Contents

• A little history: 1753 – 2019
• A short outline of a taxonomic monograph
• The concept of a Genus and of an Accepted Taxon
• *Triticum, Aegilops, Amblyopyrum, x Aegilotriticum*
• A tale of 2 Codes – “Botanical” vs “Cultivated”
• Some earlier classifications
• Winners and losers in the re-order
• Where have the perennial *Triticum* taxa gone to?
• Phylogenies and Distribution
• Agronomy: a scene from the *real* field
A little history... The “original 7”
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 meilleurs Blés (1906)
A little more history - a few more 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


- 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

**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
(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”.

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

_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: Å. triticoides) – the spontaneous hybrid of Ae. geniculata (♀) (as Å. ovata) × T. aestivum subsp. aestivum (♂) (as: T. sativum)
  - x Aegilotriticum speltiforme (as: Å. 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

• 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 Vilmorianus* precedes

  • Set against the *morphological-concept* overviews of, e.g. Alefeld (1866), Körnicke (1885), Flaksberger (1915, 1935), Percival (1921), Dorofeeiv & Korovina (1979) – the latter ones based on evolutionary concepts
A proposed classification of *Triticum* based on the Gene Pool Concept

- 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* ♂
<table>
<thead>
<tr>
<th>Section</th>
<th>Group of species</th>
<th>Species</th>
<th>2n</th>
<th>Genomes</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>T. boeoticum Boiss.</td>
<td>14</td>
<td>A&lt;sup&gt;b&lt;/sup&gt;</td>
</tr>
<tr>
<td></td>
<td></td>
<td>T. sinskajae A. Filat. &amp; Kurk.</td>
<td>14</td>
<td>A&lt;sup&gt;b&lt;/sup&gt;</td>
</tr>
<tr>
<td>Naked</td>
<td></td>
<td>T. dicoccum (Schrank) Schübl.</td>
<td>28</td>
<td>BA&lt;sup&gt;u&lt;/sup&gt;</td>
</tr>
<tr>
<td></td>
<td></td>
<td>T. ispahanicum Heslot</td>
<td>28</td>
<td>BA&lt;sup&gt;u&lt;/sup&gt;</td>
</tr>
<tr>
<td></td>
<td></td>
<td>T. durum Desf.</td>
<td>28</td>
<td>BA&lt;sup&gt;u&lt;/sup&gt;</td>
</tr>
<tr>
<td></td>
<td></td>
<td>T. polonicum L.</td>
<td>28</td>
<td>BA&lt;sup&gt;u&lt;/sup&gt;</td>
</tr>
<tr>
<td></td>
<td></td>
<td>T. aethiopicum Jakubz.</td>
<td>28</td>
<td>BA&lt;sup&gt;u&lt;/sup&gt;</td>
</tr>
<tr>
<td></td>
<td></td>
<td>T. carthlicum Nevski</td>
<td>28</td>
<td>BA&lt;sup&gt;u&lt;/sup&gt;</td>
</tr>
<tr>
<td></td>
<td></td>
<td>T. spelta L.</td>
<td>42</td>
<td>BA&lt;sup&gt;u&lt;/sup&gt;D</td>
</tr>
<tr>
<td></td>
<td></td>
<td>T. vavilovii (Tum.) Jakubz.</td>
<td>42</td>
<td>BA&lt;sup&gt;u&lt;/sup&gt;D</td>
</tr>
<tr>
<td></td>
<td></td>
<td>T. compactum Host</td>
<td>42</td>
<td>BA&lt;sup&gt;u&lt;/sup&gt;D</td>
</tr>
<tr>
<td></td>
<td></td>
<td>T. sphaerococcum Perciv.</td>
<td>42</td>
<td>BA&lt;sup&gt;u&lt;/sup&gt;D</td>
</tr>
<tr>
<td></td>
<td></td>
<td>T. timopheevii (Zhuk.) Zhuk.</td>
<td>28</td>
<td>GA&lt;sup&gt;u&lt;/sup&gt;</td>
</tr>
<tr>
<td></td>
<td></td>
<td>T. zhukovskyi Menabde &amp; Ericzjan</td>
<td>28</td>
<td>GA&lt;sup&gt;u&lt;/sup&gt;</td>
</tr>
<tr>
<td></td>
<td></td>
<td>T. palmovae G.Ivanov (syn. T. erebuni Gandil.)</td>
<td>28</td>
<td>DA&lt;sup&gt;b&lt;/sup&gt; (DA&lt;sup&gt;u&lt;/sup&gt;)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>T. dimoccocum Schiemann &amp; Staudt</td>
<td>42</td>
<td>GA&lt;sup&gt;u&lt;/sup&gt;D</td>
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<td>T. soveticum Zhebrak</td>
<td>56</td>
<td>BA&lt;sup&gt;u&lt;/sup&gt;GA&lt;sup&gt;u&lt;/sup&gt;</td>
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<tr>
<td></td>
<td></td>
<td>T. borisii Zhebrak</td>
<td>70</td>
<td>BA&lt;sup&gt;u&lt;/sup&gt;DGA&lt;sup&gt;u&lt;/sup&gt;</td>
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<tr>
<td></td>
<td></td>
<td>T. flaksbergeri Navrozb.</td>
<td>56</td>
<td>BA&lt;sup&gt;u&lt;/sup&gt;</td>
</tr>
</tbody>
</table>

_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.
It has come to this...

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

**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 Aegilotropicum 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

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

*Dasypyrum* – 9

*Anthosachne* – 6

*Catapodium*, hybrid genera – 5

*Amblyopyrum*, *Hordeum* – 4

*Australopyrum*, *Desmazeria* – 2

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

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

- 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