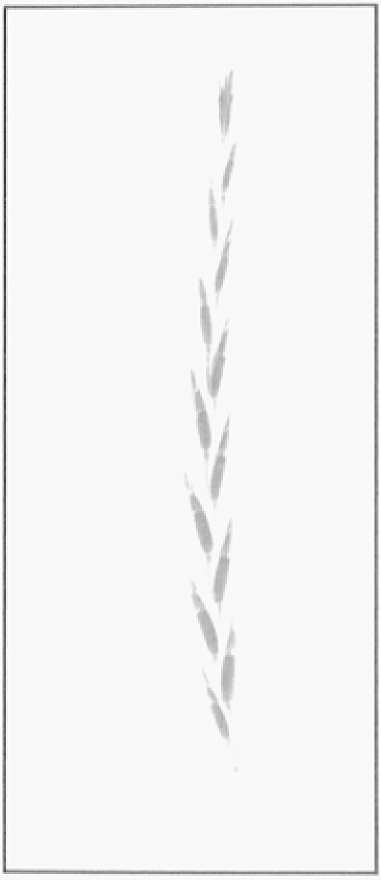
Wild Wheat

An Introduction

Gordon Kimber
and
Moshe Feldman



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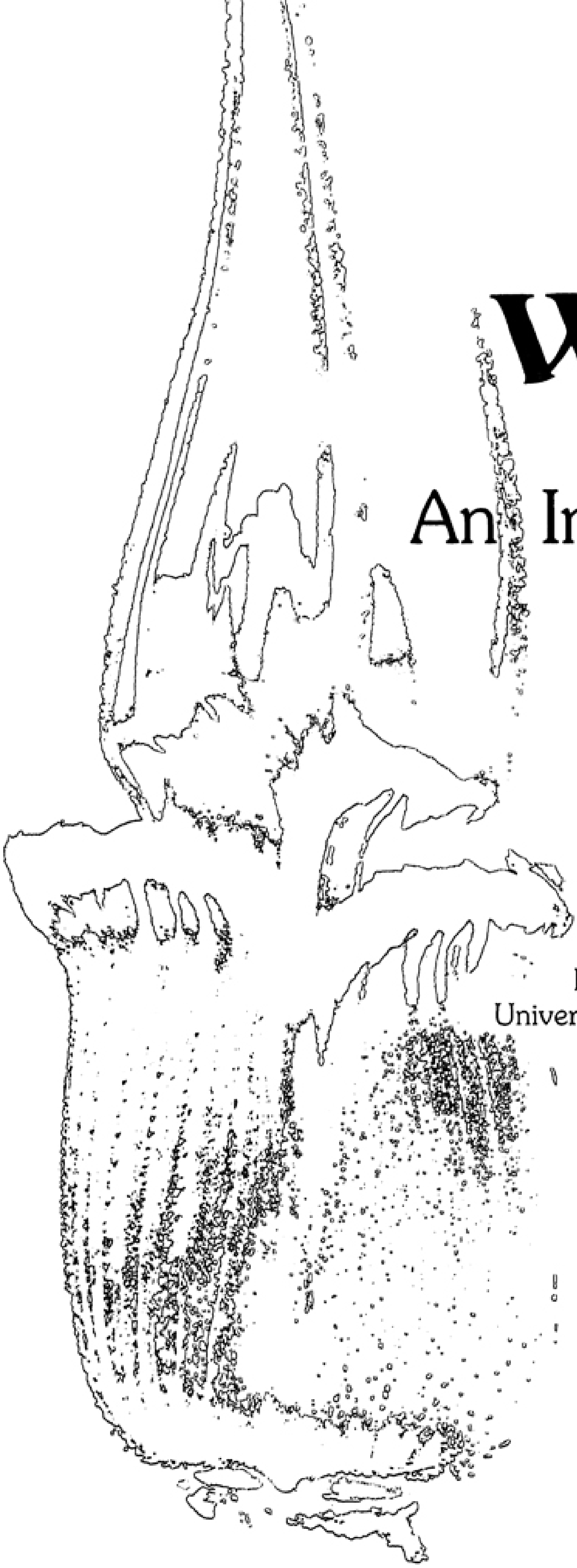

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PREFACE

Considerable interest has developed in recent years in the wild wheats. This interest has two major aspects. First, classical taxonomic, cytological and evolutionary studies and second, more pragmatic considerations such as the introduction of alien variation into the cultivated forms by the techniques of chromosome and genetic engineering. This blossoming of interest has been manifested in new collecting expeditions, the establishment of gene banks and the worldwide distribution of stocks of both the wild and cultivated species. It is also accompanied by much confusion in the identification, taxonomy and genomic relationships of the species. This small book is aimed at a resolution of these problems.

There has been, and it seems there perhaps always will be, considerable dispute concerning the generic and specific epithets employed in the description of this group. It is not our concern to enter into these arguments. Rather, it seems to us, it is much more important to be able to identify a particular genetic entity. The appending of a preferred epithet is perhaps superficial to the genomic, cytological, evolutionary or pragmatic status of the plant. Consequently there is no priority intended or implied by the choice of names. A table of the more common synonyms is given.

A new key has been developed to aid in the identification of the wild species. It has been tested by the authors on species in cultivation, in collections and in the wild. Several of our colleagues (especially R. J. Metzger and J. Mattatia) have also used the key and made suggestions for its improvement. For this and other help, we are very grateful. Following the key are tables comparing characteristics of species most often confused.

We would like to thank L. Avivi for her critical reading of the other parts of the manuscript.

Species descriptions, based largely on the monograph of Eig (1929) and our own observations, are provided. Considerable new information concerning the distribution, evolutionary, and genomic relationships, and some other data is appended. Each description is faced with photographs of the species. The photographs were taken from plants grown in greenhouses either at the University of Missouri-Columbia or at the Monsanto Company in St. Louis. The photographs with black backgrounds were taken by scanning photomacrographic techniques in order to obtain sufficient depth of focus.

Chapters dealing with geographical distribution, ecological affinities, natural and artificial hybrids, cytogenetics, genomic analysis, evolution, and the use of alien variation follow the species descriptions. A bibliography is placed at the end.

This book is intended as an introduction and as a field and laboratory guide. It is bound so that it may be carried to the field or greenhouse where it should be useful for identifying growing material. It is not to be construed as a taxonomic monograph.

The purchase of the Dynaphot, on which the scanning photomacrographs were made, and the printing expenses were paid by the provision of a most generous gift from the Monsanto Company. This gift, the growth of plants in the Monsanto greenhouse, and the support and constant encouragement of our colleagues in the Monsanto Company are most gratefully acknowledged.

Funds for the printing and distribution of an additional 1000 copies were most generously provided by the International Board for Plant Genetic Resources.

The authors are indebted to Dr. E. R. Sears for his many helpful suggestions, ideas and advice, and, in particular, for his critical reading of the entire manuscript.

INTRODUCTION

Linnaeus (1753) named seven genera in the tribe **Triticeae** including both **Triticum** and **Aegilops.** The genus **Triticum** contained species with cultivated forms, while **Aegilops** encompassed the wild relatives.

It would seem that this dichotomy was upheld by taxonomists for some 200 years. Eig (1929) and Zhukovsky (1928), for example, were both clear in calling the non-cultivated species **Aegilops.** Kihara's (1959) classification was essentially similar and also employed the **Aegilops** epithet. Hammer (1980) in a more recent monograph would also separate the two genera. A similar conclusion was reached by Gupta and Baum (1986). Stebbins (1956), however, proposed that the two genera be amalgamated into one since there were essentially no genetic barriers between them. Similarly, Bowden (1959) proposed a classification including both **Aegilops** and **Triticum** in the one genus **Triticum.** This classification was adopted essentially unchanged by Morris and Sears (1967).

A more radical re-classification, including the annual **Triticeae,** has recently been proposed by Löve (1982) on the premise that taxonomy should reflect phylogeny. This proposal places those species which are genomically the same into a single genus. There are at least two problems with this idea. First, finding agreement on what constitutes similar genomic constitutions and; second, the choice of names for the many new, and frequently monotypic, genera. Few would disagree, however, with the use of evolutionary relationships as a basis for classification.

The present text follows the classification of Morris and Sears (1967) but with some modifications. Since this usage is not universally accepted a list of the more frequent synonyms is given later in this work.

Nomenclatural disputes in this tribe are not limited to the choice of generic epithets. Many specific names have been coined, used, misused and confused. The choice of the specific names used here must not be taken as justification for them. They are used simply so that individual entities may be recognized. Again, reference should be made to the list of synonyms.

Of the wild forms, genomically identical to the cultivated species, only three are recognized. The name **T. monococcum** is used to include all the A-genome diploid species. The AB-genome tetraploids are collectively titled **T. turgidum**, while the AG-genome tetraploids are called **T. timopheevii.** The hexaploid form of **T. timopheevii** (var. **zhukovskyi**), genomically AAAAGG, is not placed in the key.

Two forms of **T. speltoides** (**ligustica** and **aucheri**) are keyed out. They have been variously named in other treatments, are recognizably different but are cross-breeders, totally interfertile, and they often grow sympatrically. Also within the **Sitopsis** section of the former genus **Aegilops** the two forms which are combined in the classification of Morris and Sears into **T. longissimum** are given specific rank here as **T. longissimum** and **T. sharonense.** They do not grow in the same habitat, flower at different times and differ by a reciprocal translocation. The new species **T. searsii** described by Feldman and Kislev (1978) since the classification of Morris and Sears (1967) is also accorded specific rank.

Polyploid taxa with forms that differ by a single genome have generally been divided into separate species. The hexaploid **T. syriacum** is probably genomically distinct from the hexaploid form of **T. crassum**, of which it has been described as a sub-species. This has been recognized in this treatment. It was originally collected by Vavilov in Syria (Salamick) and named **Ae. crassa** var. **vavilovi** by Zhukovsky (1928). It was also described by Eig (1928, 1929) as **Ae. crassa** var. **palaestina.** This form was named **Ae. vavilovi** by Chennaveeraiah (1960) and this synonym was used by Bowden (1959) for the new name **T. syriacum.** The genomic constitution was proposed by Kihara (1963) on the basis of morphological comparisons. Since it appears that this species is genomically distinct from the hexaploid **T. crassum,** we accord it specific rank with the name proposed by Bowden (1959).

The tetraploid and hexaploid forms of **T. triaristatum** are separated by the key and given the names **T. neglecta** and **T. recta** respectively.

The two species **T. kotschyi** and **T. peregrinum** are keyed out, the latter at two places (**T. peregrinum** and **T. peregrinum** (**cylindrostachys**)).

One of the characteristics of this group of species is their ability to exchange genetic material from one to another. Not only is material exchanged between sympatric polyploids sharing a common genome, as demonstrated by Zohary and Feldman (1962), but also between diploids and related polyploids (Vardi, 1973). These reticulate patterns of evolution of course tend to produce an increased range of variation and consequent difficulties in the identification of species. In addition it is quite common to find several species of similar morphology growing at the same location (**T. ovatum** and **T. umbellulatum**, for example). It is the intent of this work to allow workers, both in the field and in the laboratory, to identify the forms with which they are working. The nomenclatural justification of the names of these forms is clearly outside the domain of the present authors.

This approach should have several advantages. It avoids dispute by ignoring it. The resolution of the many taxonomic problems associated with this genus is clearly beyond an introductory book. The taxonomy of this group has changed in the past and, no doubt, will change again in the future. Consequently, it seemed that the ability to be able to place some name on a plant found in the field was much more important than the perhaps endless modification of a taxonomic treatment.

The species descriptions are largely based on the authors' translation of the descriptions of Eig (1929) and on their own observations. The descriptions are accompanied by photographs to assist in the recognition of diagnostic characters and to aid the identification of the species. They are placed so that each description faces the photographs of the species. The photographs are all of greenhouse-grown specimens. As a supplement to the species descriptions, information is given on the distribution of the species, its habitat, its genomic constitution and various other items.

The increased interest in the wild species of this group as a source of genetic material of practical consequence has led many workers to a much closer contact with these forms. They need to be sure of the genomic constitution of their material in order that they may most effectively introduce the desirable alien variation into the cultivated forms. The development of gene banks at many locations have also produced a need for the consistent identification of the materials that are maintained and also placed in their herbaria. This work is, in part, directed to these needs.

The genomic constitution of the various species is referred to at various points in the text, and there is a chapter describing genomic analysis. The list of symbols presented at the 6th International Wheat Genetics Symposium in Kyoto, Japan (Kimber and Sears, 1983) is given later in this text and is used whenever genome symbols are given. The genomic analysis of wheat and its relatives provides both an insight into the evolutionary past of the genus and a sound basis for the pragmatic use of both wild and cultivated forms. Both the evolution and the utilization of alien variation are described in separate chapters. The ploidy level is also given in the species descriptions, and there is a brief chapter outlining the cytology of the genus. Known artificial hybrids are listed in tabular form and also referred to in the text. A bibliography is given at the end.

TRITICUM KEY

The key starting on the next page is not perfect; however, its use together with the descriptions and photographs should allow the identification of the wild **Triticum** species. The imperfections stem from various sources. The conflict between efforts at simplification in order to reduce the key to manageable proportions and the inclusion of the nuances essential for the recognition of the many forms found in this polymorphic and inter-breeding genus is perhaps the greatest source of imperfection.

Each specific name in the key is followed by square parentheses **[]** containing the page number on which the description can be found, and on the page facing the description are photographs of the species.

On the pages facing the key are notes providing clarification of the terms or descriptions in the key. Some of the notes are accompanied by numbers in the form: 5/6. This indicates that this note refers to the dichotomy in entry number 5 that leads to entry number 6.

Some species are easily confused, **T. umbellulatum** and **T. ovatum** for example. Consequently several tables are provided following the key that should assist in the resolution of this type of difficulty.

The length of the spike, where given, both in the key and in the individual species descriptions, does not include the length of any awns.

KEY

1) Spike bilaterally compressed, two-rowed, wedge-shaped disarticulation into individual spikelets at maturity..4

Spike round in section, barrel-shaped or entire-spike disarticulation (if awnless, may have wedge-shaped disarticulation)..2

2) Spike round in cross section, long, parallel or slightly tapering, barrel-shaped disarticulation at maturity..9

Spike cylindrical, ovoid or lanceolate, whole-spike disarticulation (if awnless, may have wedge-shaped disarticulation)..3

3) Spike cylindrical, one-rowed spike, awnless, or awns on lateral spikelets, if present, less developed than the large awns on the terminal spikelet..............14

Spike ovoid to lanceolate, awns on glumes more developed than on lemmas.....................................22

4) Hairs on rachis internode, glume with well-developed keel, grain free at maturity............................5

Rachis internode devoid of hair.........................7

5) Grain bilaterally appressed, fertile terminal spikelet generally in the same plane as the laterals, one grain per spikelet, sometimes two in the center of the spike, palea membranous, splitting along the keel at maturity.............................**T. monococcum** [42]

Grain ovoid to round in section, terminal spikelet at right angles to the plane of the laterals..............6

6) Spike parallel and long, spikelets wedge-shaped, awns well developed, keel on the glume well-developed, glumes usually not hairy................**T. turgidum** [46]

Spike strongly bilaterally compressed, tapers to tip and base, spikelet ovoid, awns weak, keels on glumes less pronounced, glumes usually hairy.....**T. timopheevii** [44]

Notes for entries 1-6

1/4 For photographs of typical spikes see plates on pages: 27, 29, 31, 43, 45 and 47.

2/9 For photographs of typical spikes see plates on pages: 67, 69, 71, 73, 75 and 77.

3/14 For photographs of typical spikes see plates on pages: 23, 25, 33, 35, 37 and 39.

3/22 For photographs of typical spikes see plates on pages: 49, 51, 53, 55, 57, 59, 61, 63 and 65.

4/5 See spikelet from **T. monococcum** (photograph on page 43) showing hairs on the rachilla.

4/7 See plates on pages 27, 29, and 31.

7) Truncate glume with a thickened edge, sometimes with a small tooth on the margin. Awns on lemmas of lateral spikelets.................**T. speltoides** (**ligustica**) [26]

Glume without thickened edge, glumes with two teeth or a tooth and a small awn....................................8

8) Spike lax, spikelet 8-13 mm long, lemma awns in upper spikelet with two basal teeth...**T. sharonense** [30]

Spike compact, spikelet 5.5-8.5 mm long, lemma awns without basal teeth.......................**T. bicorne** [28]

9) Glumes truncate with thickened rim, never awned, do not overlap. Awns on lemma triangular in cross section ....**T. tauschii** [66]

Glumes with teeth, or teeth and awns..................10

10) Lemmas on lateral spikelets not awned, lemmas on terminal spikelet strongly awned, awns triangular in cross section, always the longest awns on the spike. Glumes of lateral spikelets with two teeth, one of which is sometimes elongated into a short awn, progressively longer to the tip of the spike. Spikelet cylindrical, narrow, usually shorter than the adjacent rachis internode, glumes more than three-quarters the length of the spikelet.........................**T. cylindricum** [68]

Spikelets pear-shaped or somewhat inflated...........11

11) Spikelet pear-shaped, usually constricted below the top, spike markedly like a string of beads, edge of glume strongly overlapping...........**T. ventricosum** [70]

Spikelets not pear-shaped. Awns of lemmas on lateral spikelets stronger than glume awns on the same spikelet 12

12) Spikelets cylindrical to slightly inflated at the base, at least three times longer than broad, lemmas of terminal spikelet with a long, flat awn with a prominent central nerve and two basal teeth.......**T. syriacum** [76]

Awns of the lemmas of the terminal spikelet either flat and without basal teeth or triangular with two basal teeth or three awns.................................13

Notes for entries 7-12

7 See also **T. speltoides** var **aucheri** (entry 16) and plates on page 25. These two varieties are cross fertile and intermediate types can be found.

8 Comparison of the plates and descriptions on pages 28 through 31 should be made to clarify any difficulties encountered with these two species.

The shapes of the spikelets, while being somewhat variable, provide a good first indication of the species in entries 9 through 13. See plates on pages 67, 69, 71, 73, 75 and 77. See also the table comparing the characters of **T. syriacum**, **T. juvenale** and **T. crassum** on page 20.

13) Fertile spikelets 4-7, glumes with 2-4 awns, sometimes reduced to teeth, when only two often with a wide gap, lemmas of terminal spikelet with a single awn, triangular in section, with two basal teeth or sometimes three awns..............................**T. juvenale** [74]

Fertile spikelets 7-12, glumes with 1-3 teeth or in the upper spikelets with a short, slender awn, lemmas of the terminal spikelet gradually tapering into a flat awn with two small basal teeth...............**T. crassum** [72]

14) Spike awnless, long with many spikelets (10-15, or more), florets equally spaced on a long rachilla, glume one third to one half length of spikelet, glumes shaped as inverted trapezoid, wedge-shaped disarticulation at maturity...........................**T. tripsacoides** [22]

Spike with awns......................................15

15) Awns, usually two, present only on the lemmas of the terminal spikelet, awns on the glumes, if present, are much reduced....................................16

Awns usually more developed on glumes than on lemmas..18

16) Glume truncate, often with a small tooth, glume about one-third to one half-the length of spikelet...................**T. speltoides** (**aucheri**) [24]

Glumes with two teeth usually separated by a membraneous edge...17

17) Awns on the terminal spikelet approximately equal in length, shorter than the spike, triangular in cross section. Glumes are half to three quarters the length of the spikelet. Upper two thirds of the spike disarticulates as a unit at maturity. Caryopsis adherent, plant tall (70-110cm) .....**T. longissimum** [32]

Awns of the terminal spikelet clearly unequal in length and width, the longest flat and longer than the spike. Glumes three quarters or more as long as the spikelet. Spike disarticulates as a unit at maturity above the lowest spikelet. Caryopsis more or less free, plant short (20-50cm)..........................**T. searsii** [34]

Notes for entries 13-17

13 See table on page 20 for a comparison of these two species and also **T. syriacum.** The plates on pages 73, 75 and 77 should also be examined.

14 This species can easily be recognized by the length of the spike and the many spikelets. There is no other species like it in the group.

15/16 See plates on pages 25, 33 and 35.

15/18 See plates on pages 37, 39, 41, 61 and 65, and the two tables on pages 18 and 19.

16 and 17 The species keyed out in these entries are the alternate forms to **T. sharonense** and **T. speltoides** var **ligustica** keyed out in entries 7 and 8. The two forms of **T. speltoides** will hybridize and intermediate forms can be found. There does not seem to be an alternate form to **T. bicorne** with only terminal awns. Some authors wish to include **T. longissimum** and **T. sharonense** into one species. They are kept separate in this treatment.

17 The distinction between these two species may be difficult. The essential differences are listed in the two parts of the entry. Photographs are to be found in the plates on pages 33 and 35.

18) Glumes of lateral spikelets never with more than one awn. Upper glume in the terminal spikelet with one or three awns.......................................19

Glumes of lateral spikelets with 2-3, awns sometimes reduced to teeth. Upper glume in the terminal spikelet with 2 or 3 awns, sometimes reduced to teeth..........21

19) Spike long, cylindrical, 4-8 spikelets ....**T. dichasians** [36]

Spike short, usually tapering, 2-3 spikelets..........20

20) Awns on lateral spikelets, glumes of lateral spikelets with a large, triangular tooth separated from the awn by an angle. Awn on the terminal spikelet wider than the awns of the lateral spikelets. Usually three basal rudimentary spikelets.........**T. uniaristatum** [40]

Usually no awns on the lateral spikelets, if present then much reduced. Lower glume of the terminal spikelet with three awns, seldom one. Basal rudimentary spikelets usually one....................**T. comosum** [38]

21) Central awn on the glumes of terminal spikelet is longer and broader than its laterals and also is the longest awn on the spike. Awns of lateral spikelets triangular in cross section. Spikelet elliptical to lanceolate. Glumes at least three quarters as long as the rachis segment. Caryopsis free...**T. triunciale** [60]

Awns on glumes of terminal spikelet variable, central awn not always the largest. Awns of lateral spikelets, if present, are flat. Spikelets inflated in the upper part. Glumes about two-thirds as long as the spikelet. Caryopsis adherent..**T. peregrinum** (**cylindrostachys**) [64]

22) Spikes ovoid, glumes on lower spikelets suddenly inflated, usually 4-7 awns on glumes of lowest fertile spikelet...23

Usually less than 4 awns on the glumes................24

Notes for entries 18-22

18/19 Usually the awns on the glume of the terminal spikelet are very well developed, see plates on pages 37, 39 and 41.

18/21 The species **T. peregrinum** (**cylindrostachys**) is most variable and may cause difficulty in using this, or any other, key.

19 The distinction based on the length of the spike and the number of spikelets is consistent, see plates on pages 37, 39 and 41.

21 See note 18/21. Perhaps the most constant character allowing distinction between these species is the free or adherent grain. The large central awn of the glumes of the terminal spikelet coupled with the small central awn of the lower spikelets is also a combination of characters that is consistent for **T. triunciale.**

22/23 The sudden inflation of the glumes is usually very clear. There are forms with less than 4 awns on the glumes of the lowest spikelet.

22/24 The occurrence of 4 awns is very unusual.

23) Glume abruptly inflated above the middle, basal rudimentary spikelets 3, 4-6 spikelets, internodes of the upper spikelets usually equal or longer than the adjacent spikelet, lemmas of lower fertile spikelets with 8-12 veins near the top........**T. umbellulatum** [48]

Glume abruptly inflated at middle or below, basal rudimentary spikelets 1 (seldom 0 or 2), 2-4 (usually 3) spikelets, internodes of upper spikelets usually equal to or shorter than the adjacent spikelet, lemmas of the lower fertile spikelets usually with 5-7 veins near the top..**T. ovatum** [50]

24) Spike abruptly narrows, due to reduction in upper spikelet size, upper spikelets fertile or infertile, shorter than rachis internode............................25

Spike tapers or is parallel.............................27

25) Both glumes of lateral fertile spikelets with two awns, one much broader than the other. Usually 5 spikelets (4-6), spike 4-6 cm long.....**T. columnare** [58]

Glumes of lateral fertile spikelets usually with three awns (rarely 4) of equal width or one glume three-awned and the other with two awns unequally broad. Usually 4 (2-5) spikelets, spike 2-3 cm long....................26

26) Florets of terminal spikelets fertile, lemma longer than glume..........................**T. recta** [54]

Spike suddenly narrows, uppermost spikelets infertile, lemma equal in length to the glume......**T. neglecta** [52]

27) Nerves on central part of the lower glumes equally broad, approximately parallel, glume length about two-thirds of spikelet, grain adherent....................28

Glume nerves unequally broad, grain free..............29

28) Spikelets small, linear. Glumes usually with three narrow, equal-sized awns which are equal in length to the lemma awns.........................**T. kotschyi** [62]

Spikelets broad, inflated in upper parts. Glume awns usually unequal in length and width, sometimes reduced to teeth, but if present then usually longer than the lemma awns.........................**T. peregrinum** [64]

Notes for entries 23-27

23 See species descriptions and plates on pages 48 and 50. The table on page 18 contains a list of the differences of these two species.

24/25 The sudden narrowing of the spike is often, particularly in **T. columnare**, very marked. In some forms of **T. neglecta** and **T. recta** the upper rachis segments are also reduced in length, but again the spike becomes suddenly narrow.

27 The two forms keyed out in 27/28 and in entry 28 are very variable and often difficult to distinguish. Both of them have grain that is adherent and this character is consistent. See plates on pages 63 and 65.

29) Spike long (4-6 cm), central awn on glumes of terminal spikelet longer and broader than its laterals and also is the longest awn on the spike. Awns on lateral spikelets usually triangular in cross section. Lemma awns on lateral spikelets absent or weakly developed. Basal rudimentary spikelets usually 3. ....**T. triunciale** [60]

Spike short (2-3cm), glumes of terminal spikelet with awns of equal size, which are larger than all other awns. Awns of lateral spikelets flat. Lemma awns at least one. Basal rudimentary spikelets 1 (seldom 2). ....**T. macrochaetum** [56]

Tables listing contrasting characters of species that are sometimes incorrectly ascribed.

	sharonense	**bicorne**
Plant size	large	small
Spike/spikelet size	large	small
Lemma awn	no adjacent teeth	1 or 2 teeth
Rachis	lax to compact	very compact, zig-zag
Ratio of rachis segment to spikelet	2/3	1/2
Grain	long and plump	short and narrow

*****

	longissimum	**searsii**
Plant size	tall (70-110cm)	short (20-50cm)
Awns on terminal spikelet	equal, shorter than spike, triangular	unequal, one longer than spike, flat
Ratio glume/ spikelet	1/2 - 3/4	3/4 or more
Grain	adherent	± free

*****

	comosum	**uniaristatum**
Basal rudimentary spikelets	1	2-3
Terminal spikelet	fertile, large	sterile, small
Glumes	2 teeth	triangular large tooth, small awn

*****

	cylindricum	**dichasians**
Spikelets	8-10	4-8
Disarticulation	with adjacent rachis segment	entire spike
Large awns of terminal spikelet	on lemmas, shorter than spike, triangular	on glumes, longer than spike, flat
Glume awns of lower spikelets	short, triangular awn and blunt tooth	2 teeth or tooth and small awn

*****

	ovatum	**umbellulatum**
Basal rudimentary spikelets	1	3
Spikelets	3	5
Glume inflation	middle or below	above middle
Length of rachis segment of upper spikelet/adjacent spikelet	shorter	longer
Veins on lemma of lowest spikelet	5-7	8-12
Chromosome number	28	14

*****

	kotschyi	**peregrinum**
Spikelets	linear, appressed	urn shaped to elliptical, not appressed
Glume awns	fine	coarse
Lemma awns	equal to or slightly shorter than glume awns	weak, often missing

*****

	columnare	**recta/neglecta**
Glumes of fertile spikelets	always 2 awns, one much broader than the other	3 awns, sometimes 2 on one glume 3 on other

See notes in species description of **T. columnare**

*****

	recta	**neglecta**
Terminal spikelets	fertile	sterile
Spike	narrows	suddenly narrows
Spikelets	lemma longer than glume	lemma equals glume
Chromosome number	42	28

*****

	syriacum	**juvenale**	**crassum**
Fertile spikelets	5-10	4-7	7-12
Glumes	truncate	1-4 small flat awns	blunt, 2 triangula awns
Awn of lemma of terminal spikelet	long, broad with central nerve	triangular	flat

*****

INDEX OF SPECIES DESCRIPTIONS AND PLATES

The order in which the species are listed is based, partly, on their relationships. The monotypic Mt-genome species is listed first followed by the S-genome species and then the other diploids. The three groups of polyploids that are based on the A-, U- and D-genome diploids are described in that order with the diploid first. The polyploids of the U-genome group are listed with the M-genome species first, then the C- and finally the S-genome species.

T. TRIPSACOIDES

Synonyms: **Ae. mutica, Amblyopyrum muticum.**

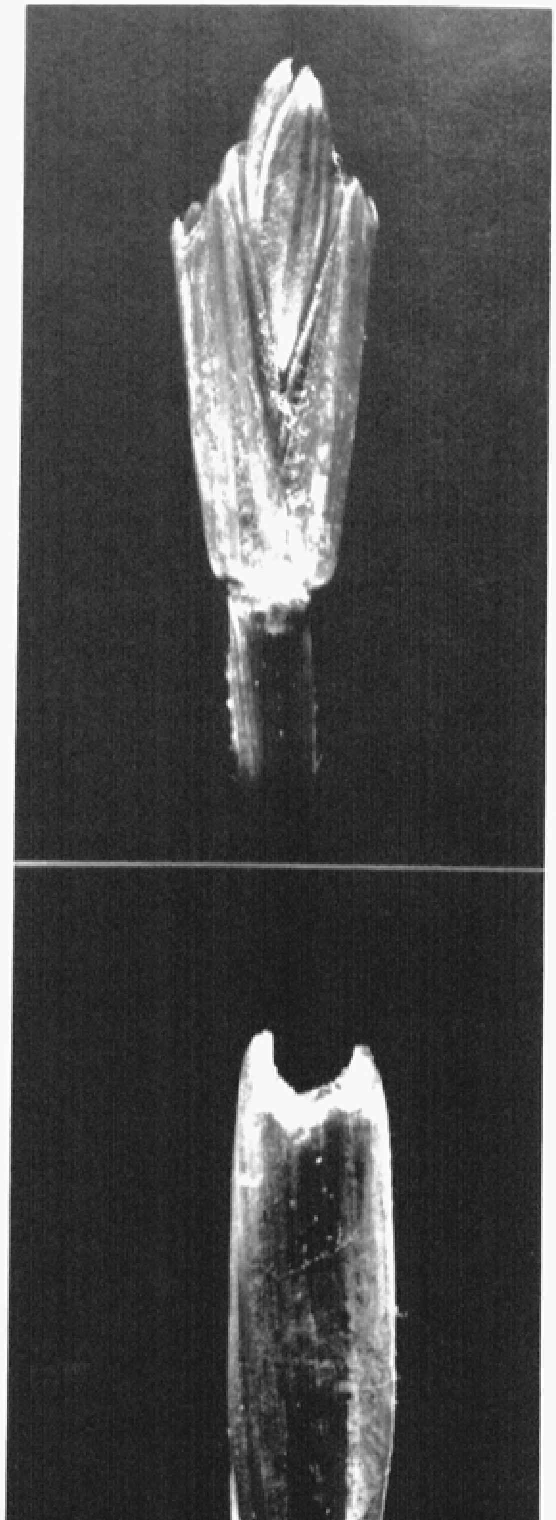
Annual, 70-80 cm high, mostly upright culm, sparsely foliated. Spike very long (up to 30 cm), thin, cylindrical, one-rowed, many spikelets (10-15, sometimes 20 or more), awnless. Sometimes tough rachis at maturity or else disarticulates into individual spikelets each with its associated rachis segment. Spikelets 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. Florets 5-8, upper 1-3 sterile. Glumes trapezoid with the upper edge being larger than the base. Upper margin with 2-4 short blunt teeth separated by notches. Lemma leathery, about the same length as the glume. Caryopsis adherent.

A very variable species; however, only awnless forms are known. Glumes sometimes covered with dense bristles, hairy or glabrous. Floral parts and rachis segregates for red, black and colorless and for width. Grows in mixed stands in which many forms can be seen. Some taxonomists would place this species in a monotypic genus, **Amblyopyrum** or as a primitive species linking **Triticum** and **Agropyron.**

W. Asiatic: Turkey (Anatolian Plateau, S.E. Turkey, Turkish Armenia), Caucasus (S. Ciscaucasia, S. Transcaucasia), W. Iran and N.E. Syria. May also occur in N. Iraq. Grows on sandy, stony or steppic-grey soils in abandoned fields, edges of wheat fields or roadsides. Secondary or unstable habitats. In the center of its distribution it forms dense stands, in E. Turkey occurs more sporadically in wadis and lower slopes. Alt: 700-1200 m.

Diploid, Mt genome. Hybridized with several species, seems to have no genomic homology with other species in the group. Segregates for the ability to suppress the **Ph** mechanism of **T. aestivum** and **T. turgidum.** Some populations contain plants with B chromosomes. Habitually out-pollinated or even self-incompatible.

PLATE 1. Left, spike x0.85, note 20 spikelets; upper right, spikelet x10; lower right, glume x10.



T. SPELTOIDES (AUCHERI)

Synonyms: **Ae. aucheri**, **Ae. speltoides** var **aucheri**.

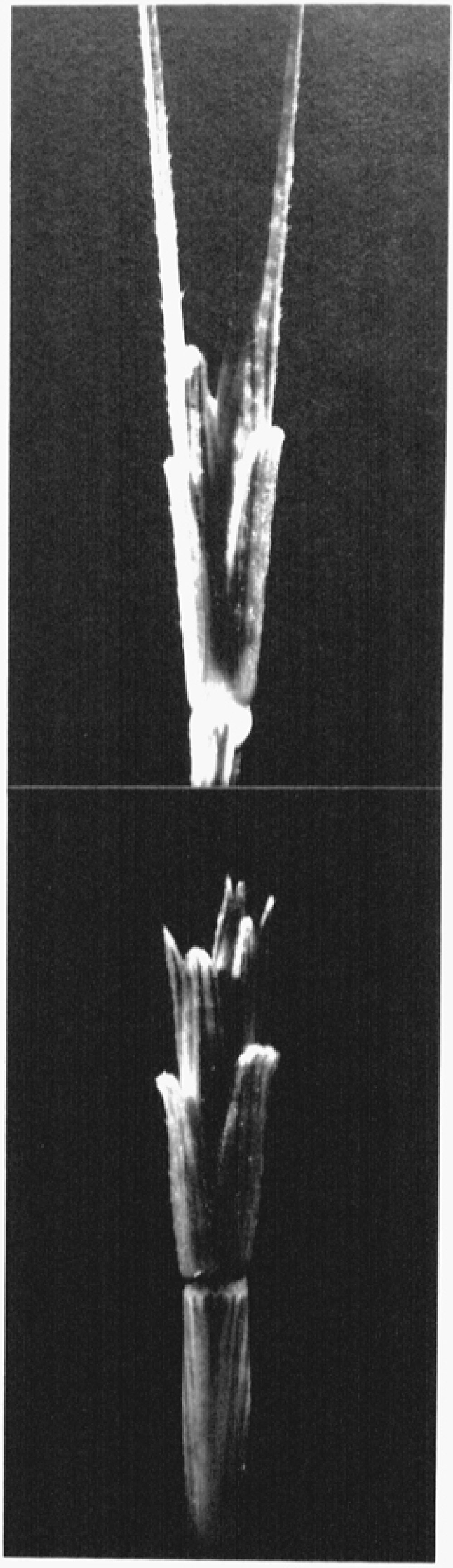
Annual, 40-70 cm high. Leaves usually hairy, sometimes pendant. Spike linear, narrow, tapers to the tip, 6-18 (usually 8-11) cm, disarticulates above the basal rudimentary spikelet at maturity. Rachis segments curved or somewhat bent. Spikelets, 6-15, lanceolate or linear, longer than the adjacent rachis segment in the lower parts of the spike, equal or even shorter in the upper parts of the spike. 4-8 (usually 4-6) florets, upper 1-3 sterile. Glumes truncate, about 2/3 as long as the lemma, with a slanting or blunt tip, sometimes a small point on the inner side of glume of the lower spikelets. Lemmas not awned in the lower spikelets but the lemmas of the terminal spikelet with long convex awns. Caryopsis adherent at maturity.

Limited morphological variation of mainly spike characteristics; differences between var. **aucheri** and var. **ligustica** controlled by several, tightly linked genes, generally inherited as a single Mendelian unit (**ligustica** type dominant). The var. **ligustica**, having the wedge type of disarticulation, is probably the primitive form. Center of variation is in N. Syria, S.E. Turkey.

E. Mediterranean: Israel (coastal plain), Jordan, Lebanon, Syria, N. Iraq, W. Iran, Turkey (S.E. and Anatolian Plateau) and S.E. Balkan peninsula (N.E. Greece, European Turkey, and S. Bulgaria). Grows on terra rosa or alluvial soil, in openings or degraded deciduous oak forest and steppe maquis, open steppe-like herbaceous formations, alluvial plains and wadi beds, edges of cultivation and recently disturbed habitats. Common, locally abundant in the fertile crescent, more sporadic as a weedy type in the west. Few adventitious plants in Italy, Crimea and N. Africa. Alt: 50-1150 m.

Diploid, S genome. Hybridized with many species. Segregates for the ability to suppress the **Ph** mechanism of **T. aestivum** and **T. turgidum**. Some populations contain plants with B-chromosomes. Habitually out-pollinated. Resistant to leaf and stem rust, a useful forage grass.

PLATE 2. Left, spike x2; upper right, terminal spikelet x8; lower right, lower spikelet x8, note truncate glumes with blunt tip.



T. SPELTOIDES (LIGUSTICA)

Synonyms: **Ae. speltoides, Ae. ligustica, Ae. speltoides** var **ligustica.**

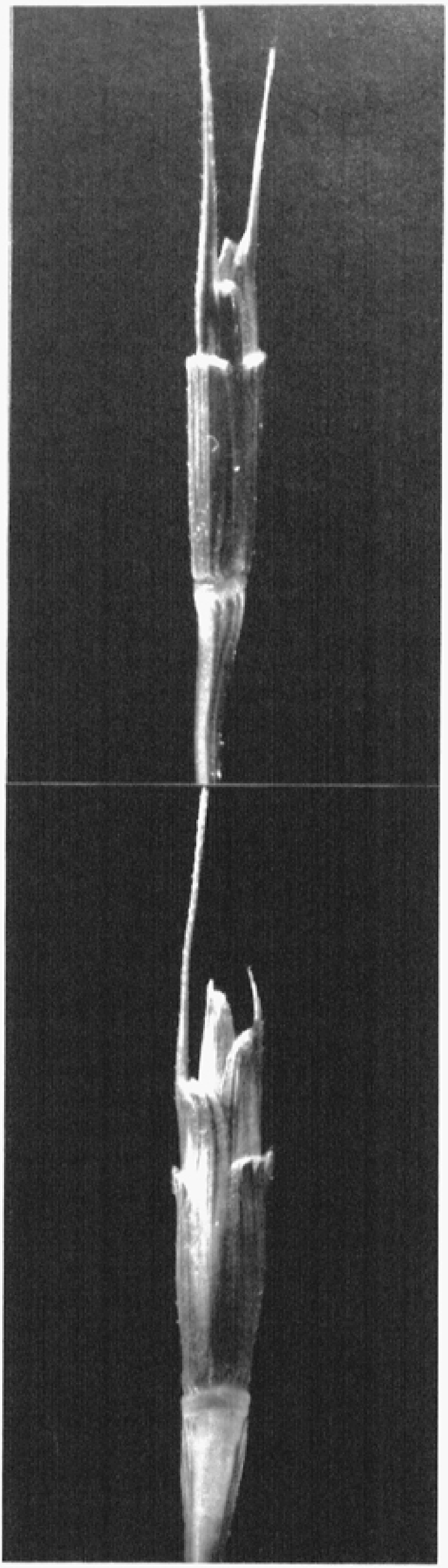
Annual, culm 40-60 cm high, upright, sparsely foliated, hairy leaves. Spike broad-linear, two rowed, tapers to the tip, 6-12 (usually 7-9) cm. Spikelets, 7-11, lanceolate or linear all more or less equal in length or longer than the adjacent rachis segment. 4-6 (usually 4-5) florets, upper 1-3 sterile. Disarticulates into individual spikelets at maturity each with its associated rachis segment. Usually only one rudimentary spikelet at the base of the spike. Glumes truncate, about 2/3 as long as the lemma, with a slanting or blunt tip, sometimes a small point on the inner side of the glumes of the lower spikelets. Lemmas tipped with a short triangular awn which becomes longer in the upper spikelets. Caryopsis adherent.

Limited morphological variation of mainly spike characteristics; differences between var. **aucheri** and var. **ligustica** controlled by several, tightly linked genes, generally inherited as a single Mendelian unit (**ligustica** type dominant). The var. **ligustica,** having the wedge type of disarticulation, is probably the primitive form. Center of variation is in N. Syria, S.E. Turkey.

E. Mediterranean: Israel (coastal plain), Jordan, Lebanon, Syria, N. Iraq, W. Iran, Turkey (S.E. and Anatolian Plateau) and S.E. Balkan peninsula (N.E. Greece, European Turkey, and S. Bulgaria). Grows on terra rosa or alluvial soil, in openings or degraded oak forest and steppe maquis, open steppe-like herbaceous formations, alluvial plains and wadi beds, edges of cultivation and recently disturbed habitats. Common, locally abundant in the fertile crescent, more sporadic as a weedy type in the west. Few adventitious plants in Italy, Crimea and N. Africa. Alt: 50-1150 m.

Diploid, S genome. Hybridized with many species. Segregates for the ability to suppress the **Ph** mechanism of **T. aestivum** and **T. turgidum.** Some populations contain plants with B-chromosomes. Habitually out-pollinated. Resistant to leaf and stem rust, a useful forage grass.

PLATE 3. Left, spike x2; upper right, terminal spikelet x9; lower right, lower spikelet x9.



T. BICORNE

Synonym: **Ae. bicornis.**

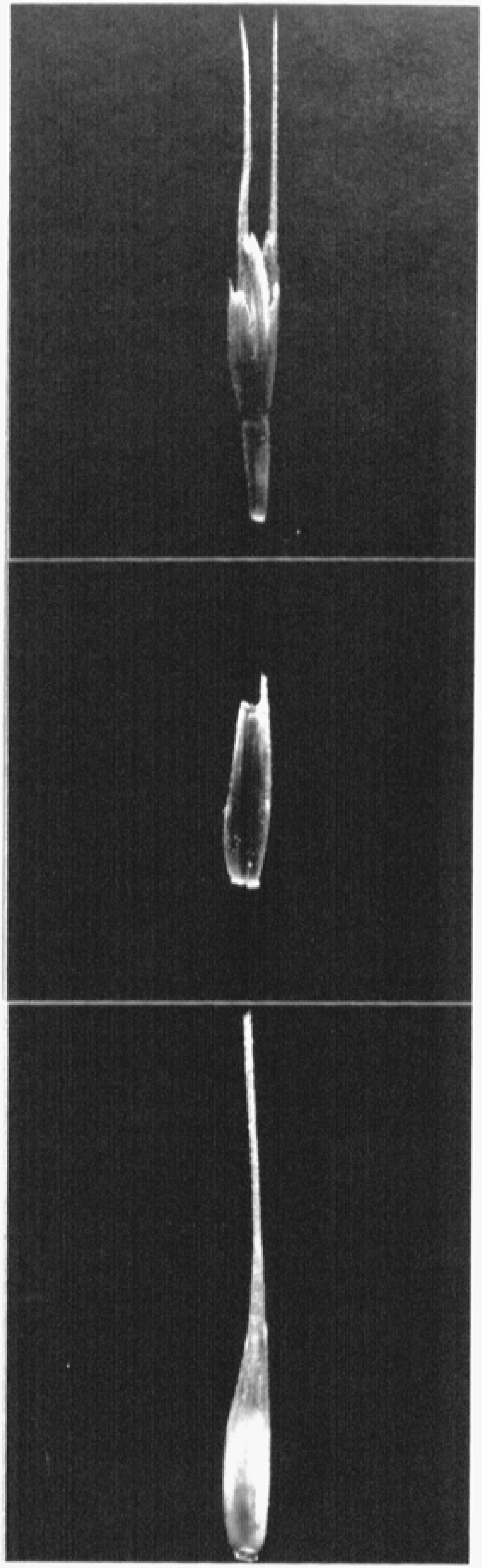
Annual, culm 15-45 cm, bushy, culm prostrate then turning upwards, upper parts defoliate. Spike linear, compact, 4-8 cm, does not taper to the tip, two-rowed and awned (sometimes missing). Zig-zag rachis, each segment weakly bent or straight. Spikelets elliptical to linear, longer than the adjacent rachis segment and not becoming smaller to the tip of the spike. Florets 3, upper 1-2 sterile. Disarticulates into individual spikelets at maturity, each with its associated rachis segment. Glumes of the lateral spikelets with two teeth separated by an angle. Lemma canoe-shaped, triangular awn, short or absent in the lower spikelets but longer in the upper. There are no teeth at the sides of the awn. Caryopsis adherent.

Limited morphological variation involving mainly spike and spikelet size, plant size and degree of awn development. Awnless forms have been observed. Close to **T. boeoticum** in spike morphology. May have originated in the southern part of the fertile crescent. Currently, center of variation is in lower Egypt and Sinai.

S.E. Mediterranean: Libya (Cyrenaica), Egypt (lower Egypt and Sinai), S. Israel (Negev) and S. Jordan (Edom). One population was also found in N.E. Cyprus. Grows on stable sandy soils in open dwarf shrub or herbaceous steppe-like or desert-like formations, xeric coastal and desert plains, edges of cultivation and roadsides. Common, sometimes dense populations in coastal plain of S. Israel, Sinai and lower Egypt. Sporadic in inner sandy deserts. Alt: 0-200 m.

Diploid, S genome. More difficult to hybridize than other S-genome species. Variation in the ability to suppress the **Ph** gene of **T. aestivum** has not yet been demonstrated. A very early type.

PLATE 4. Left, spike x2; upper right, spikelet x6; middle right, glume x10; lower right, lemma x6.



T. SHARONENSE

Synonyms: **Ae. sharonensis** and **Ae. longissima** var **sharonensis**.

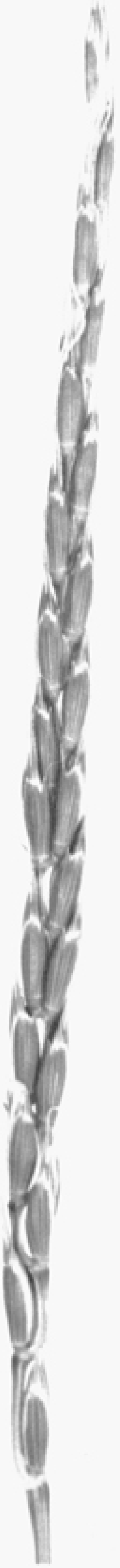
Annual, culm 40-100 cm, prostrate then turning upright, sparsely foliated in the lower parts. Spike more or less broad linear, two rowed, usually awned, 7-13 cm. Rachis zig-zaged, each segment being bow shaped. Spikelets linear elliptical, getting smaller to the tip, more or less flattened. Florets 3-5, upper 1-3 sterile. Disarticulates as individual spikelets at maturity, each with the associated rachis segment. Glumes with two small points, one of which is sometimes elongated into a small awn. Lemmas with a 40 - 60 mm awn at the base of which are two short broad teeth, awns increasing in length to the tip of the ear. Caryopsis adherent.

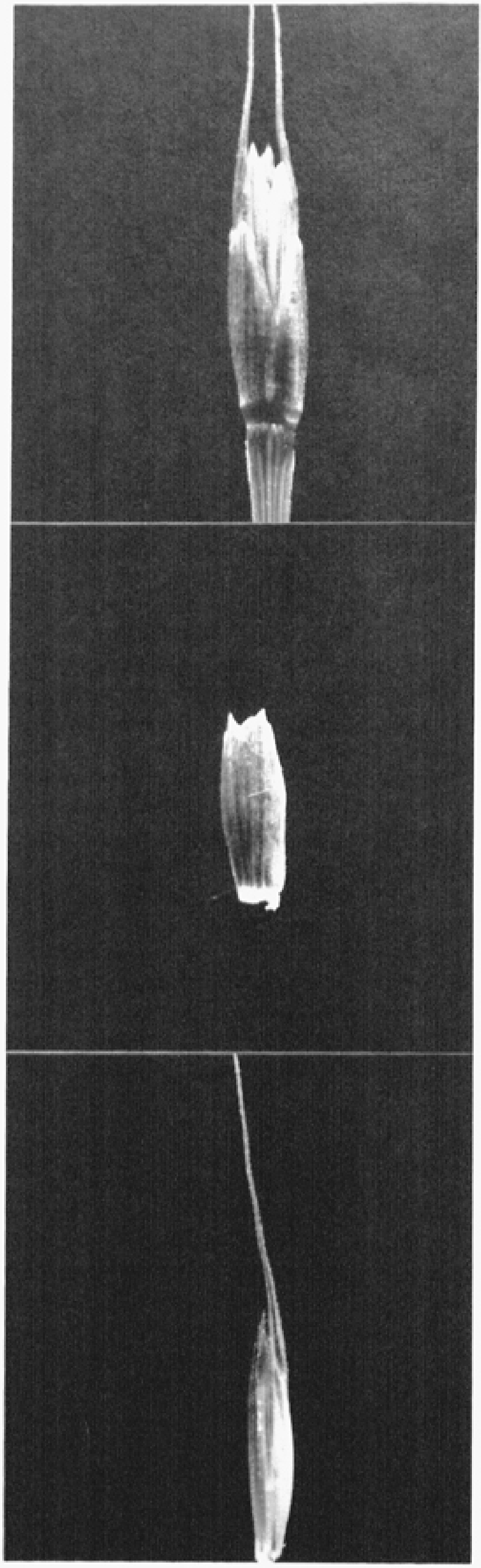
Limited morphological variation involving spike size, spikelet number and size, degree of expression of two-rowed nature and awn development. Awnless forms have been observed. Morphologically similar to **T. bicorne** but larger. Shares some characters with **T. longissimum.** Edaphically closer to **T. bicorne** than to **T. longissimum** though sympatric with the latter. A relatively young species, endemic to light soils in the coastal plains of Israel and Lebanon. Probably derived from **T. bicorne** by introgression from **T. longissimum.**

E. Mediterranean: coastal plain of Israel and Lebanon. Well drained sandy loams, sandy soils and consolidated sand dunes in open park-, shrub-, and herbaceous-formations, abandoned fields, disturbed habitats and roadsides. Common, often in dense stands. Alt: 0-100 m.

Diploid, S genome. Probably involved in the parentage of **T. peregrinum.** Hybridizes with many species. Some forms have genetic mechanisms able to suppress the **Ph** gene in **T. aestivum** and **T. turgidum.** Resistant to leaf and stem rust, some forms grow in salt-marshes (N. of Haifa) and may contain genes for salt tolerance.

PLATE 5. Left, spike x2; top right, spikelet x9, note awns on lemmas; center right, glume x9, note teeth and membraneous edge; lower right, lemma x9.





T. LONGISSIMUM

Synonym: **Ae. longissima.**

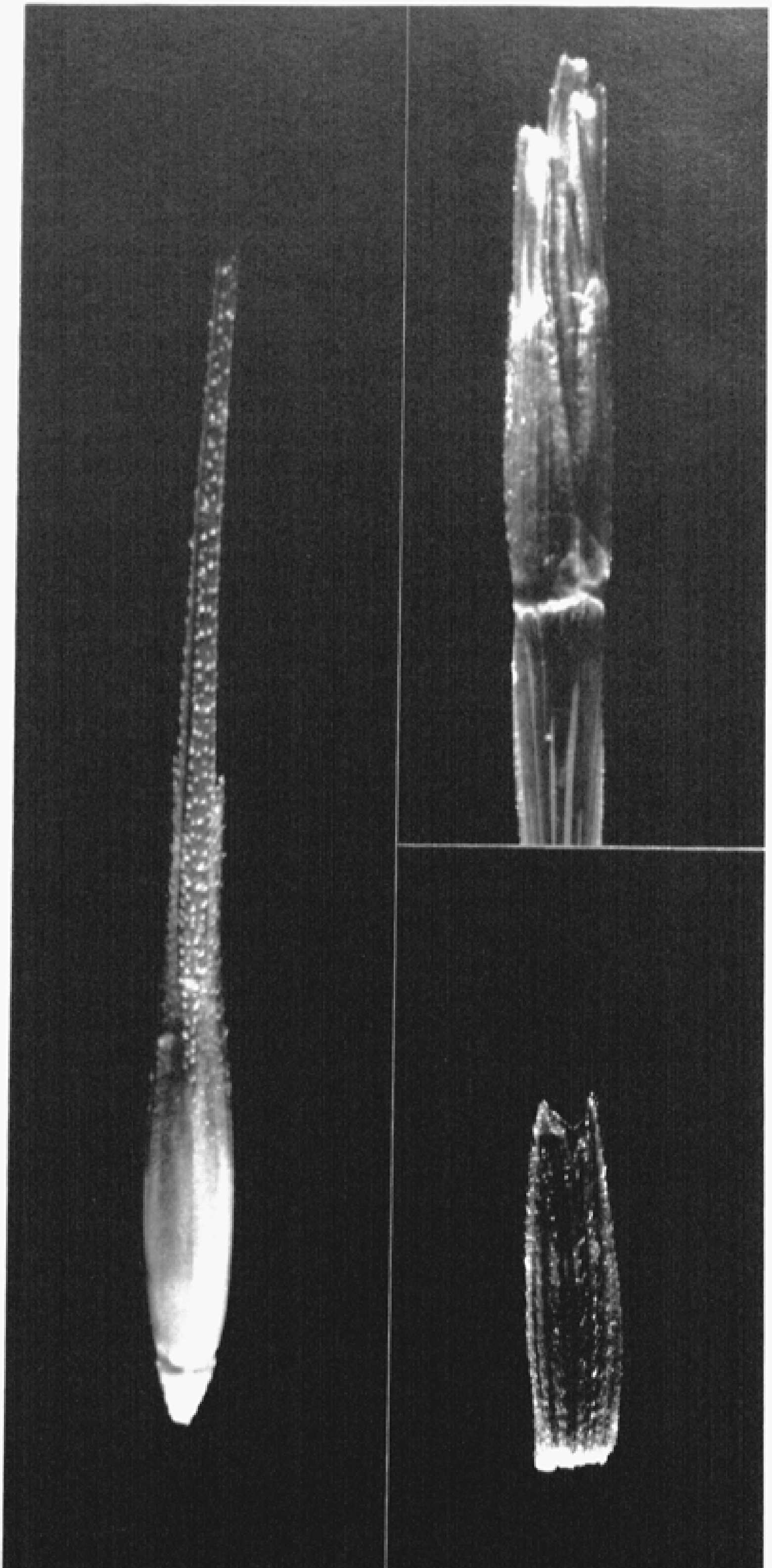
Annual, culm 40-110 cm, prostrate then turning upright, sparsely foliated in lower parts. Spike narrow, linear, one-rowed, tapering slightly to the tip, 10 to 20 cm. At maturity fragile near, but usually not at, the base. Spikelets 8-15, becoming thinner and shorter to the tip of the spike, appressed to the rachis segment. Florets 3-5, upper 1-3 sterile. Glumes rough, usually two teeth separated by a membranous edge, glumes of terminal spikelet sometimes with three, teeth the center one of which may be elongated into a very short awn. Lemmas of the lateral spikelets canoe-shaped, not awned. Lemmas of the terminal spikelet with a long, broad, convex awn often with a small tooth on each side. Caryopsis adherent.

Limited morphological variation involving mainly spike length, spikelet number, rachis form (zig-zaged or straight) and awn length. It is taller and later than **T. sharonense** and **T. bicornis.** Center of variation in steppic regions of Israel and Jordan.

S.E. Mediterranean: Egypt (lower Egypt and Sinai), Israel, Jordan, Lebanon (S. coastal plain) and Syria. Sandy loams, rarely on somewhat heavier soil, in the coastal plain of Egypt, Israel and Lebanon, and on sand derived from Nubian sandstone, in grey calcareous steppe soil or loess in the inland steppe and desert regions, in open dwarf shrub or herbaceous steppe-like or desert-like formations, plains, abandoned fields, edges of cultivation and roadsides. Common, often abundant in the coastal plain and in several steppic habitats bordering on the Mediterranean region in Israel and Jordan. Alt: 0-900 m.

Diploid, S genome. Probably involved in the parentage of **T. peregrinum**, **T. kotschyi** and **T. syriacum.** Hybridizes with many species. Some forms have genetic mechanisms able to suppress the **Ph** gene in **T. aestivum** and **T. turgidum.** It would appear that there is similarity between the cytoplasm of this species and the cytoplasms of the tetraploid and hexaploid cultivated wheats. Resistant to mildew, leaf and stem rust. Heat and drought tolerance, high grain protein.

PLATE 6. Left, spike x1; center, lemma of terminal spikelet x12, note small lateral teeth; upper right, spikelet x9; lower right, glume of lower spikelet x9, note two teeth separated by membraneous edge.



T. SEARSII

Synonym: **Ae. searsii.**

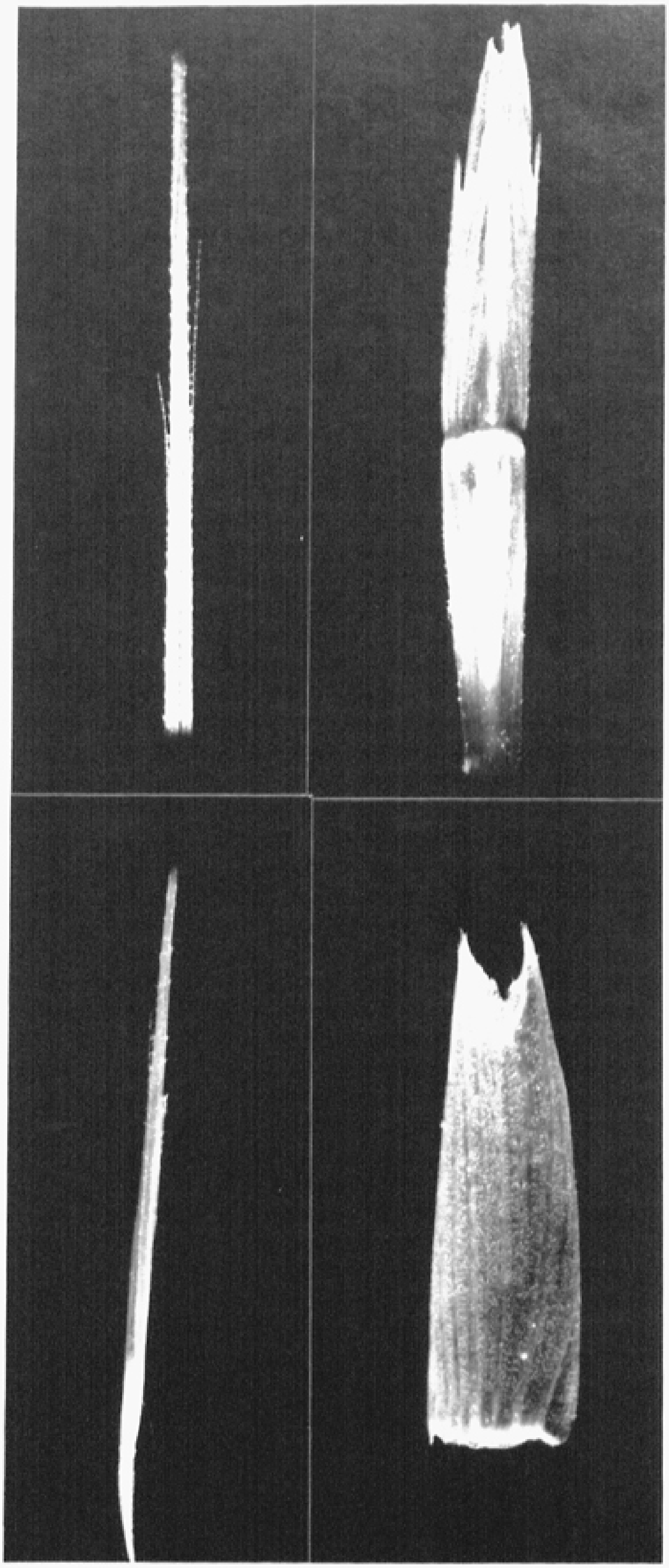
Annual, culm 20-50 cm, prostrate then turning upright, sparsely foliated in the lower parts. Spike narrow, linear, 5-11 cm, one rowed, tapering slightly towards the tip. At maturity disarticulates above the lowest spikelet. Spikelets 8-12, linear, florets 3, uppermost sterile. Glumes with two teeth separated by a membranous edge. Glumes 3/4 of the length of the spikelet or longer. Lemmas of the terminal spikelet awned. One floret with a short awn, triangular in cross section, the other floret with a very long (equal to or longer than the spike), flat awn. Caryopsis more or less free at maturity.

Limited morphological variation involving mainly spike size, spikelet number and awn length. Center of variation in Israel and Jordan, where it probably originated.

S.E. Mediterranean: Israel (Judea, Samaria and the Golan Heights), Jordan (Gilead, Ammon and Moav), S.E. Lebanon and S.W. Syria; grows on terra rosa or basalt soil in open-park herbaceous formations, in the degraded deciduous steppe-maquis, in small shrub (batha) formations, abandoned fields and edges of cultivation. Common, sometimes dense stands in S. Judea. Alt:200-1000 m.

Diploid, S genome. Probably involved in the parentage of **T. turgidum**, **T. kotschyi** and **T. peregrinum**. This is the only diploid wheat species that grows in mixed populations with **T. turgidum** in the southern fertile crescent. It also has massive contact with **T. monococcum**. Hybridizes with many species. Variation in the ability to suppress the **Ph** gene has not yet been demonstrated.

PLATE 7. Left, spike x1, note large and small awns or terminal spikelet; upper center, central portion of the large awn x6, note two lateral awnlets; lower center, entire lemma with small awn x6; upper right, spikelet and associated rachis segment x8; lower right, glume of spikelet from the center of the spike x12; note the two teeth separated by a membranous edge.



T. DICHASIANS

Synonyms: **Ae. caudata, Ae. markgrafii.**

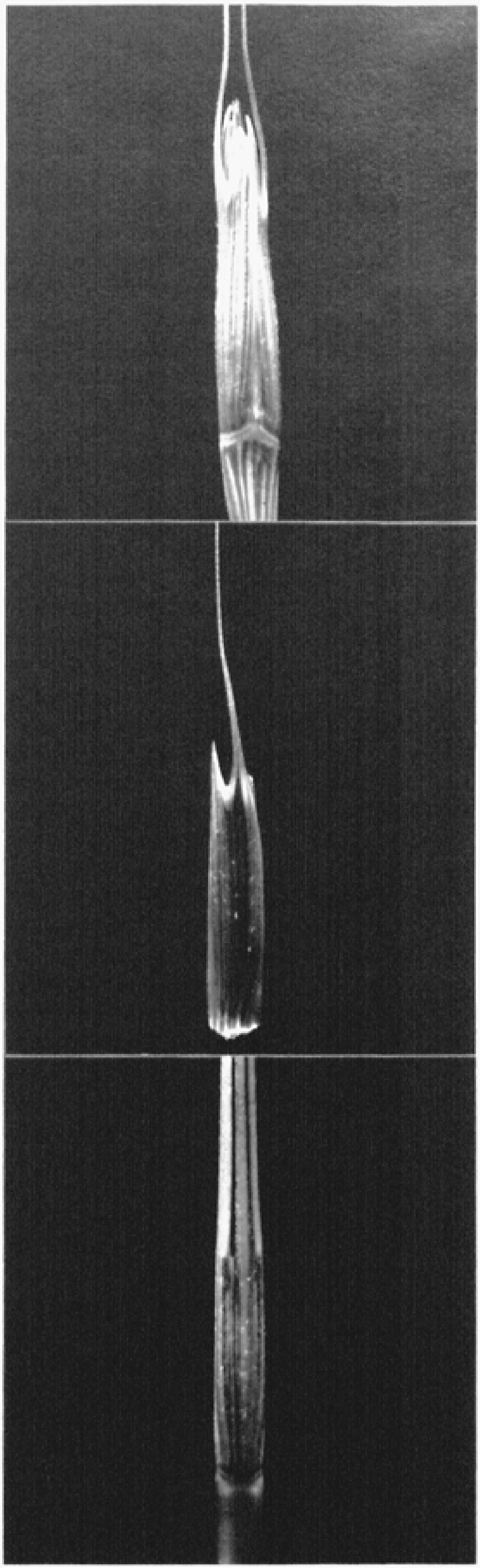
Annual with upright culms 20-40 cm high, leaves hairy. Spike linear, narrow, tapering little to the tip, 6-8 cm, disarticulates as entire spike at maturity. Spikelets 4-8, cylindrical, equal in length to the adjacent rachis segment, florets 3-4, upper 1-2 sterile. Usually two basal sterile spikelets. Glumes rough, upper parts overlap. Glumes of lower spikelets with two teeth, or with a sharp tooth and a short, thin awn separated from the tooth by an acute angle. Glumes of terminal spikelet gradually tapering into a long, broad awn, longer than the entire spike, with a small adjacent tooth separated by a gap (no angle), the awns diverging sharply from each other. Lemma membranous, upper parts thickened, 2-3 teeth from which weak, short awns can develop in the terminal spikelet. Adherent caryopsis.

Limited morphological variation involving mainly the number and size of spikelets, awn length and development on the lateral spikelets. In some spike characteristics it is similar to **T. comosum**; however it is more primitive, its spike less specialized and shows a greater resemblance to the basic spike structure of the group. Its area of distribution overlaps with the center and the massive part of the genus distribution. Center of diversity in Turkey and Iran, where it probably originated.

N.E. Mediterranean and Central Asiatic: S. Yugoslavia, S. Bulgaria, Greece (inc. Crete, Rhodes and the Aegean region), Turkey, Cyprus, Lebanon, Syria, N. Iraq, Iran and Afghanistan. Grows on a variety of soils from terra rosa to grey-calcareous steppe soil as well as on stony slopes at the edge of and openings in sclerophyllous and deciduous oak forests and maquis, open herbaceous park formations, open dwarf shrub steppe-like formations, abandoned fields, edges of cultivation and roadsides. Common throughout most of its distribution. Alt: almost sea level-1200 m.

Diploid, C genome. Involved in the parentage of **T. cylindricum** and **T. triunciale.** Hybridized with many species, several artificial amphiploids. Segregates for the ability to suppress the **Ph** mechanism of **T. aestivum** and **T. turgidum.**

PLATE 8. Left, spike x3; upper right, spikelet x6; center right, glume of lower spikelet x6; lower right, glume of terminal spikelet x6.



T. COMOSUM

Synonyms: **Ae. comosum, Ae. comosum** var **heldrechii, Ae. heldrechii.**

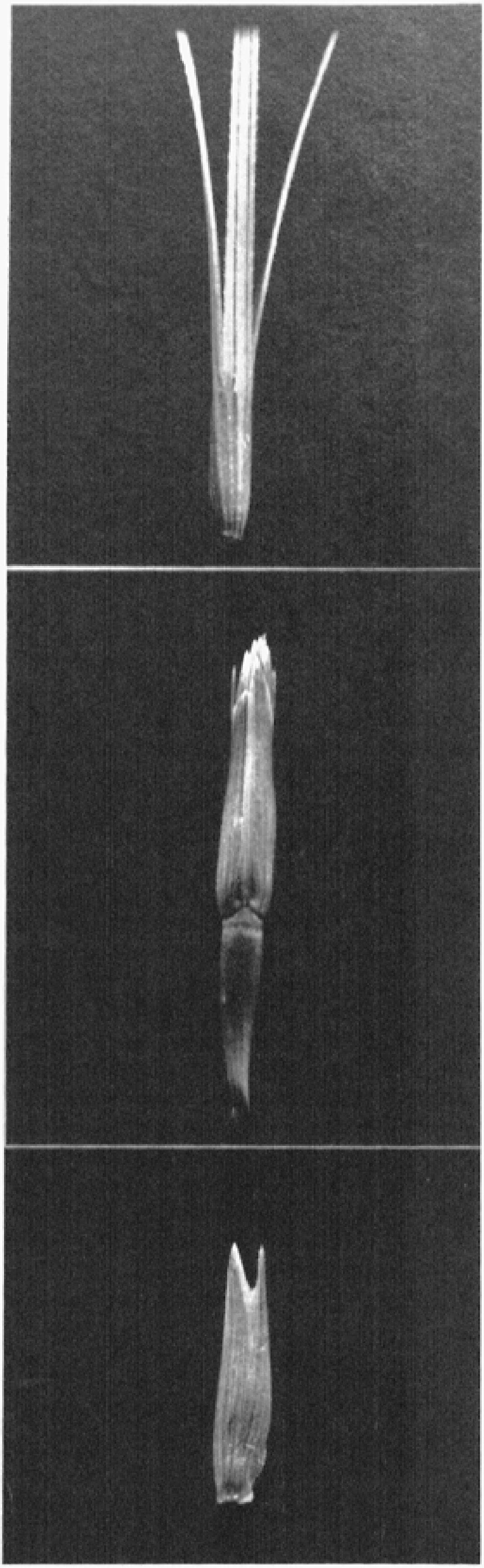
Annual, many-tillered, thin culm, 15-30 cm high, usually upright, with narrow, usually hairy leaves. Spike linear-lanceolate to narrow-elliptical to narrow-oval, short (2-7 cm), usually rough or hairy, gradually tapering to the tip. The entire spike disarticulates at maturity. Spikelets 3, long narrow to oval, shorter than the adjacent rachis segment, rudimentary spikelets 1 (rarely 2). Florets 3-4, upper 1-2 sterile. Glumes more or less rough or hairy, upper parts overlap, glumes of lateral spikelets with two teeth with an angle between, sometimes one of the teeth developing into a small awn, the glumes of the terminal spikelet with 3 (seldom 1)-9 large awns. The awns on each glume spread laterally from each other and the central awn of each glume diverges laterally from the central awn of the other glume. Lemma membranous, cartilaginous in the upper parts, seldom awned in the upper spikelets. Adherent caryopsis.

Highly polymorphic species, variation involves spike and spikelet structure and number and length of awns. Spp. **heldreichii** is regarded by some as a separate species. The spikelets of ssp. **heldreichii** are more inflated and the number of awns on the terminal spikelet is 1+3 and not 3+3 as in **T. comosum.** The awns of ssp. **heldreichii** are usually shorter and the uppermost spikelet is smaller. Intermediate forms are frequent.

N.E. Mediterranean: Greece (incl. Aegean Islands), W. Turkey. Grows on terra rosa soil in the edges of sclerophyllous and deciduous oak forests and maquis, open and degraded dwarf shrub (batha) formations, cleared areas, pastures, abandoned fields, edges of cultivation and roadsides. Common, frequently abundant and forms dense stands. Alt: almost sea level-1000 m.

Diploid, M genome. Probably involved in the parentage of **T. ovatum, T. macrochaetum, T. neglecta, T. recta** and **T. columnare** of the U-genome group and of **T. crassum, T. juvenale** and **T. syriacum** of the D-genome group. Hybridized with many species. Resistant to yellow rust.

PLATE 9. Left, spike x2; upper right, glume of terminal spikelet x6; center right, lower spikelet x6, note glumes overlapping in upper parts; lower right, glume of lower spikelet x6.



T. UNIARISTATUM

Synonym: **Ae. uniaristata.**

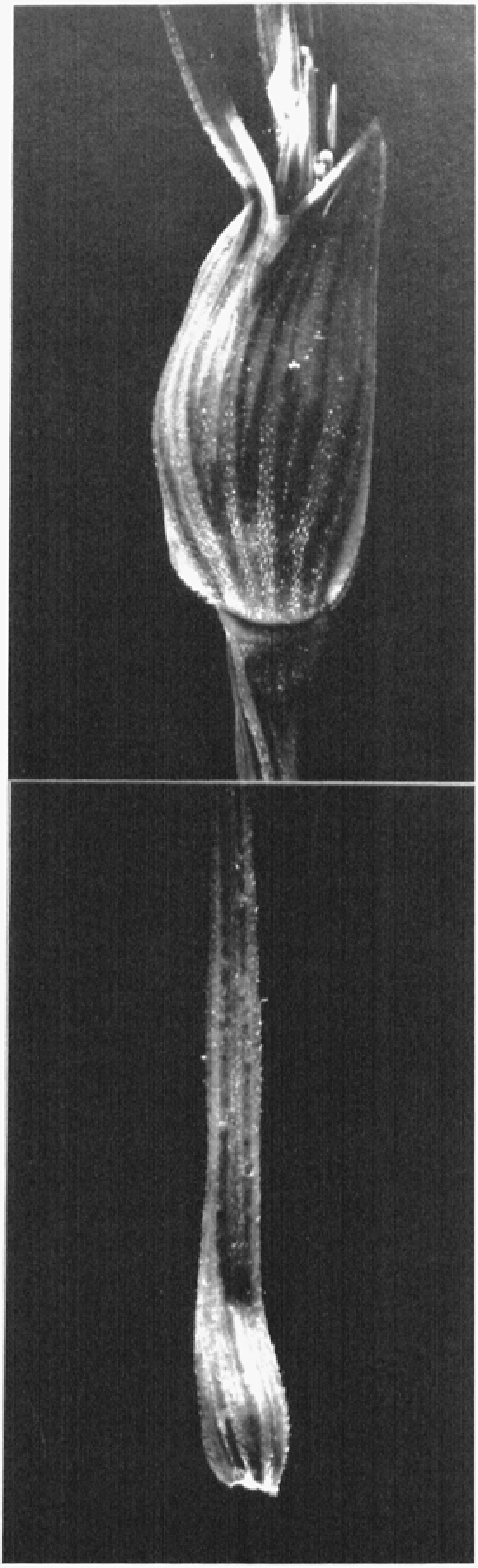
Annual, many culms 10-30 cm high, usually prostrate then turning upwards; narrow, linear leaves, usually hairy, leaf sheaths usually hairy in the upper parts. Spike short (1.5 - 3.5 cm), lanceolate to oval-lanceolate, glabrous, tapering rapidly to the tip, disarticulates as entire spike. Spikelets 2 or 3, terminal spikelet usually sterile, basal rudimentary spikelets also 2-3. Florets 4, upper 1-2 sterile. Glumes of lateral spikelets with a conspicuous triangular tooth separated from an awn by an acute angle, glume of the terminal spikelet stepwise or abruptly ending in a broad, flat awn sometimes with an accompanying tooth. The middle nerve of the awn of the terminal glume is strongly projecting and is a continuation of the projecting nerve of the glume. Lemmas of the lateral spikelets with small teeth which are sometimes elongated into small awns, those of the terminal spikelet with a weakly developed awn and 1-2 adjacent teeth. Caryopsis adherent.

Limited morphological variation, mainly involving spike and spikelet size. Morphologically close to **T. comosum**, particularly to several forms of ssp. **heldreichii**, from which it differs by several characters: its glumes carry only one awn and those of the lateral spikelets have a large, triangular tooth. It possibly derived from ssp. **heldreichii** in N. Greece or N.W. Turkey.

N.E. Mediterranean: Yugoslavia (Adriatic region), Albania, Greece (including Crete), N.W. Turkey. Grows on terra rosa soil in edges of sclerophyllous Mediterranean oak forest and maquis, open or degraded dwarf shrub formations, pastures, disturbed habitats, edges of cultivation and roadsides. Sporadic in Turkey and Greece, more common in Adriatic region of Yugoslavia. Alt: 0-600 m.

Diploid, Un genome. Originally given an M^u genome symbol indicating a genome modified from the M genome of **T. comosum**. Now thought to have a unique genome. Involved in the parentage of **T. ventricosum** and the hexaploid **T. recta.** Hybridized with some other species. May contain genes for aluminum tolerance.

PLATE 10. Left, spike x3; upper right, spikelet x7, note large triangular tooth separated by angle from awn on glume; lower right, glume of terminal spikelet x7.



T. MONOCOCCUM

Synonyms: **T. aegilopoides**, **T. boeoticum**, **T. thaoudar**, **T. urartu.**

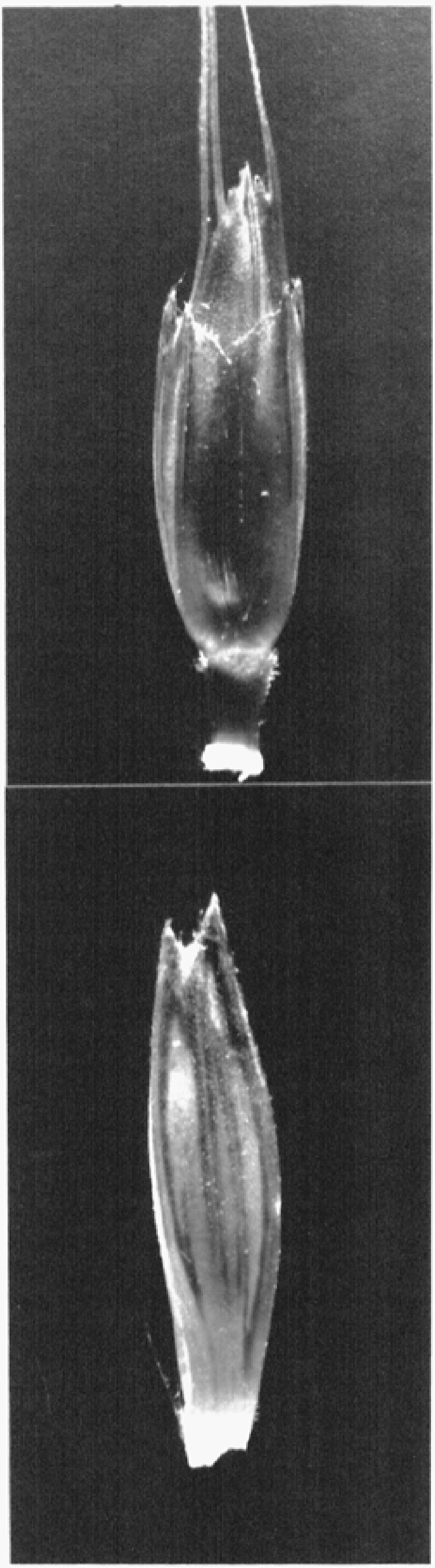
Annual, culm 30-70 cm high, jointed at base then upright. Spike bilaterally compressed, indeterminate, two rowed, 8-12 cm, awned. Basal rudimentary spikelets 2-3. Disarticulates into individual spikelets each with its associated rachis segment at maturity. Hairs on the rachis internode. Spikelets compressed, top fertile spikelet generally in the same plane as those below. One grain per spikelet, sometimes two in the center of the spike. Glume with two well-developed keels, two unequal teeth usually not developed into awns. Lemma tapering into a long awn with a lateral tooth. Palea membranous, splitting along the keel at maturity. Caryopsis free, laterally compressed.

Polymorphic species with variation involving spike and spikelet size, color, hairiness, number of grains per spikelet and awns. Two main types: var. **boeoticum** and var. **urartu.** The former with two forms **aegilopoides** with a relatively small spike, spikelets mostly 1-grained and with one awn, and **thaoudar** with larger spikes, spikelets frequently 2-grained and two awns. Intermediates are common. Var. **urartu** is characterized by a smaller, second tooth on the glume, smaller anthers by a two-awned spikelet and red grain color.

N.E. Mediterranean and W. Asiatic: S. Yugoslavia, S. Bulgaria, Albania, Greece, Turkey, Syria, Lebanon, N. Iraq, N.W. Iran and S. Russia (Crimea, Ciscaucasia and Transcaucasia). Grows on terra rosa, basalt and several types of alluvial soils in the edges and degraded deciduous oak forest and maquis, deciduous steppe maquis, open herbaceous-park forest, open dwarf shrub steppe-like formations, pastures, abandoned fields, edges of cultivation and roadsides. Very common, locally abundant in the fertile crescent. Alt: 100-1600 m.

Diploid, A genome. Still cultivated in very small areas on poor soils in Turkey, Greece, Yugoslavia and Italy. Involved in the parentage of the wild and cultivated polyploid wheats. Contributed at least six (possibly not 4A) chromosomes to **T. aestivum.** Involved in many artificial hybrids.

PLATE 11. Left, spike x3; upper right, spikelet x8, note hairs on rachis segment; lower right, glume x12.



T. TIMOPHEEVII

Synonyms: **T. araraticum**, **T. turgidum** var **timopheevii**, **T. turgidum** var **tumanianii**, **T. dicoccoides** var **nudiglumis**.

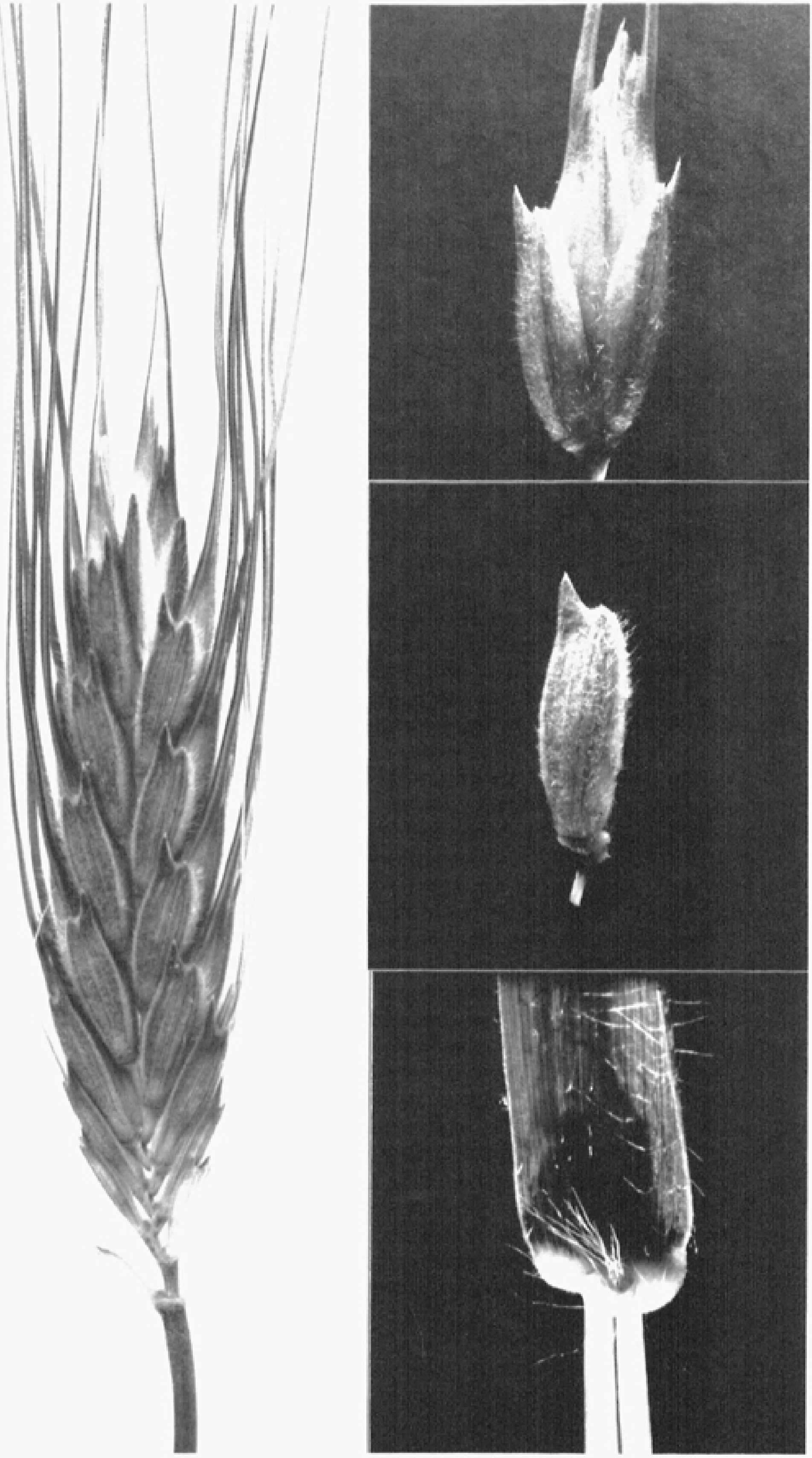
Annual, culm upright 100 cm high. Entire plant clothed with stiff hairs which may be as long as 3 mm on the leaf sheaths. Leaf blades hairy. Spike strongly bilaterally compressed, two rowed, 10 cm or less, ovoid, tapering to both the base and tip, very hairy. Disarticulates into individual spikelets at maturity, each with its associated rachis segment. Rachis internodes covered with dense, white hairs. Spikelets ovoid with 3 florets, upper floret usually sterile. Glume very hairy, keel less developed, shorter than the lemma, two teeth on the upper margin, one larger and pointed separated from the other by an acute angle. Lemma membranous, hairy, central nerve prolonged as narrow awn. Caryopsis free.

Morphological variation involves mainly spike and spikelet size and shape, glume and awn colors and hairiness, plant height, growth habit and leaf width.

W. Asiatic: E. Turkey, N. Iraq, W. Iran and S. Russia (Ciscaucasia and Transcaucasia). Grows on terra rosa, basalt and other soils that were produced from hard limestone bedrock in the herbaceous cover of the oak park forest, dwarf shrub formations, semi-steppe herbaceous formation, pastures, abandoned fields and edges of cultivation. Common, locally abundant in the northern part of the fertile crescent. Alt: 300-1600 m.

Tetraploid, genomically AG, cytoplasm similar to that of **T. speltoides.** Progenitor of the cultivated form, and a hexaploid cultivated form (**T. timopheevii** var **zhukovskyi**) genomically AAG. The cultivated forms have a very restricted distribution in S. Russia. Though the G genome is assumed to be derived from the S genome of **T. speltoides**, it seems to be more closely related to the B genome of the polyploid wheats than to any diploid genome. It also contains the **Ph** gene, presumably on the long arm of chromosome 5G, that suppresses the pairing of homoeologous chromosomes. The cytoplasm is different from that of the AB polyploid wheats and this difference has been used to produce male sterility in **T. aestivum** for the production of hybrid wheats. Resistant to leaf and stem rust and also powdery mildew.

PLATE 12. Left, spike x3; upper right, spikelet x6; center right, glume x6; lower right, lamina and ligules x6, note long hairs.



T. TURGIDUM

Synonyms: **T. carthlicum**, **T. dicoccoides**, **T. dicoccon**, **T. durum**, **T. polonicum**.

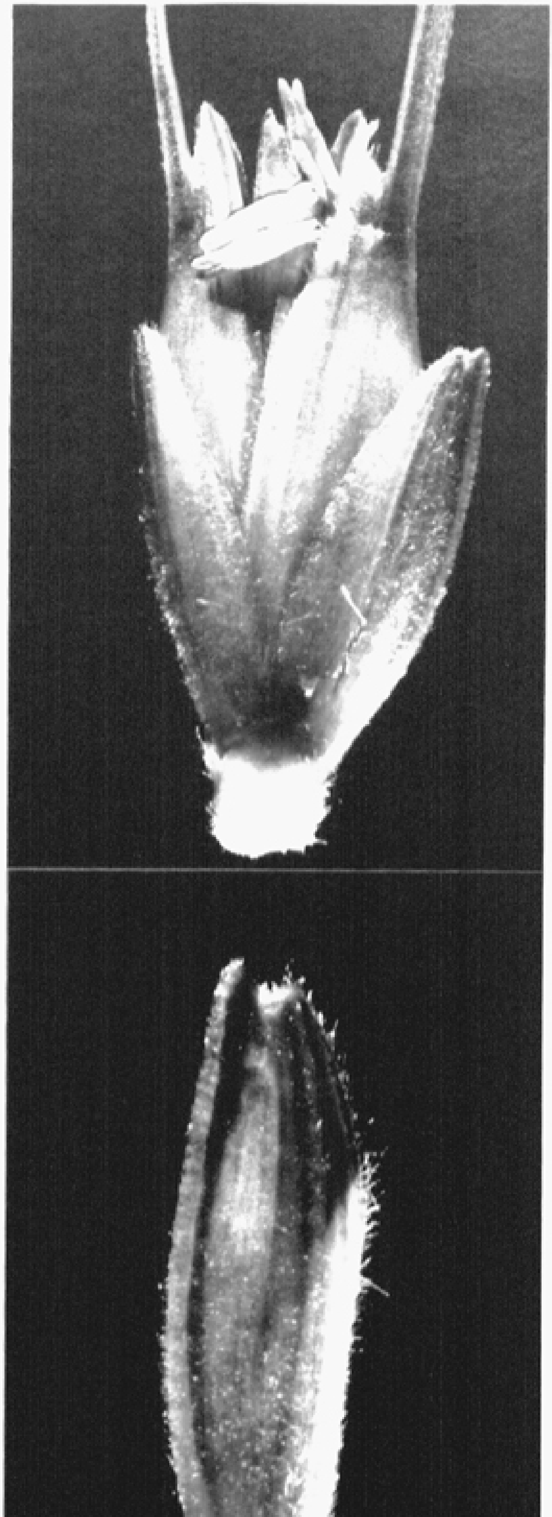
Annual, culm erect up to 160 cm high, stiff, lower internodes hollow, uppermost usually solid. Leaves linear, pointed, up to 60 cm long. Spike bilaterally compressed, determinate, two-rowed, parallel and up to 15 cm. Disarticulates into individual spikelets at maturity each with its associated rachis segment. Terminal spikelet at right angles to plane of lateral spikelets. Spikelet lanceolate, florets 3, upper usually sterile. Basal rudimentary spikelets 2-3. Hairs on the rachis internode. Glumes with strong keel, usually not hairy, with two teeth one usually larger than the other. Lemma with a strongly developed awn and a small basal tooth. Caryopsis free.

Wide morphological variation involving mainly spike and spikelet size and shape, glume and awn color and hairiness, grain color and size, plant height, growth habit and leaf width.

E. Mediterranean: Israel, Jordan, Lebanon, Syria, E. Turkey, N. Iraq and W. Iran. Grows on terra rosa or basalt soil in the herbaceous cover of the oak park forest, dwarf shrub formations, pastures, abandoned fields and edges of cultivation. Common, locally abundant in the southern part of the fertile crescent where it occupies a variety of primary and secondary habitats, less frequent in the northern part of the fertile crescent. Alt: 200 below sea level - 1600 m.

Tetraploid, genomically AB. Cytoplasm similar to that of **T. longissimum**. The large grains of this species attracted pre-agricultural hunter/collectors who eventually domesticated it - presumably in the southern part of the fertile crescent. Progenitor of the cultivated forms with tough rachis and free-threshing grains - the macaroni (durum) wheats of commerce. Origin of the A and B genomes of **T. aestivum**, with which it makes fertile hybrids. These hybrids and their derivatives can be found on the edges of wheat fields throughout the fertile crescent. Many artificial hybrids. The amphiploid of the cultivated form with rye is commercially grown as triticale. Resistant to yellow and leaf rust; contains genes for high grain-protein content, large grains, earliness and many other useful characters.

PLATE 13. Left, spike x3; upper right, spikelet x7, note awns on lemmas; lower right, glume x10.



T. UMBELLULATUM

Synonym: **Ae. umbellulata.**

Annual, bushy branched, many jointed culm bent upwards, 10-30 cm high, leaves linear, 2-5 cm long, more or less hairy. Spike lanceolate-ovoid, 2.5-4 cm, usually rough. Entire spike disarticulates at maturity. Rudimentary basal spikelets 3 (2-4). Spikelets 5 (3-6), upper 1-3 sterile, so the ear suddenly becomes narrow. The rachis segment of the lower spikelets is much shorter than the adjacent spikelet. Florets 4, upper 2 sterile. The rachis segment of the upper spikelets is much longer than the adjacent spikelet causing the narrow upper part of the spike to protrude from the lower wider part. Glumes are suddenly inflated above the middle, above which they narrow to a deeply incised margin. Glumes of the lower spikelets with 4-5 (3-6) awns all similar in shape, glumes of upper spikelets similar to the lower but with 3-5 awns. Lemma awns resembling the glume awns but usually shorter and 1-3 in number. All awns diverge at maturity producing a characteristic umbel shape. The lemma of the lower spikelet has 8-12 veins near the upper margin. Caryopsis free.

Morphological variation involves mainly spike size, color and hairiness.

W. Asiatic: Greece (including Rhodes and the Aegean Islands), Turkey, Syria, N. Iraq, W and N. Iran and S. Russia (Transcausia and possibly Ciscaucasia). Grows on terra rosa, basalt, alluvial and grey calcareous steppe soils in the edges and openings of sclerophyllous or deciduous oak forest or maquis of the Mediterranean region, deciduous steppe maquis, degraded dwarf shrub formations, open dwarf shrub semi-steppe and steppe-like formations, abandoned fields, edges of cultivation and roadsides. Common, locally abundant. Often grows as a weed in cultivated areas. Alt: 100-1600 m.

Diploid, U genome. A most important species, a parent of several polyploids. Many features of this species (glume awns, sudden narrowing of the spike, free caryopsis, inflation of the glumes and whole spike disarticulation) are found in its related polyploids. Several artificial hybrids. Resistant to leaf rust.

PLATE 14. Top, spike x3; lower left, lowest spikelet x6, note sudden inflation; lower center, glume x6; lower right, uppermost two spikelets x6, note rachis segment of terminal spikelet is longer than adjacent spikelet.

T. OVATUM

Synonyms: **Ae. ovata, Ae. geniculata.**

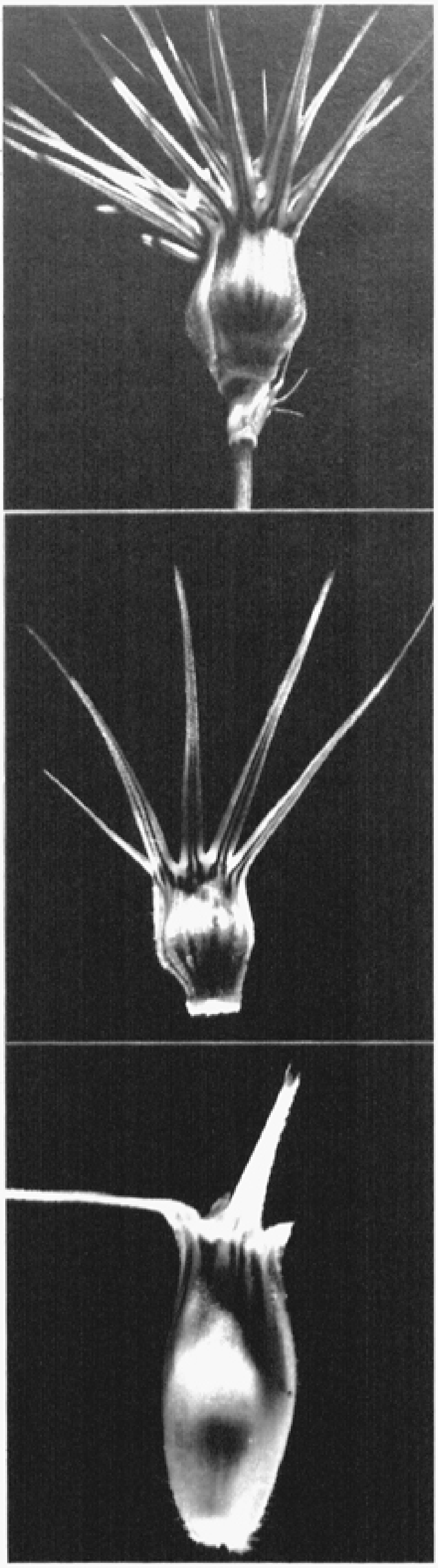
Annual, bushy branched, many jointed, upright culms 10-20 cm high with many hairy or glabrous leaves near the ground, upper 1/3 or 1/4 defoliate. Leaf blade usually short, 2-5 cm. Spike, broad-oval to narrow-elliptical, usually does not become suddenly narrow, 1-3 cm, usually awned, whole spike disarticulates at maturity. Basal rudimentary spikelets 1 (rarely 2, sometimes 0, then the spike does not disarticulate). Spikelets 3 (2-4), appressed to the rachis, all potentially fertile but the terminal usually sterile. The rachis segments usually shorter than the adjacent spikelet. Florets 5, upper 3 sterile. Glume inflated at the middle, margin usually with 2-5 (usually 4) awns (2.0-3.5 cm), usually more awns on the upper spikelets. Lemma awns shorter than glume awns, usually 2 on lower spikelets, 3 on upper. All awns diverge at maturity. Lemma of the lower spikelets have 5-7 veins near the upper margin. Caryopsis free.

Wide morphological variation in spike shape, size, hairiness, and compactness, spikelet shape, site of glume inflation, and number, length and structure of awns. In the western part of its distribution there is a compact form with irregular awns.

Mediterranean: Macaronesia (Madeira, Teneriffe), Portugal, Spain, S. France, Italy, Yugoslavia, Bulgaria, Albania, Greece, S. Russia (Crimea, Ciscaucasia, possibly S. Ukraine and Transcacausia), Turkey, N. Iraq, W. Iran, Syria, Lebanon, Cyprus, Israel, Jordan, Egypt (possibly), Libya, Tunisia, Algeria and Morocco. In several regions of Africa it penetrates into the Sahara. Grows on terra rosa, basalt, rendzina, calcareous sandstone and alluvial soils. Found in edges and openings of sclerophyllous oak forest, shrub and herbaceous formations and disturbed habitats. Often in dense stands. Alt: almost sea level - 1600 m.

Tetraploid, genomically UM, cytoplasm similar to that of **T. comosum**, grows with its two diploid parents in W. Turkey and Greece. Distribution larger than that of parents. Many natural and artificial hybrids.

PLATE 15. Upper left, spike x3; lower left, spike x3, note compact rachis; upper right, lowest fertile spikelet and rudimentary spikelet x6, note inflation of glumes and four awns; center right, glume of lowest spikelet x6; bottom right, lemma from lower spikelet x9, note two awns.



T. NEGLECTA

Synonyms: **Ae. triaristata** (4x), **T. triaristatum** (4x).

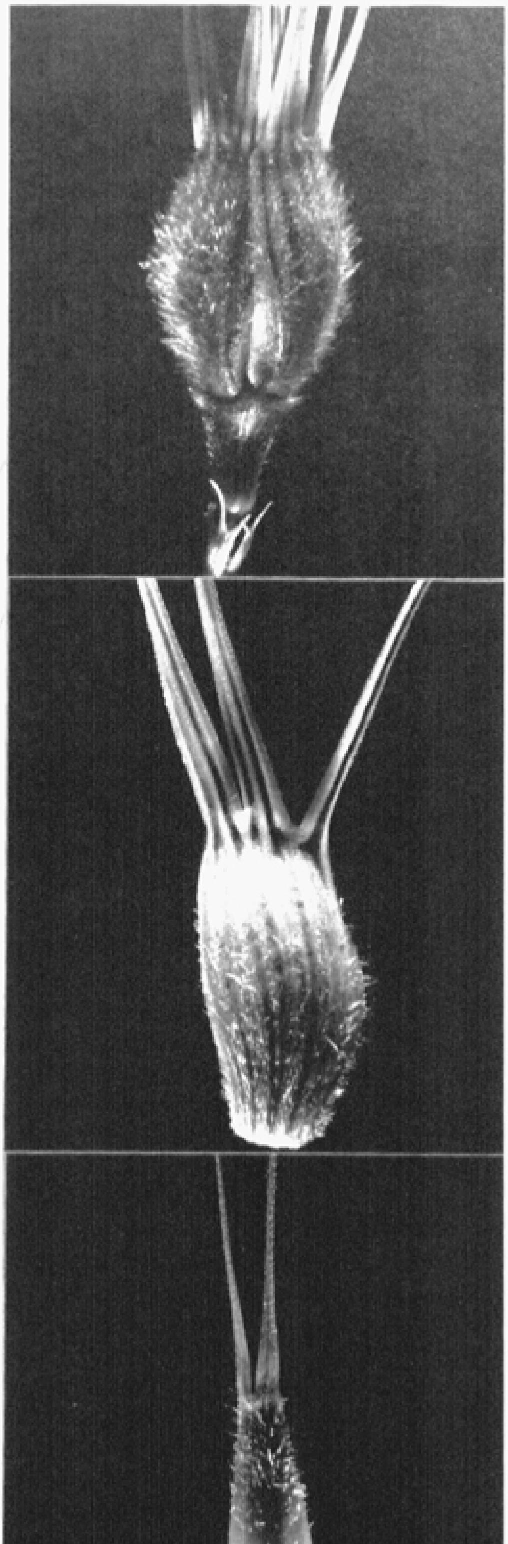
Annual, culm without many joints, 25-30 cm high, upright or somewhat jointed near the ground, upper 1/4 or 1/3 defoliate. Leaves more or less hairy, often with ciliate margins. Spike lanceolate, compact, 2.3-3.5 cm, generally becoming suddenly narrow in the upper parts, awned. The entire spike disarticulates at maturity. Basal rudimentary spikelets 3, seldom 2. Spikelets 3-6 (usually 4), the two lowest narrow to broad-elliptical, proportionally large and lying against each other, the upper two sterile and projecting conspicuously from the lower. Florets 4, upper 2 sterile. Glumes broad, with curved, unequally broad, flattened nerves, awned, equal in length to the lemma. Glume awns usually 3 (3.5-4.5 cm), those of the lower spikelets 3-2 in number, those of the upper spikelets almost always 3. Lemma awns 2-4 (usually 2) on lower spikelets, usually 0 in upper, if they exist then weakly developed. Often the awns of this species decrease in length in the upper spikelets so that all awns end at the same height. The awns of the mature spike are generally weak, seldom strong. Caryopsis free.

Wide morphological variation of spikelet number, shape and size, hairiness, awn number and development. Sometimes confused with **T. columnare.** See note page 58.

Mediterranean: Portugal, Spain, S. France, Italy, Yugoslavia, Hungary (possibly), Bulgaria, Albania, Greece, S. Russia (Crimea, Cis- and Transcaucasia), Turkey, N. Iraq, W. Iran, Syria, Lebanon, Libya, Tunisia, Algeria and Morocco. Grows on terra rosa, basalt, rendzina and alluvial soils in the edges and openings of sclerophyllous and deciduous oak forests and maquis and of dwarf-shrub formations, semi-steppe herbaceous formations, pastures, abandoned fields, edges of cultivation, disturbed and eroded areas and roadsides. Common, locally abundant. Alt: almost sea level - 1300 m.

Tetraploid, genomically UM, cytoplasm similar to that of **T. umbellulatum.** Two parents have contact in W. Turkey and Greece. Distribution much wider than its parents. Many artificial hybrids.

PLATE 16. Left, spike x3; upper right, spikelet x6; center right, glume of lower spikelet x6; lower right, lemma of lower spikelet x6.



T. RECTA

Synonyms: **Ae. triaristata** (6x), **T. triaristatum** (6x), **Ae. recta.**

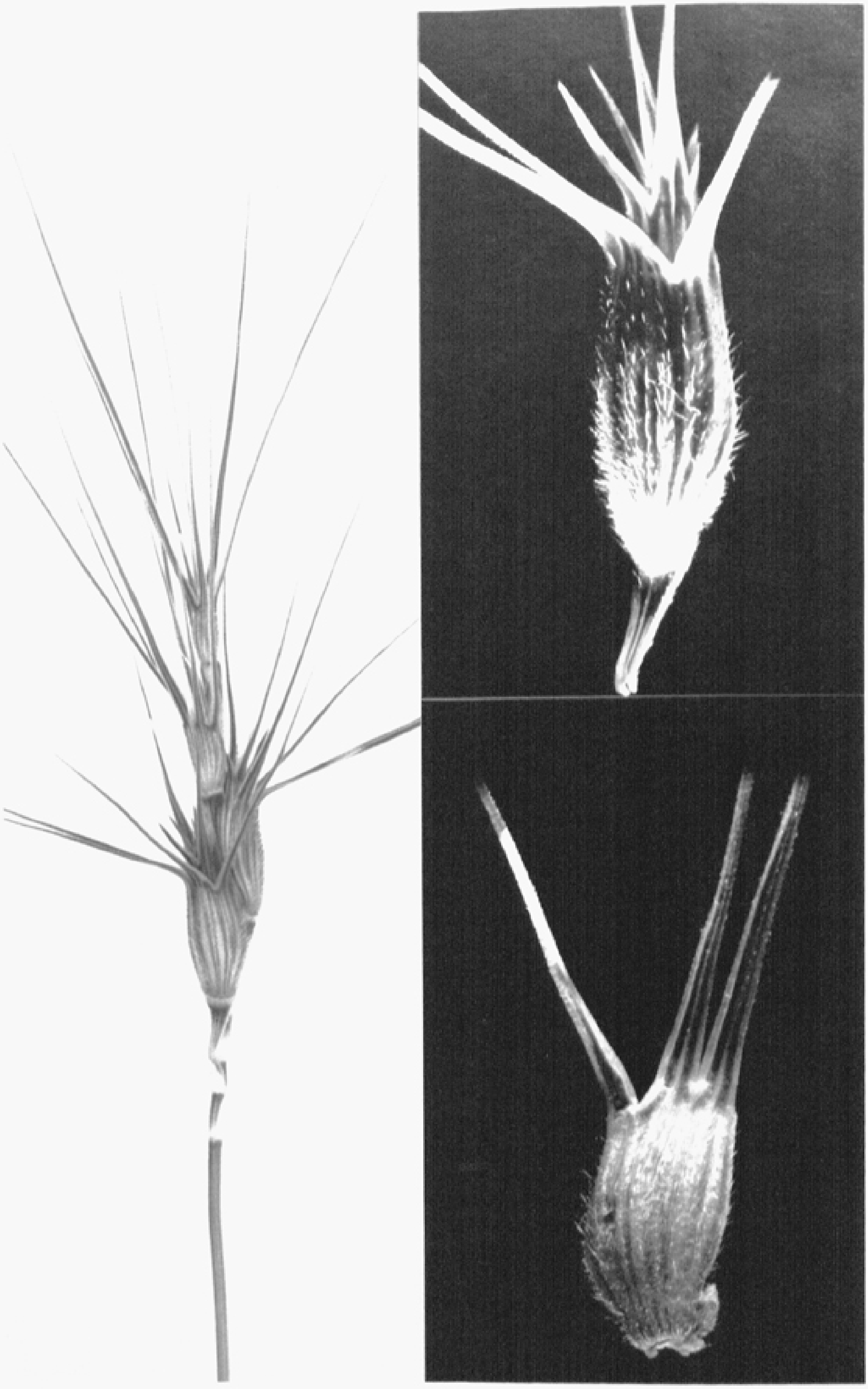
Annual, culm without many joints, 25-30 cm high, upright or somewhat jointed near the ground, upper 1/4 or 1/3 defoliate. Leaves more or less hairy, often with ciliate margins. Spike lanceolate, compact, 2-3.5 cm, generally becoming narrow in the upper parts. The entire spike disarticulates at maturity. Basal rudimentary spikelets 3, seldom 2. Spikelets 3-6 (usually 4), the two lowest narrow to broad-elliptical, proportionally large and lying against each other, the upper two fertile and projecting from the lower. Glumes broad, with curved, unequally broad, flattened nerves, awned, shorter than the lemma. Glume awns usually 3, those of the lower spikelets 3-2 in number, those of the upper spikelets almost always 3. Lemma awns 2-4 (usually 2) on lower spikelets, usually 0 in upper, if they exist then weakly developed. Often the awns of this species decrease in length in the upper spikelets so that all awns end at the same height. The awns of the mature spike are generally weak, seldom strong. Caryopsis free.

Relatively limited morphological variation involving spike size, color and hairiness. Sometimes confused with **T. columnare.** See note page 58.

Mediterranean: Portugal, Spain, France, Italy, Yugoslavia, Greece, and W. Turkey. Grows on terra rosa soil in edges and openings of sclerophyllous oak forests and maquis and dwarf-shrub formations, in abandoned fields, edges of cultivation, disturbed and eroded areas and roadsides. Relatively common in W. Turkey and Greece. Sporadic in Italy and W. Europe.

Hexaploid, genomically UMUn, cytoplasm similar to that of **T. umbellulatum.** Its two parents have contact in S. Balkans and W. Turkey where it presumably originated. Its distribution is larger than that of its diploid parent but smaller than the tetraploid. Many artificial hybrids.

PLATE 17. Left, spike x3; upper right, spikelet x6, note lemma longer than glume; lower right, glume of lower spikelet x6.



T. MACROCHAETUM

Synonyms: **Ae. biuncialis, Ae. lorentii.**

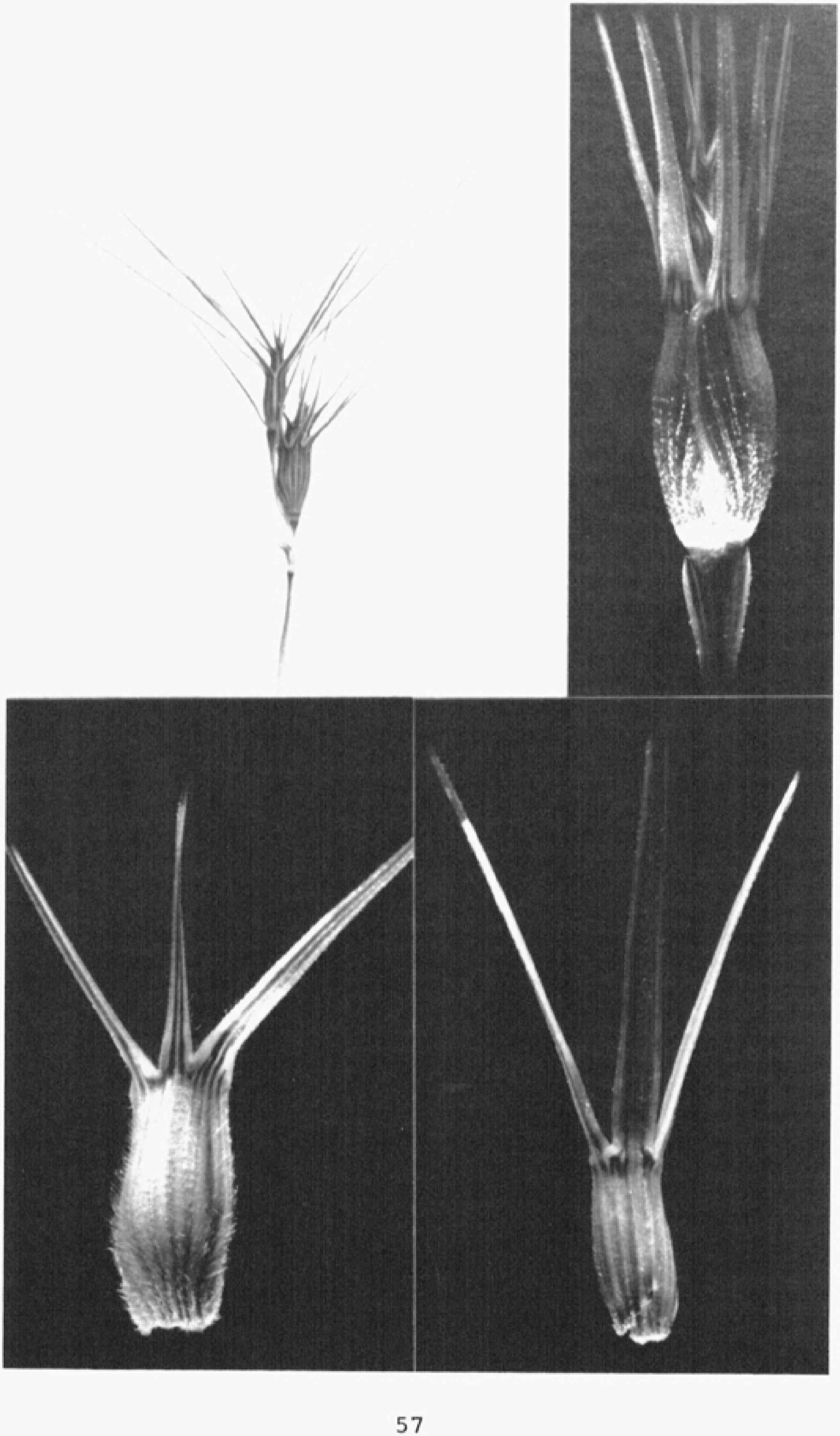
Annual, many-jointed culm, 15-30 cm high, uppermost 1/3 or 1/4 defoliate. Leaves glabrous or ciliate, seldom hairy, short (2-5 cm) narrow-linear. Spike narrow-lanceolate to narrow-elliptical, lax, 2.0-3.0 cm, awned, usually 2 spikelets the uppermost of which is not significantly smaller. Entire spike disarticulates at maturity. Basal rudimentary spikelets 1, seldom 2. Spikelets narrow to broad elliptical, sometimes lower parts slightly inflated, florets 4, upper 2 sterile. Glumes with curved, unequally broad nerves. Glume awns usually smooth underneath, equally broad, gradually tapering to the tip, unequally long in different spikelets. Glume awns of terminal spikelet 3, much longer and broader than those of the lateral spikelets, the middle awn sometimes longer than its laterals, those of the lateral spikelets 2-3, when 3 middle awn shorter than its laterals. Lemma membraneous, usually awned but the awns are more weakly developed than the glume awns, plainly shorter and reduced in number. Lemma awns always more than one per spikelet, usually 2 in lateral spikelets, 3-4 in the terminal spikelet. All the awns diverge laterally at maturity. Caryopsis free.

Relatively limited morphological variation involving mainly spike shape (elliptical to lanceolate), size (2 or 3 fertile spikelets), color, hairiness and width and length of the awns.

Mediterranean: Portugal (possibly), Spain, S. France, Italy, Yugoslavia, Romania, Bulgaria, Albania, Greece, S. Russia (Crimea, S. Ukraine, Cis- and Transcaucasia), Turkey, N. Iraq, W. Iran, Syria, Lebanon, Cyprus, Israel, Jordan, Libya, Tunisia (possibly), Algeria, and Morocco (possibly). Grows on terra rosa, basalt and rendzina soils in the edges and openings of the sclerophyllous and deciduous oak forests and maquis, in degraded shrub formations, in semi-steppe herbaceous formations, in stony hillsides, abandoned fields, edges of cultivation, disturbed and eroded areas and roadsides. Common, locally abundant and forms dense stands. Alt 400-1650 m.

Tetraploid, genomically UM, cytoplasm similar to that of **T. umbellulatum.** Its parents overlap in W. Turkey and Greece. Distribution larger than that of parents.

PLATE 18. Upper left, spike x1; upper right, spikelet x6; lower left, glume of lower spikelet x6; lower right, glume of upper spikelet x7.



T. COLUMNARE

Synonym: **Ae. columnaris.**

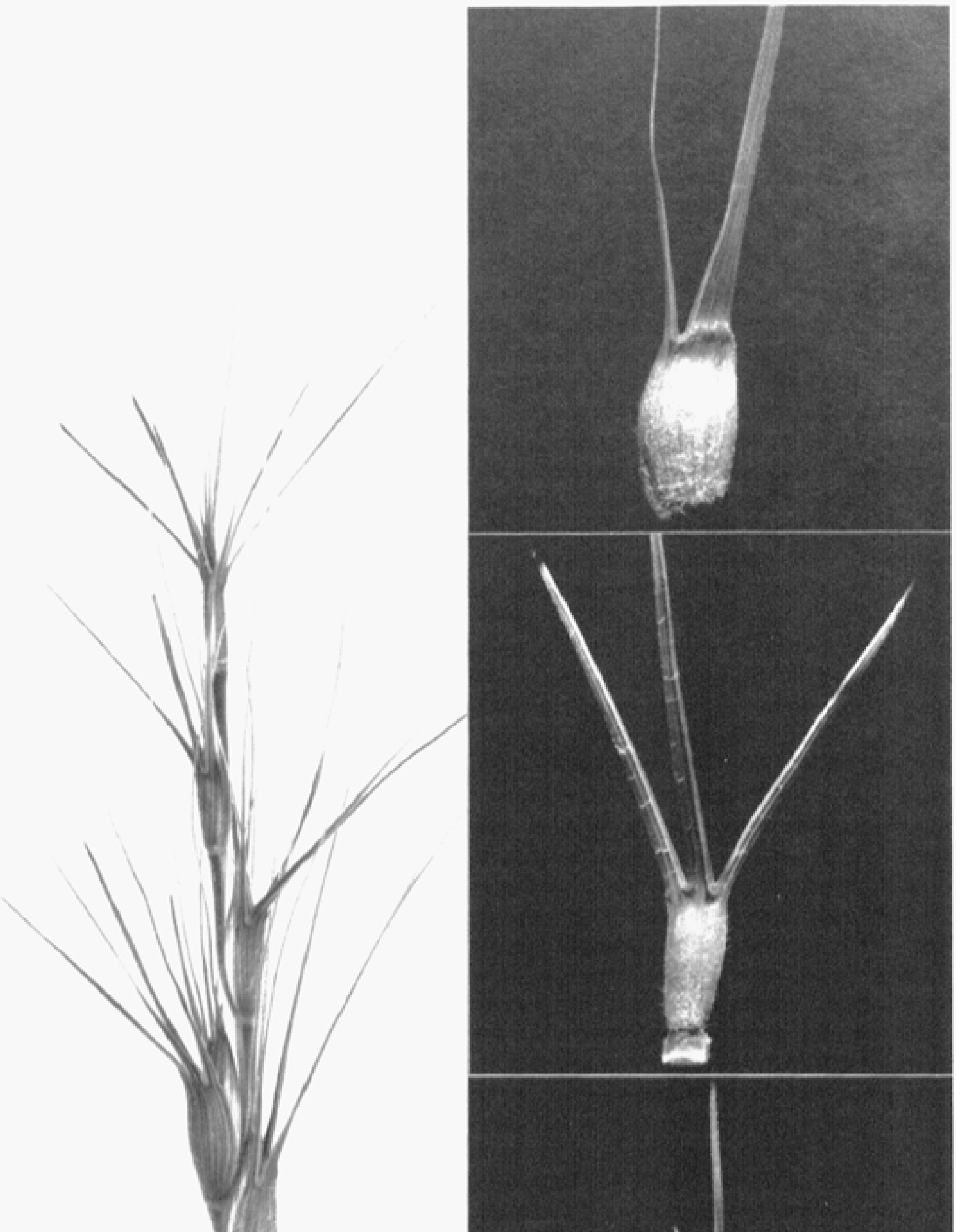
Annual, culm jointed at the base, 20-30 cm high, leaves narrow, generally hairy. Spike lanceolate, becoming suddenly narrow in the upper half, generally hairy and awned, 3.5-7.0 (usually 3.5-5.5) cm. Entire spike disarticulates at maturity. Basal rudimentary spikelets 2-4 (usually 3). Spikelets 4-6 (usually 5), the lowest two (seldom 3) elliptical and longer than the adjacent rachis segment, the upper equally long or shorter than the adjacent rachis segment, upper spikelets not fertile or with small seed. Glumes elliptical, with two awns one very much wider than the other with a deep cleft between, glumes on upper spikelets often with 3 awns, shorter than the awns on the lower spikelets. Lemma awns much weaker than glume awns, generally present in all spikelets, 1-2 per lemma. Caryopsis free.

Relatively little morphological variation involving spike size, number of fertile and rudimentary spikelets and awn development. Sometimes difficult to distinguish from **T. neglecta** and **T. recta** when those species have only two awns per glume. Generally **T. columnare** has two awns, one very much wider than the other, on the glumes of all the lateral spikelets, while **T. neglecta** and **T. recta** can sometimes have a glume with two awns and a glume with three awns on some of the lower spikelets.

W. Asiatic: Turkey, Syria, E. Lebanon, N. Iraq (rare), Iran and possibly Transcaucasia. Grows on terra rosa, basalt or grey-calcareous steppe soils in degraded deciduous oak forest, deciduous steppe maquis, degraded dwarf-shrub formations, open dwarf-shrub steppe-like formations, pastures, abandonded fields, edges of cultivation, disturbed areas and roadsides. Common in marginal Mediterranean dwarf-shrub and steppical regions. Alt: 300-1700 m.

Tetraploid, genomically UM, cytoplasm similar to that of **T. umbellulatum.** Its two putative diploid parents make contact in W. Turkey and Greece; however, the distribution of **T. columnare** is east of this contact area. Many artificial hybrids. Often found growing with other species.

PLATE 19. Left, spike x2; upper right, glume of lowest spikelet x5, note very unequal awns; center right, glume from terminal spikelet x6; lower right, lemma from lowest spikelet x7, note weak awns.



T. TRIUNCIALE

Synonym: **Ae. triuncialis.**

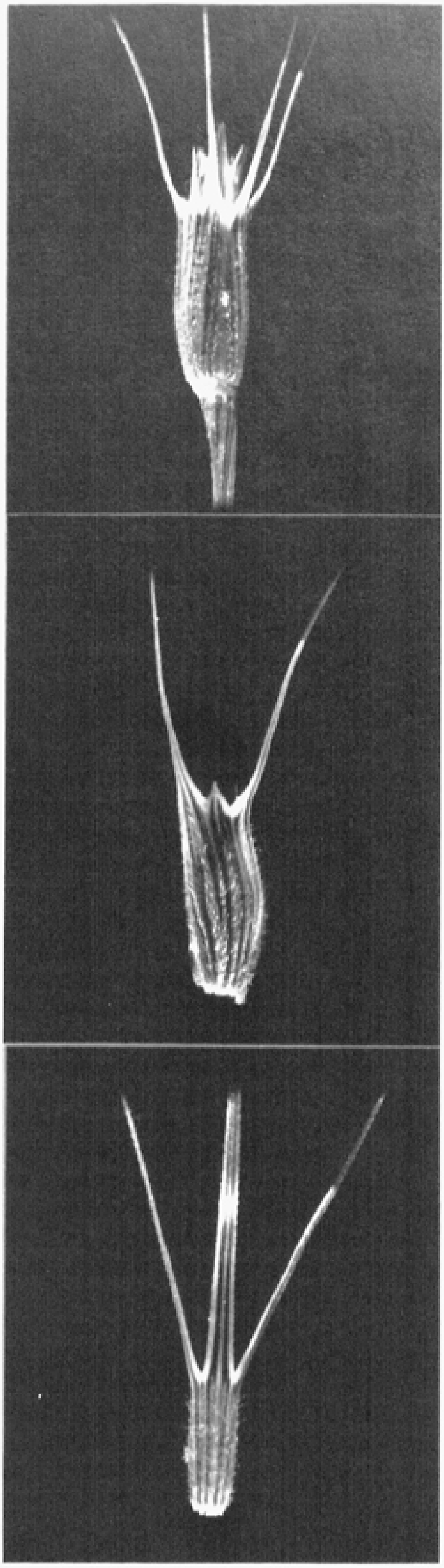
Annual, culm without many joints, usually prostrate then turning upright, 20-35 cm high, upper 1/4 defoliate. Leaves usually hairy, narrow linear, 2-6 cm long. Spike narrow-lanceolate, 3.0-6.0 cm, usually awned, tapering to the tip, well clear of the flag leaf on a long peduncle. Entire spike disarticulates at maturity, seldom into individual spikelets each with adjacent rachis segment. Basal rudimentary spikelets 3 (seldom 2). Spikelets 3-8 (usually 4-5), narrow elliptical, usually all potentially fertile, florets 4, upper 2 sterile. Glumes with curved, unequally wide nerves, often being covered with short, silvery hairs. Glume awns 3, usually smooth underneath, gradually tapering to the tip, unequal in length. Central awn of glumes of lower spikelets shorter (or a tooth) than its laterals, central awn of glumes of the terminal spikelet longer (4.5-7.0 cm) and wider than its laterals and often the longest awn on the spike, and it diverges almost at right angles to the spike axis. Lemma awns weak or not developed. Caryopsis free.

Wide morphological variation involving mainly awn development (presence or absence), length and number, spike color and hairiness. One form (**persicum**) has a terminal spikelet with no awns on the lemmas and 1 (1-3) awn on the glumes, spike sometimes disarticulates into individual spikelets each with its adjacent rachis segment. Hammer (1980) lists 17 forms and varieties.

Mediterranean and C. Asiatic: Morocco, Algeria, Portugal, Spain, France, Italy, Yugoslavia, Greece, Bulgaria, Albania, Cyprus, Turkey, Lebanon, Israel, Syria, Iraq, Iran, Kuwait, Saudi Arabia, Southern Russia, Afghanistan, and Pakistan. Grows on a variety of soils in open areas and degraded forest and maquis, dwarf-shrub formations, steppe-like formations, pastures and disturbed habitats. Common. Alt: 150-1800 m.

Tetraploid, genomically UC, some forms of ssp **eutriunciale** contain cytoplasm similar to **T. dichasians** while others contain cytoplasm similar to **T. umbellulatum**. Many artificial hybrids. Introduced, with cultivated species, into U.S.A.

PLATE 20. Left, spike x3; upper right, spikelet x5; center right, glume from lowest spikelet x5, note center awn reduced to a tooth; lower right, glume from terminal spikelet x5, note central awn is the largest on the spike.



T. KOTSCHYI

Synonyms: **Ae. kotschyi.**

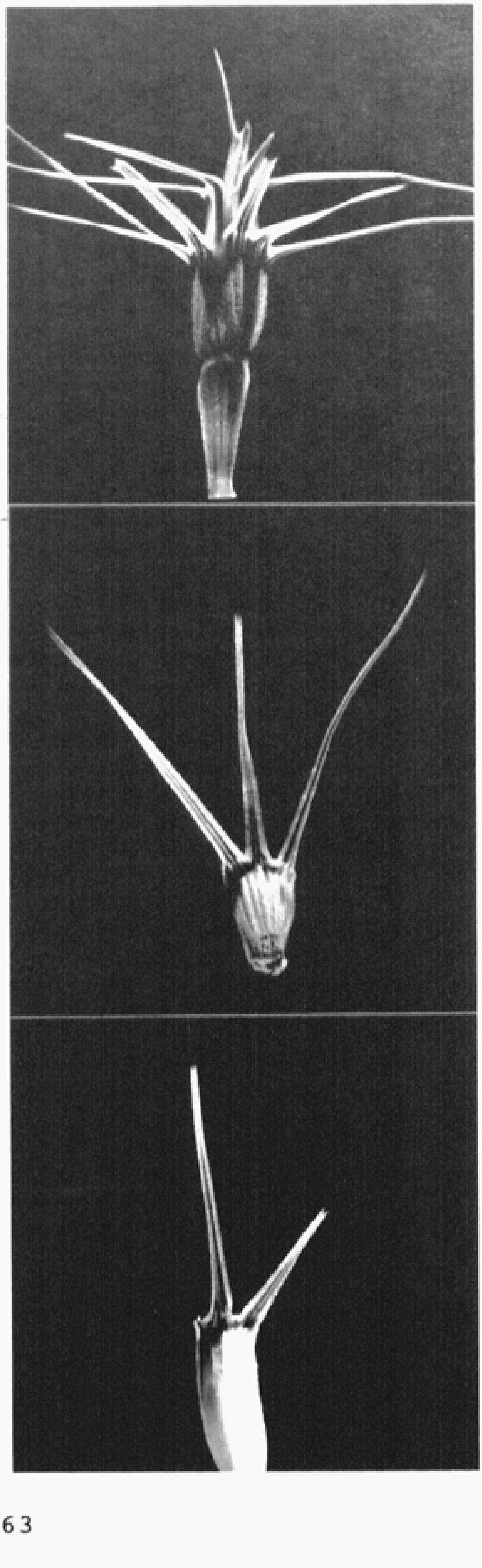
Annual, 15-25 cm high, culm usually bushy, many-jointed near the ground, upper parts upright. Leaves usually glabrous. Spike narrow-lanceolate, 2.0-3.0 cm, becoming narrow to the tip, awned, entire spike disarticulates at maturity. Basal rudimentary spikelets 2-4 (usually 3). Spikelets 2-6 (usually 4), usually linear, appressed to rachis or to each other, lowest spikelets usually longer than the adjacent rachis segment. All spikelets usually fertile, uppermost with small seed, florets 3-4, upper 1-2 sterile. Glume usually shorter than lemma, with narrow, equally wide, parallel nerves. Glume awns usually 3, sometimes 2, then central awn replaced with a tooth or gap, awns flat gradually tapering to the tip. Lemma awns 1-3, equal to or slightly shorter than glume awns. The total number of awns on the spike is 8-14, awns tend to spread at maturity. Caryopsis adherent.

Wide morphological variation involving mainly spike shape (ratio of length to width), compactness, spikelet size, awn length and development. Many intermediates occur in the contact zone with **T. peregrinum**.

S.E. Mediterranean and C. Asiatic: S. Asiatic USSR, S. Russia (Transcaucasia), Afghanistan, Pakistan, Iran, Iraq (Mesopotamia), Kuwait, Saudi Arabia, S. E. Turkey, Syria, Lebanon, Cyprus (possibly), Israel, Jordan, Egypt (lower Egypt and Sinai), Libya and Tunisia. Grows on grey-calcareous steppe soil, white rendzina, loess, sandy-clay and sandy soils, in deciduous steppe maquis, in dwarf-shrub steppe-like formations, in marginal dwarf-shrub formations, steppical plains, wadis, edges of cultivation, disturbed habitats and roadsides. Very common, locally abundant forming very dense populations in open, disturbed habitats of the warm steppes, sporadic in primary, stable habitats. Alt: 100-1100 m.

Tetraploid, genomically US, cytoplasm possibly similar to that of **T. longissimum**. Its two putative parents may have sporadic contact in semi-steppical, steppical or sub-Mediterranean regions in Syria. Its distribution is much larger than that of its parents. Hybridized with many species. Many artificial hybrids. Contains genes for drought, heat and salt tolerance.

PLATE 21. Left, spike x3; upper right, spikelet x6; center right, glume x6; lower right, glume x6.



T. PEREGRINUM

Synonyms: **Ae. peregrina, Ae. variabilis.**

Annual, bushy branched culm 15-40 cm high, branched and prostrate near the ground, upper parts upright. Leaves hairy or glabrous. Spike broad oval, linear to cylindrical, 1.2-7.5 cm, entire spike disarticulates at maturity, usually awned. Basal rudimentary spikelets 2-4 (usually 3, exceptionally 1). Spikelets 2-7 (usually 3-5), urn-shaped to elliptical, not appressed to the rachis or to each other, becoming smaller to the tip of the spike, seldom the uppermost spikelet becoming suddenly smaller, florets 3-6, usually 4-5, upper 1-3 sterile. Glume usually tough and rough, nerves weak, narrow, parallel, equally long and wide. Glume awns of terminal spikelet 3, lateral spikelets 2-3, when 2 central awn replaced by tooth or gap. Number of awns never exceeds 3. Glume awns narrow and flat at the base, strongly polymorphic and variable in number, width and length, spread out at maturity. Glume awns equally broad, or those of the lower spikelets broader, or one of them (particularly in the lower spikelets) considerably broader, equally long or differ in length (by 4-8 mm), or middle awn shorter or longer than its laterals. Lemma awns weakly developed, often missing, when present 1, very seldom 3, always shorter than glume awns, often more or less long teeth. Caryopsis adherent.

Very wide morphological variation. Two main forms: ssp. **euvariabilis** (described above) and ssp. **cylindrostachys** in which the spike is linear and long, lateral spikelets poorly awned or awnless. Many intermediate forms.

S. Mediterranean: S. Italy (including Sicily), S. Greece (including Crete and Rhodes), S. Turkey, Iraq (lower Mesopotamia), Syria, Lebanon, Cyprus, Israel, Jordan, Egypt (lower), Libya, Tunisia, Algeria and Morocco. Grows on a large variety of soils, in edges and openings of sclerophyllous oak forest, maquis, dwarf shrub formations, herbaceous formations, pastures, abandoned fields, edges of cultivation, disturbed areas and roadsides. Very common, locally abundant in open unstable secondary habitats. Alt: 0-1600 m.

Tetraploid, genomically US, cytoplasm similar to that of **T. searsii** or **T. longissimum.** Many artificial hybrids.

PLATE 22. Left, spike x3; center, spike x3 of ssp. **cylindrostachys**; top right, spikelet, x7; lower right, glume, x7.

T. TAUSCHII

Synonym: **Ae. squarrosa.**

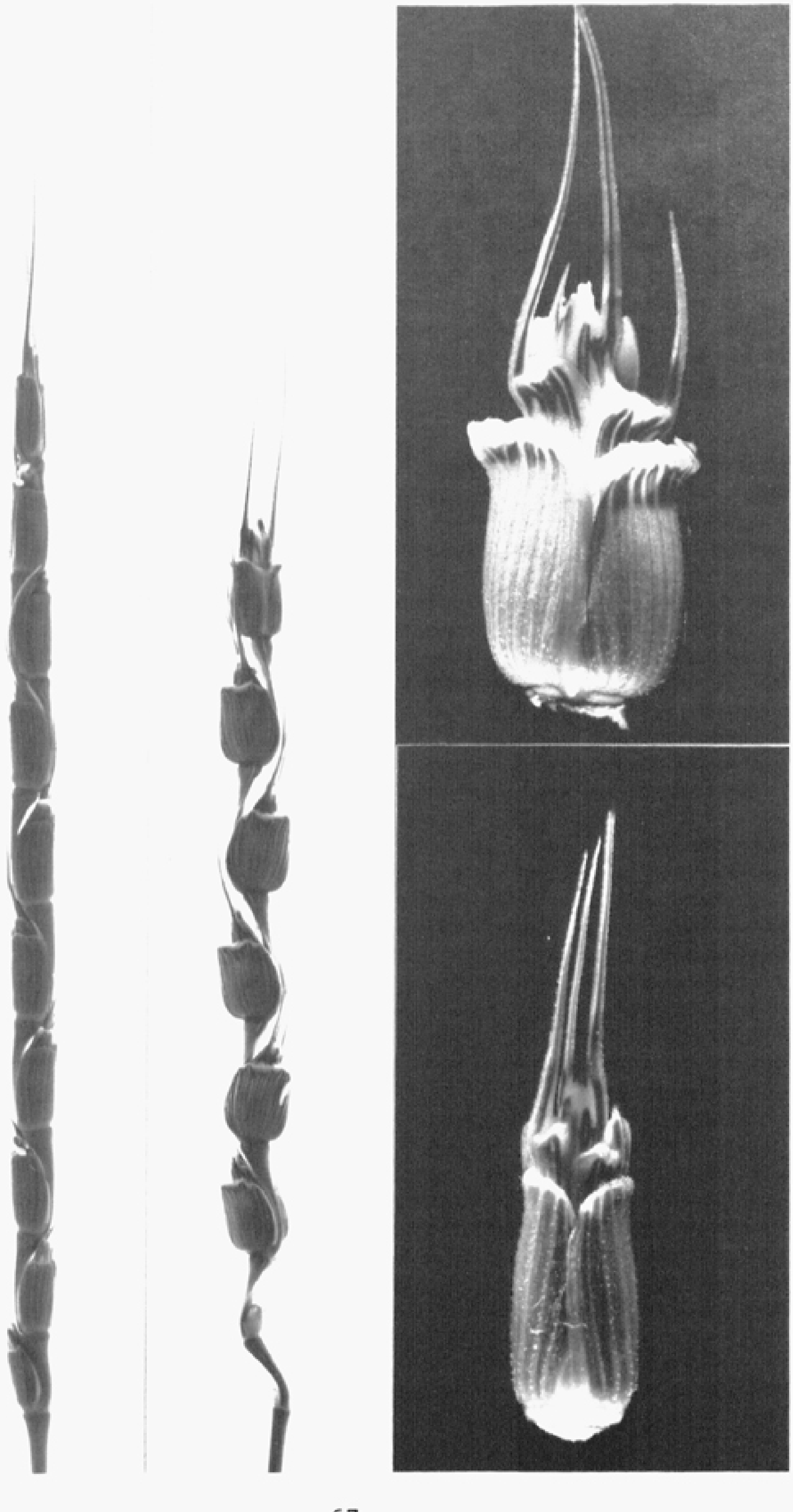
Annual. Thin culm single or branched, usually upright, 20-30 cm high, defoliate in lower parts at maturity, leaves usually long. Spike cylindrical, sometimes constricted, thick or thin, one-rowed, tapering slightly to the tip, relatively long. Disarticulates at maturity into individual spikelets, each with the adjacent rachis segment. Spikelets, 5-13, cylindrical, barrel-shaped, usually equal in length to the adjacent rachis segment, florets 3-5, usually 4, upper 1-3 sterile. Basal rudimentary spikelets 0, sometimes 1 or 2. Glume almost rectangular, narrow equally-spaced small nerves. The tip of the glume, truncate, blunt with a clearly thickened edge, one tooth or no teeth. Lemma membranous, with a keel terminated with a small tooth or awn, sometimes accompanied by 1-2 short, wide lateral teeth. The awn is triangular in cross section and is shorter on the lower spikelets. Caryopsis adherent.

Relatively little morphological variation. The variety **strangulata** has a curved rachis segment noticeably longer and narrower than the adjacent spikelet, giving the spike a markedly moniliform appearance.

C. Asiatic: S. Russia (Cis- and Transcaucasia, possibly Crimea), S. Asiatic USSR, Afghanistan, China (W. slopes of Himalayas), India (Kashmir), Pakistan, Iran, Iraq, E. Turkey and possibly N.E. Syria. Grows on grey-calcareous steppe, marl, alluvial, and sandy soils in open areas of deciduous steppe maquis, dwarf-shrub steppe-like formations, steppical plains, wadis, abandoned fields, edges of cultivation, disturbed habitat and roadsides. Weed of cultivation. Very common. Alt 150-1400 m.

Diploid, D genome. A most important species. The donor of the D genome to **T. aestivum**, the bread wheat of commerce to which it conferred baking quality and cold hardiness. Also the pivotal genome to a group of polyploid species. Many hybrids and it, as do some of its polyploid relatives, carries a gene, **Ph2**, on the short arm of chromosome 3D affecting chromosome pairing in hybrids similar to but less effective than the **Ph1** gene on chromosome 5B of **T. aestivum.**

PLATE 23. Left, spike of var. **eusquarrosa** x2; center, spike of var. **strangulata** x3; upper right, spikelet of var. **strangulata** x9; lower right spikelet of var. **eusquarrosa** x9.



T. CYLINDRICUM

Synonym: **Ae. cylindrica.**

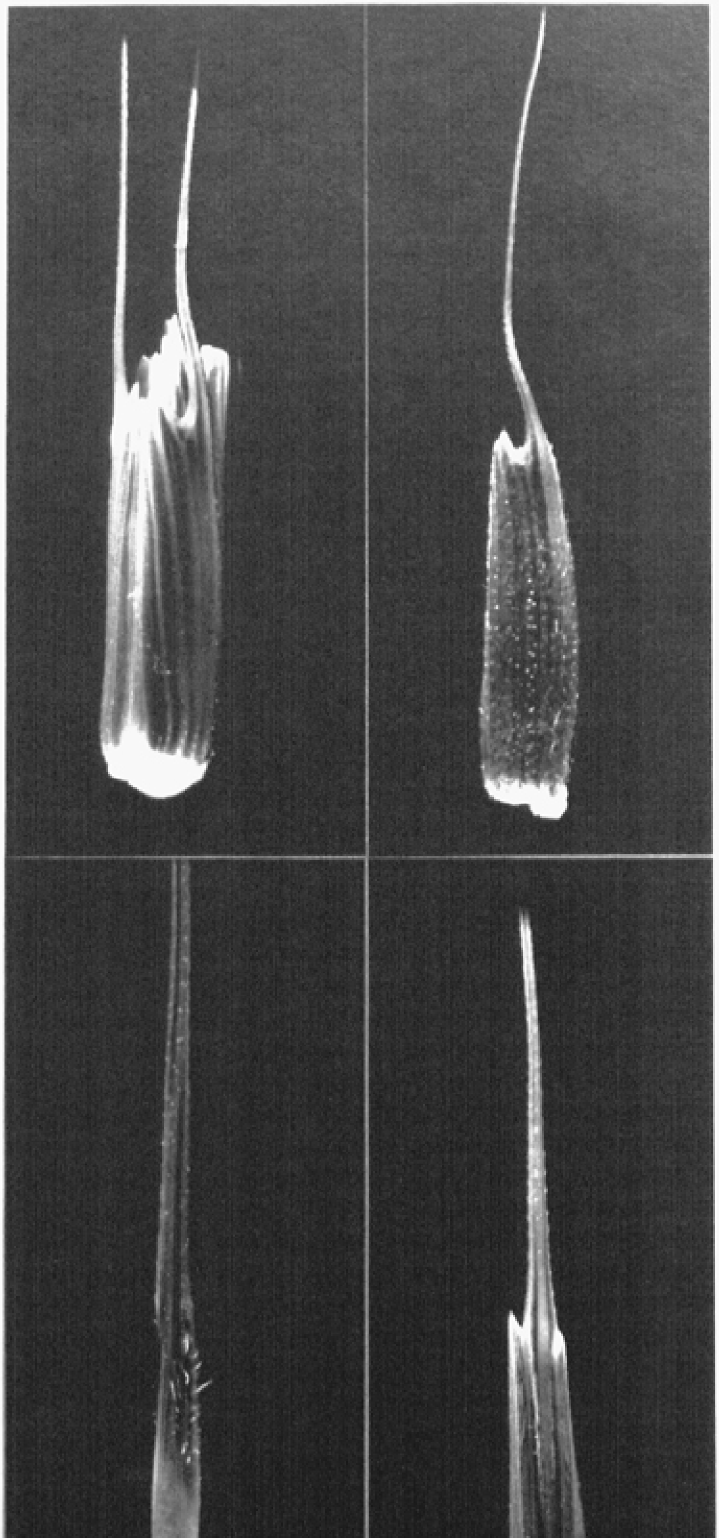
Annual, bushy branched, culm prostrate near the ground then upright, 20-40 cm high. Leaves narrow, linear, smooth or hairy. Spike long, cylindrical, one-rowed, more or less awned, 8-10 spikelets, becoming smaller to the tip of the spike. Barrel-shaped disarticulation into individual spikelets, each with the adjacent rachis segment, or entire ear separates from the culm. Rudimentary spikelets 1-2, seldom 0. Spikelets cylindrical, three or more times longer than broad, almost equal in length and appressed to rachis segment. Glumes with a short triangular awn and an associated short, broad, blunt tooth making an obtuse or acute angle with the awn. Awns on glumes of lower spikelets shorter than on upper. Lemmas solid in their upper parts, nerved, 2-3 toothed, always 3 in the terminal spikelet with the middle tooth elongated into an awn thicker and longer than the awns on the glumes. Awns of lemmas of lower spikelets shorter (or absent) than associated glume awns. Adherent caryopsis.

Wide variation in spike length, spikelet number and size, awn development, hairiness and color. More awns on the glumes but the lemma awns are more developed. Intermediate forms with **T. triunciale** are found.

N. Mediterranean and C. Asiatic: S. France, Italy, Yugoslavia, Hungary, Romania, Bulgaria, Albania, Greece (incl. Crete), S. Russia (S. Ukraine, Crimea, Cis- and Transcaucasia), S. Asiatic USSR, Afghanistan, Iran, N. Iraq (rare), Turkey and Syria. Occasionally adventive as an introduced weed of cultivation in Britain, Sweden, N.W. Russia and America (mid-west and Pacific northwest). Grows in many soils at the edges and in openings of deciduous Mediterranean and steppical oak forest and maquis, dwarf shrub, dwarf shrub steppe-like shrub formations, plains, pastures, abandoned fields, edges of cultivation, disturbed habitats and roadsides. Common, locally abundant. Persistent weed of cultivated fields. Alt: 300-1750 m.

Tetraploid, genomically CD, cytoplasm similar to that of **T. tauschii.** Frequent natural hybrids with cultivated wheats. Many artificial hybrids.

PLATE 24. Left, spike x1; upper center, lower spikelet x6; upper right, glume of lower spikelet x6; lower right, glume of terminal spikelet x6; lower center, lemma of terminal spikelet x6.



T. VENTRICOSUM

Synonym: **Ae. ventricosa.**

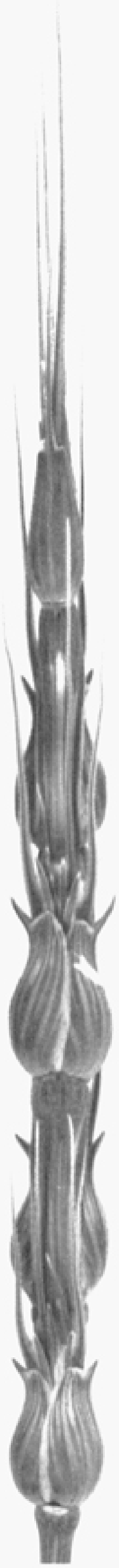
Annual, many rather thick culms, 20-30 cm high, entire length foliated, leaves broad linear, glabrous seldom hairy. Spike mostly long, 4-6 (rarely up to 12) cm, 5-10 spikelets like a string of beads, more or less rough, usually awned. Disarticulates into individual spikelets each with its adjacent rachis segment; sometimes the whole spike disarticulates at the base. Spikelets oval, equal in length to the rachis segment, suddenly becoming inflated in the lower parts (urn-shaped), florets 4-5, upper 1-3 sterile. Glumes strongly overlapping, curved nerves, tips somewhat thickened with two teeth separated with a broad sinus, one tooth may be lengthened into an awn which is usually shorter than the lemma awn. Tips of the glumes of the terminal spikelet 3-toothed, the center one of which is usually elongated into an awn. Lemma membraneous, thickened in the upper parts, weak keel the tip of which is elongated into an awn at the base of which are 1-2 small teeth. Awns triangular, lemma awns stronger than glume awns, all awns becoming longer to the tip of the spike. Adherent caryopsis.

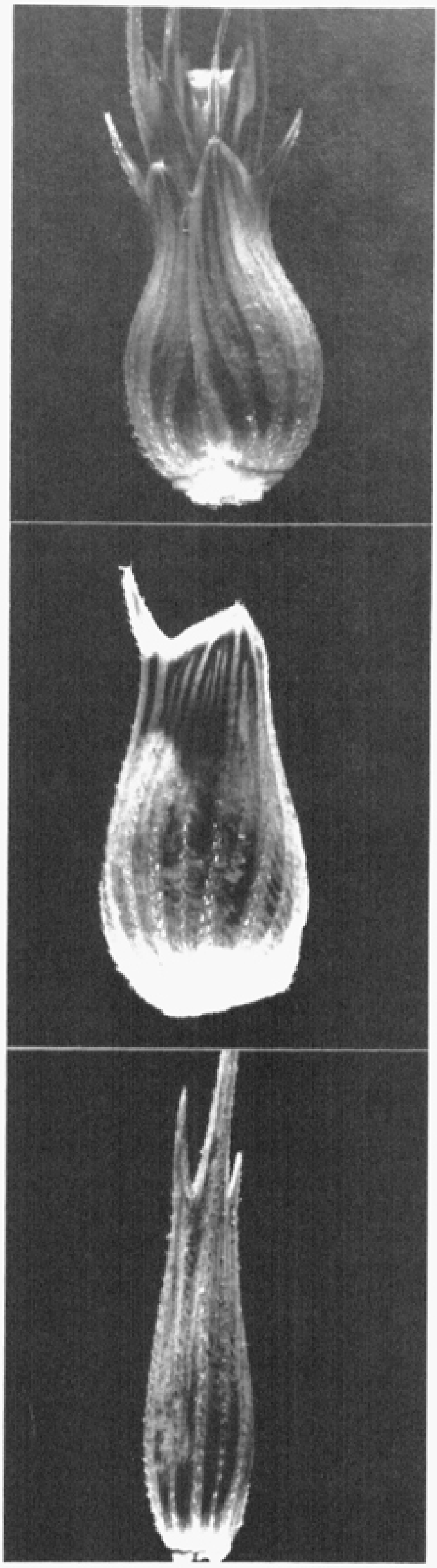
Limited variation, mainly narrowness of the upper part of the spikelets, spike length and width, spikelet number and awning. Some spike and spikelet characters similar to **T. uniaristatum** but basic characters indicate it belongs to the D-genome species cluster.

W. Mediterranean: Portugal, Spain, S. France, Italy, Egypt (near Alexandria, rare), Libya, Tunisia, Algeria and Morocco. Grows on terra rosa, rendzina and light sandy soils in the edges and openings of deciduous and sclerophyllous Mediterranean forests and maquis, in degraded dwarf-shrub and semi-steppical formations, pastures, abandoned fields, edges of cultivation, disturbed habitats and roadsides. Common in a wide array of habitats. Weed of cultivation. Alt: almost sea level - 2000m.

Tetraploid, genomically DUn, cytoplasm similar to that of **T. tauschii.** Interestingly its distribution does not overlap with either of its diploid progenitors (**T. tauschii** and **T. uniaristatum**). Its distribution area is larger than **T. uniaristatum** but smaller than **T. tauschii**. Hybrids known with many species. Resistant to eyespot, tolerant to aluminum.

PLATE 25. Left, spike x3; upper right, spikelet x8; center right, glume of lower spikelet x10; lower right, glume of terminal spikelet x10.





T. CRASSUM

Synonym: **Ae. crassa.**

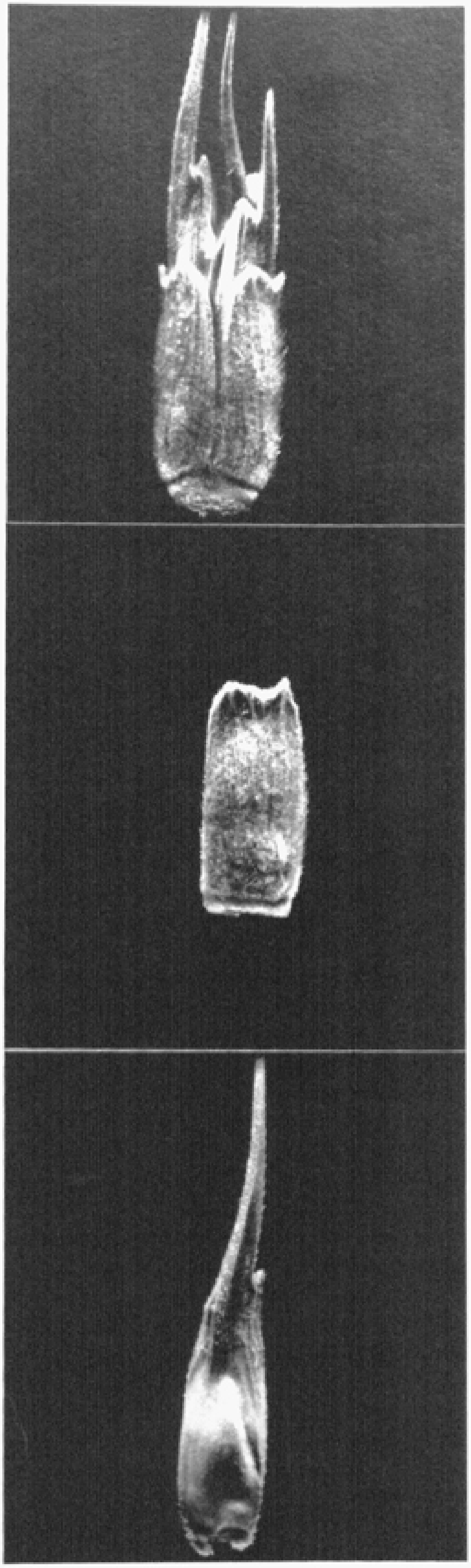
Annual, culm many-jointed, sometimes thick, 20-30 cm high, often whole length foliated. Spike usually long (4-8 cm), thick, cylindrical, somewhat like a string of beads, tapering to the tip, usually hairy, barrel-shaped disarticulation, each spikelet with its adjacent rachis segment, 0-2 rudimentary spikelets. Spikelets (5-11) somewhat inflated in the lower parts, equal to or slightly shorter than the adjacent rachis segment, florets 3-5, upper 1-3 sterile. Glumes somewhat or not fully overlapped, covered with fine silvery hairs, glume tip blunt, thickened, with 1-4, usually 2, teeth separated by a broad and shallow sinus, usually not awned or seldom with a short awn. Glume awns are slender, triangular and weaker than the lemma awns of the same spikelet. Lemma membraneous or cartilaginous, somewhat keeled usually tipped with a tooth or an awn flanked by 1-2 lateral teeth. The lemma awns are mostly broad and more strongly developed in the upper spikelets. Caryopsis adherent.

Very wide morphological variation (this species and **T. peregrinum** are the most variable species), involving all the diagnostic characters such as spike and spikelet size, form, structure, color, awn development, form and place of attachment.

C. Asiatic: S. Russia (Transcaucasia), S. Asiatic USSR (Turkestan, Pamir-Alai), Afghanistan, Iran, Iraq (Iraqi Kurdistan and Mesopotamia), N.E. Syria and S.E. Turkey. Grows on grey-calcareous, loess and alluvial soils and on stony slopes and gravel, in degraded deciduous steppe maquis, juniperous forests, dwarf-shrub steppe-like formations, steppical plains, wadis, edges of cultivation, disturbed habitats and roadsides. Common. A common weed of cultivation. Alt: 200-900 m.

Both tetraploid and hexaploid morphologically indistinguishable cytotypes are known, genomically DM and DDM respectively, cytoplasm similar to that of **T. tauschii.** There is evidence that the D genomes in the hexaploid and possibly the M genomes in both forms are substantially modified. Many artificial hybrids are known, makes natural hybrids with wheat in cultivation.

PLATE 26. Left, spike x2; upper right, spikelet x6; center right, glume x6; lower right, lemma x6, note broad awn.



T. JUVENALE

Synonyms: **Ae. juvenalis, Ae. turcomanica.**

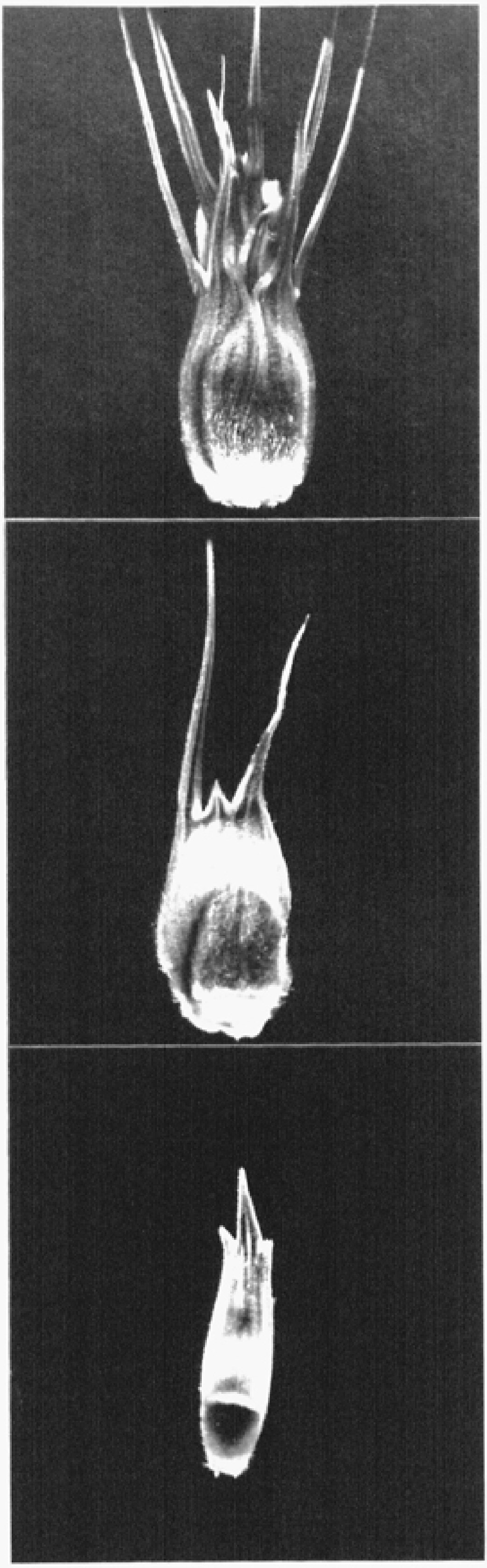
Annual, 20-40 cm high, jointed in the lower parts then upright, glabrous or almost so. Leaves broad. Spike medium-sized, 4-8 cm, thick, one-rowed, somewhat like a string of beads, becoming narrower to the tip, hairy, with 4-7 (usually 5) spikelets. Rudimentary spikelets 1-2, seldom 0. Disarticulates into individual spikelets each with its adjacent rachis segment. Spikelets, elliptical, weakly inflated in the lower parts, somewhat incised above. Glumes hairy and overlapping in the upper parts. Tips of the glumes of lateral spikelets with 1-4 small, narrow and flat awns separated from each other by an interval, glume of the terminal spikelet with a flat awn and two flanking teeth, or with 2 or 3 awns. Lemma leathery, hairy at the top and about one-third longer than the glume, with a flat awn and two lateral teeth or seldom with 3 awns. Lemma awns more strongly developed than glume awns. Caryopsis adherent.

Limited morphological variation. Thellung, who first described this species, thought it was a hybrid between **T. crassum** and **T. triunciale.** It resembles **T. crassum** in many characters but differs from it by its many flat awns on the glumes and lemma and by shorter and wider glumes, all of which are characters of **T. umbellulatum.**

C. Asiatic: S. Asiatic USSR, Iran, Iraq (Mesopotamia) and N.E. Syria. Grows on grey calcareous and alluvial soils, stony ground, gravel and open steppical habitat, edges of cultivation and roadsides. Weed of cultivation. Sporadic distribution, mainly in secondary disturbed habitats, throughout the warm steppes of central Asia. Adventive in S. France (Port Juvenal - from where it receives its name). Alt: 50-900 m.

Hexaploid, genomically DMU, cytoplasm similar to that of **T. crassum,** i.e., that of **T. tauschii.** Some evidence that at least the D and M genomes have been substantially modified. Many artificial hybrids. Its distribution overlaps that of its tetraploid parent but is much more restricted.

PLATE 27. Upper left, spike x1; lower left, spike of awnless form x1; upper right, spikelet x6, note overlapping glumes; center right, glume x6; lower right, lemma x4.



T. SYRIACUM

Synonyms: **Ae. crassa, Ae. crassa** var **vavilovi**, also var **palaestina, Ae. vavilovi**.

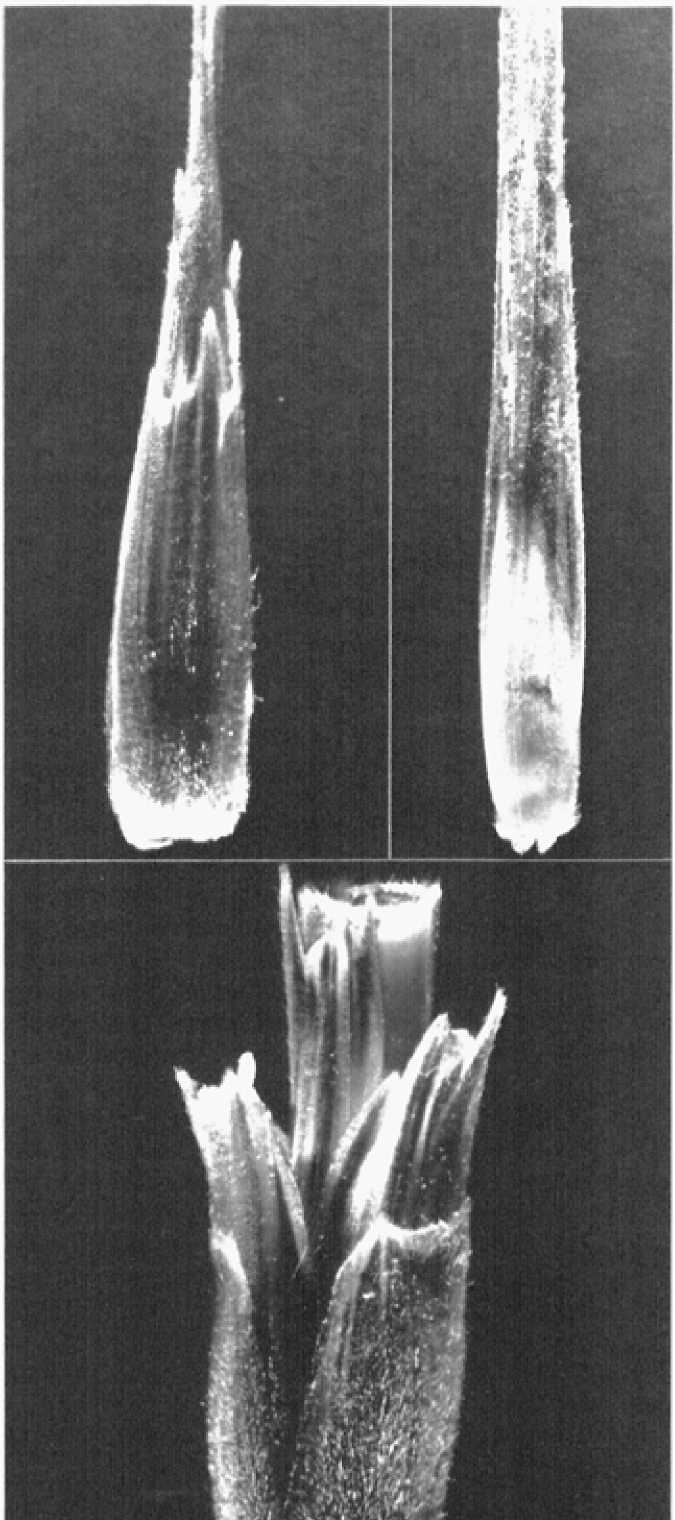
Annual, culm many-jointed, thick 20-30 cm high. Spike 10-15 cm, 5-10 spikelets, cylindrical or more or less zig-zag, 0-3, usually 1, basal rudimentary spikelets. Disarticulates into individual spikelets at maturity each with its adjacent rachis segment. Spikelets cylindrical to slightly inflated at the base, edges of the glumes overlap slightly. Glumes truncate, covered with fine silvery hairs, about 2/3 to 3/4 as long as the lemmas, with 2-3 teeth. Lemma also with 2-3 teeth one of which may be extended into a small awn. Lemmas of the terminal spikelet with strong, broad awns 5-8 cm long with a prominent central nerve, awn flanked with two small teeth. Caryopsis adherent.

Limited morphological variation. It differs from **T. crassum** by its long cylindrical and sometimes zigzagged spike and by the absence of awns on the lateral spikelets while those of the uppermost spikelet are very long, all of which are characters that were derived from its S genome parent.

S.E. Mediterranean: Egypt (Sinai), S. and E. Israel, Jordan, Lebanon and Syria. Grows on grey calcareous, rendzina, alluvial or sandy soils in the edges of dwarf-shrub steppe-like formations, wadis, stony slopes edges of cultivation and disturbed habitats. Rare, mainly in secondary habitats of the high elevations of the S.E. Mediterranean steppes, also in sandy habitats of the Sinai coastal plain and dry and semi-desert habitats in Eastern Syria and Jordan. Alt: 50-1100 m.

Hexaploid, genomically DMS, cytoplasm similar to that of **T. crassum**, i.e., **T. tauschii**. Its distribution partially overlaps that of its diploid parent, but much more restricted. Several artificial hybrids known.

PLATE 28. Left, spike x2; upper center, terminal spikelet x9; upper right, lemma of terminal spikelet x12; lower right spikelet x10.



SYNONYMS

The large number of generic and specific epithets of this variable and inter-breeding group stems not only from the penchants of various taxonomists but represents the diversity of the species themselves. To provide a complete tabulation is clearly beyond this work. If greater detail is required the reader is referred to the extensive work of Hammer (1980).

Only the most commonly used names are given in the following list. Further, the listing of any name is not to be taken as a demonstration of priority. The names used in this publication are printed in bold face to aid in their location and to facilitate the use of the list.

Ae. aucheri = **T. speltoides (aucheri)**
Ae. bicornis = **T. bicorne**
Ae. biuncialis = **T. macrochaetum**
Ae. caudata = **T. dichasians**
Ae. columnaris = **T. columnare**
Ae. comosum = **T. comosum**
Ae. crassa = **T. crassum**
Ae. cylindrica = **T. cylindricum**
Ae. geniculata = **T. ovatum**
Ae. heldreichii = **T. comosum**
Ae. juvenalis = **T. juvenale**
Ae. kotschyi = **T. kotschyi**
Ae. ligustica = **T. speltoides (ligustica)**
Ae. longissima = **T. longissimum**
Ae. longissima var. sharonensis = **T. sharonense**
Ae. lorentii = **T. macrochaetum**
Ae. markgrafii = **T. dichasians**
Ae. mutica = **T. tripsacoides**
Ae. neglecta = **T. neglecta,** T. triaristatum (4x)
Ae. ovata = **T. ovatum**
Ae. peregrina = **T. peregrinum**
Ae. persica = **T. triunciale**
Ae. recta = **T. recta,** T. triaristatum (6x)
Ae. searsii = **T. searsii**
Ae. sharonensis = **T. sharonense**
Ae. speltoides = **T. speltoides (ligustica)**
Ae. squarrosa = **T. tauschii**
Ae. tauschii = **T. tauschii**
Ae. triaristata (4x) = **T. neglecta**
Ae. triaristata (6x) = **T. recta**
Ae. tripsacoides = **T. tripsacoides**
Ae. triuncialis = **T. triunciale**
Ae. turcomanica = **T. juvenale**
Ae. umbellulata = **T. umbellulatum**

Ae. uniaristata = **T. uniaristatum**
Ae. variabilis = **T. peregrinum**
Ae. vavilovi = **T. syriacum**
Ae. ventricosa = **T. ventricosum**
T. aegilops = **T. tauschii**
T. aegilopoides = **T. monococcum**
T. araraticum = **T. timopheevii**
T. bicorne = Ae. bicornis
T. boeoticum = **T. monococcum**
T. carthlicum = **T. turgidum**
T. columnare = Ae. columnaris
T. comosum = Ae. comosa, Ae. heldreichii
T. crassum = Ae. crassa, Ae. vavilovi
T. cylindricum = Ae. cylindrica
T. dichasians = Ae. caudata, Ae. markgrafii
T. dicoccoides = **T. turgidum**
T. dicoccum = **T. turgidum**
T. durum = **T. turgidum**
T. juvenale = Ae. juvenalis, Ae. turcomanica
T. kotschyi = Ae. kotschyi
T. longissimum = Ae. longissima
T. macrochaetum = Ae. biuncialis, Ae. lorentii
T. monococcum = T. aegilopoides, T. boeoticum,
= T. monococcum, T. urartu
T. neglecta = Ae. neglecta, Ae. triaristata (4x)
T. ovatum = Ae. ovata, Ae. geniculata
T. peregrinum = Ae. peregrina, Ae. variabilis
T. persicum = **T. turgidum**
T. polonicum = **T. turgidum**
T. recta = Ae. triaristata (6x)
T. searsii = Ae. searsii
T. sharonense = Ae. sharonensis,
= Ae. longissima var. sharonensis
T. speltoides (aucheri) = Ae. aucheri
T. speltoides (ligustica) = Ae. speltoides,
= Ae. ligustica
T. syriacum = Ae. vavilovi, Ae. crassa var.
vavilovi or var. palaestina
T. tauschii = Ae. squarrosa
T. timopheevii = T. timopheevii, T. araraticum
= T. timopheevii var. zhukovskyi
T. timopheevii var. zhukovskyi = **T. timopheevii**
T. triaristatum = Ae. triaristata, Ae. recta,
= Ae. neglecta, T. rectum
T. tripsacoides = Ae. mutica
T. triunciale = Ae. triuncialis
T. turgidum = T. carthlicum, T. dicoccoides,
= T. dicoccum, T. durum,
= T. persicum, T. polonicum
T. umbellulatum = Ae. umbellulata
T. uniaristatum = Ae. uniaristata
T. urartu = **T. monococcum**
T. ventricosum = Ae. ventricosa

GEOGRAPHICAL DISTRIBUTION AND ECOLOGICAL AFFINITIES

The 27 species of the genus **Triticum** are distributed in the Mediterranean basin and in southwest and central Asia. The genus is distributed in the area between 10° W and 85° E and between 26° and 50° N. It is rectangular in shape, with its width being about four times its length. The center of the distribution is in S.E. Turkey (38° N, 36-37° E). The western border of distribution is in Madeira and the Canary Islands (**T. ovatum**); to the north it reaches into northern Hungary or even to southern Czechoslovakia in Europe (**T. cylindricum**) and up to the Aral-Caspian deserts and Altai in Asiatic USSR (**T. cylindricum**); to the south it includes the Canary Islands and the northern border of the Sahara Desert in N. Africa (**T. ovatum**) and up to southern Iran in Asia (**T. crassum**); while the eastern border is on the western slopes of the Himalayan Mountains and the banks of the Indus (**T. tauschii**) (Zhukovsky, 1928; Eig, 1929; and Kihara, 1954).

Within the borders of its distribution the genus has massive, wide and almost continuous distribution. Species of **Triticum** are found in almost every place except high mountains (above 1800 m.) and deserts (**T. kotschyi** even penetrates in to semi-desert areas). All the islands of the Mediterranean Sea are also inhabited by some species. The genus can be regarded as having a very wide adaptation and it occupies almost all habitats available to it. Its distribution is limited by sea or desert in the west or south, by high mountains in the east and by cold climate in the north. The cool deciduous forest on one side and true desert on the other are the extreme ecological formations for the genus **Triticum**. The climate of most of the genus distribution is marked by a short, mild and rainy winter and a long, hot and dry summer. The genus has developed in and adapted itself to the conditions between these extremes in that all the species are annuals (grow in the winter and pass the dry, hot summer as seed), most of them are predominantly self-pollinated and have large, well protected grains for the safe and rapid reestablishment of the stand (Feldman, 1976).

Most of the species grow in the central part of the genus distribution (Table 1). Countries like Turkey, Syria, Iraq and Iran contain 17-20 of the 27 species in the genus, while peripheral countries like those of Western Europe and North Africa in the west, or South Asiatic USSR, Afghanistan and Pakistan in the east contain few (six or fewer) species. Thus Turkey, Syria, Iraq and Iran (the area between 20° and 40° East and 35° and 45° North - the northern part of the fertile-crescent belt), is not only the geographical center of the genus distribution but also this area contains the greatest concentration of species. This is presumably the center of origin and development of most of the species. From this primary center the genus spread centrifugally.

Five diploid species (**T. tripsacoides, T. monococcum, T. speltoides, T. dichasians** and **T. umbellulatum**) are distributed in the central part of the genus distribution (Table 1). Several species of the S-genome group (**T. longissimum, T. searsii, T. sharonense** and **T. bicorne**) are found south of the center and the species of the M/Un -genome group (**T. comosum** and **T. uniaristatum**) west of the center, while **T. tauschii** is in the eastern part of the genus distribution. Some of the diploid species are characterized by relatively large distribution areas (**T. monococcum, T. umbellulatum, T. dichasians** and **T. tauschii**), or by a medium-sized area (**T. speltoides**), while others are characterized by a small distribution area (**T. tripsacoides, T. bicorne, T. searsii, T. sharonense, T. longissimum, T. uniaristatum** and **T. comosum**). Some species are endemics (**T. sharonense** and **T. searsii**). The geographical distribution of the various diploid species indicates that the genus has undergone an extensive differentiation in its early stages of development.

The polyploid (particularly tetraploid) species have, in general, a wider distribution than the diploids (Table 1) (Zohary and Feldman, 1962; Feldman, 1963). The polyploids of the U-genome group have the widest distribution, those of the D-genome group an intermediate one and those of the A-genome group have a relatively restricted distribution. The polyploids of the U-genome group are distributed in the central and western parts of the genus distribution (except **T. triunciale** and **T. columnare** which extend to the east and **T. kotschyi** found only in the south-east), those of the D-genome group in the eastern part (except **T. ventricosum** which is found in the western part and **T. cylindricum** which is distributed all over the northern part), while those of the A-genome group are distributed in the central parts of the genus distribution.

The genus consists of species which are Mediterranean or steppical (Irano-Turanian) elements. Actually, the center of origin and development of the genus, which is in the fertile crescent belt, is characterized by marginal Mediterranean conditions. From this center the various species have spread to more typical Mediterranean or steppical areas.

All of the species have, more or less, continuous distributions and usually occupy open habitats in the edges and openings of Mediterranean formations, in herbaceous park-forest formations (of which some of the species are natural components), in pastures, abandoned fields, edges of cultivation and roadsides (Zohary and Feldman, 1962; Feldman, 1963 and Feldman and Zohary, unpublished). Some of the habitats are primary in well-defined and balanced ecological conditions, while most of the habitats are secondary in disturbed and degraded areas. Many of the species also grow as weeds in cultivated fields. In disturbed and newly opened habitats, some of the species (particularly the tetraploids) can form massive and very dense stands, usually consisting of several species. Their genetic system provides them with the ability to colonize such newly-opened areas quickly and efficiently.

There are striking differences between the patterns of geographical distribution and ecological affinities of the diploid and tetraploid species (Zohary and Feldman, 1962; Feldman, 1963). All the diploids are distributed either in or around the center of the distribution of the genus (except **T. tauschii** which grows in the eastern part). They are relatively restricted in their distribution (Table 1) and are much more specialized than the tetraploids in their ecological requirements, usually occupying well-defined habitats with specific edaphic or climatic conditions. Some of the diploids show wider ecological amplitudes correlated with their weedy and segetal tendency.

In general the polyploids have larger distribution areas and wider ecological amplitudes than the diploids. The distributions of some of them, such as **T. triunciale**, **T. ovatum**, **T. neglecta**, **T. macrochaetum** and **T. cylindricum** occupy large parts of the distribution area of the genus. They grow well in a very wide array of edaphic and climatic conditions and so do not show the marked ecological specificity of the diploids. Their weedy nature is reflected in their ability to colonize rapidly and efficiently a variety of newly disturbed and secondary habitats. Undoubtedly, the expansion of agriculture and the opening up of many segetal habitats, played a key role in the massive distribution of these polyploid species throughout the range of the genus.

Many tetraploid species are sympatric (Table 2) and tend to grow in mixed stands, usually with several species in each population (Feldman, 1965a, Feldman and Zohary, unpublished). However, in various parts of the genus distribution one tetraploid is the massive, dominant species. Thus, **T. cylindricum** is such a species in the northern part of the genus distribution, **T. triunciale** in the central and western parts, **T. peregrinum** in the southern part, **T. kotschyi** in the southeastern part and **T. crassum** in the eastern part. This interregional kind of vicarism reflects the ability of the various tetraploids to adapt themselves to different climatic conditions.

The distribution areas of most of the tetraploids overlap, completely or partly, with that of their two diploid parents. Exceptions are **T. columnare** and **T. crassum**, which do not overlap with the distribution area of the M genome donor and **T. ventricosum** which does not overlap with the distribution of either of its parents, the Un and D genome donors. Most of the putative diploid parents of the various tetraploids have spatial contact, either sympatric or allopatric. Only **T. tauschii** and the donors of the M and Un genomes have no such contacts.

The distribution areas of all seven tetraploid species of the U-genome group and that of **T. cylindricum** from the D-genome group is larger than that of each of their diploid parents (only that of **T. columnare** is equal or somewhat smaller than that of **T. umbellulatum**). The distribution area of each of the other tetraploids of the D-genome group, **T. ventricosum** and **T. crassum**, is larger than that of the M- or Un-genome donors but smaller than that of **T. tauschii**, the D-genome donor. The distribution area of the tetraploids of the A-genome group is smaller than that of either of their parents. The ecological amplitude of most of the tetraploids is much larger than that of their diploid parents.

In contrast to the wide distribution of the tetraploid species, the distribution area of the hexaploid species is, in all cases, smaller than that of their tetraploid and diploid parents. Only **T. recta** has a larger distribution area than that of its diploid parent, **T. uniaristatum**. The relatively restricted distribution area of the hexaploids tends to lie close to the center of the distribution of the genus. Also their ecological amplitudes are much more restricted than those of the related tetraploids and even the diploid parents. They grow in a smaller number of habitats and then often only sporadically. The morphological variation of the hexaploids is also relatively limited.

Table 1. The occurrence of the species of **Triticum** in different countries. Solid circles indicate confirmed presence; open circles indicate possible presence.

Page 85. Central Asiatic and East Mediterranean countries.

Page 86. Other Mediterranean and Southern European countries.

Country	Tripsacoides 2x	Speltoides 2x	Bicorne 2x	Sharonensis 2x	Longissimum 2x	Searsii 2x	Dichasians 2x	Comosum 2x	Uniaristatum 2x	Monococcum 2x	Timopheevii 4x	Turgidum 4x	Umbellulatum 2x	Ovatum 4x	Neglecta 4x	Recta 6x	Macrochaetum 4x	Columnare 4x	Triunciale 4x	Kotschyi 4x	Peregrinum 4x	Tauschii 2x	Cylindricum 4x	Ventricosum 4x	Crassum 4x,6x	Juvenale 6x	Syriacum 6x	Species/country
USSR (Transcaucasia)	●									●	●		●	○	●		●	○	●	●		●	●		●			11 (13)
USSR (South Asiatic)																			●	●		●	●		●	●		6
Afghanistan							●												●	●		●	●		●			6
China (Himalayas)																						●						1
India (Kashmir)																						●						1
Pakistan																			●	●		●						3
Iran	●	●					●			●	●	●	●	●	●		●	●	●	●		●	●		●	●		17
Iraq	○	●					●			●	●	●	●	●	●		●	●	●	●	●	●	●		●	●		17 (18)
Kuwait																			●	●								2
Saudi Arabia																			●	●								2
Turkey	●	●					●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●		●			20
Syria	●	●			●	●	●			●		●	●	●	●		●	●	●	●	●	○	●		●	●	●	19 (20)
Lebanon		●		●	●	●	●			●		●		●	●		●	●	●	●	●						●	15
Cyprus							●							●			●		●	○	●							5 (6)
Jordan		●	●		●	●						●		●			●			●	●						●	10
Israel		●	●	●	●	●						●		●			●		●	●	●						●	12
Egypt			●		●									○						●	●			○			●	5 (7)

Country	Portugal	Spain	France	Italy + Sicily	Yugoslavia	Hungary	Romania	USSR (Ukraine)	USSR (Crimea)	USSR (Ciscaucasia)	Bulgaria	Albania	Greece + Crete	Libya	Tunisia	Algeria	Morocco
Tripsacoides 2x										●							
Speltoides 2x									○		●		●				
Bicorne 2x														●			
Sharonensis 2x																	
Longissimum 2x																	
Searsii 2x																	
Dichasians 2x											●		●				
Comosum 2x													●				
Uniaristatum 2x					●							●	●				
Monococcum 2x					●					●	●	●	●				
Timopheevii 4x										●							
Turgidum 4x																	
Umbellulatum 2x										○			●				
Ovatum 4x	●	●	●	●	●			○	●	●	●	●	●	●	●	●	●
Neglecta 4x	●	●	●	●	●	○			●	●	●	●	●	●	●	●	●
Recta 6x	●	●	●	●	●								●				
Macrochaetum 4x	○	●	●	●	●		●	●	●	●	●	●	●	●	○	●	○
Columnare 4x																	
Triunciale 4x	●	●	●	●	●			○	●	●	●	●	●		●	●	●
Kotschyi 4x														●	●		
Peregrinum 4x				●									●	●	●	●	●
Tauschii 2x									○	●							
Cylindricum 4x			●	●	●	●	●	●	●	●	●	●	●				
Ventricosum 4x	●	●	●	●										●	●	●	●
Crassum 4x,6x																	
Juvenale 6x																	
Syriacum 6x																	
Species/country	5 (6)	6	7	8	8	1 (2)	2	2 (4)	5 (7)	9 (10)	8	7	13	7	6 (7)	6	5 (6)

ADDITIONAL INFORMATION ON INDIVIDUAL SPECIES DISTRIBUTIONS

T. tripsacoides.

Relatively limited distribution in the central region of the distribution of the genus, sub-steppical (Irano-Turanian) element; restricted mainly to the steppes of the Anatolian Plateau, Eastern Turkey and Western Iran (area with 300 mm annual rainfall). Grows mainly in secondary, disturbed habitats. In some of these sites it grows in dense stands. In eastern Turkey occurs more sporadically in wadis and lower slopes. Sympatric with the following species: **T. speltoides**, **T. dichasians**, **T. monococcum**, **T. umbellulatum**, **T. ovatum**, **T. neglecta**, **T. macrochaetum**, **T. columnare**, **T. triunciale**, and **T. cylindricum**. Allopatric with **T. timopheevii** and **T. tauschii.**

T. speltoides (**aucheri** and **ligustica**)

A medium-sized distribution in the central and south central regions of the distribution of the genus. Eastern Mediterranean element extending into steppical (Irano-Turanian) region. It occupies primary and secondary habitats. The two forms grow, in most cases, in mixed stands and are cross-fertile; intermediates are usually found. The center of variation is in N. Syria - S. E. Turkey which is also probably the center of origin. Presumably **ligustica**, having the wedge-type dispersal unit which is typical of many **Triticinae** species, is the primitive form. Sympatric with the following species: **T. tripsacoides**, **T. dichasians**, **T. monococcum**, **T. timopheevii**, **T. turgidum**, **T. umbellulatum**, **T. ovatum**, **T. neglecta**, **T. macrochaetum**, **T. columnare**, **T. triunciale**, **T. peregrinum**, and **T. cylindricum.** Allopatric with the following species: **T. sharonense**, **T. longissimum**, **T. searsii**, **T. comosum**, **T. recta**, **T. tauschii**, **T. crassum**, and **T. juvenale.**

T. bicorne

A relatively limited distribution in the south central region of the distribution of the genus. It occupies the driest part of the Mediterranean, a semi-desert (Saharo-Arabian) element. This is the only diploid species that grows in Africa west of Egypt. Close to **T. boeoticum** in spike morphology. Might have originated in the southern part of the fertile crescent. Currently its center of variation is in lower Egypt and Sinai. Sympatric with the following species: **T. longissimum**, and **T. kotschyi.** Allopatric with **T. peregrinum** and in Libya with **T. ventricosum.**

T. sharonense

Very limited distribution in the south central region of the distribution of the genus. Sub-Mediterranean element. A relatively young species, endemic to the light soils of the coastal plain of Israel and Lebanon. It is probably derived from forms of **T. bicorne** that penetrated the coastal plain and absorbed genes from **T. longissimum** via introgressive hybridization. Sympatric with **T. longissimum**, and **T. peregrinum.** Allopatric with **T. speltoides,** and **T. ovatum.**

T. longissimum

Relatively limited distribution in the south-central region of the distribution of the genus. Steppical (Irano-Turanian) element extending into sub-Mediterranean and desert (Saharo-Arabian) regions. Hybrid swarms with **T. sharonense** can be found in the coastal plain. Like **T. bicorne,** it grows in the hot and dry parts of the S. E. Mediterranean, but its distribution area is closer to the center of the distribution of the genus. The center of variation is in the steppic regions of Israel and Jordan, where it presumably originated and from which it invaded the coastal plain. Sympatric with the following species: in the coastal plain with **T. sharonense**, and **T. peregrinum**, and in the steppical region with **T. bicorne, T. kotschyi** and **T. syriacum.** Allopatric with the following species: **T. speltoides, T. searsii, T. umbellulatum**, **T. ovatum**, **T. macrochaetum**, and **T. crassum.**

T. searsii

Relatively limited distribution in the south-central region of the distribution of the genus. Occupies the marginal E. Mediterranean region. Grows in primary and secondary habitats. Its center of variation is in Israel and Jordan, where it presumably originated. Sympatric with the following species: **T. monococcum** (in Lebanon and Syria), **T. turgidum, T. ovatum, T. macrochaetum, T. triunciale**, and **T. peregrinum.** Allopatric with the following species: **T. speltoides, T. longissimum, T. dichasians, T. umbellulatum,**

T. neglecta, **T. columnare**, and **T. kotschyi.**

T. dichasians

Relatively large distribution in the central and eastern regions of the distribution of the genus. A bi-regional species of the Mediterranean and steppical (Irano-Turanian) regions. Occupies primary and secondary habitats. Sympatric with the following species: **T. tripsacoides**, **T. speltoides**, **T. comosum**, **T. monococcum**, **T. timopheevii**, **T. turgidum**, **T. umbellulatum**, **T. ovatum**, **T. neglecta**, **T. recta**, **T. macrochaetum**, **T. columnare**, **T. triunciale**, and **T. cylindricum.** Allopatric with the following species: **T. searsii**, **T. uniaristatum**, **T. kotschyi**, **T. peregrinum**, **T. tauschii**, **T. crassum**, and **T. juvenale.**

T. comosum

Relatively limited distribution in the central-western region of the distribution of the genus. Mediterranean element. Together with **T. uniaristatum** it occupies the western part of the distribution of the diploid species of this group. Sympatric with the following species: **T. dichasians**, **T. uniaristatum**, **T. umbellulatum**, **T. ovatum**, **T. neglecta**, **T. recta**, **T. macrochaetum**, and **T. triunciale.** Allopatric with the following species: **T. speltoides**, **T. monococcum**, **T. peregrinum**, and **T. cylindricum.**

T. uniaristatum

Limited distribution in the central western part of the distribution of the genus. Mediterranean element. Occupies the northwestern corner of the distribution area of the diploid species. It also occupies the most mesophytic of all the habitats of the diploid species. It grows sympatrically with **T. comosum** (in Greece and Turkey), usually with ssp. **heldreichii** - the mesophytic form of **T. comosum.** The record for Turkey (Sea of Marmara) is for only two specimens. Subsequent search (Metzger and Kimber, unpublished data) did not result in additional collections. Sympatric with the following species: **T. comosum**, **T. ovatum**, **T. neglecta**, **T. recta**, **T. macrochaetum**, and **T. triunciale.** Allopatric with the following species: **T. dichasians**, **T. umbellulatum**, and **T. cylindricum.**

T. monococcum

Relatively large distribution in the central part of the distribution of the genus. E. Mediterranean element extending to the steppical (Irano-Turanian) region. The form **aegilopoides** of var. **boeoticum** is common in the Balkans, the Anatolian Plateau and the fertile crescent region; **thaoudar** is found mainly in the fertile crescent while var. **urartu** is distributed in S. Russia (Cis- and Transcaucasia), E. Turkey, Syria and Lebanon, in many sites in mixed populations with var. **boeoticum.** Sympatric with the following species: **T. tripsacoides, T. speltoides, T. searsii, T. dichasians, T. timopheevii, T. turgidum, T. umbellulatum, T. ovatum, T. neglecta, T. recta, T. macrochaetum, T. columnare, T. triunciale,** and **T. cylindricum.** Allopatric with the following species: **T. comosum, T. peregrinum, T. tauschii, T. crassum,** and **T. juvenale.**

T. timopheevii

Relatively restricted distribution in the central region of the distribution of the genus. E. Mediterranean element extending into marginal and semi-steppical regions. Occupies a variety of primary and secondary habitats. While the distribution of **T. timopheevii** overlaps that of both of its putative parents (**T. monococcum** and an S-genome species), it is much more restricted. The putative parents have massive contact in the northern part of the fertile crescent and this is the presumed center of origin. Sympatric with the following species: **T. speltoides, T. dichasians, T. monococcum, T. umbellulatum, T. macrochaetum, T. columnare, T. triunciale,** and **T. cylindricum.** Allopatric with the following species: **T. tripsacoides, T. turgidum** (In the northern part of the fertile crescent the contact may be more intimate, and may, in some populations, be sympatric.), **T. ovatum, T. neglecta, T. tauschii, T. crassum,** and **T. juvenale.**

T. turgidum

Relatively restricted distribution in the north-central region of the distribution of the genus. E. Mediterranean element extending into marginal regions. Occupies a variety of primary and secondary habitats. The center of variation of **T. turgidum** is in the upper Jordan valley and the slopes of Mt. Hermon, which is assumed to be the center of origin. It presumably spread into the northern part of the fertile crescent with the development of agriculture. Its cultivated derivative var. **dicoccum** was brought to this area and most probably introgressed with wild **T. timopheevii.** The donor of the A genome, **T. monococcum,** has contact with **T. searsii** and more sporadic contact with **T. longissimum** in the southern part of the fertile crescent. The distribution of **T. turgidum** overlaps and is larger than that of **T. searsii** but is smaller than the distribution area of **T. monococcum.** Sympatric with the following species: **T. speltoides** (in the northern part of the fertile crescent), **T. searsii, T. dichasians, T. monococcum, T. ovatum, T. macrochaetum, T. triunciale,** and **T. peregrinum.** Allopatric with the following species: **T. timopheevii, T. umbellulatum, T. neglecta, T. columnare,** and **T. cylindricum.** The allopatric contact in the northern part of the fertile crescent with **T. timopheevii** is more intimate and may, in some populations, be sympatric.

T. umbellulatum

Wide distribution in the central region of the distribution of the genus. E. Mediterranean element extending into the steppical (Irano-Turanian) region. Occupies a large variety of primary and secondary habitats. There are two forms which differ in spike size. They sometimes grow in mixed populations and in these stands intermediates may be found. Sympatric with the following species: **T. tripsacoides, T. speltoides, T. dichasians, T. comosum, T. monococcum, T. timopheevii, T. ovatum, T. neglecta, T. recta, T. macrochaetum, T. columnare, T. triunciale, T. peregrinum, T. tauschii,** and **T. cylindricum.** Allopatric with the following species: **T. longissimum, T. searsii, T. uniaristatum, T. turgidum, T. kotschyi, T. crassum,** and **T. juvenale.**

T. ovatum

Very wide distribution in the central and western part of the distribution of the genus. Mediterranean element. With the exclusion of **T. bicorne** and **T. syriacum,** both of which grow in xeric habitats, **T. ovatum** has contact with all the species of the group. It usually grows in mixed stands and introgresses particularly with those species belonging to the U-genome cluster. It is common, locally abundant, forming dense stands throughout its range in both primary and secondary habitats. It is sporadic in marginal and semi-steppical regions. The two diploid parents grow together in western Turkey and in Greece and this is presumably the center of origin of the species. Its distribution area and its ecological affinities are much wider than those of its parents. Sympatric with the following species: **T. speltoides**, **T. searsii**, **T. dichasians**, **T. comosum**, **T. uniaristatum**, **T. monococcum**, **T. turgidum**, **T. umbellulatum**, **T. neglecta**, **T. recta**, **T. macrochaetum**, **T. triunciale**, **T. peregrinum**, **T. cylindricum**, and **T. ventricosum.** Allopatric with the following species: **T. tripsacoides**, **T. sharonense**, **T. longissimum**, **T. timopheevii**, **T. columnare**, **T. kotschyi**, **T. tauschii**, **T. crassum**, and **T. juvenale.**

T. neglecta

Wide distribution in the western and central region of the distribution of the genus. Mediterranean element extending into marginal and steppical regions. Occupies a large variety of primary and secondary habitats. Hybrids and intermediate forms of this species and other species of the U-genome cluster, which usually grow in mixed stands, are occasionally found. The two putative parents have spatial contact in W. Turkey and in Greece which is the presumed center of origin. Its distribution and ecological affinities are much greater than those of its diploid parents. Sympatric with the following species: **T. tripsacoides**, **T. speltoides**, **T. dichasians**, **T. comosum**, **T. uniaristatum**, **T. monococcum**, **T. umbellulatum**, **T. ovatum**, **T. recta**, **T. macrochaetum**, **T. columnare**, **T. triunciale**, **T. cylindricum**, and **T. ventricosum.** Allopatric with the following species: **T. searsii**, **T. timopheevii**, **T. turgidum**, **T. peregrinum**, **T. tauschii**, **T. crassum**, and **T. juvenale.**

T. recta

A medium-sized distribution in the western part of the distribution of the genus. Mediterranean element. Usually grows in mixed stands with other species with which it introgresses. Its two parents have contact in Western Greece and Yugoslavia. Its distribution overlaps that of its two parents, is larger than that of **T. uniaristatum** but smaller than that of **T. neglecta.** Sympatric with the following species: **T. dichasians**, **T. comosum**, **T. uniaristatum**, **T. monococcum**, **T. umbellulatum**, **T. ovatum**, **T. neglecta**, **T. macrochaetum**, and **T. triunciale.** Allopatric with **T. speltoides**, and **T. ventricosum.**

T. macrochaetum

Very wide distribution in the western and central parts of the distribution of the genus. Mediterranean element extending into semi-steppical (W. Irano-Turanian) region. Occupies a wide variety of primary and secondary habitats. Usually grows in mixed stands with other species, particularly those belonging to the U-genome cluster, with which it introgresses. Its two parents have contact in Western Turkey and Greece, where it presumably originated. Its distribution overlaps with and is larger than that of its two parents. Sympatric with the following species: **T. tripsacoides**, **T. speltoides**, **T. searsii**, **T. dichasians**, **T. comosum**, **T. uniaristatum**, **T. monococcum**, **T. timopheevii**, **T. turgidum**, **T. umbellulatum**, **T. ovatum**, **T. neglecta**, **T. recta**, **T. columnare**, **T. triunciale**, **T. peregrinum**, **T. cylindricum**, and **T. ventricosum.** Allopatric with the following species: **T. longissimum**, **T. kotschyi**, **T. tauschii**, **T. crassum**, and **T. juvenale.**

T. columnare

A medium-sized distribution in the central part of the distribution of the genus. Irano-Turanian element penetrating into the marginal Mediterranean region. Occupies mainly open, secondary habitats. Usually grows in mixed stands with other species, with which it introgresses, particularly with other U-genome polyploids. Its two putative parents have spatial contacts in W. Turkey and in Greece. However, the distribution area of **T. columnare** is east of this area and overlaps, to some extent, that of **T. umbellulatum.** It does not have contact with its second parent, **T. comosum.** Sympatric with the following species: **T. tripsacoides**, **T. speltoides**, **T. dichasians**, **T. monococcum**, **T. timopheevii**, **T. umbellulatum**, **T. neglecta**, **T. macrochaetum**, **T. triunciale**, **T. tauschii**, **T. cylindricum**, **T. crassum**, and **T. juvenale.** Allopatric with the following species: **T. searsii**, **T. ovatum**, **T. kotschyi**, and **T. peregrinum.**

T. triunciale

Very large distribution (the largest in the group) overlapping with almost all of the distribution of the genus, except the S. E. corner of the Mediterranean basin. A bi-regional species occupying both Mediterranean and Irano-Turanian elements. It is similar in this respect to one of its parents, **T. dichasians.** It is the most massive species in its distribution area with a very wide ecological amplitude. It occupies a very large number of primary and secondary habitats. Usually grows in mixed stands with other species, with which it introgresses. While ssp. **eu-triuncialis** is distributed throughout all of the area of the genus, ssp. **persicum** (=**orientalis**) is distributed only in the Asiatic area of the species range. Introduced, with cultivated wheat, into the U.S.A. Its two parents have massive contacts throughout Greece, Turkey and Iran. The distribution area of **T. triunciale** is much wider than those of its two parents. Sympatric with the following species: **T. tripsacoides**, **T. speltoides**, **T. searsii**, **T. dichasians**, **T. comosum**, **T. uniaristatum**, **T. monococcum**, **T. timopheevii**, **T. turgidum**, **T. umbellulatum**, **T. ovatum**, **T. neglecta**, **T. recta**, **T. macrochaetum**, **T. columnare**, **T. peregrinum**, **T. tauschii**, **T. cylindricum**, **T. ventricosum**, **T. crassum**, and **T. juvenale**. Allopatric with **T. kotschyi** and **T. syriacum**.

T. kotschyi

A relatively large distribution in the south, central and eastern part of the distribution of the genus. Steppical (Irano-Turanian) element penetrating into the desert (Saharo-Arabian) region. It is a vicaric species to **T. peregrinum**, the latter growing massively in Mediterranean habitats while **T. kotschyi** grows massively in the warm steppes of the south-central region of the distribution of the genus. It is the southern-most species of the group and grows out of contact with other species at many sites. In various parts of its distribution it grows sympatrically with one of its putative parents, **T. longissimum**, and in other parts it has allopatric contact with its second parent, **T. umbellulatum**. In the central and eastern part of its distribution it grows in mixed populations with other steppical species with which it introgresses. Its two putative parents have sporadic contact in semi-steppical, steppical or sub-Mediterranean regions of Syria. It is possible that this species originated there and then spread both south- and eastward. Its distribution area is much larger than that of its two parents. It hybridizes well with many species. Sympatric with the following species: **T. bicorne**, **T. longissimum**, **T. crassum**, **T. juvenale**, and **T. syriacum**. Allopatric with the following species: **T. searsii**, **T. dichasians**, **T. umbellulatum**, **T. ovatum**, **T. macrochaetum**, **T. columnare**, **T. triunciale**, **T. peregrinum**, **T. tauschii**, and **T. cylindricum**.

T. peregrinum

A medium-sized distribution in the southwestern part of the distribution of the genus. Mediterranean element. Like **T. triunciale** in the central and northern parts of the genus area, **T. peregrinum** is the massive species in the southwestern part of the genus area. Its ecological amplitude is exceptionally large. It differs from its related species, **T. kotschyi**, in that it grows sympatrically with both its diploid parents. Usually grows in mixed populations with other species, with which it introgresses. Its two putative diploid parents may have sporadic contact in semi-steppical, steppical and sub-Mediterranean regions of Syria, in which **T. peregrinum** might have originated and then spread south and west. Its distribution area is much larger than those of its parents. There are many intermediate forms with **T. kotschyi** in the contact zone between the two species and to **T. ovatum**, **T. macrochaetum** and **T. triunciale** in their mixed populations in the Mediterranean habitats. Sympatric with the following species: **T. speltoides**, **T. sharonense**, **T. longissimum**, **T. searsii**, **T. dichasians**, **T. turgidum**, **T. umbellulatum**, **T. ovatum**, **T. macrochaetum**, and **T. triunciale.** Allopatric with the following species: **T. bicorne**, **T. comosum**, **T. monococcum**, **T. neglecta**, **T. columnare**, **T. kotschyi**, and **T. syriacum.**

T. tauschii

Large distribution in the eastern part of the distribution of the genus. Irano-Turanian element. The most easterly distributed species. Its distribution in the east is limited by the Himalayan Mountains, southward by the deserts of southern Pakistan and Iran and northwards by the cold steppes of Central Asia. Its western border is not clear but is presumably from Caucasia in the north, through Turkish Armenia, Turkish and Iraquish Kurdistan and probably also in S. E. Syria. In many sites it grows alone. Very common and widely distributed in open, primary and secondary habitats in steppes and in marginal regions. One of the annual constituents of the dwarf shrub-steppe or semi-tragacantic formations and also occupying a wide array of disturbed, secondary habitats. Grows as a weed in cultivated fields. Sympatric with the following species: **T. umbellulatum**, **T. columnare**, **T. triunciale**, **T. cylindricum**, **T. crassum**, and **T. juvenale.** Allopatric with the following species: **T. tripsacoides**, **T. speltoides**, **T. dichasians**, **T. monococcum**, **T. timopheevii**, **T. ovatum**, **T. neglecta**, **T. macrochaetum**, and **T. kotschyi.**

T. cylindricum

Large distribution in the northern and central parts of the distribution of the genus. Mediterranean and steppical (Irano-Turanian) element, a biregional species, in this respect it is similar to one of its parents **T. dichasians.** Occupies a wide variety of primary and secondary habitats. Grows in mixed populations with many species, with which it introgresses. Its two parents overlap in E. Turkey, Iran and Afghanistan, where this species may have originated and then spread both west and north. Its distribution area is larger than those of its diploid parents. Sympatric with the following species: **T. tripsacoides**, **T. speltoides**, **T. dichasians**, **T. monococcum**, **T. timopheevii**, **T. umbellulatum**, **T. ovatum**, **T. neglecta**, **T. macrochaetum**, **T. columnare**, **T. triunciale**, **T. tauschii**, **T. ventricosum**, **T. crassum**, and **T. juvenale.** Allopatric with the following species: **T. comosum**, **T. uniaristatum**, **T. turgidum**, **T. kotschyi**, and **T. syriacum.**

T. ventricosum

Medium-sized distribution in the western part of the distribution of the genus. Mediterranean element. It is relatively isolated from the rest of the group. Interestingly, its distribution does not overlap with either of its diploid parents, **T. tauschii** and **T. uniaristatum.** It is closer, however, to **T. uniaristatum** than to any other diploid species (excluding **T. bicorne** with which it may have contact in Libya). Sympatric with the following species: **T. ovatum**, **T. neglecta**, **T. macrochaetum**, **T. triunciale**, and **T. cylindricum.** Allopatric with the following species: **T. bicorne**, **T. recta**, and **T. kotschyi.**

T. crassum

A relatively large distribution in the eastern part of the distribution of the genus. Steppical (Irano-Turanian) element penetrating into semi-desert regions. Occupies a wide range of primary and secondary habitats. It has no contact with M-genome species. It is closer morphologically to **T. tauschii** than its vicaric species **T. ventricosum.** The two cytotypes (4x and 6x) are indistinguishable. The hexaploid form grows, together with the tetraploid, in N. Afghanistan, N. E. Iran and S. Asiatic USSR. According to Kihara (1954) the tetraploid originated in Asia Minor and the hexaploid in Afghanistan. The distribution area of both of the cytotypes is somewhat smaller than that of **T. tauschii**, but much larger than that of the M-genome species. Sympatric with the following species: **T. columnare, T. triunciale, T. kotschyi, T. tauschii, T. cylindricum**, and **T. juvenale**. Allopatric with the following species: **T. speltoides, T. longissimum, T. dichasians, T. monococcum, T. umbellulatum, T. ovatum, T. neglecta, T. macrochaetum**, and **T. syriacum**.

T. juvenale

Medium-sized distribution in the eastern part of the distribution of the genus. Steppical (Irano-Turanian) element. The two progenitors have contact in Iran, N. Iraq and E. Turkey, where this species presumably originated. Sympatric with the following species: **T. columnare, T. triunciale, T. kotschyi, T. tauschii, T. cylindricum**, and **T. crassum**. Allopatric with the following species: **T. speltoides, T. dichasians, T. monococcum, T. timopheevii, T. umbellulatum, T. ovatum, T. neglecta**, and **T. macrochaetum**.

T. syriacum

Relatively limited distribution in the south-central part of the distribution of the genus. Steppical (Irano-Turanian) element. The two parents may have contact in N. E. Syria where this species presumably originated and spread southward. It is relatively isolated from most of the other species of the group. Sympatric with **T. longissimum** and **T. kotschyi**. Allopatric with the following species: **T. triunciale, T. peregrinum, T. cylindricum**, and **T. crassum**.

TABLE 2. The number of species that each species has sympatric, allopatric or no contact.

Species		Contact Symp.*	Allo.	No cont.
Tripsacoides	2x	10	2	14
Speltoides	2x	13	8	5
Bicorne	2x	2	1	23
Sharonense	2x	2	2	22
Longissimum	2x	5	6	15
Searsii	2x	6	7	13
Dichasians	2x	14	7	5
Comosum	2x	8	4	14
Uniaristatum	2x	6	3	17
Monococcum	2x	14	5	7
Timopheevii	4x	8	7	11
Turgidum	4x	8	5	13
Umbellulatum	2x	14	8	4
Ovatum	4x	15	9	2
Neglecta	4x	14	7	5
Recta	6x	9	2	15
Macrochaetum	4x	18	5	3
Columnare	4x	13	4	9

Natural hybridization between diploid species is a very rare phenomenon. In spite of the fact that several of the diploids have massive spatial contact (Table 2), to the best of our knowledge, interspecific hybrids have been reported between only two of these species, **T. longissimum** and **T. sharonense**, whose F_1 hybrids and hybrid derivatives have been repeatedly found in disturbed sites in the Israeli coastal plain (Ankori and Zohary, 1962; Feldman, unpublished). The two species are closely related and differ from each other mainly by a reciprocal translocation. The F_1 hybrid between them is highly fertile and the only isolation between them is their differential ecological requirements (**T. sharonense** grows on sandy soil while **T. longissimum** grows on heavier sandy loams). In the contact zone between these two types of soils many hybrid swarms can be found. Actually lines of **T. longissimum** collected on the coastal plain differs from lines of that species collected in the steppical region of Israel mainly by characters derived from **T. sharonense.** Interestingly, although **T. longissimum** grows in many sites in the Israeli Negev together with **T. bicorne**, a close relative of **T. sharonense**, no evidence has been found for hybridization and gene exchange between these two species.

In clear contrast to the rarity of interspecific hybridization at the diploid level, hybridization between tetraploid species, particularly between those sharing a common genome, is a frequent phenomenon (Feldman, 1963). Such tetraploid species tend to grow in mixed stands, and many F_1 hybrids as well as backcrossed progeny were repeatedly found in many localities in Israel, Turkey and Greece (Zohary and Feldman, 1962; Feldman, 1965a and unpublished, and Metzger and Kimber, unpublished). Actually, a full range of morphological intermediates between tetraploids growing together in one mixed stand is a common phenomenon.

Interspecific hybridization and introgression was repeatedly found in the tetraploid species of the U-genome group (Zohary and Feldman, 1962; Feldman, 1963, 1965a). In southern Judea in Israel numerous hybrid swarms were found in mixed populations of **T. peregrinum** and **T. kotschyi.** This part of Israel is a transition between the Mediterranean and steppical regions, and the two vicaric species grow together and introgress. In the Mediterranean parts of Israel numerous hybridizations were found between **T. peregrinum**, **T. ovatum** and **T. macrochaetum.** In northern Israel, in the eastern Galilee and the Golan Heights, hybridization was noticed between these species and **T. triunciale.** In Turkey and Greece hybrid swarms were repeatedly found between **T. neglecta** and **T. columnare** as well as between these species and **T. ovatum, T. macrochaetum** and **T. triunciale.** Hybridization was also found between **T. triunciale** and **T. cylindricum** in several sites in Turkey.

Considerable evidence was obtained for spontaneous hybridization also between tetraploid and diploid species (Vardi, 1973; Zohary and Feldman, unpublished data). Triploid F_1 hybrids between **T. peregrinum** and **T. longissimum** or **T. sharonense** or between **T. kotschyi** and **T. longissimum** were found in several sites in Israel. Hybrids between **T. triunciale** and **T. dichasians** were found in Turkey. These triploid hybrids were found in mixed populations where the diploid parent was the main constituent. Judging from the morphology of the dispersal unit from which the triploid hybrid germinated, the female parent in these hybridizations was always the tetraploid species. Pollination of the highly sterile F_1 by the tetraploid parent resulted, in several cases, in partially fertile hybrid derivatives. The occurrence of such hybrid derivatives in mixed natural populations indicates the possibility of gene flow from diploid to tetraploid species.

Hence, hybridization between tetraploids, particularly between those sharing one common genome and, to a lesser extent, between tetraploids and diploids, facilitates a rapid build-up of genetic variability at the tetraploid level. The differential genomes, which are isolated from one another at the diploid level where emphasis is on divergence and specialization, are brought together and allowed to recombine at the tetraploid level. Thus the ability to exchange genetic material through spontaneous interspecific hybridization promotes the convergent evolution of these species.

Natural hybrids also occur between the wild and the cultivated species. Hybrids have been recorded between cultivated **T. turgidum** and its wild progenitor var. **dicoccoides** as well as with **T. longissimum, T. ovatum, T. triunciale, T. cylindricum** and **T. ventricosum.** Similarly, hybrids have been recorded between **T. aestivum** and **T. monococcum, T. umbellulatum, T. turgidum** var. **dicoccoides, T. ovatum, T. triunciale, T. peregrinum, T. cylindricum** and **T. ventricosum.**

In addition to the many natural hybrids observed between the wild species and also between them and the cultivated forms, considerable efforts have been made by many workers to produce hybrids between the species of the **Triticeae.** These hybrids have been used for a variety of purposes including genomic analysis, studies of speciation and evolution, and as the starting point for efforts at the introduction of alien variation into cultivated forms.

A data base of hybrids of which at least one parent is a species of **Triticum** and for which there is at least some meiotic information is maintained by Kimber (Kimber and Abu Bakar, 1979). Information from this data base can be obtained on request. The data can also be used to construct tables showing which hybrid combinations are included in the data base. Table 3, which follows, shows all those hybrids in which both parents are within the genus **Triticum.**

Table 3. Artificial hybrid combinations recorded in the data base maintained by Kimber.

The species names of the female parents are arranged alphabetically on the left, and following them is a two-letter code. This code is also printed at the head of the table to identify the species name of the male parent. A plus (+) indicates that there is information in the data base, a minus (-) indicates a lack of information.

Table 3 does not show all the hybrid combinations in the data base but only those in which both of the parents are in the genus **Triticum.** Altogether there are, at the time of writing, some 1229 entries representing 339 hybrid combinations involving 50 species. Hybrids with species of six other genera are known. The meiotic information of individual hybrids can be recovered using different search keys. The full data base also contains 306 bibliographic references.

TRITICUM X TRITICUM HYBRIDS

FEMALE	CODE	MALE																								
		TA	TB	TY	TC	TI	TX	TF	TJ	TK	TL	TP	TM	TO	TS	TR	TD	TG	TN	TQ	TW	TT	TU	TE	TH	TZ
T. aestivum	TA	+	−	+	+	+	+	+	+	+	+	+	+	+	+	−	+	+	+	+	+	+	+	−	+	+
T. bicorne	TB	+	−	−	−	−	−	−	−	−	−	−	+	−	−	−	+	−	−	+	−	−	+	+	−	−
T. columnare	TY	−	+	−	+	+	−	+	−	+	−	+	−	−	+	−	−	−	−	−	+	−	+	+	−	−
T. comosum	TC	+	−	−	+	−	−	−	−	−	+	−	−	−	−	−	+	−	−	+	−	+	−	+	−	−
T. crassum	TI	+	+	+	−	+	+	+	−	+	+	−	−	+	+	−	+	−	−	+	+	+	+	+	+	−
T. cylindricum	TX	−	−	−	−	+	−	+	+	−	−	+	+	+	−	−	+	−	+	−	+	+	−	−	+	−
T. dichasians	TF	−	+	−	+	−	+	−	−	−	+	+	−	−	+	−	+	+	−	+	−	+	+	+	−	−
T. juvenale	TJ	+	−	+	−	+	+	+	−	−	+	−	−	−	+	−	+	−	−	+	+	−	+	+	+	−
T. kotschyi	TK	+	−	+	−	−	−	+	−	+	+	+	−	+	+	−	−	+	−	−	−	+	+	−	−	−
T. longissimum	TL	+	+	−	+	−	+	+	−	+	+	−	+	−	+	−	−	+	−	+	−	+	+	+	−	−
T. macrochaetum	TP	−	+	+	+	+	−	+	−	+	+	−	−	+	+	−	−	−	+	−	+	−	−	−	−	−
T. monococcum	TM	−	+	−	−	−	−	−	−	−	−	−	+	−	+	−	+	−	−	+	−	+	−	+	−	−
T. ovatum	TO	−	−	+	+	−	−	+	−	+	+	−	+	−	+	−	+	+	+	−	+	+	+	+	+	−
T. speltoides	TS	−	+	−	+	−	−	+	−	−	+	−	+	−	−	−	+	−	−	+	−	+	−	−	−	−
T. syriacum	TR	−	−	−	−	−	+	−	−	−	−	−	−	−	−	−	+	−	−	−	−	−	−	−	+	−
T. tauschii	TD	+	+	−	−	−	+	−	−	−	−	−	−	−	−	−	−	−	−	+	−	−	−	+	+	−
T. timopheevii	TG	+	+	−	+	−	+	+	−	−	+	−	+	−	+	−	+	+	−	−	+	+	+	+	+	−
T. triaristatum	TN	−	−	+	−	+	+	+	−	+	−	+	−	−	+	−	−	−	+	−	+	+	−	+	+	−
T. tripsacoides	TQ	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−
T. triunciale	TW	+	−	−	−	−	−	+	−	+	−	−	−	−	−	−	−	−	+	−	−	+	−	−	+	−
T. turgidum	TT	+	+	−	+	−	+	+	−	−	+	−	+	+	+	−	+	+	+	+	+	+	+	+	+	−
T. umbellulatum	TU	−	+	−	+	−	+	+	−	−	−	−	−	−	+	−	+	−	−	+	−	−	−	+	+	−
T. uniaristatum	TE	−	+	−	+	−	−	+	−	−	−	−	−	−	−	−	−	−	−	+	−	−	+	−	−	−
T. ventricosum	TH	+	−	−	−	+	+	+	−	−	−	−	+	+	+	+	+	+	−	−	−	+	−	+	−	−
T. zhukovskyi	TZ	+	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	+	−	−	−	−	−	−	−	−

CYTOGENETICS

"The history of the earth is recorded in the layers of its crust; the history of all organisms is inscribed in the chromosomes"

Hitoshi Kihara

The study of the wheat group has been facilitated by several fortuitous factors. First, the supreme commercial importance of several of the species, which gave the often-needed justification to conduct basic scientific investigations; second, the relative ease with which hybrids could be made; and third, the small number of quite large chromosomes. It is this third factor which allowed the early determination of the basic number of the genus (7), and the recognition that many of the species are polyploid. Since these early and essential steps, the study of the cytology of the wheat group has cast the clearest light on the evolutionary patterns in the genus and at the same time has undergone an evolution of its own.

The earliest work on wheat-group chromosomes relied on reconstructions made from serial sections of root tips and anthers. This is a technically difficult and time-consuming process that also carries with it possibilities of misinterpretation. The development of the smear technique for anthers and the squash technique for root tips not only reduced the possibilities of misinterpretation but allowed larger numbers of plants to be cytologically determined.

The karyotypes of many of the species of the group were produced by Senyaninova-Korchagina (1932) and Chennaveeraiah (1960), and even though there are many, and subtle, differences it is possible to separate the diploids into two categories. First, those diploids without chromosomes with subterminal centromeres and second, those with such chromosomes. The former include the A-, S-, Mt- and D-genome species, while the C-, M-, Un- and U- genome species have as many as four chromosomes with sub-terminal centromeres. The B and G genomes found only in polyploid species also do not have chromosomes with sub-terminal centromeres. Stebbins (1950) considered asymmetry of centromere position more advanced than the approximate isobrachial condition since it was found in those diploids with increased specialization of the lemmas, the rachis (with respect to fragility) and awn development.

The development of the asymetric centromeric position in polyploid species is not clearly related to any evolutionary advantage, although several of the U-genome polyploids (**T. triunciale** in particular) have wide distributions. However, all of the commercial forms, both diploid and polyploid, (**T. monococcum, T. turgidum, T. timopheevii** and **T. aestivum**) have exclusively sub-median centromeric positions. Interestingly, the related forms **Hordeum vulgare** and **Secale cereale,** both of which are cultivated, also have chromosomes with centromeres near the center.

As might be anticipated, the karyotypes found in the diploids are reflected in the polyploids derived from them. The U-genome sub-terminal chromosomes, for example, are easily seen in such species as **T. ovatum, T. kotschyi** and **T. columnare.** However, the use of karyotype analysis as a means of determining evolutionary relationships has severe limitations. Just because two chromosomes from putatively related species have the same arm ratio does not mean they are homologous (or even homoeologous); it simply means they have the same arm ratio. The genetic content of the chromosomes should be the determinant of evolutionary relationships, and centromeric position is independent of genetic content. Similarly the use of the number and size of satellited chromosomes has limited usefulness in determining evolutionary relationships. To distinguish between closely related diploids and to propose genomic homology on the basis of satellites is to ignore the genetic content of most of the chromosomes simply on the basis of the presence or absence of a small piece of chromatin distal to a secondary constriction in one or two chromosomes. The B genome of the cultivated wheats was ascribed to **T. speltoides** (Riley, Unrau and Chapman, 1958) partly on the basis of the similarity of the satellites of that diploid and the putatively related polyploids. It has since been demonstrated (Waines and Kimber, 1972 and Sallee and Kimber, unpublished) that there is variation for satellite size in the S-genome species and that other species in the group, e.g. **T. searsii** (Feldman, 1978) have satellites similar to those of the B genome as well. Satellited or sub-terminal chromosomes can be very useful however, as cytological markers for studies of chromosome behaviour at meiosis or mitosis. For example, Avivi, Feldman and Brown (1982a and b) used satellited chromosomes to study the spatial relationships in the common-wheat nucleus.

Chromosomes 1B and 6B carry nucleolar organizers on their short arms. These secondary constrictions are proximal to the large satellites. Less conspicuous secondary constrictions and satellites are also found on the short arms of chromosomes 1A and 5D. The chromosomes of the D genome tend to be shortest. Chromosome 1B is the longest; chromosome 5B is the most heterobrachial, with an arm ratio of 2.19:1 (Larsen and Kimber, 1973). The remainder of the chromosomes of the karyotype are not conspicuously different from each other.

The Giemsa C-banding pattern of most of the species and the N-banding pattern of some species has been produced by various workers. Similarities of pattern have been observed between diploids and related polyploids, but the interpretation of these results has sometimes been both confusing and contradictory. A detailed consideration is beyond the scope of this book, but a cautionary note may be in order. There seems to be a tendency to assume that just because two chromosomes have the same banding pattern they are homologous. This type of reasoning is also applied, with perhaps slightly more justification, to the identification of genomes on the basis of the similarity of the banding pattern of several chromosomes in the donor and the putative recipient. The reliability of this method of genomic analysis is positively related to the number of the bands and uniqueness of their distribution. The method does suffer, however, from the restriction that a band represents many replications of a small piece of DNA and is thus viewed out of proportion to the genetic effect of that DNA. Also most of the DNA is not banded and therefore its genetic contribution is totally ignored.

The banding of chromosomes is, however, a particularly useful technique for other cytogenetic studies. Gill and Kimber (1977), by the use of C-bands, were able to demonstrate both translocations between two different wheat chromosomes and also between wheat and rye chromosomes. The extensive use of C-banding in **Triticale** has been described by Gustafson (1983), and the use of N-banding for genetical and cytological studies in wheat has been discussed by Jewell and Mujeeb-Kazi (1983).

Studies in somatic and meiotic cells (Feldman, Mello-Sampayo and Sears, 1966; Feldman and Avivi, 1973, 1984; Avivi and Feldman, 1980; Avivi, Feldman and Brown, 1982a and b; Yacobi, Levanony and Feldman, 1985a and b) indicated that the chromosomes of common wheat are distributed non-randomly with respect to one another, occupying definite positions in the nucleus. Within each of the three homoeologous genomes composing the common wheat nucleus, homologous chromosomes are located most closely to each other, exhibiting so called somatic association. Non-homologous chromosomes of the same genome are situated further apart, yet closer to each other than chromosomes of different genomes, either homoeologous or non-related. The relative separation of chromosomes of different genomes in common wheat indicates that each genome maintains its integrity and occupies a distinct region of the wheat nucleus. The arrangement of the non-homologues within each genome is also non-random. The centromere and microtubular components are the chromosomal region and sub-cellular structure responsible for positioning the chromosomes in their respective nuclear location (Feldman, 1966c; Avivi and Feldman, 1973; Feldman and Avivi, 1984). Association of homologous chromosomes in somatic and premeiotic cells is a requisite for their regular pairing at meiosis (Feldman, 1966c, 1968). Pairing behaviour at meiosis is modified when chromosomal associations in somatic cells are modified either by alterations in the dosage of the **Ph** genes or by premeiotic treatment with anti-microtubular agents. In **T. aestivum** suppression of somatic association can result in partial asynapsis of homologues, increase in homoeologous pairing and a high frequency of interlocking bivalents (Feldman, 1966; Feldman and Avivi, unpublished).

The meioses of almost all the species of **Triticum** are characterized by regular bivalent formation. The hexaploid form of **T. timopheevii** (var **zhukovskyi**), with the proposed genomic constitution AAAAGG, does produce, as expected, quadrivalents at first meiotic metaphase (Upadhya and Swaminathan, 1963 and Sallee and Kimber, 1975). Similar multivalents were not observed by Chennaveeraiah (1960) in the hexaploid form of **T. crassum**, which has the proposed genomic constitution of DDDDMM and should thus be an autoallohexaploid like the hexaploid form of **T. timopheevii**. The other polyploids show a diploid-like meiotic pairing pattern characteristic of allopolyploids. The uniform bivalent formation at meiosis in the tetraploid **T. turgidum** and **T. timopheevii** is regulated by a small number of genes, the most potent of which is found on the long arm of chromosome 5B (and also 5G?). The pattern of approximation to genetic autopolyploidy coupled with strict cytological allopolyploidy confers a significant evolutionary advantage on these species.

Chromosome aberrations seem to be widespread intra-specifically in the wild forms, particularly in the polyploid species, are not uncommon in inter-specific hybrids, and are well documented in the cultivars of **T. aestivum.** There is a reciprocal translocation in **T. longissimum** relative to the other S-genome diploids, **T. sharonense, T. bicorne,** and **T. speltoides** (Kimber, 1961) and **T. searsii** (Feldman, Strauss and Vardi, 1979). It is possible that some of the multivalents observed in hybrids involving polyploid forms may be due to homoeologous chromosome pairing rather than reciprocal translocations (Alonso and Kimber, 1981); however, many translocations have been demonstrated by several workers. Inversions in pentaploid hybrids between **T. aestivum** and **T. turgidum** have been recorded by Love (1941) but do not appear to be widespread in the genus. The presence of B-chromosomes, and their effect on the regulation of meiotic pairing in hybrids, has been recorded in both the diploid out-breeding species **T. tripsacoides** (Dover, 1973) and **T. speltoides** (Mendelsson and Zohary, 1972).

The unique feature of the cytology of the wheat group is both the concept and practical demonstration of the homoeologous relationships of the chromosomes of the cultivated **T. aestivum** and their relationships to the chromosomes of other species. By the development of stocks in which one chromosome was absent (nullisomic) and another chromosome was present four times (tetrasomic) Sears (1966) was able to show that the deficiency of a particular chromosome could be compensated for by extra dosage of only two other chromosomes. Within these groups of three chromosomes any nulli-tetra combination produced compensation. There is no compensation between the chromosomes of different groups. In addition, the three chromosomes of a single group were found to come one from each of the three genomes present in **T. aestivum.** Thus it is possible to place the 21 different chromosomes in an orthogonal classification of seven groups of three. The chromosomes of each group are termed homoeologous (=similar) and they are considered to have a common evolutionary origin. The homoeologous classification of the wheat chromosomes allows the chromosomes to be identified by a numbering system that conveys information about their genome and homoeologous group.

There have also been cytological demonstrations of the genetic homoeology identified by nulli-tetra compensation tests. Riley and Chapman (1966) showed that telocentrics of the same group were often associated in the same multivalent when the activity of chromosome 5B was suppressed. Riley and Kempanna (1963) showed that translocations produced from the multivalents formed in the absence of chromosome 5B were between homoeologous chromosomes and Feldman and Avivi (1973, 1984) have shown the somatic association of homoeologous telocentrics in the absence of chromosome 5B. However, in its presence, the homoeologues are separated and the three genomes occupy different regions in the wheat nucleus (Avivi, Feldman and Brown, 1982b).

	Genomes		
	A	B	D
Group 1	1A	1B	1D
Group 2	2A	2B	2D
Group 3	3A	3B	3D
Group 4	4A	4B	4D
Group 5	5A	5B	5D
Group 6	6A	6B	6D
Group 7	7A	7B	7D

The homoeologous classification of the chromosomes of **T. aestivum.**

This pattern of homoeology is not limited to **T. aestivum** but is widespread in the group. Clearly, this is a consequence of the divergence of diploids from a common archetype followed by the convergence of the differentiated genomes in polyploids. This feature is well recognized by the ability of alien chromosomes to preferentially substitute only for their homoeologues. The basic homoeology of the seven chromosomes of the **Triticeae** extends to genera such as **Agropyron, Haynaldia, Hordeum,** and **Secale.**

As may be anticipated, the chromosomes of a homoeologous group have similar genetic functions. Homoeoalleles may be found on the chromosomes of one group. One of the advantages of allopolyploidy is the maintenance of the heterozygosity of homoeoalleles (Galili and Feldman, 1983). Interestingly genes causing reaction to pathogenic agents do not seem to be similarly distributed on the chromosomes of a homoeologous, group giving rise to the speculation that they are of recent evolutionary origin. A full listing of gene symbols, linkage measurements and chromosome assignments has been produced by McIntosh (1983).

The triplication of genetic material in the hexaploid **T. aestivum** has allowed the development of a full range of aneuploids (Sears, 1954). The production of this set of tools has resulted in the analysis of wheat and its relatives with a degree of precision not available in any other species group (Kimber and Sears, 1980). The ability to substitute chromosomes of an alien species generally for wheat chromosomes of only one homoeologous group can be taken as a clear indication of the homoeology of the alien chromosome to similar chromosomes in wheat and consequently provide cytological evidence of their evolutionary relationship.

The meiosis of the polyploid cultivated wheats is characterized by very regular bivalent formation and only a small percentage of pairing failure. The synapsis of homoeologous chromosomes is rarely, if ever, seen when the homologue of each chromosome is present. This is remarkable in view of the extensive triplication of the genetic content of the chromosomes. The resolution of this apparent anomaly occurred with the recognition of the genetic control of the regular bivalent formation at meiosis (Okamoto, 1957; Riley and Chapman, 1958; Sears and Okamoto, 1958; see also reviews by Riley and Law, 1965; and Sears, 1976).

The most potent of the meiotic pairing regulators is the gene **Ph1** located on the long arm of chromosome 5B. When this gene is present, there is normal meiotic pairing, with synapsis apparently limited to strictly homologous chromosomes. In its absence, not only homologous chromosomes synapse but homoeologous also, giving rise to a very complex meiotic pairing pattern. The gene **Ph1** is found in all forms of **T. aestivum** and **T. turgidum** and a gene of similar, if not identical effect is found in **T. timopheevii** (Feldman, 1966a). A less potent pairing regulator (**Ph2**) is found on the short arm of chromosome 3D in **T. aestivum.** Minor suppressors of pairing are found on the short arms of chromosomes 3A and 3B (Mello-Sampayo and Canas, 1973) and on the long arms of chromosomes of group 2 (Ceoloni, Strauss and Feldman, 1986). Pairing promoters are found in **T. aestivum** on the long and short arms of chromosomes 5A and 5D and on the short arm of chromosome 5B (Feldman, 1966c and 1968) as well as on the long arms of chromosomes of group 3 (Mello-Sampayo and Canas, 1973) and on the short arms of group 2 (Ceoloni, Strauss and Feldman, 1986). The evolutionary advantage of a system with duplicated or triplicated genetic content and at the same time regular meiotic behavior and its attendant fertility is most obvious; such polyploids are fully fertile, with increased chromosomal stability and disomic inheritance. The latter may result in permanent heterozygosity between homoeologous loci, i.e., similar genes in different genomes.

The mode of action of the **Ph1** locus has been a subject for intensive study. From the effect of extra dosage of **Ph1** on chromosome pairing, Feldman (1966c) and Feldman and Avivi (1973 and 1984) concluded that this gene regulates chromosome pairing in common wheat by operating at premeiotic stages and determining the specific spatial relationships between homoeologous and between homologous chromosomes. In the normal situation of two doses of **Ph1**, homologues associate with each other while homoeologues are relatively separated. Since close association of homologues or homoeologues at the premeiotic stage is a requisite of their regular pairing at meiosis, then in plants with two doses of **Ph1** only homologues can pair. Further studies (Avivi and Feldman, 1973 and Ceoloni, Avivi and Feldman, 1983) indicated that **Ph1** affects the sensitivity of spindle microtubules to antitubulins and consequently, it is concluded it controls the spatial separation of chromosomes in the nucleus by affecting some of the assembly and organization characteristics of the spindle microtubules. Consequently, **Ph1** may code for a microtubule-associated protein.

The action of the **Ph** system in hybrids may be perceived in a similar manner. In its presence homoeologous genomes may be well separated and thus pair but infrequently, while in its absence (or mutation or suppression) homoeologues would be expected to be more closely associated. Kimber (1983b) showed that the best-fit model in a series of hybrids involving **T. aestivum** and **T. kotschyi** with different doses of **Ph1** and **Ph2** did not change even though the level of chromosome pairing did. These observations are consistent with the concept of **Ph** affecting the spatial association of premeiotic chromosomes.

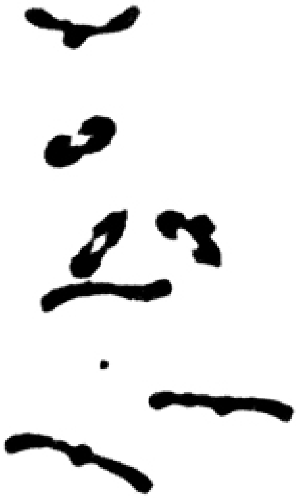
In addition to the genes in the A-genome polyploids affecting chromosome pairing, there are genes in other species the effect of which may be observed in hybrids. The ability of **T. speltoides** to suppress the activity of **Ph1** was recognized by Riley, Unrau and Chapman in 1958. Since then it has been shown (Kimber and Athwal, 1972; and Dvorak, 1972) that **T. speltoides** varies in its ability to suppress **Ph1**. Similar variation in the ability to suppress **Ph1** has been recorded from hybrids involving **T. longissimum** and **T. tripsacoides** (Mello-Sampayo, 1971; Dover and Riley, 1972). Genes affecting chromosome pairing in hybrids have also been recorded for **T. umbellulatum** (Riley, Chapman and Miller, 1973) and **T. dichasians** (Abu Bakar, 1980). Abu Bakar and Kimber (1982) have shown that some nine wild species were unable to compensate for the absence of **Ph1** and eight of them were not able to compensate for the absence of **Ph2** in hybrids. It would seem that the regular bivalent formation of many of the wild species without a D genome can be ascribed to differential affinity. The hexaploid species **T. juvenale**, which carries a D genome, can compensate for the absence of **Ph2**, but not **Ph1**, and therefore has at least some measure of genetic regulation of chromosome pairing. McGuire and Dvorak (1982) also concluded that other wild polyploids may contain gene systems regulating diploid meiotic behaviour.

The appreciation of the cytogenetical structure of the wheat group provides not only the satisfaction of understanding the cytological development of the species over evolutionary time but also the basis for the practical utilization of the genetic resources of the wild species.

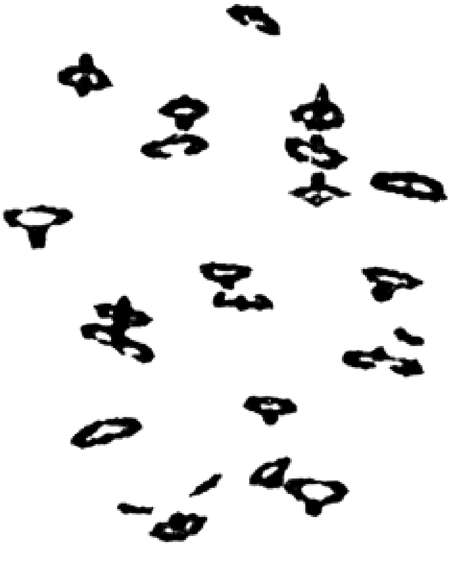
PLATE 29. Mitotic and meiotic chromosomes of wheat species and hybrids. a) **T. bicorne** (2n=14), root-tip cell, note two pairs of different sized satellites and chromosomes with sub-median centromeres. x1600. b) **T. aestivum** (2n=42), root-tip cell, note four approximately equal sized satellites, and chromosomes with sub-median centromeres. x850. c) **T. umbellulatum** (2n=14) first meiotic metaphase, three ring and four rod bivalents. x1600. d) First meiotic metaphase in a di-monotelosomic line of **T. aestivum**, 20" + t" + t'. x850. e) First meiotic metaphase of a hybrid between **T. cylindricum** (2n=28; genomically CCDD) and **T. tauschii** (2n=14; genomically DD). Note six bivalents, one trivalent and six univalents demonstrating homology between two of the genomes. The trivalent probably results from a translocation. x850. f) First meiotic metaphase in a tri-generic hybrid involving **T. timopheevii** (2n=28; AAGG), **Hordeum bogdanii** (2n=14; HH) and **Secale cereale** (2n=14; RR). Note 28 univalents demonstrating a total lack of homology; the large chromosomes of **S. cereale** are clustered together near the top of the cell. x850.

a

b



c



d

e

f

GENOMIC ANALYSIS

Genomic analysis is the general term used to describe, particularly for a polyploid series, both the processes and the results of investigations designed to demonstrate evolutionary relationships.

Different investigators have employed a range of techniques each with individual inherent advantages and disadvantages. Each technique is expected to measure, either directly or indirectly, the similarity of the DNA of the related species. Clearly, those methods which measure the similarity, or dissimilarity, of the greatest amount of DNA will generally provide the most consistent and reliable of data.

The effects of nucleus substitution has been used by several workers (Maan, 1973; Tsunewaki, 1980) to determine the relationships of the wild and cultivated species of the wheat group. More recently Ogihara and Tsunewaki (1982) have made restriction enzyme analyses of the chloroplast DNA of the **Triticum** species and Terachi, Ogihara and Tsunewaki (1985) for mitochondrial DNA. These techniques make comparisons or identify very small amounts or regions of the DNA; consequently it is to be expected that this type of investigation will provide unequivocal but perhaps contradictory results. However, the evolution of cytoplasmic DNA is thought to be very slow; therefore if paternal transmission is uncommon, then this type of evidence can provide a good indication of the origin of the cytoplasm.

Immunochemical reactions or protein electrophoresis may also provide clear, but contradictory, results. For example, Aniol (1974) and Jaaska (1976) by the use of immunochemical and electrophoretic methods, respectively, identified **T. speltoides** as the donor of the B genome of cultivated polyploid wheats. Johnson (1975) also from electrophoretic evidence equally clearly identified as the B-genome donor **T. urartu**, a species now known to have an A genome (Dvorak, 1976; Chapman, Miller and Riley, 1976).

Giemsa-banded chromosomes, or **in situ** DNA hybridization, or any other method dependent on the presence of repeated sequences of DNA often provides very clear indications of homology. However it must be remembered that the same repeated sequences may occur at several locations on unrelated chromosomes, that the same sequences may occur in distant non-lineal relatives and that over 95% of the DNA may not be considered in the conclusions drawn.

The problems associated with the use of karyotype analysis as a means of determining evolutionary relationships were discussed in the previous chapter.

The genomic relationships implied in the construction of a taxonomic classification have proven to be largely consistent. This consistency is based on the fact that the assemblage of characters used to describe individual species represents the effects of many loci and thus is vicariously comparing substantially more DNA than the methods previously discussed. There are three possible problems associated with the use of taxonomic classifications in the wheat group: first, the demonstration (Vardi, 1973) of introgression of characters both from diploid species to sympatric polyploids and vice versa; second, the frequent hybridization between related polyploids growing at the same site (Zohary and Feldman, 1962); and third, the suppression of characters of generic importance in wide crosses involving polyploids (Kimber, 1983a).

Where possible, the production of synthetic amphiploids, their crossing with their natural equivalents and the regularity of chromosome pairing in the derivatives provides perhaps the clearest genomic data possible. The construction by McFadden and Sears (1944, 1946) of a synthetic **T. aestivum** and a synthetic **T. triunciale** by Sears (1941) are the two best examples in the wheat group.

Genomic analysis by the "analyser-method" (Kihara and Nishiyama, 1930; see review, Lilienfeld, 1951) has provided the most consistent recognition of genomic similarities in the wheat group. Rosenberg (1909), observing the meiosis in a hybrid between two species of **Drosera**, concluded that 10 of the 20 chromosomes of the polyploid form were homologous to those of the diploid, since he observed 10 bivalents at meiosis in the triploid hybrid. This simple and elegant observation is the basis of classical genomic analysis. A hybrid is made, preferably between a diploid and a tetraploid. Chromosome pairing in multiples of the basic number in the meiosis of the hybrid is taken as an indication of genomic similarity. Even though chromosome pairing may not represent identity of the DNA at a locus, and even though the amount of chromosome pairing may be affected by the genotype of the species involved, it is a consequence of comparisons of some DNA along the entire length of every chromosome (a crucial point which is easily demonstrated by the observation of the characteristic meiotic figures produced as a consequence of translocations, inversions or other aberrations). Therefore this method of genomic analysis should be more reliable than any other method.

There are, of course, difficulties associated with the use of chromosome pairing as a method of genomic analysis in a polyploid series. Hybrids may be difficult to produce. Hybrids between diploid species are essentially useless for genomic analysis by the analyser-method, for there is the assumption that the chromosomes present in the hybrid must be able pair preferentially in order to show homology, and this requires the presence of at least three sets of chromosomes. Subjective judgements must be made if the chromosome pairing is not exactly in multiples of the basic number. Finally, in tetraploid or higher ploidy hybrids it is often not possible to determine which sets of chromosomes are pairing, or not pairing. Despite these difficulties, a largely consistent picture of the genomic relationships of the wheat group has emerged by the use of the analyser-method.

Recently numerical methods have been developed (Kimber, Alonso and Sallee, 1981; Alonso and Kimber, 1981; Kimber and Alonso, 1981 and Espinasse and Kimber, 1981) that allow not only the determination of the amount of chromosome pairing (equivalent to the analyser-method) but also the pattern of genomic affinity in hybrids. The genomic assignments made by Kihara and his co-workers by the analyser-method have remained essentially unaltered. The C^u genome symbol given to the diploid analyser **T. umbellulatum** has been given separate rank and the symbol U (Kimber and Abu Baker, 1981) and the M^u symbol for the diploid analyser **T. uniaristatum** has been also given separate rank and changed to Un (Kimber, Pignone and Sallee, 1983). Both of these changes indicate that the species are now recognized as not having genomes modified from some other diploid but are distinct and differentiated genomes.

The relationships of the genomes in the polyploid species of **Triticum** have also been clarified, but much work remains to be accomplished. First indications of the effect of the genetic systems involved in the regulation of chromosome pairing are that they do not change the relative affinity of the genomes present in a hybrid but that they alter the amount of chromosome pairing (Kimber, 1983b). This means that genomic analysis based on chromosome pairing in hybrids can now be considered even more reliable than previously, for the effect of the pairing regulators can be assessed and not just dismissed as a potential source of confusion.

T. monococcum	A
T. speltoides	S
T. bicorne	S^b
T. longissimum	S^l
T. searsii	S^s
T. tripsacoides	Mt
T. tauschii	D
T. comosum	M
T. uniaristatum	Un
T. dichasians	C
T. umbellulatum	U

Proposed genome symbols of the diploid species of the genus **Triticum** (Kimber and Sears, 1983).

The U-genome group of species has been extensively investigated by Feldman and Zohary in a series of publications. Zohary and Feldman (1962) presented morphological evidence for the occurrence of natural hybridization between most of the tetraploid U-genome species. A hypothesis was advanced that the polyploid species of the **Triticum** group can be regarded as three groups of species. Within each cluster species are characterized by an unaltered genome (designated pivotal) and one, or two in the hexaploids, modified genome(s) (designated differential). Most polyploids within each of the three species clusters are considered to be hybridization derivatives from a more limited number of primordial amphiploids. Feldman (1956a, 1965b and 1965c) documented the chromosome pairing, fertility and morphological features of the U-genome group, clearly establishing the cytological, genomic and evolutionary status of this group of species.

The relationships of the group of species containing D genomes have been investigated by Zhao and Kimber (1984), Kimber and Zhao (1983), and Kimber and Zhao (1984). A total of 21 hybrids have been investigated of which 10 have not previously been recorded. The D-genome species can be divided into three groups. The first group contains **T. cylindricum, T. ventricosum** and

T. aestivum, and the D genomes in these species seem to have been little modified from the D genome of the diploid progenitor **T. tauschii**. The second group consists of the tetraploid and hexaploid forms of **T. crassum**, and the D genomes in these forms are somewhat modified from the D genomes of the first group of species. In fact it would seem that the two D genomes present in the hexaploid **T. crassum** pair preferentially with each other to the exclusion of the D genome of **T. tauschii**. The D genomes present in the third group (**T. juvenale** and **T. syriacum**) are substantially modified from all other D genomes.

The A-genome cluster of species includes, obviously, the cultivated wheats. The A genome present in the hexaploid, and presumably in the tetraploids also, is essentially unaltered from the A genome of the diploid wheats. Kimber and Hulse (1978) and Kimber, Alonso and Sallee (1981) calculated the similarity of the A-genome chromosomes of diploid wheats to the telocentrics of the A-genome chromosomes of **T. aestivum**. With the exception of chromosome 4A, which is not homologous to any A-genome chromosome (Miller, Shepherd and Riley, 1981), there was clear indication that the A-genome chromosomes of **T. aestivum** were essentially unaltered derivatives of the chromosomes of diploid wheat. Kimber (unpublished) calculated the relative affinities of the series of 20 hybrids between hexaploid and diploid wheats produced by Miller and Reader (1981). The values of x ranged from 1.000 to 0.952, clearly showing that the A genome of diploid wheat was homologous to the A genome of hexaploid wheat. The D-genome chromosomes of the hexaploid **T. aestivum** are also essentially unaltered (Kimber and Zhao, 1983). Since the B genome is not unequivocally assigned to a diploid species, it is possible that it may be the differential genome of the A-genome cluster of species.

No diploid with a genome homologous to the B or G genomes has been identified, neither has the relationship of the B to the G genome been clarified. The chromosome pairing in tetraploid hybrids involving **T. aestivum** and S-genome species seems to be that pattern expected from two clusters of two similar genomes (Kimber and Alonso, 1981). Alonso (1981) by the use of complex hybrids in which the **Ph1** gene was suppressed and involving telocentric chromosomes that the pairing pattern does indeed involve two clusters of chromosomes and they are A-D and B-S. In addition the pairing frequency in each of these clusters was about the same. It is probable that the S-genome diploids are in fact closer to the B (or G) genome than any other diploid species investigated. However, if homology of the B and S genomes is proposed, then similarly homology of the A and D genomes would be implied. For a diploid species to have unequivocal homology with the B (or G) genome the chromosome pairing in a hybrid of that species and **T. aestivum** would have to be very similar to that observed in the hybrids between **T. aestivum** and either **T. monococcum** or **T. tauschii**.

T. turgidum	AB
T. timopheevii var **zhukovskyi**	AAG
T. aestivum	ABD
T. ventricosum	DUn
T. crassum (4x)	D$\underline{M}$
T. crassum (6x)	$\underline{DDM}$
T. syriacum	$\underline{DMS}$
T. juvenale	$\underline{DMU}$
T. kotschyi	U$\underline{S}$
T. ovatum	U$\underline{M}$
T. neglecta	U$\underline{M}$
T. recta	U$\underline{MUn}$
T. macrochaetum	U$\underline{M}$
T. columnare	U$\underline{M}$
T. triunciale	UC
T. cylindricum	CD

The proposed symbols of the polyploid species of the genus **Triticum** modified from Kimber and Sears (1983).

Underlined symbols represent substantially modified genomes.

In contrast to the origin of the A and D genomes, that of the B genome has, so far, defied conclusive identification. Morphological, cytological and genetic evidence implicate a species with an S-like genome (Feldman, 1978). In addition, the cytoplasm of common wheat is similar to that of **T. longissimum** (Tsunewaki, 1980). Similar data would indicate that the G genome of **T. timopheevii** also had its origin from a species with an S-like genome. Also the cytoplasm of **T. timopheevii** is very similar to the cytoplasm of **T. speltoides.**

The two tetraploids (**T. turgidum** and **T. timopheevii**) could have had a monophyletic origin and diverged following introgression from other diploid species or, alternatively, they could have arisen independently and then hybridized with each other and with other diploid species. Consequently the B could have differentiated from the G, or the G from the B or both from some S-like genome progenitor. Any of these possible scenarios would implicate an S-like genome in the parentage of both the B and G genomes and, at the same time, provide the grounds for the difficulty of unequivocal identification of the genomes in the polyploids.

EVOLUTION

Evolution in the **Triticeae** is a complex anastomosis of general processes and singular events which have occurred over long periods of time and which are still proceeding in a dynamic environment.

Perhaps the most conspicuous feature of the group is the divergence of several (10 or more) forms at the diploid level and their convergence in various and subsequently modified combinations at the polyploid level. This reticulate pattern of evolution provides the basis for many of the characteristics of individual species and the often unclear demarcations between closely or partially related species.

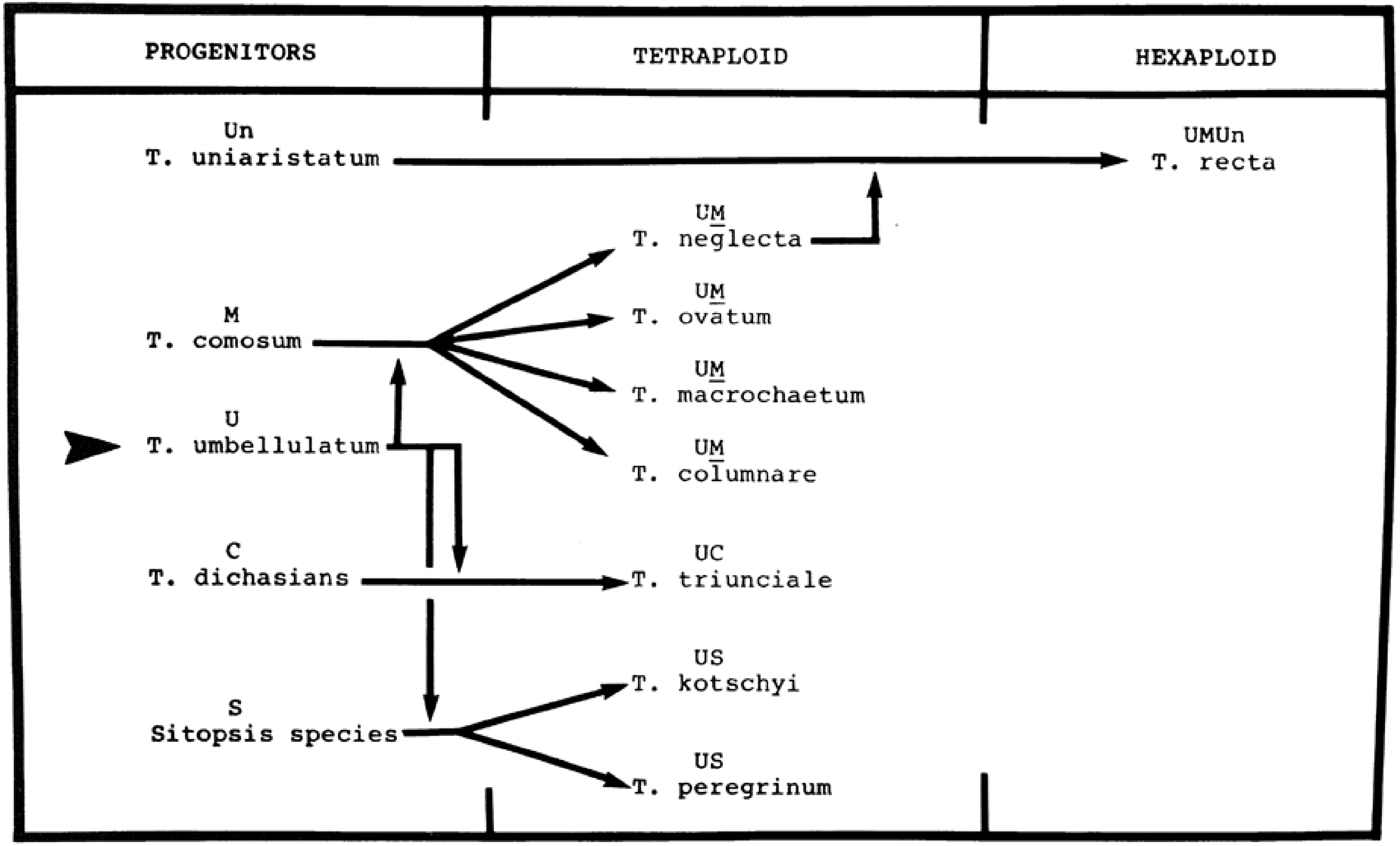
Although the diploid species are presumably descended from a common ancestor, they have diverged considerably from one another. Cytogenetic studies have shown that almost every species has a distinct genome. The homoeologous chromosomes of the different genomes exhibit varying degrees of reduced affinity for one another, and hence they do not pair regularly at meiosis in interspecific diploid hybrids. Consequently almost all of the interspecific hybrids are completely or almost completely sterile and are thus genetically isolated from each other. Thus the diploid level is characterized by chromosomal and genetic divergence which is expressed in the great morphological and ecogeographical specialization which is evident in the well-defined dispersal unit marking each diploid species.

Zohary and Feldman (1962) pointed out that morphologically and cytogenetically the polyploid species of the genus **Triticum** fall into three natural groups: one sharing the U genome of **T. umbellulatum**, one the D genome of **T. tauschii**, and one the A genome of **T. monococcum**. The species of each group share one common genome and differ in their other genome or genomes. In basic morphology and particularly in the structure of the seed dispersal unit, the polyploids of each group resemble the diploid donor of the common genome and differ in features of the other genomes.

This characteristic genomic structure of the polyploids accounts for the relatively high rate of successful hybridization (and hence gene flow) between the polyploids. Hybridizations of this type are facilitated by the shared genome, which acts as a buffer ensuring some fertility in the resulting hybrids. In such cases, the different genomes, which are brought together from different diploid parents, can exchange genetic material and form new recombinant genomes. Thus in each natural group of polyploid species, there is almost continuous variation between the characteristics of the differentiated genomes.

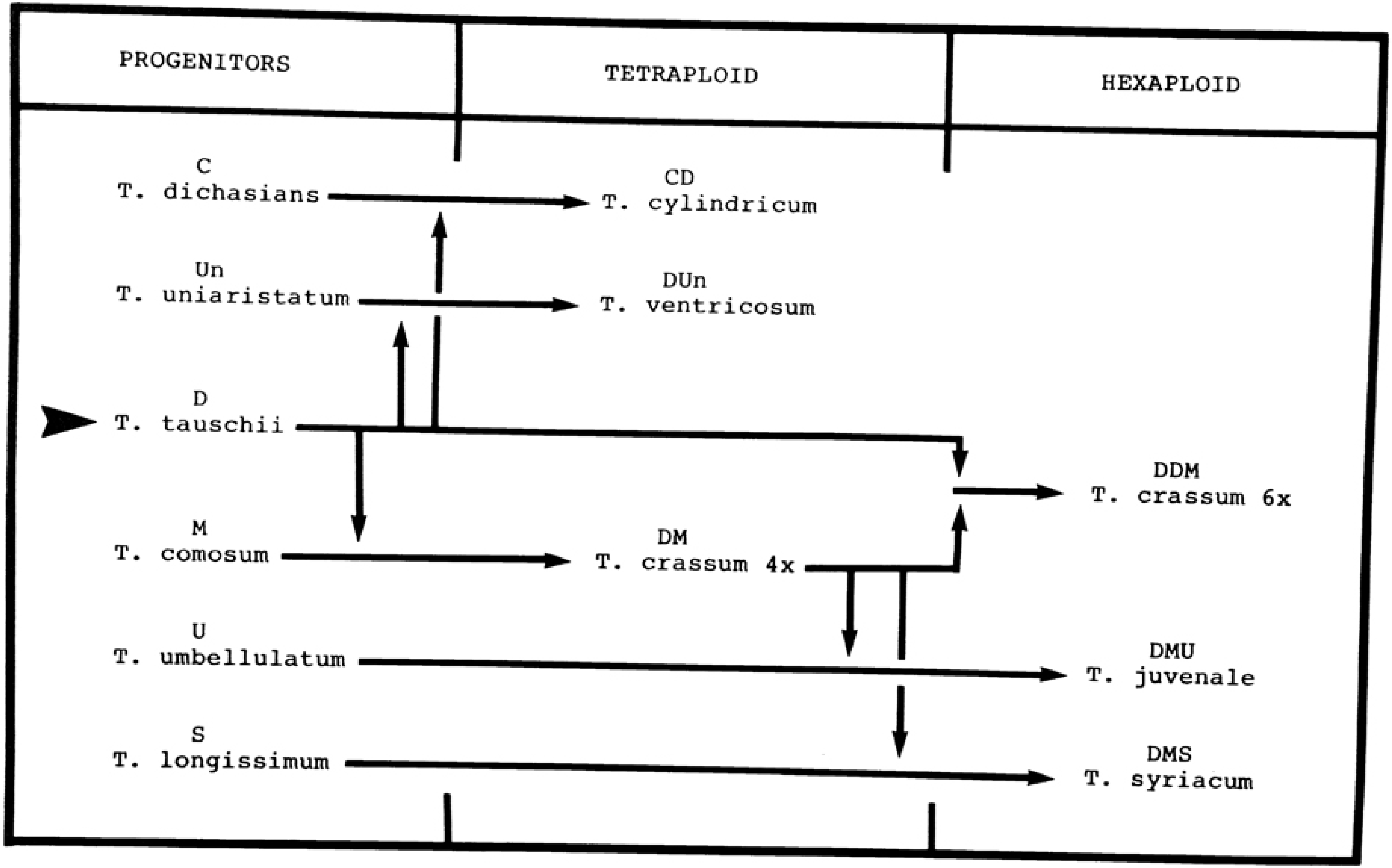
The U-genome cluster (Plate 30) was investigated by Zohary and Feldman (1962), and they suggested the pivotal-differential hypothesis of evolution in this group. It is proposed that the U genome present in the polyploid species has not been substantially modified but the other genome or genomes present have undergone extensive modification. The modification of the differential genomes has possibly occurred following hybridization between U-genome tetraploids differing in their second genome. Clear evidence was provided of the presence of several U-genome tetraploids in one population and of the introgression of characters from one to another. In addition to the introgression of characters from one tetraploid to another, it is also clear that there is introgression of characters both to and from diploids which are sympatric with the mixed tetraploid populations. Even though it is quite possible to recognize the tetraploid species as individual entities, there is not only an overlapping of diagnostic features but also a relatively free exchange of genetic material between them.

Plate 30. A diagrammatic representation of the major evolutionary features of the U-genome wild wheat species. Two groups of species are shown diverging from single hybridization events for the purposes of diagrammatic simplicity. It is quite possible that each group is polyphyletic in origin and in addition there is an anastomosing network of hybridization following the origin of the tetraploid amphiploids. The **Sitopsis** species involved in the evolutionary origin of **T. kotschyi** and **T. peregrinum** are not yet finally resolved.


PROGENITORS
TETRAPLOID
HEXAPLOID
Un
T. uniaristatum
UMUn
T. recta
UM
T. neglecta
UM
T. ovatum
M
T. comosum
UM
T. macrochaetum
U
T. umbellulatum
UM
T. columnare
C
T. dichasians
UC
T. triunciale
US
T. kotschyi
S
Sitopsis species
US
T. peregrinum

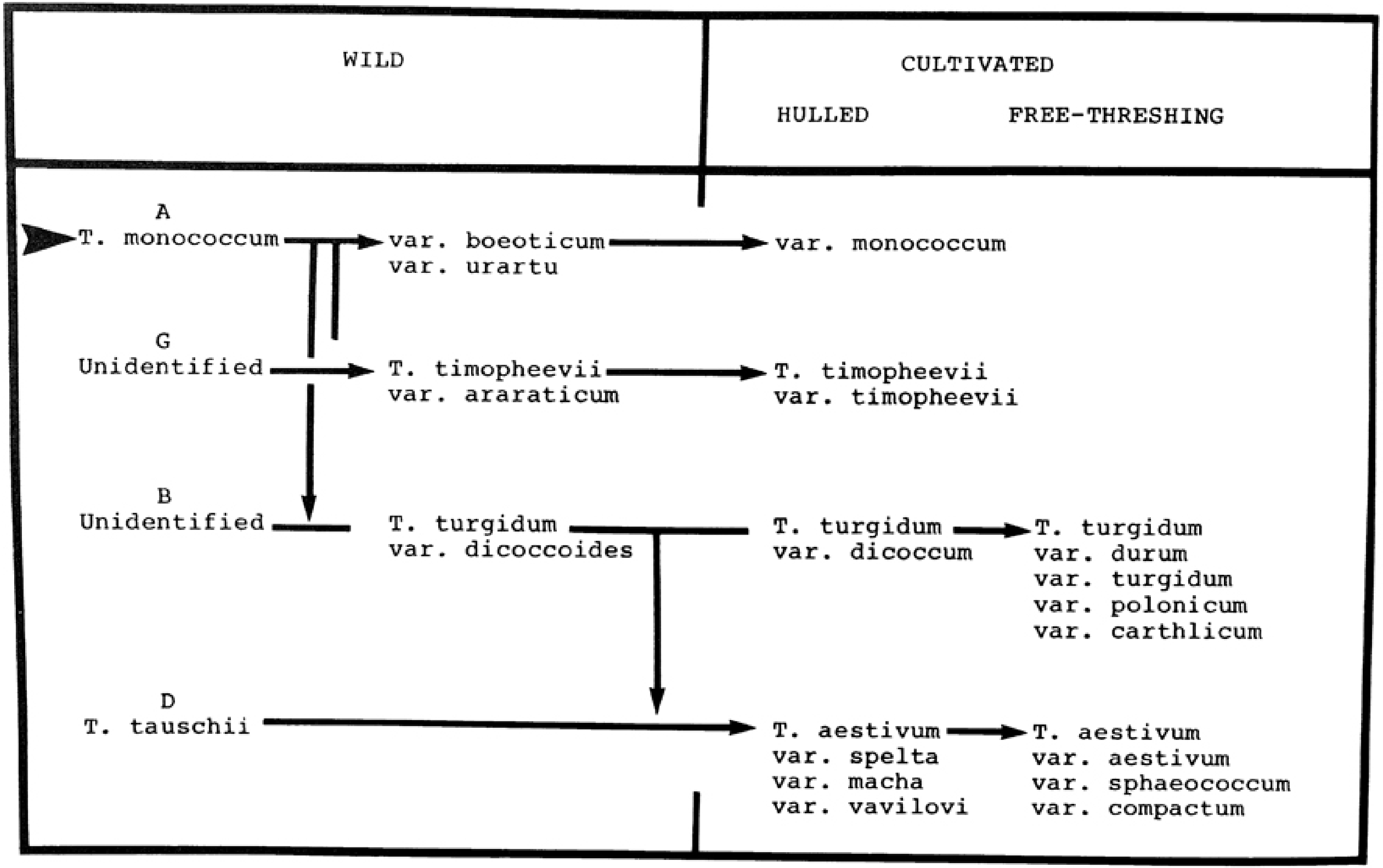
The pivotal-differential pattern of evolution in the D-genome cluster is not quite so clear. Zhao and Kimber (1983) and Kimber and Zhao (1983) have shown that the D-genome cluster can be divided into three groups on the basis of the modification of the D-genome. Thus it can be considered as a pivotal genome only in the broadest sense. Nevertheless there is a clear group of species, each with the characteristic barrel-shaped disarticulation into individual spikelets, and other features inherited from **T. tauschii.** Another interesting feature of this group is the three different hexaploids that share the D and M genomes of **T. crassum.**

Plate 31. A diagrammatic representation of the major evolutionary features of the D-genome wild wheat species. There have been two major evolutionary events in this group. First, the evolution of the two tetraploids **T. cylindricum** and **T. ventricosum** in both of which the D genome is essentially unaltered; and second, the evolution of **T. crassum** at the tetraploid level from which three hexaploid species, **T. crassum** (6x), **T. juvenale** and **T. syriacum**, each with substantially modified D genomes were derived.


PROGENITORS
TETRAPLOID
HEXAPLOID
C
T. dichasians
CD
T. cylindricum
Un
T. uniaristatum
DUn
T. ventricosum
D
T. tauschii
DDM
T. crassum 6x
M
T. comosum
DM
T. crassum 4x
U
T. umbellulatum
DMU
T. juvenale
S
T. longissimum
DMS
T. syriacum

The A-genome group of species includes all the cultivated forms. The A genome of the polyploids is closely related to the A genome of the diploid, although it can be shown (Miller, Shepherd and Riley, 1981) that chromosome 4A of **T. aestivum** is not homologous to any A-genome chromosome. Since the B and G genomes are not known to be homologous to any diploid investigated, then only 13 of the chromosomes (six A-genome and seven D-genome) of **T. aestivum** are homologous to their diploid analysers. The D genome of **T. aestivum** is essentially unmodified from that in the D-genome progenitor, **T. tauschii**, and was added after the union of the A and B genomes.

Plate 32. A diagrammatic representation of the major evolutionary features of the A-genome wild and cultivated wheat species. The A-genome cluster differs from the U- and D-genome clusters in that it contains species of paramount commercial importance. In addition, the cultivated forms exist at all three ploidy levels. For the purposes of diagrammatic simplicity possible introgression between the tetraploid species is not shown.


WILD
CULTIVATED
HULLED
FREE-THRESHING
A
T. monococcum
var. boeoticum
var. urartu
var. monococcum
G
Unidentified
T. timopheevii
var. araraticum
T. timopheevii
var. timopheevii
B
Unidentified
T. turgidum
var. dicoccoides
T. turgidum
var. dicoccum
T. turgidum
var. durum
var. turgidum
var. polonicum
var. carthlicum
D
T. tauschii
T. aestivum
var. spelta
var. macha
var. vavilovi
T. aestivum
var. aestivum
var. sphaeococcum
var. compactum

The relationships of the B to the G genome fall into an intermediate category. Sallee and Kimber (1978) calculated a similarity of the B and G genomes based on the pairing of the B-genome telocentrics with G-genome chromosomes from the data of Feldman (1966b) and Winkle (1976). Kimber, Alonso and Sallee (1981) extended these observations and showed that the G genome was some 47 per cent similar to the B genome. The wild forms of these two species do grow together in the fertile crescent and also in association with cultivated forms. There is obviously the opportunity for introgression between the B and the G genome, and so it is possible that these genomes may now not be homologous to any particular diploid.

The evolutionary relationships of the wild wheats are not confined to the generic boundaries of **Triticum**. It is obvious from the ability of chromosomes of alien species generally to substitute for the chromosomes of only one homoeologous group that homoeologous relationships exist between the chromosomes of the genus **Triticum** and other genera in the **Triticeae** which are similar to those that exist between the chromosomes of **T. aestivum** and its closer relatives. The species of the genus **Triticum** can therefore be viewed as part of a greater continuum of genetic relationships extending to many other grasses.

UTILIZATION OF ALIEN VARIATION

The eroding genetic base of the cultivated wheats has led workers to investigate the possibility of utilizing the genetic variation present in the wild relatives (Feldman and Sears, 1981). These wild gene pools contain many economically important genes that might be transferred to cultivated wheats and utilized in their improvement and in creating potentially new variation. If the genomic constitution of a wild form shows little similarity to the genomes present in the cultivated wheats, then the probability of the introduction of desirable variation will be severely limited. Clearly, in order to utilize this variation effectively it is essential to understand the genomic and cytological relationships of the wild and cultivated species.

At least three criteria must be met in order to develop a cultivar involving alien variation. First, the desirable character must be located in another species. This implies a simple and effective screening technique allowing the clear recognition of the character. Second, the genetic mechanism controlling the character must be simply inherited. Physiological characteristics such as photosynthetic activity, or quantitative characteristics such as yield are probably affected by many genes. It would be very difficult, if not impossible, to transfer these characteristics successfully. Third, the genetic mechanism must be expressed satisfactorily in the genetic background of the cultivar. Providing that these criteria can be met then it is possible to actually choose the method for the introduction of alien variation that has the highest probability of success.

The limitations placed or implied by the three criteria tend to limit the choice of characters for introduction mainly to disease resistance. Disease resistance is often simply inherited. Screening is generally easy, both of the accessions of the wild species and of the large number of plants in the derived generations. Since the pioneering work of Sears (1956), several such genes were transferred into cultivated wheat. Sharma and Gill (1983) list a large number of alien genes for disease resistance introduced from wild species. Similarly, McIntosh (1983) in the catalogue of gene symbols lists many of the introduced genes and actually ascribes symbols to them.

Recently there has been increased interest in characters other than disease resistance. Avivi (1978, 1979) showed very high grain-protein percentage in the wild form **T. turgidum** var. **dicoccoides.** In some lines proteins as high as 30 per cent were recorded. Some of the genes involved were transferred to hexaploid and tetraploid cultivars, resulting in an increase of 3 to 5 per cent of grain protein without loss of yield (Avivi, Levy and Feldman, 1983; Levy and Feldman, 1986). Wild species such as **T. kotschyi** or **Agropyron junceum**, which grow in dry and saline places, may contain genes for drought and salt tolerance. The ability to introduce characters such as these into cultivated wheats will greatly increase the value of the crop or increase its range of cultivation so that it may grow in conditions that are currently impossible.

On the assumption that the three criteria are met, then the choice of the method for the introduction of the alien variation can be made on the basis of the genomic and cytological relationships of the genomes of the wild form to the genomes in the cultivated varieties. Again, three situations can be envisioned.

First, if the pattern and level of chromosome pairing indicates homology, then the alien transfer can be accomplished simply by recombination.

Second, if the pattern of chromosome pairing indicates that there is substantial homoeology between the alien genomes and the wheat genomes even though the level of pairing may be low, then it is possible to increase the level of pairing by using wheat lines either deficient or mutant for the pairing regulators **Ph1** or **Ph2** (Sears, 1972 and 1981). An example of this type of hybrid would be **T. aestivum** x **T. kotschyi**, where it can be shown that the five genomes present can be divided into two groups, one of three genomes and the other of two, and that this pattern still persists at high levels of induced chromosome pairing (Kimber, 1984).

Third, if the pattern of chromosome pairing indicates that the alien chromosomes do not pair frequently with the wheat chromosomes and also the level of pairing is very low (for example, hybrids such as **T. aestivum** x **Secale cereale** or **T. aestivum** x **Hordeum vulgare**), then it may be necessary to resort to techniques allowing the breaking and fusion of chromosomes (Sears, 1956, and 1972; Driscoll and Jensen, 1964; Kimber, 1971; and Feldman,1983).

Increasing the genetic base of the stocks of wild wheats (including land races) is clearly the first step providing material for future use. The value of such collections is inestimable and can only represent one of the best investments that it is possible to make. The recognition of this simple fact is reflected in the choice of words to describe the depositories of these materials: gene bank. In order to maximize the value of these collections, the species must be properly identified, and their cytological, genomic and evolutionary status must be understood. It is our hope that this small book will contribute to that end.

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