), or only partly so (*Ae. caudata and Ae. umbellulata*); one diploid spread mainly to the east (*Ae. tauschii*). In this old group speciation is relatively strong as is shown by the reported sterility of artificial hybrids of the Sitopsis species.

Coinciding with the speciation has been a gradual change in fertilization mechanism within the diploids from allogamy (*A. muticum* and *Ae. speltoides*), to facultative autogamy (*Ae. longissima, Ae. caudata, Ae. comosa*). Higher levels of autogamy are associated with lower values for anther length x width (as scored by Hammer 1980). This development

happened at the lowest, most primitive ploidy level. This model of distribution, speciation, and change to autogamy can also be applied to the wild taxa of *Triticum*. Hammer (1980) notes that the anther length of diploid *Triticum* is shorter than those of Sitopsis species, while other characters could be interpreted as reductions or subsequent changes in any of the two groups, e.g., two versus only one keel, hairy versus glabrous rachillae, and 1–2 versus 2–3 kernels per spikelet. This, as well as the distribution patterns, underline the development of both groups out of a common ancestor, with according to Hammer, the flower biology of the diploid *Triticum* considered more derived and of *Aegilops* more-closer to the common ancestor.

At the early stage during the late Pleistocene, it is supposed that *A. muticum*, an obligate allogamous species, separated from the common stock during the westward migration through Asia minor (Hammer 1980). Eig (1929b) considered this an old species, being most closely related to the oldest section of Aegilops (Sitopsis) and showing relatively little plasticity in its morphology. Many morphological characters place this species apart from all *Aegilops* species while karyotype analysis showed similarity with what Hammer (1980) considered the most primitive *Aegilops*, i.e., *Ae. speltoides* (Chennaveeraiah 1960).

Out of the initial distribution of the diploids, the allotetraploids spread further westwards along the Mediterranean basin as well as in more northern, southern and eastern directions. This process continued until halted by natural boundaries and lack of suitable environments, such as the Saharan and Arabian deserts, the central Asian steppes, the Tian Shan and Himalayan Mountains or the coldness of the continental climate affecting the spread to the north and east.

The complicated interactions that happened in the process of allopolyploidization resulted in an intergrading network of forms and reproduction strategies that make it impossible to point at any direction of the evolution at this stage. The tetraploid stage is apparently dominant and a further development into hexaploids has been limited.

Amblyopyrum separated from the ancestral *Aegilops* lineage at an early stage, of which *Ae. speltoides* is thought to be the most primitive representative of *Aegilops*. Phylogenetic speculation that assumes a change from obligatory allogamy (as in *A. muticum*) towards almost complete autogamy (as in species of *Aegilops*, *Eremopyrum*, *Heteranthelium*, *Henrardia* and *Triticum*), coinciding with a divergent development in morphology, makes a separation at an early stage from the ancestral *Aegilops* lineage plausible (Hammer 1980).

Based on karyomorphological studies, Senjaninova-Korczagina (1932) concluded that the karyotype of *A. muticum* is similar to those of *Ae. tauschii* and *Ae. comosa* but is very different from those of *Ae. caudata* and *Ae. umbellulata*. Chennaveeraiah (1960), found that *A. muticum* has large chromosomes with median or sub-median centromeres, of which two pairs have fairly large satellites on their short arms. He argued that the karyotype of *A. muticum* is different from those of *Ae. comosa* and *Ae. tauschii*, and is more similar to those of the species of section Sitopsis, especially to that of *Ae. speltoides*. The karyotype analysis of these species by Giorgi and Bozzini (1969) confirmed the finding of Chennaveeraiah (1960), displaying a similar though not identical karyotype of *Ae. speltoides* and *A. muticum.* Thus, also from a karyomorphological view, a close phylogenetic relationship exists between *A. muticum* and *Ae. speltoides.* However, according to Jones and Majisu (1968), this karyotype similarity does not seem to be indicative of any greater homology between these genomes. In spite of that, since most species of the Triticeae, and particularly those that belong to the Arctic-temperate group, have large chromosomes with median or sub-median centromeres, it is assumed that this type of karyotype is characteristic of the prototype of the tribe. Hence, *A. muticum* having large chromosomes and symmetric karyotype is one of the primitive species in the sub-tribe Triticineae.

Analysis of the cytoplasm of *A. muticum* pointed at a close genetic relationship with the cytoplasm of the allotetraploid species *Ae. geniculata* (Maan 1977). Ohsako et al. (1996), studying variation in chloroplast and mitochondrial DNA by PCR-SSCP analysis, found that the level of intraspecific variation in *A. muticum* was lower than that in *Ae. speltoides* and, consequently, suggested that *A. muticum* is not older than *Ae. speltoides*. This suggestion is in contrast to the hypothesis of Hammer (1980) and Ohta (1990, 1991) that *A. muticum* is an ancestral species in the group. In the phylogenetic trees, *A. muticum* was included in different cluster than the other *Aegilops* and *Triticu*m species (Ohsako et al. 1996). Yamane and Kawahara (2005) conducted phylogenetic studies by analyzing chloroplast DNA sequences from four regions of the diploid species of the wheat group and found that *A. muticum* was included in the most terminal clade close to *Ae. umbellulata*. Likewise, Terachi et al. (1984) and Murai et al. (1989) studied chloroplast DNA and suggested that *A. muticum* is close to *Ae. umbellulata* while Terachi and Tsunewaki (1992), based on mitochondrial RFLP analysis, suggested that it is close to *Ae. tauschii*. This poses a discrepancy between molecular phylogeny and classification based on morphology.

Sasanuma et al. (2004) pointed out that discrepancy also exists between results of chromosomal pairing in interspecific hybrids and molecular data from plasmon analysis. They studied intra- and inter-specific variation in seven diploid *Aegilops* species (including *A. muticum*) using AFLP technique. Of the seven species, the cross-pollinating *Ae. speltoides* and *A. muticum* showed the highest levels of intraspecific variation. In their study, *A. muticum* did not form a clear cluster with any other *Aegilops* species.

Dvorak and Zhang (1992), analyzing repeated DNA sequences, concluded that *A. muticum* is close to *Ae. caudata*, *Ae. comosa*, *Ae. uniaristata* and *Ae. umbellulata*. Wang et al. (2000) compared the internal transcribed spacer (ITS) region of the ribosomal DNA in the diploids of the wheat group (including *A. muticum*) and observed wide divergences of this sequence between species. The highest divergence was between *Ae. speltoides* and *A. muticum.* In-situ hybridization with repeated DNA markers and C-banding patterns suggest that *A. muticum* occupies an isolated position but relatively closer to the Sitopsis species than to other species of *Aegilops* (Badaeva et al. 1996a). Sallares and Brown (2004), who analyzed the transcribed spacers of the 18S ribosomal RNA genes, reached a similar conclusion, namely, that *A. muticum* has a basal position and that it is close to *Ae. speltoides*. Yet, in several phylogenetic analyses based on nuclear DNA sequences *Amblyopyrum* is a good, monophyletic genus (Frederiksen and Seberg 1992; Frederiksen 1993). Most morphological and molecular trees included *Amblyopyrum* in the *Aegilops* clade (e.g., Seberg and Petersen 2007) and in other molecular trees several species of *Elymus* (=Agropyron) are also included in this clade (Mason-Gamer et al. 1998), even though, the relationships of *Amblyopyrum* within the *Aegilops* clade remains at present somewhat vague.

Based on their molecular phylogenetic studies, Marcussen et al. (2014) concluded that the A and B (=S) lineages, the early *Triticum* and *Aegilops speltoides* forms, diverged from a common ancestor about 7 MYA, and that these ancestral forms gave rise to the D-genome lineage through homoploid hybrid speciation 1–2 million years later. Since then, more complex evolutionary scenarios with several rounds of hybridization have been proposed (Li et al. 2015; El Baidouri et al. 2017). However, these studies involved only a number of the diploids of the wheat group. In contrast, Glémin et al. (2019) obtained and analyzed a comprehensive genomic dataset including all extant diploid species of *Amblyopyrum*, *Aegilops* and *Triticum,* and developed a new framework to test intricate hybridization scenarios. Owing to these new developments, Glémin et al. (2019) were able to propose a core reference scenario for the history of diploid *Aegilops*/*Triticum* species. They confirmed the occurrence of an ancient hybridization event that gave rise to the D lineage, but showed (i) that this lineage includes 9, not only 5, of the 13 diploid species of the wheat group, and (ii) that the hybridization scenario involved a different parental species, *A. muticum* instead of *Ae. speltoides*. Glémin et al. (2019) pointed out that *A. muticum* has been an overlooked species with a debated phylogenetic position, and that their results plead for reconsideration and extensive study of this key species in the history of wheat relatives. To reconcile with the hypothesis of Marcussen et al. (2014) . with that of Glémin et al. (2019), it is suggested that the homoploid hybridization scenario involved the ancestral genome S/T before the divergence of *Ae. speltoides* from *A. muticum*.

Similar to Glémin et al. (2019), also Bernhardt et al. (2020) hypothesize that most of the diploid species of the wheat group were shaped by a primordial homoploid hybrid speciation event, that is the *Triticum* lineage merged with the ancestor of *A. muticum* to form all other species of *Aegilops* except *Ae. speltoides*. These results highlight the pivotal role of *A. muticum*, instead of *Ae. speltoides*, in the formation of the wild diploids of the wheat group. This hybridization event was followed by multiple introgressions affecting all taxa except *Triticum*. Mostly progenitors of the extant species were involved in these processes, while, according to Bernhardt et al. (2020), recent interspecific gene flow seems insignificant.

The results of Glémin et al. (2019) and Bernhardt et al. (2020) highlight the key role of *A. muticum*, instead of *Ae. speltoides*, in the formation of the diploid species of *Aegilops*. This hybridization event, was estimated to have occurred about 5.5 MYA based on whole genome sequences (Li et al. 2022). It was followed by multiple ancient introgressions affecting all taxa except *Triticum*. In contrast with Glémin et al. (2019), Bernhardt et al. (2020) do not find introgression of *Triticum* into *A. muticum*, instead their results indicated that *A. muticum* may have been introgressed by the *unbellulata/caudata* (U/C) group. Introgression to *A. muticum* from *Ae. umbellulata* (genome U) was also suggested from chloroplast phylogenetic research (Yamane and Kawahara 2005; Bordbar et al. 2011; Bernhardt et al. 2017). Hence, the maternal lineage of *A. muticum* does not group with *Ae. speltoides*, although both are sister taxa in nuclear phylogenies, but it shares a common ancestor with *Ae. umbellulata*.

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