Review Article

Taxonomy and phylogeny in Triticeae: a historical review and current status

Abstract

The Triticeae is an economically important tribe within the Poaceae. Because a number of cereal crops and forage grasses belong to the tribe it has attracted much scientific attention covering many species: taxonomy, phylogeny, genetics, cytogenetic, genome analyses (crossing ability and chromosome pairing), isoenzymes, molecular biology (RFLP, RAPD, PCR sequencing) and breeding. This paper contains a brief historical outline of the taxonomy of the tribe. Phylogenetic hypotheses regarding this tribe inferred from different methods, techniques and approaches, are reviewed. The different phylogenies are discussed and compared and conflicts are elucidated.

Keywords: triticeae, phylogeny, taxonomy, poaceae, perennial species, durum wheat, phylogenies, genetic diversity, cytogenetics, molecular biology, chromosomes, perennial, caespitose, thizomatous species

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Introduction

The tribe *Triticeae* Dum is economically the most important tribe in the grass family (Poaceae). It encompasses between 350 and 500 annual or perennial species,[1–3] including the important cereal crops wheat (*Triticum aestivium* L.), durum wheat (*T. turgidum sup. durum* (Desf. MacKay) barley (*Hordeum vulgare* L.), rye (*Secale cereal* L.) and triticale (*Triticosecale* Wittm). In addition, this diverse group of grasses also includes some often overlooked, but agronomically important perennial forage grasses, mainly species of *Agropyron* Gaertn., *Thinopyron* A. Löve, *Elymus* L., *Psedoroegneria* (Nevski) A. Löve, *Pascopyron* A. Löve, *Leymus* Hochst. and *Psathyrostachs Nevski*.[4] Naturally, this tribe has received much attention because of the economical importance of some members, but it is also an excellent model group for research in genetics, genetic diversity, cytogenetics, molecular biology, taxonomy, phylogeny and speciation.

The *Triticeae* have been placed together with *Brachypodieae* (Hack.) Hayek and *Bromeae* Dum, in the monophyletic subgroup *Triticeae* Macfarlane and Watson of the *Pooideae* A. Brown[5,6] characterized by having endosperm with simple and rounded starch grains (type 1 of Tateoka[7]). In addition the Iodicules are nearly always hairy and the hilum is linear and as long as the grain. By using the rest of the Pooideae as an out group, the three tribe's can each is characterized by the following autopomorphies: distinct apical appendages on the ovary (the *Bromeae*), small chromosomes and racemose inflorescences (the *Brachypodieae*) and spicate inflorescences (the *Triticeae*). This grouping based on morphology is party in accordance with classification based on molecular techniques.[8,9] Clayton et al.,[10] included *Brachypodium P*. Beauv. In the *Triticeae* as an aberrant member. Some studies, morphological[11] and molecular[12] have *Brachypodium* as sister group to a clade including the *Triticeae* and *Bromus* L. However, new molecular studies[9] and new morphological studies[13] indicate that *Brachpodium* is not closely related to the *Triticeae* at all, but that *Bromus* is the sister group to the monophyletic *Triticeae*. Chloroplast DNA restriction site studies by Soreng et al.,[14] did not contradict the monophyletic nature of *Triticeae*. It was also revealed that *Bromus* is more closely related to the *Triticeae* than to *Brachypodium*, thus contradicting *Clayton et al.*[10] as cited above. We can therefore conclude that the most appropriate outgroup for the tribe will be *Bromus*.

Definition

The *Triticeae* encompasses annual and perennial, caespitose or thizomatous species. The culms are slender to robust and most often erect. The leaves have linear leaf blades, are usually articulate at the orifice and have open or rarely more or less closed sheaths; the ligules are membranaceous and usually truncate. The inflorescences are usually spicate with, at maturity, a tough or fragile rachis and are erect or nodding. The spikelets are alternate in two opposite rows, single or in groups 9 2–3 (rarely more). The spikelets are sessile or sub sessile, all alike (very rarely lacking), with the broad side to the rachis and with 1–12 perfect florets; incomplete or sterile spikelets may occur together with female fertile ones. The rachises are prolonged and usually articulate beneath each flower. The glumes are persistent (or rarely lacking), awned, muticous or awnless, coriaceous to membranaceous and conspicuously 1–9 veined. The lemmas are herbaceous to coriaceous, with 3–100 veins and, when present, with terminal straight or recurved awns.

The paleas are well developed and 2–keeled. The two lodicules are hairy and membranaceous. The ovaries are hairy, without any appendages and the caryopses are hairy at the apex, free or adherent to the lemma and palea and have a longitudinal groove and linear hilum. The embryos are rather small and the endosperm has simple starch grains. The chromosomes are large, the basic number is 7 and diploids (2n–2x=14) to dodecaploids (2n–12x=94) occur. The polyploids are predominantly of alloploid origin, but autoploidy occurs. Photosynthesis is C3. The type genus is Triticum L.

Classification concepts

The classificatory methods and concepts have changed with time. Artificial classifications prevailing in the pre–Darwinian period grouped organisms on the basis of few, easily identifiable character such as we see today in modern wildflower books. This system has very little to do with phylogeny. Evolution is composed of cladogenesis, the process which splits one existing species into two and anagenesis, where a species differentiates through character changes. Today most scientists agree that classification should reflect the evolutionary history. However, classificatory methodology does not take both processes into account and this has always divided the taxonomists, especially the ones dealing with difficult groups such as the *Triticeae*. Since the turning point of neodarwinism in the 1940s, controversies between three schools have existed, viz. the eclectic, the strict phonetic and the phylogenetic (cladistics), respectively. A phonetic classification, which here also includes artificial classification, reflects observable similarities and differences and the higher taxa emerge as Operational Taxonomic Units with greatest possible overall similarity. A phylogenetic classification should reflect the evolutionary history and accepts only monophyletic groups and the clades are identified by synapmorphies. It assumes that evolution is divergent.

However, more than 46% of the species in the *Triticeae* are polyploids[15] and most of them are of hybrid origin (hybridization followed by polyploidy). This implies difficulties for a direct cladistics analysis of the tribe and complicates the phylogenetic reconstruction. The conflict between strict monophyletic classification and the Linnaean hierarchal model leaves the question open whether mono–and paraphyletic groups should be accepted. It has been documented[16–18] that a cladistics analysis is only appropriate for mono genomic groups, i.e. taxa which have only one genome. Only mono genomic groups are accepted as terminal taxa, but the hetero genomic groups, i.e. taxa that have a combination of two or more genomes, can be superimposed and added to the phylogeny shown as reticulations.[19] The implication of genome analyses in evolutionary hypotheses has been criticized as these have been demonstrated to be inconsistent with phylogenetic reconstruction.[20,21] The eclectic (evolutionary, traditional) classification defines and classifies on the basis of phenotype, but also includes that are not defined phylogenetic aspects.

Taxonomic classification of the tribe – A historical review

Within the *Triticeae* classification, especially at the generic level, is complicated by the large variability, the frequent lack of synapomorphies and the numerous supposed alloploids and thus be reticulate evolution. Different concepts, strict phonetic to genomic classification, have been applied and have lately caused considerable debate and conflicting treatments. The extreme points are Krause[22] Stebbins[23] and Stebbins et al.,[24] on the one hand who proposed that all species should be united in a single genus and Löve[2,25] who on the other advocated genomical defined genera and thus split the tribe up into 37 genera. Recently most treatments recognize a number of genera between 1 and 37, but still genera are predminantly defined genomically, i.e. mono genomic taxa having one genome and hetero genomic taxa having combinations of two or more genomes.[19,25]

The history of the tribe Titiceae started with Linnaeus[26] who included 5 genera that still remain the tribe plus Lolium L. and Nardus L.; one species (Agropyron critstum (L.) Gaertner was placed in *Bromus*. The artificial classifications by Beauvois[27]) were also solely based on a few inflorescence characters. Bentham[28] recognized the tribe as Hordeae Spen. Defined by simple spikes and included 12 genera. Six of these have later been excluded from the tribe. Bentham's classification was similar to that of Hackel Hochst[29] Both were based on a broad generic concept and both used a wide range of morphological characters. During the Phenetic period from 1933 and up to now. 24 new generic names have been proposed. However, many of these names have proved to be superfluous and have been reduced to synonyms.

Nevski[30,31] was the first who adopted a phylogenetic approach and his taxonomy differed from Bentham's more traditional phonetic concept. Nevski's generic circumscriptions were rather narrow and he recognized 25 genera of which 5 were new. The tribe (called Hordeae Benth.) was subdivided into seven sub tribes (including the Brachypodiinae Holmb). Nevski came up with some evolutionary theories for the tribe in which a change from grouped to solitary spikelets and tough to brittle rachis, respectively, entered parallelly several times in the different evolutionary groups. Three major evolutionary groups were observed among the sub tribes. The first included the subtribes Elyminae Nevski and Agropyrinae Nevski, with Leymus and Aneurolepidium Nevski derived from a common ancestor and the former genus was regarded as an evolutionary line leading to Elytrigia Desv. and Agropyron. The evolution of this group should have taken place in the eastern Mediterranean region. The second group included the sub tribes Clinelyminae Nevski and Roegneria Nevski, with Terellia Lunn, as the most primitive one leading to Elymus, Hystrix and Roegneria C. Koch. He suggested that this group evolved in the Pacific Floristic center with connections to Asia and South America. The third group, the sub tribes Hordeinae Nevski and Aegilopinae Nevski had Hordeum as the primitive member and included Heteranthelium, Hordelymus (Jessen) Hartz and Psathyrostachys. The evolution of this diverse group should have occurred in central and western parts of the Mediterranean. Nevski[30,31] based his taxonomy not only on morphology, but also on anatomical, geographical and cytological data. In the beginning of the thirties the latter was in its initial phase of development. Presently, few taxonomists accept his phylogenetic theories, mainly because he was not aware of the role of polyploidy in the evolution of the tribe. Some general of his system have been rejected, but Nevski's influence on later classifications[32,33] cannot be underestimated.

Bentham's[28] morphological approach had an influence on[34] treatment of North American *Triticeae* and also partly on Melderis[35] in his work with European species. Compared to Bentham, Hitchcock[34] only included two additional genera, viz. Aegilops and Sitanion Raf. in the tribe. Melderis[32] recognized 21 general, mainly based on morphology, but he included anatomical and cytological information and thus, some of Nevski's[30,31] generic concepts. The biosystem work of Stebbins[24] resulted in a classification where all species were lumped into one large genus. The large variability and very often the lack of crossing barriers make this a defendable suggestion, but because of the importance of some of the genera, not practical. His school argued that Bentham's artificial classification just as well could be used, because the weak crossing barriers between many species will make it impossible to construct a generally recognized phylogenetic classification of the Triticaeae. Runemark et al.,[36] advocated a broad concept and combined data from morphology, mainly based on spikelet characters (number of spikelets per node, number of florets), anatomy and cytology, basically the same criteria as the ones later used by Sakamoto.[37] The recognition of genera was nearly identical between authors. Runmark et al.,[36] classified the tribe into 6 morphologically distinct groups viz. the Hordeum, Henrardia, Elymus, Triticum, Secale and Heteranthelium groups, but within and among the groups no phylogenetic hypothesis was proposed.

Baum[38] proposed a classification based on various phenetic techniques. This classification suffers from several flaws. Some of

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Baum's taxa were allowed to overlap and some species were allowed to belong to more than one genus "depending on the purpose of the user". The phenetic, numerical approach was retained by Macfarlane & Watson[5] in the classification of the subfamily Pooideae, which they divide into five and three tribes, respectively. This study was based on 90 morphological characters. The numerical analysis of the Poaceae by Watson et al.,[39] included 298 mainly morphological, anatomical, physiological and cytological characters. The eclectic study by Clayton et al.,[10] was based on a very broad concept. It mainly included morphological and anatomical features. These were also used by Watson et al.,[6] who expanded the number of characters to cover all aspects of variation. They regarded cladistics computer techniques as inappropriate to be used at the super species level and advocated prior recognition of phenetic groups before cladistics inferences. Macfarlane et al.,[5] Watson et al.[39] and Watson et al.,[6] all used overall similarity as an indication of phylogenetic relationship; however, by this procedure both mono– and paraphyletic groups may appear.

During the last few decades the classification of the *Triticeae* has been based primarily on genome analyses. This method was founded Kihara.[40] After accumulation of cytogenetic information Löve[25] and Dewey[1] proposed a classification of the whole tribe and the North American perennial species, respectively, solely based on genomic relationship. The basic concept is that species with the same genome, or the same combination of genomes, are united in a single genus. This naturally creates monophyletic and/or non–monophyletic groups.

Genome analysis is founded on the assumption that like (homologous) chromosomes pair completely; similar, but not identical (homologous) chromosomes pair to a certain degree and unlike (non–homologous) chromosomes do not pair at all during meiosis. The chromosome–pairing level (chiasma frequency) in an inter specific or intergeneric hybrid meiotic metaphase I (MI) indicates the degree of relationship between the species. The genomic system of classification immediately gained worldwide attention and considerable research in this discipline has been carried out in the Triticaeae resulting in a number of phylogenetic hypotheses.[41–43] However, apart from the practical difficulties, criticism of the implication of genome analysis for elucidating evolutionary relationship (phylogenetic reconstruction) has appeared recently mainly from advocates of the cladistic school. The theoretical, methodological and biological criticism can be summarized as follows:

i. A phylogenetic analysis is only appropriate for mono genomic groups;
ii. Pairing is a plesiomorphic character state;
iii. The definition of homology I morphology and molecular biology is clear, but in genome analyses homology becomes purely operational;
iv. Chromosome pairing is distance data, not discrete character data (except when full or no pairing occur) and thus not transformable to character data;
v. A division to arbitrary categories based on the degree of pairing (chiasma frequency level) is subjective;
vi. The questions of auto–/allysyndese and pairing suppressing/promoting genes are often not considered or are used at random, respectively;
vii. The biological basis of using an average chiasma value for inferring relationships is dubious;
viii. Genomic genera may be a mixture of monophyletic and non–monophyletic groups;
ix. The nature of the genomes is ambiguous; and
x. The genomic genera are not practical units.

The arguments against the use of genome analyses for phylogenetic reconstruction seem reasonable. So the observed correspondence between the genomically defined genera and traditional classifications may be coincidental. The only data from genome analyses, which can be used for phylogenetic inference, are those when no pairing occurs between species (non–homology). However, genome analysis should not be neglected, as it is important and usable for plant breeding because it indicates the difficulty of transferring genetic material between species.

The first phylogenetic (cladistics) investigation of the *Triticeae* was made by Baum.[44] However, this analysis suffers from several inconsistencies. The main criticisms are that some characters are overlapping and their polarities are determined by Ad hoc criteria, the algorithms will not find the most parsimonious trees and that Psathyrostachys is used as an outgroup. The same criticisms, plus the large number of unknown character states, can be raised when Baum[44] evaluates Löve's[2,25] genomic system of classification cladistically. However, in both of Baum's studies[44] it was documented that parallelism prevails in the tribe.

A phylogenetic analysis of the mono genomic genera based on morphology was made by Kellogg.[19] The mono genomic genera were used as terminal taxa, but the hetero genomic general of Löve[25] was then added afterwards to the final tree as reticulations. However, when the data were reexamined with newer algorithms a completely unresolved consensus tree appeared.[19] Morphological data are often unstable and due to homoplasy (parallelism and convergence), inadequate for phylogenetic reconstruction in the *Triticeae*.[19] Frederiksen et al.,[16] followed the same principles as Kellogg[19] but included additional characters and further taxa. Their consensus tree is well resolved although weakly supported. Frederiksen et al.,[16] also reexamined their data and a nearly completely resolved tree appears.

Lately, modern techniques have been applied to the phylogenetic classification of the *Triticeae*, but often with deviating results and often with a limited number of taxa. Cladistic analyses have been made by McIntyre[45] based on the electrophoretic variation of isozymes and by Monte et al.[46] and Mason–Gamer et al.,[47] based on plastid restriction fragment length polymorphism (RFLP) variation. Sequence data of nuclear, ribosomal and/or chloroplast DNA based on PCR (polymerase chain reaction) are also accumulating. It has resulted in hypotheses of phenetic relationships[45] and phylogenetic relationships.[17,18,47] Petersen et al.,[48] and Mason–Gamer, et al.,[47] reanalyzed the data sets of Kellogg et al.,[17] Hsiao et al.[18] and Mason–Gamer et al.,[47] and combined the data sets. Limited congruence was found but also the bootstrap support in many of the trees was rather low. RAPD (random amplified polymorphic DNA) techniques have been applied in phylogenetic studies of the *Triticeae*.[49,50] However, the reproducibility and reliability of this technique have been questioned.

Unfortunately, a cladistics analysis of the whole tribe does not exist. A phylogenetic hypothesis based on morphology exists for the mono genomic genera and from an eclectic point of view the latest taxonomic treatment of the tribe by Watson & Dallwitz[6] seems at present appropriate. Several phylogenetic hypotheses based on molecular studies exist, but the gene trees are often in conflict with the morphology–based hypotheses and/or with each other.[19] The incongruence among gene trees is often attributed to poor support, intra specific polymorphism and inference of different histories, hybridization introgression, or methodological causes. Some of the conflicts may be solved through the total evidence approach.[51] However, the hybridogenous origin of many *Triticeae* species implies that taxonomic congruence may provide useful information. The evolutionary trees derived from different sequence studies all show more or less congruence with many recurring clades. When congruence between several hypotheses are found they deserve credence and it is likely that they represent the phylogeny quite accurately. The discrepancies of phylogenetic studies based on morphology might be faults in the outgroup comparison scoring non–homologous characters. Having the discrepancies with the hetero genomic genera and the cladistics hypothesis in mind, main efforts should be continued on the phylogeny of the mono genomic genera as suggested by Kellogg et al.[19] Hopefully, the results of morphological and molecular studies an in the future be incorporated in a comprehensive cladistics analysis.

Conclusion

The perspective of future *Triticeae* research can be found under the following headlines and future success will depend on the establishment of networks and collaboration between research groups:

i. Systematics, phytogeography and ecology;
ii. Phylogeny and evolution;
iii. Cytogenetics and wide hybridization;
iv. Genetic diversity and genetic resources; and
v. Breeding.

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Conflict of interest

The author declares no conflict of interest.

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