On the taxonomy of *wheat*

Classifications and Nomenclature

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Contents

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- A short outline of a taxonomic monograph
- The concept of a Genus and of an Accepted Taxon
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A little history… The “original 7”

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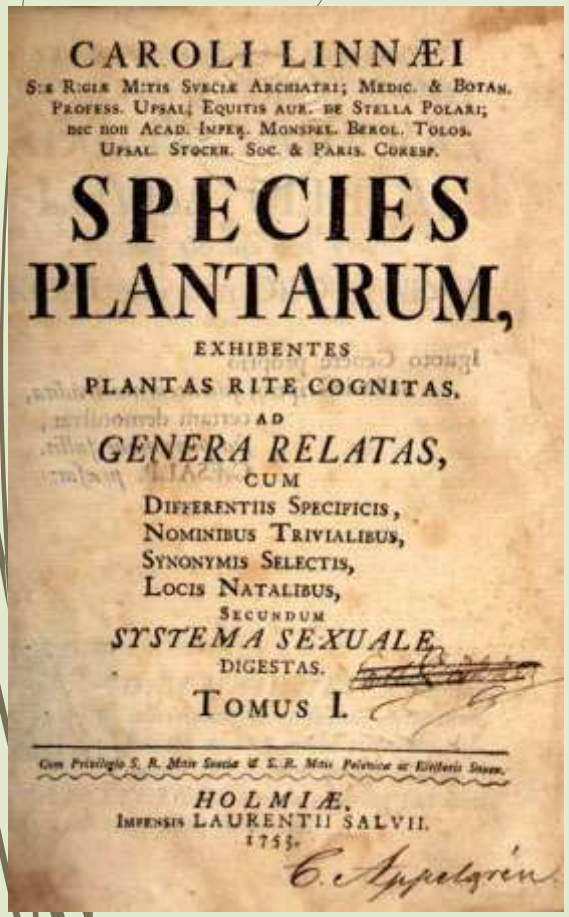


CAROLI LINNÆI

SUÆ REGIÆ MAJESTATIS SVECIÆ ARCHIATRI; MEDIC. & BOTAN. PROFESS. UPSAL; EQUITIS AUR. DE STELLA POLARI; NEC NON ACAD. IMPER. MONSPEL. BEROL. TOLOS. UPSAL. STOCKH. SOC. & PARIS. CORESP.

SPECIES PLANTARUM,

EXHIBENTES

PLANTAS RITE COGNITAS,

AD

GENERA RELATAS,

CUM

DIFFERENTIIS SPECIFICIS,
NOMINIBUS TRIVIALIBUS,
SYNONYMIS SELECTIS,
LOCIS NATALIBUS,

SECUNDUM

SYSTEMA SEXUALE

DIGESTAS.

TOMUS I.

Cum Privilegio S. R. Majt. Suecia & S. R. Majt. Poloniæ ac Electoris Saxon.

HOLMIÆ,
IMPENSIS LAURENTII SALVII.
1753.

C. Appelgren

Hordeum floſculis omnibus hermaphroditis. *Hort. cliff* 24. *Roy. lugdb.* 69.
Hordeum polyſtichon vernum. *Bauh. pin.* 22. *theatr.* 439.

β. Hordeum floſculis omnibus hermaphroditis, ſeminibus decorticatis. *Hort. upſ.* 23. *cæleſte.*
Habitat - - - - ⊙

2. HORDEUM floſculis omnibus hermaphroditis ariſtatis, ſeminibus ſexfariam æqualiter poſitis. *Hort. upſ.* 23. *hexaſtichon.*
Habitat - - - - ⊙

3. HORDEUM floſculis lateralibus maſculis muticis, ſeminibus angularibus imbricatis. *Hort. upſ.* 23. *diſtichon.*
Hordeum diſtichon. *Bauh. pin.* 22.

β. Hordeum floſculis lateralibus maſculis muticis, ſeminibus angularibus imbricatis decorticatis. *nudum.*
Habitat - - - - ⊙

4. HORDEUM floſculis lateralibus maſculis muticis, ſeminibus angularibus patentibus corticatis. *Hort. upſ.* 23. *n.* 5. *zeocriton.*
Zeocriton ſ. oryza germanica. *Bauh. pin.* 22.
Habitat - - - - ⊙

5. HORDEUM floſculis lateralibus maſculis ariſtatis, *murinum.*
Hort. cliff. 24. *Fl. ſuec.* 107. *Roy. lugdb.* 69.
Gramen hordeaceum minus & vulgare. *Bauh. pin.* 8. *theatr.* 134. *Scheuch. gram.* 14.

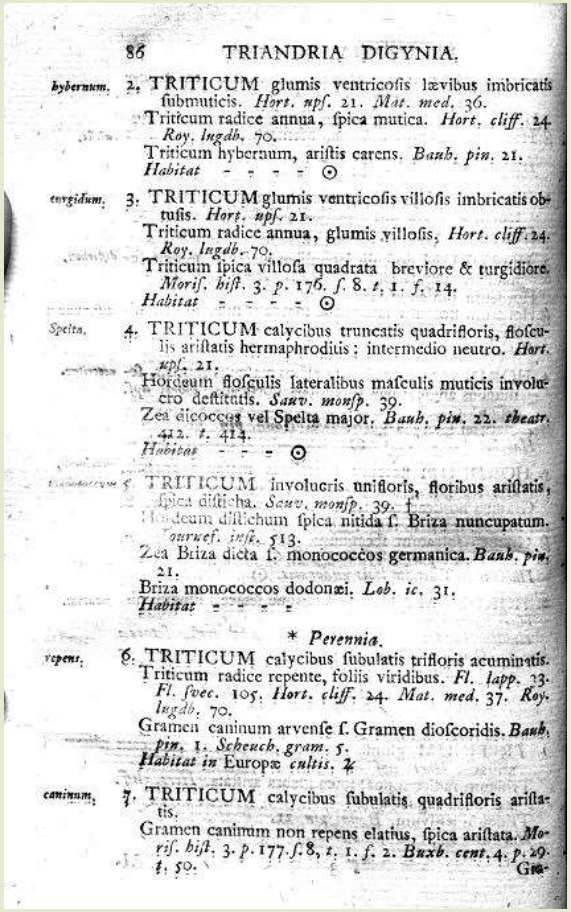
β. Gramen ſpicatum ſecalinum minus. *Scheuch. gram.* 17. *Vaill. pariſ,* 83. t. 17. f. 6.
Habitat in Europæ *locis ruderatis.* ⊙

6. HORDEUM ariſtis involucrisque ſetaceis longiſſimis. *jubatum.*
Habitat in Canada. *Kalm.*
Habitus hordei murini, ſed involucra & ariſtæ ſetaceæ quadruplo longiores, quam tota ſpica, unde ſingularis facies graminis.

TRITICA.

* *Annua.*

1. TRITICUM glumis ventricoſis glabris imbricatis ariſtatis. *Hort. upſ.* 21. *æſtivum.*
Triticum radice annua, ſpica glabra ariſtata. *Hort. cliff.* 24. *Roy. lugdb.* 170.
Triticum æſtivum. *Bauh. pin.* 21.
Habitat - - - - ⊙



hybernum. 2. TRITICUM glumis ventricoſis lævibus imbricatis ſubmuticis. *Hort. upſ.* 21. *Mat. med.* 36.
Triticum radice annua, ſpica mutica. *Hort. cliff.* 24. *Roy. lugdb.* 70.
Triticum hybernum, ariſtis carens. *Bauh. pin.* 21.
Habitat - - - - ⊙

turgidum. 3. TRITICUM glumis ventricoſis villoſis imbricatis obtuſis. *Hort. upſ.* 21.
Triticum radice annua, glumis villoſis. *Hort. cliff.* 24. *Roy. lugdb.* 70.
Triticum ſpica villoſa quadrata breviore & turgidiore. *Moriſ. hiſt.* 3. *p.* 176. *ſ.* 8. *t.* 1. *f.* 14.
Habitat - - - - ⊙

Spelta. 4. TRITICUM calycibus truncatis quadrifloris, floſculis ariſtatis hermaphroditis: intermedio neutro. *Hort. upſ.* 21.
Hordeum floſculis lateralibus maſculis muticis involucro deſtitutis. *Sauv. monſp.* 39.
Zea dicoccos vel Spelta major. *Bauh. pin.* 22. *theatr.* 422. *t.* 414.
Habitat - - - ⊙

monococcum 5. TRITICUM involucris unifloris, floribus ariſtatis, ſpica diſticha. *Sauv. monſp.* 39. †
Hordeum diſtichum ſpica nitida ſ. Briza nuncupatum. *Tournef. inſt.* 513.
Zea Briza dicta ſ. monococcos germanica. *Bauh. pin.* 21.
Briza monococcos dodonæi. *Lob. ic.* 31.
Habitat - - - -

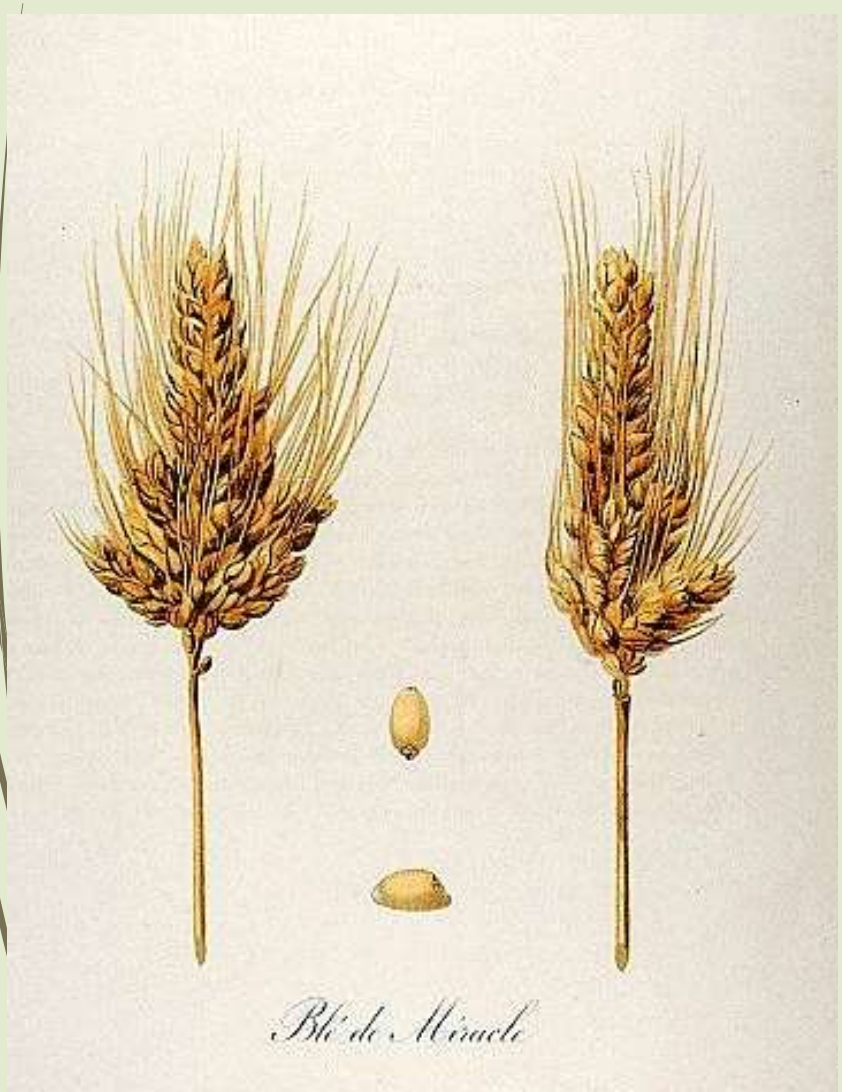
* *Perennia.*

repens. 6. TRITICUM calycibus ſubulatis trifloris acuminatis.
Triticum radice repente, foliis viridibus. *Fl. lapp.* 33. *Fl. ſuec.* 105. *Hort. cliff.* 24. *Mat. med.* 37. *Roy. lugdb.* 70.
Gramen caninum arvenſe ſ. Gramen dioſcoridis. *Bauh. pin.* 1. *Scheuch. gram.* 5.
Habitat in Europæ *cultis.* ♃

caninum. 7. TRITICUM calycibus ſubulatis quadrifloris ariſtatis.
Gramen caninum non repens elatius, ſpica ariſtata. *Moriſ. hiſt.* 3. *p.* 177. *ſ.* 8. *t.* 1. *f.* 2. *Buxb. cent.* 4. *p.* 29. *t.* 50.

Gra-

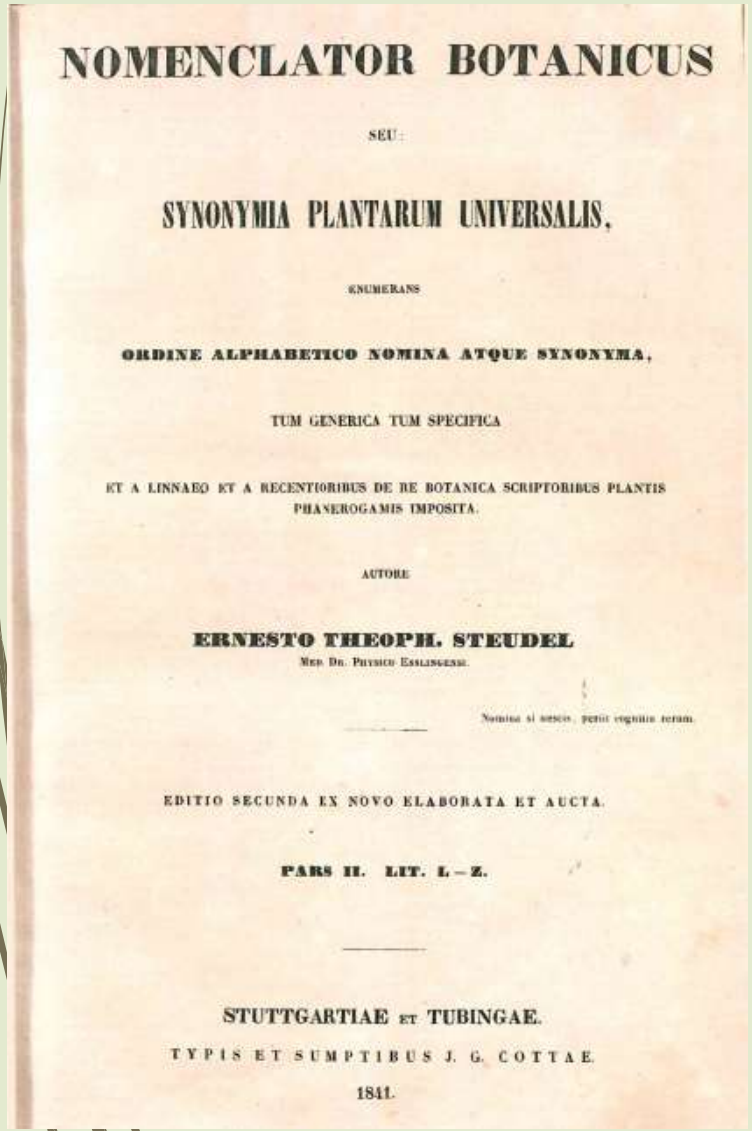
A little history… The “original 7”



- For any taxonomic monograph the “starting point” of evidence is 1 May 1753; ALL names published in *Triticum* after that date are taken into account
- Linnaeus published both *Annua* and *Perennia* in the genus
- The conspicuous *T. polonicum* L. was well-known in 1753 but only included in the second edition of the *Species plantarum* (1762: 127)
- The branched *T. compositum* L., equally well-known (e.g. depicted in Lobel’s *Icones* from 1591), only in 1774 in Linnaeus’s *Systema vegetabilium* ed. 13 (the “Murray edition”), p. 108
- The title “Tritica” on p. 85, 1753,is a typographical error

Left: *Triticum compositum* in Ph. de Vilmorin’s *Les meillieurs Blés* (1906)

A little more history - a few more names…



NOMENCLATOR BOTANICUS

SEU

SYNONYMIA PLANTARUM UNIVERSALIS,

ENUMERANS

ORDINE ALPHABETICO NOMINA ATQUE SYNONYMA,

TUM GENERICA TUM SPECIFICA

ET A LINNAEO ET A RECENTIORIBUS DE RE BOTANICA SCRIPTORIBUS PLANTIS PHANEROGAMIS IMPOSITA.

AUTORE

ERNESTO THEOPH. STEUDEL

Med. Dr. Physico Esslingensi.

Nomina si nescis, perit cognitio rerum.

EDITIO SECUNDA EX NOVO ELABORATA ET AUCTA.

PARS II. LIT. L – Z.

STUTTGARTIAE ET TUBINGAE.

TYPIS ET SUMPTIBUS J. G. COTTAE.

1841.

- 1841 – Von Steudel, *Nomenclator Botanicus, vol. II* (left): *Triticum* (annuals and perennials): **85** accepted species (and **308** names)
- 1885 – Körnicke, *Handbuch des Getreidebaues*: *Triticum* (only annuals): **3** species and **125 (*vulg.*) + 21 (*polon.*) + 4 (*mono.*) = 150** infraspecific taxa
- 1915 – Flaksberger, *Opredelitel Pshenitsa* [Determination of wheats]: *Triticum* (only annuals): **8** species and **253** infraspecific taxa
- 1979 – Dorofeev & Korovina, *Pshenitsa* [Wheat – Fl. Cult. Plants USSR, Vol. I]: *Triticum* (only annuals): **27** species and **1031/1054** (Mac Key 1988 vs. Bernhardt 2015) infraspecific taxa
- 1995 – Czerepanov (former USSR flora only): *Triticum* (only annuals): **30** species and **9** subsp.
- 2011 – Hammer *et al.*: *Triticum* (only annuals): **25** species and **2** subsp.

A short outline of a new **taxonomic monograph** - 1

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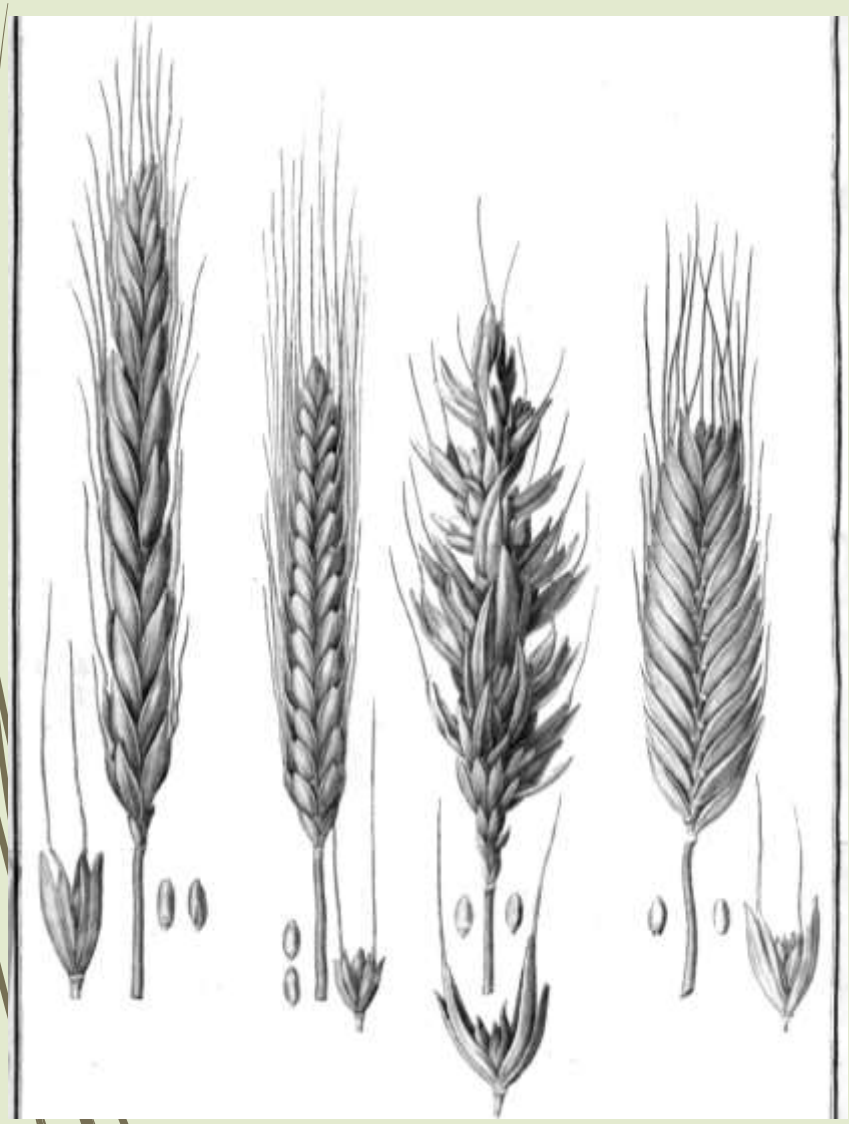


General Part:

- History (pre / post Linnaean)
- Generic Relationships in Triticinae
- Genus and Species (taxa) concept
- Phylogeny
- Geographic distribution
- [Agronomy – not relevant with "normal" botanical monographs]

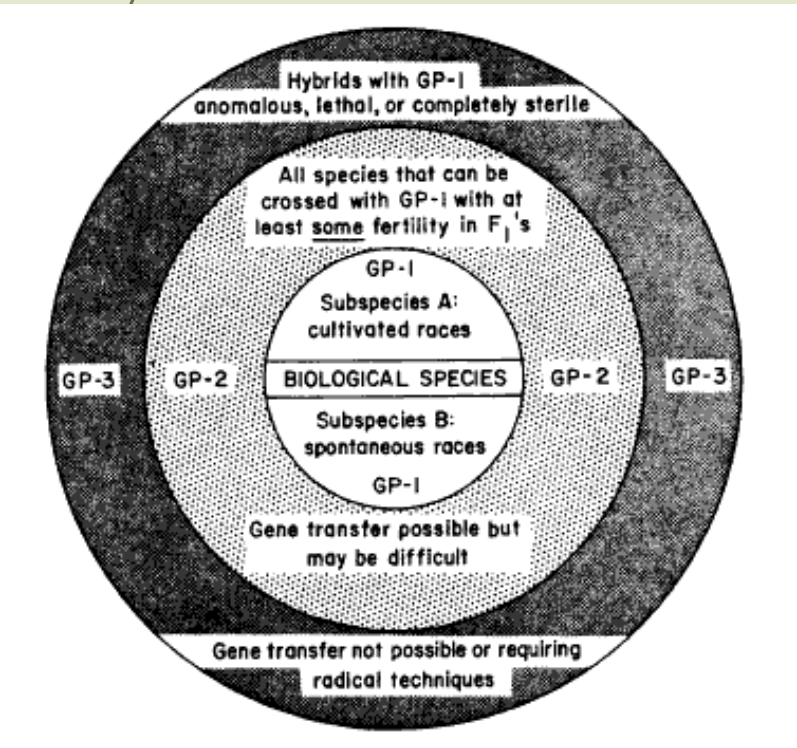
Taxonomic Part:

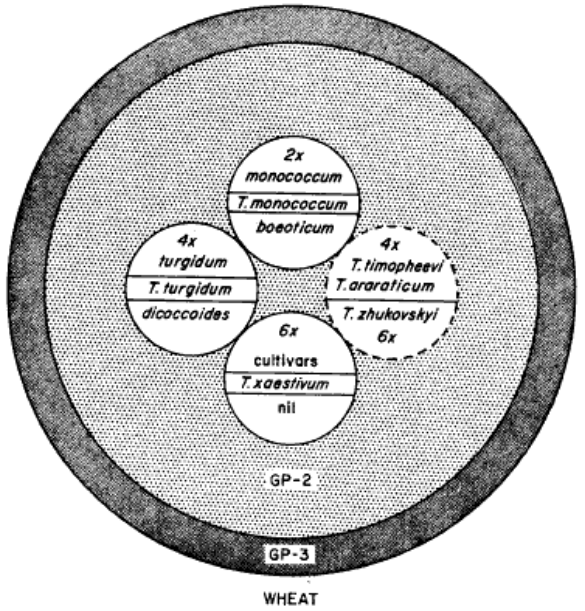
- Contains an opinion on ALL names published in the revised taxonomic unit
- Genus and species descriptions
- Key(s) to the accepted taxa
- The "Grey Zone" of sect. *Compositum*
- Excluded taxa

Left: Bellardi, Ann. Agric. Regno Italia 3(8) (1809)

A concept note: Gene Pools (Harlan & de Wet 1971)

- Subspecies level for direct, wild progenitor vs cultivated “races”; GP-1 etc. are not proposed as formal group
- Four GP1 “kernels” in the wider wheat gene pool (one is based on an accidental hybrid instead of a “species”)
- Authors reject detailed infraspecific categories

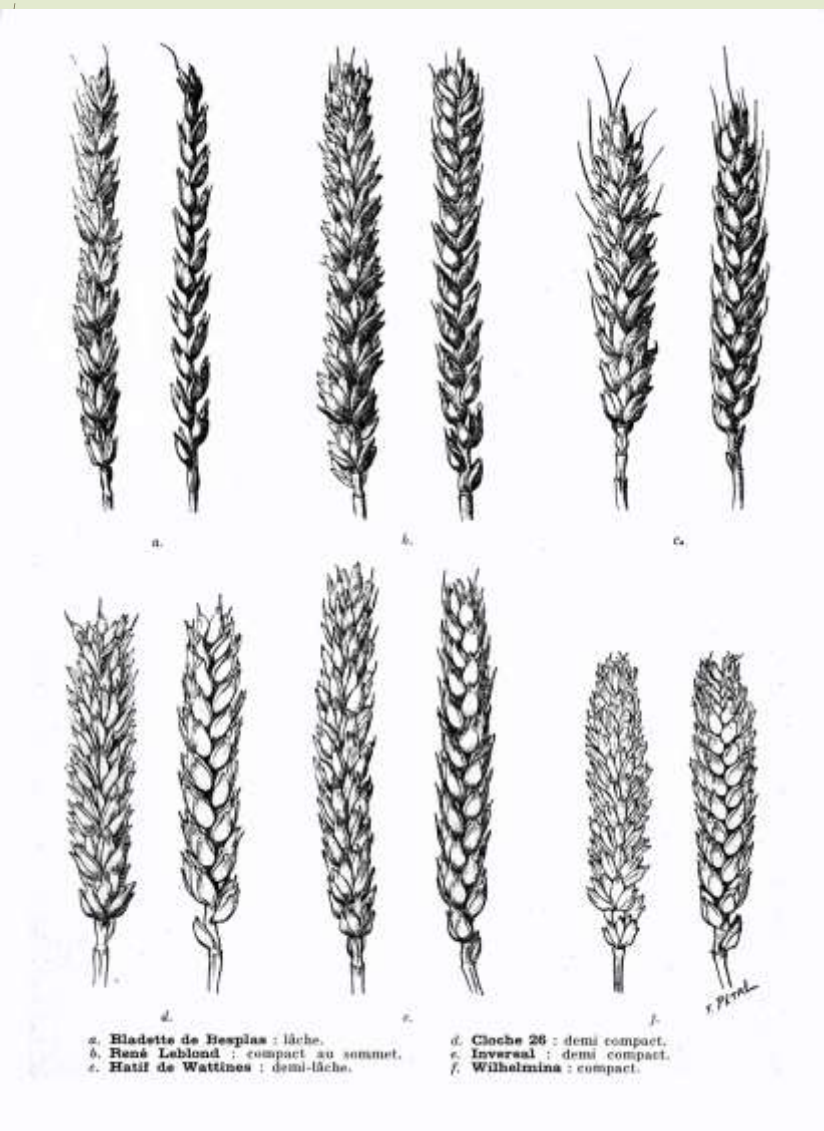




WHEAT

FIG. 2. The gene pools of wheat. The secondary gene pool is very large and includes all species of *Aegilops*, *Secale*, and *Haynaldia*, plus at least *Agropyron elongatum*, *A. intermedium*, and *A. trichophorum*. The tertiary gene pool includes several species of *Agropyron* and several of *Elymus*.

(Sub-) species concepts in *Triticum*



- "Morphologic" versus "genetic"
- **Morphologic:** level of detail within a species that can be recognised: subspecies, convar., (pro)var., forma, subforma, grex, "group", "race", etc … (*Triticum* genus comprising 27 species and 1031 subspecific taxa; cf. Dorofeev & Korovina 1979)
- Versus:
- **Genetic:** genome type = (sub-) species. Full name then Latin taxon name + registered name of cultivar, e.g. *Triticum aestivum* L. subsp. *aestivum* 'Florence Aurore' (genome BAD).
- ICNCP, Art. 2: "the Cultivar"
- Only works when "gross morphology" can be aligned with "genome type".

LEFT: *Triticum aestivum* spike variation (from: Jonard, *Les blés tendres cultivés en France* (1951))

Why 3(+) genera in Gene Pools 1 and 2 of wheat?

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Triticum L. (1753) vs *Aegilops* L. (1753)

- Most flora's have kept and still keep them apart
- Genetic research illustrates link (first formally united as *only* these two genera by Hackel 1887)
- Choice of unifying name (e.g. as "*Triticum* sensu lato") appears arbitrary from a nomenclatural point of view, and has never been proposed formally
- **Unification** would bring all three constituent genomes into one genus, but that is an argument based on genetics rather than taxonomy – would then include the hybrid genus × *Aegilotriticum* (but *Amblyopyrum* can then still be left out)
- "Taxa that are believed to be of hybrid origin need not be designated as nothotaxa." (Art. H.3 *Note 1.* of the *International Code of Nomenclature*)

Amblyopyrum Eig (1929) vs *Aegilops* L. (1753)

- Since 1851 in a separate subgenus or section within *Aegilops*
- Genome type "T" of *Amblyopyrum* not found in any other *Aegilops* species
- Better circumscription of both genera

Key to the genera of GP 1 and 2

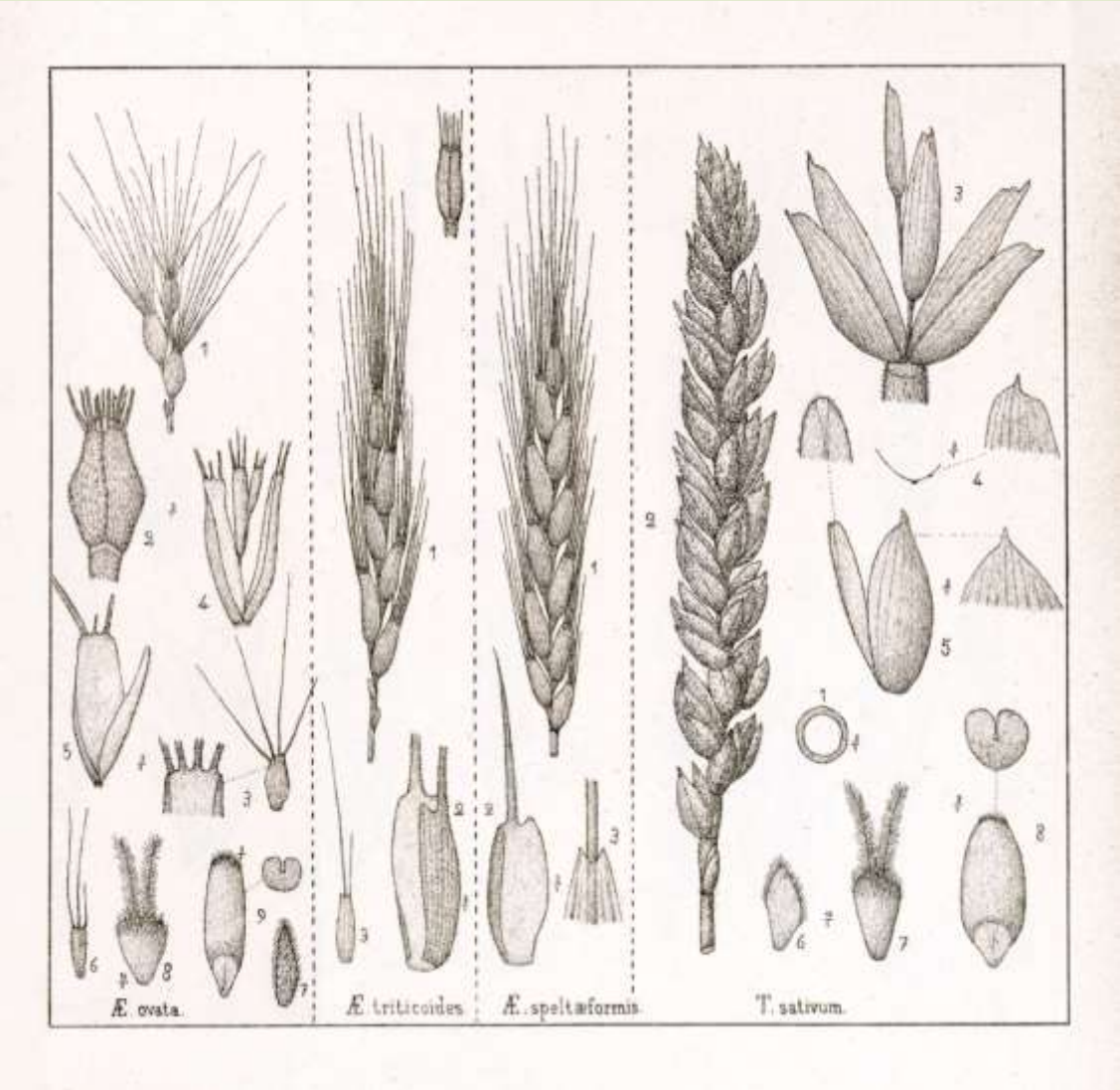
1 Distinct keel present on all glumes of lateral spikelets, ending in a broad to sharp, triangular tooth or short awn: inner side of glumes with a sharp angle at the location of the keel ..... ……***Triticum*** (wild and cultivated taxa), **x *Aegilotriticum***

1 Glumes rounded on the back or at most with a thickened dorso-ventral rim only at the location of the keel: inner side of glumes always smooth and rounded 2

2 Spikelets awnless, narrowly cylindrical; spikes (15-)20-35(-45) cm long, with (9-)12-20(-24) spikelets; glumes without teeth or awns, widest at the apex and with nerves diverging; outer surface of glumes glabrous or hispid ..... ***Amblyopyrum***

2 At least the uppermost spikelet with awned glumes and/or lemmas; spikes (narrowly) ovoid, moniliform, or (narrowly) cylindrical, 1.5-20 cm long, with 2-10(-19) spikelets; glumes with 2-5 teeth or awns, widest just above, at, or below the middle, but never at the apex, nerves converging towards the apex; outer surface of glumes glabrous, scabrous, or velutinous, but never hispid ..... ***Aegilops***

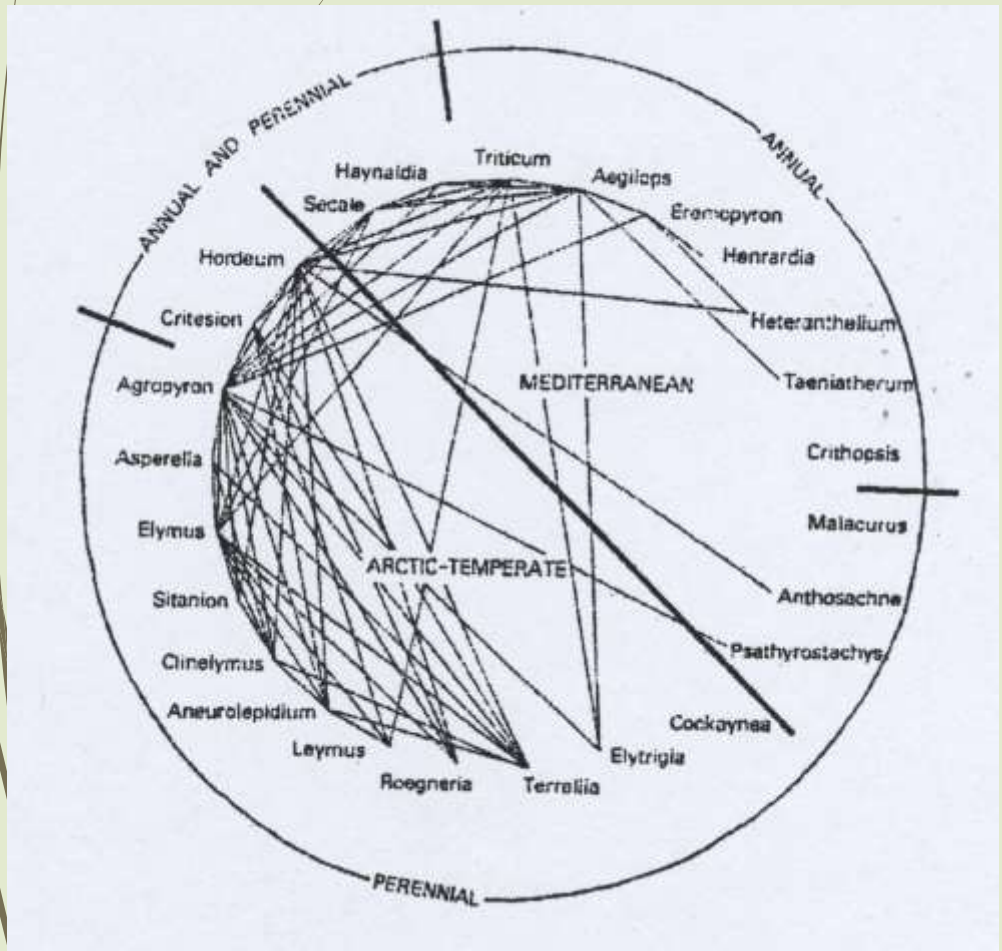
The hybrid “genus” x *Aegilotriticum* P.Fourn.



- Definition revised from MvS 1994 to include only *natural Aegilops* L. × *Triticum* L. hybrids. Examples:
- x *Aegilotriticum requienii (as: Æ. triticoides)* – the spontaneous hybrid of *Ae. geniculata* (♀) (as *Æ. ovata*) x *T. aestivum* subsp. *aestivum* (♂) (as: *T. sativum*)
- x *Aegilotriticum speltiforme (as: Æ. speltaeformis)* – the spontaneous backcross with the wheat parent, looking more like “*spelta*”
- “*Aegilops* turning into wheat” (Jordan 1856)

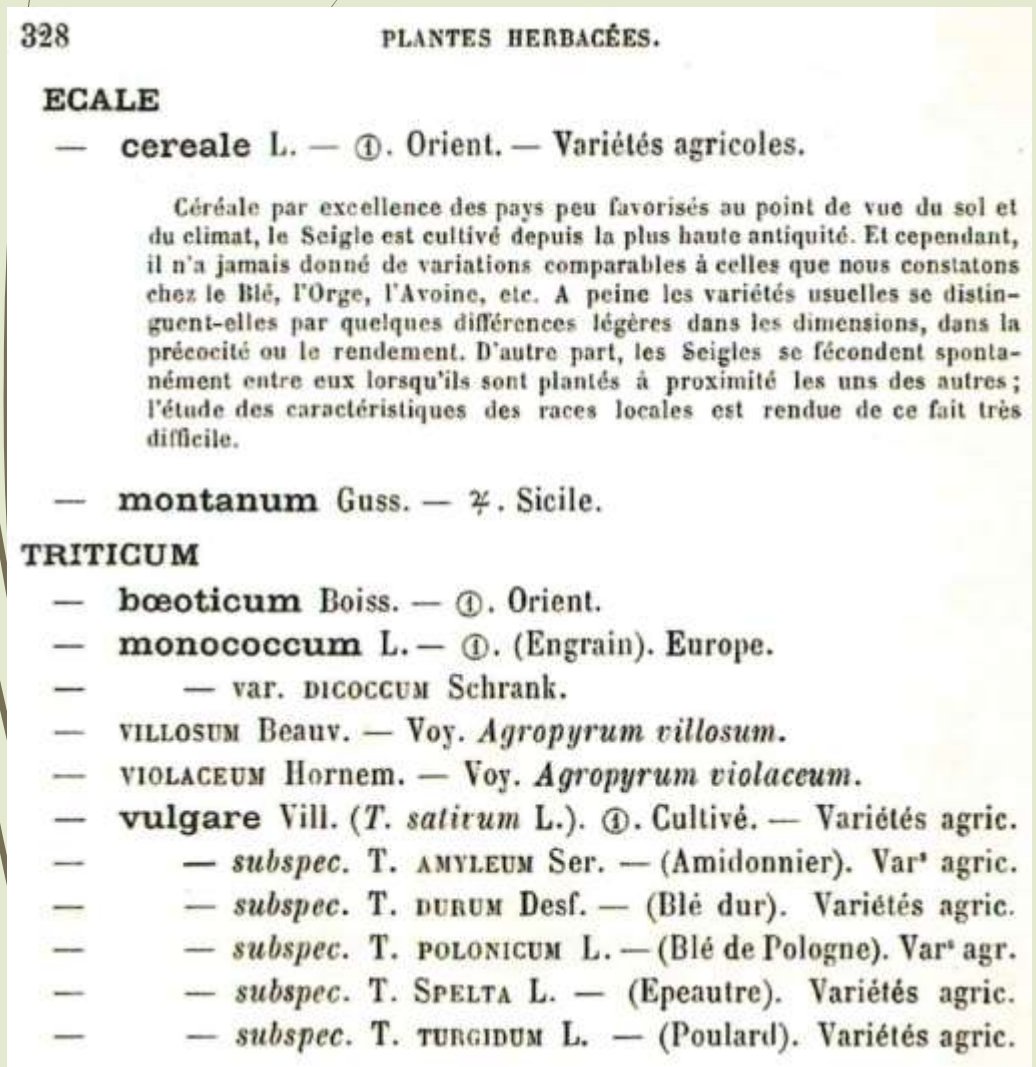
Left: from PT Husnot, *Graminées* (1899)

Relationships of *Triticum* in the subtribe Triticinae



- Genus of annuals
- Able to hybridise with many other genera in the subtribe, such as *Aegilops*, *Secale, Elymus* (incl. *Elytrigia*), *Thinopyrum*, *Hordeum* and *Leymus*
- Crossability and fertility in F1 thus a “dangerous” character
- Hybrid genera created to formalise stable “products”, whether spontaneous or created
- Consequences for generic concept: all united vs all split along “genome types”
- Evolutionary young group

The “genetic concept” is older than you think



328 PLANTES HERBACÉES.

ECALE

— **cereale** L. — ①. Orient. — Variétés agricoles.

Céréale par excellence des pays peu favorisés au point de vue du sol et du climat, le Seigle est cultivé depuis la plus haute antiquité. Et cependant, il n'a jamais donné de variations comparables à celles que nous constatons chez le Blé, l'Orge, l'Avoine, etc. A peine les variétés usuelles se distinguent-elles par quelques différences légères dans les dimensions, dans la précocité ou le rendement. D'autre part, les Seigles se fécondent spontanément entre eux lorsqu'ils sont plantés à proximité les uns des autres; l'étude des caractéristiques des races locales est rendue de ce fait très difficile.

— **montanum** Guss. — ♃. Sicile.

TRITICUM

— **bœoticum** Boiss. — ①. Orient.
— **monococcum** L. — ①. (Engrain). Europe.
— — var. DICOCCUM Schrank.
— VILLOSUM Beauv. — Voy. *Agropyrum villosum*.
— VIOLACEUM Hornem. — Voy. *Agropyrum violaceum*.
— **vulgare** Vill. (*T. satirum* L.). ①. Cultivé. — Variétés agric.
— — *subspec.* T. AMYLEUM Ser. — (Amidonnier). Var^{s} agric.
— — *subspec.* T. DURUM Desf. — (Blé dur). Variétés agric.
— — *subspec.* T. POLONICUM L. — (Blé de Pologne). Var^{s} agr.
— — *subspec.* T. SPELTA L. — (Epeautre). Variétés agric.
— — *subspec.* T. TURGIDUM L. — (Poulard). Variétés agric.

- In recent times promoted by James Mac Key in many publications between 1954 and 2005
- Taxon name as promoted by the *International Code for the Classification of Cultivated Plants* (ICNCP):
- Latin botanical name + 'culivar name'
- De Vilmorin’s (1905) *Hortus Vilmorinianus* precedes
- Set against the **morphological-concept** overviews of, e.g. Alefeld (1866), Körnicke (1885), Flaksberger (1915, 1935), Percival (1921), Dorofeev & Korovina (1979) – the latter ones based on evolutionary concepts

A tale of two *Codes* – *ICN* (2018 ed.) vs *ICNCP* (2009 ed.)

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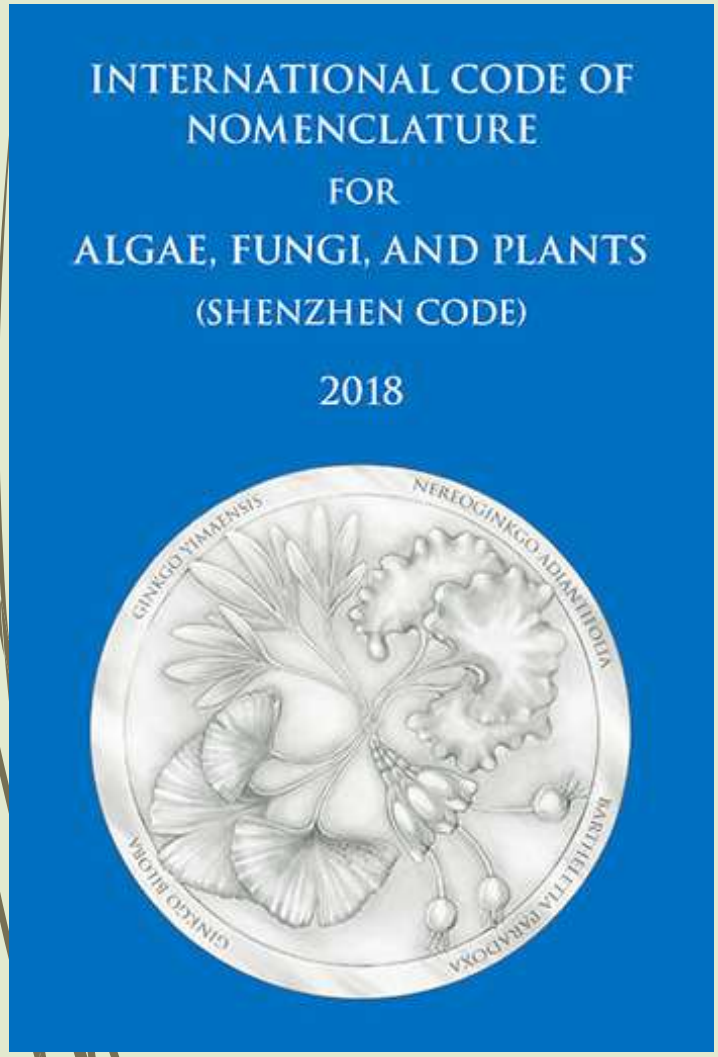

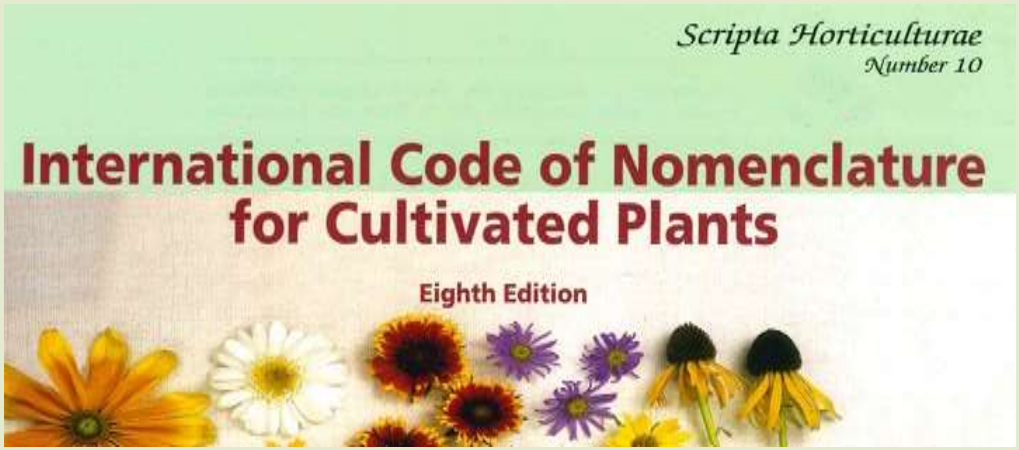

A proposed classification of *Triticum* based on the Gene Pool Concept

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- Five species, based on genome type (A, BA, GA, BAD)
- Two species are *complexes* (BA- and BAD-genomic)
- Total number of accepted taxa: **22**
- No subtaxa below subspecies; notation "[Latin name] [cultivar]"
- *Aegilops, Amblyopyrum* and *Secale* are separate genera
- x *Aegilotriticum* hybrid genus accepted as separate for natural hybrids of *Aegilops* L. ♀ × *Triticum* L. ♂ or (less common) the reverse
- x *Triticosecale* [Triticale] is a hybrid genus, separate from either parent (contrary to Mac Key)

left: x *Aegilotriticum sancti-andreae* (Degen) Soó with parents *Aegilops cylindrica* Host ♀ × *Triticum aestivum* L. subsp. *aestivum* ♂

Classifications - 1

Section	Group of species	Species	2n	Genomes
		T. boeoticum Boiss.	14	A^b
	Naked	T. sinskajae A. Filat. & Kurk.	14	A^b
Dicoccoides Flaksb.		T. dicoccum (Schrank) Schübl.	28	BA^u
		T. ispahanicum Heslot	28	BA^u
		T. durum Desf.	28	BA^u
		T. polonicum L.	28	BA^u
		T. aethiopicum Jakubz.		
		T. carthlicum Nevski	28	BA^u
		T. spelta L.	42	BA^uD
		T. vavilovii (Tum.) Jakubz.		
	Naked hexaploid	T. compactum Host	42	BA^uD
		T. sphaerococcum Perciv.	42	BA^uD

Section	Group of species	Species	2n	Genomes
Compositum N.P. Gontsch.	Hulled	T. timopheevii (Zhuk.) Zhuk.	28	GA^u
		T. zhukovskyi Menabde & Ericzjan		
		T. palmovae G.Ivanov (syn. T. erebuni Gandil.)	28	DA^b (DA^u)
		T. dimococcum Schiemann & Staudt		
		T. kiharae Dorof. & Migusch.	42	GA^uD
		T. soveticum Zhebrak		
		T. borisii Zhebrak	70	BA^uDGA^u
		T. flaksbergeri Navrozb.		

Triticum classification (Goncharov 2002 with additions according to Goncharov *et al.* 2009). Names in blue: not accepted in *Triticum proper* in view of the Gene Pool concept.

Classifications – 2

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Section Monococcon Dumort.
2n = 14

ssp. aegilopoides (Link) Thell.

ssp. monococcum

var. sinskajae (Filat. & Kurk.) Mac Key, comb. nov

T. urartu Tumanian ex Gandilyan

Section Dicoccoidea Flaksb.
2n = 28

ssp. armeniacum (Jakubz.) Mac Key

var. militinae (Zhuk. & Migusch.) Zhuk. & Migusch.

ssp. dicoccoides (Körn. ex Aschers. & Graebn.) Thell.

subsp. georgicum (Dekapr. & Menabde) Mac Key

ssp. durum (Desf.) Husn.

ssp. polonicum (L.) Thell.

Section Triticum L. (Speltoidea Flaksb.)
2n = 42

T. zhukovskyi Menabde & Ericzjan
2n = 42 (GGAAAA)

T. kiharae Dorof. & Migush.
2n = 42 (GGAADD)

ssp. spelta (L.) Thell.

ssp. compactum (Host) Mac Key

ssp. aestivum ('vulgare' (Vill.) Mac Key

Section Triticosecale (Wittm. ex Camus) Mac Key, section nov.
2n = 28/42/56

T. semisecale Mac Key, spec. nov.

T. neoblaringhemii (Wittm. ex Camus) Mac Key, comb. nov.

T. rimpaui (Wittm.) Mac Key, comb. nov.

Mac Key (2005) classification. Names in blue: not accepted as not accepted in *Triticum proper* in view of the Gene Pool concept.

It has come to this…

Taxa accepted in the wheat GENUS,	**22**
1 genus, 3 sections, 18 (sub-) species	
Taxa accepted in the wheat GENEPOOL	**2,343**
Accepted taxa (the 18 (sub-) species only)	
Infraspecific taxa (estimated 2,200; 2,065 identified so far)	
Taxa of uncertain identity but clear *Triticum* (25)	
"Evolutionary" / "theoretical" taxa (8; only 4 genepool-relevant)	
Grey Zone - mutation-based taxa (24)	
Grey Zone - *Triticum* × *Triticum* hybrids (74)	
× *Aegilotriticum* [*Triticum* × *Aegilops* hybrids] (4)	
× *Triticosecale* [*Triticum* × *Secale* hybrids; triticale] (4)	
Taxa excluded from the wheat GENUS and GENEPOOL	**701**
Genera (4), subgeneric taxa (27), species and infraspecific taxa (670)	
Grand total of *Triticum* taxa	**3,066**
Grand total of *Triticum* names	**± 4,500**

Showcasing an accepted (sub-) species

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Accepted: taxa (species / subspecies) that presently are (e.g. *aestivum*, *durum* (see below for a set of Lebanese cvs.), *monococcum*, *spelta, turanicum*) or for which distinct evidence exist that they have been cultivated in the past (e.g. *polonicum*) + their direct, wild relatives. **Taxa**: 18 at (sub-) species level.

Showcasing some “exclusions”

Excluded: all taxa that taxonomically not belonging to *Triticum* as delimitated. Mostly wild but 7 artificially created. **Taxa:** 614 – **names involved:** ± 750; x *Aegilotriticum* **taxa:** 7 – **names involved:** 14; x *Triticosecale* **taxa:** 4 – **names involved:** 20

Not all are in the tribe Triticeae!

Elymus (incl. *Elytrigia*) – 232

Thinopyrum – 71

Aegilops – 74

Brachypodium – 40

Agropyron – 31

Secale – 22

[totally unclear – 19]

Eremopyrum – 18

Micropyrum – 15

Leymus (e.g. *L. secalinus*, left), *Vulpia* – 12

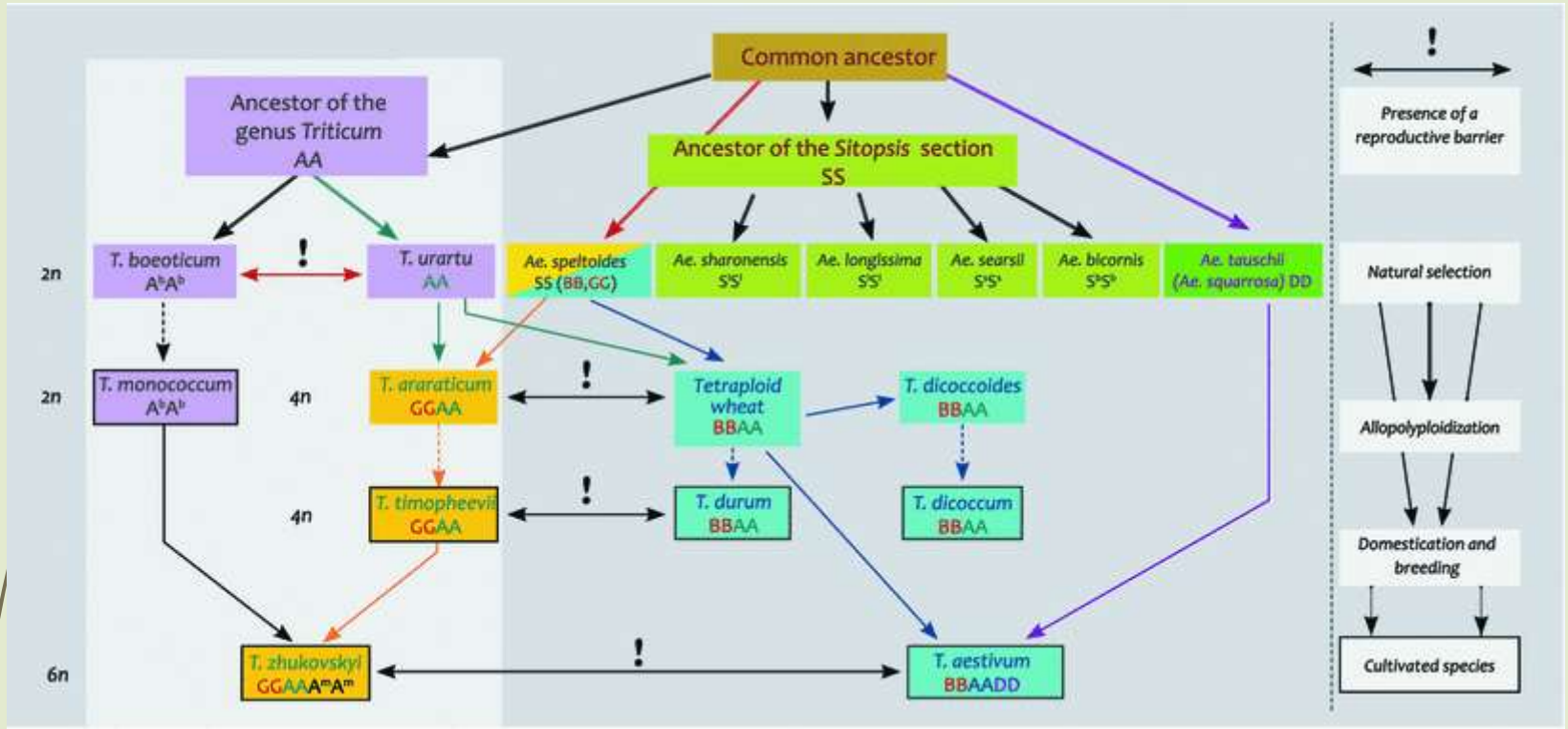
Dasypyrum – 9
Anthosachne – 6
Catapodium, hybrid genera – 5

Amblyopyrum, Hordeum – 4

Australopyrum, Desmazeria – 2

Agropyropsis, Bromus, Ctenopsis, Cutandia, Distichlis, Eleusine, Eragrostiella, Gaudinia, Halopyrum, Heteranthelium, Kengyilia, Lasiurus, Loliolum, Melampyrum (!), Narduroides, Peridictyon, Psathyrostachys, Spinifex, Stenostachys, Tribolium, Zea – 1

Phylogeny of the wheats – a first take



Goncharov (2011, Fig. 2)

Presenting the origin of cultivated bread wheat; note the pivotal S-genome of *speltoides*

Phylogeny of the wheats – a second take

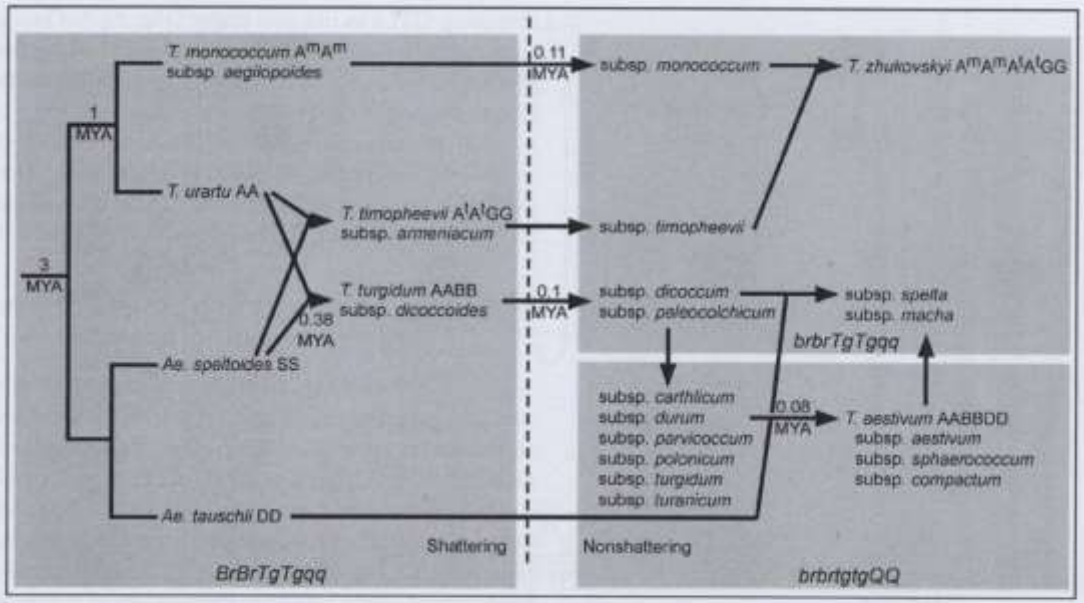


Fig. 2. Wild and domesticated diploid, tetraploid, and hexaploid wheat species, their phylogeny, timeline of evolution, and genotypic constitution with respect to domestication genes for shattering (*Br1*, *Br2* = brittle rachis; *br1*, *br2* = non-brittle rachis), tough glume (*Tg* or *Sog* = tough glume; *tg* or *sog* = soft glume), and threshing (*q* = speltoid and non-free-threshing; *Q* = square-headed and free-threshing). Modified from Li and Gill (2006).

Similarity with Mac Key (2005):

dicoccum ⟶ *spelta*

wild spp. ⟶ domestication

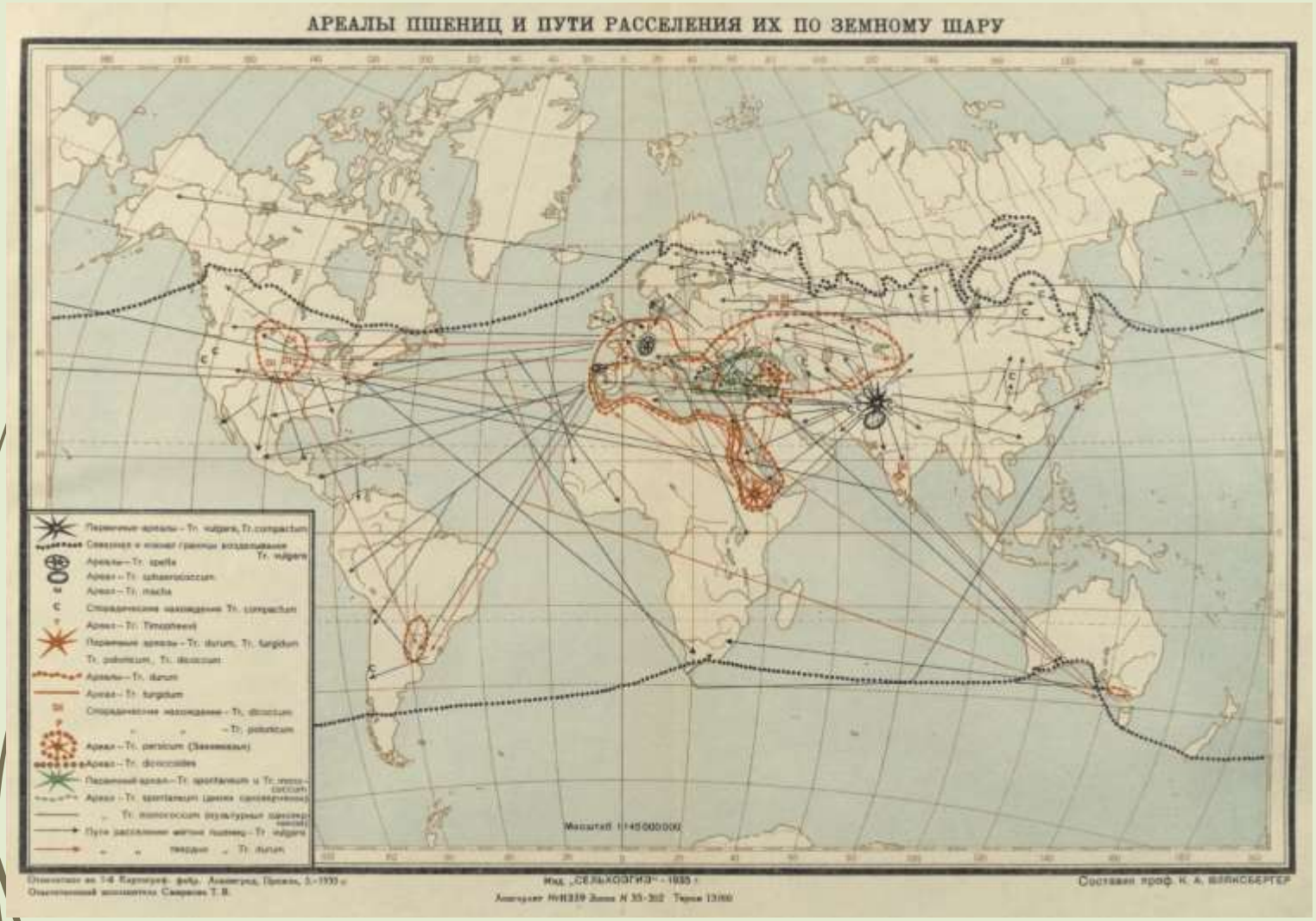
Difference with Mac Key (2005):

durum ⟶ *aestivum*

Genome notation ♂ x ♀

"Sitopsis Sect." = *Ae. speltoides*

Distribution



(From Flaksberger, *Pshnitsa* [Wheat] (1935)

Agronomy: a scene from the REAL field

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- Bread wheat: 724 million ton produced in 2016 on 221 m ha. Compare with rice: 494 million ton on 161 m ha. (FAO Food Outlook, June 2016; www.statista.com)
- Global number of “active” cultivars:

around 5000