

Twenty-one Years Later: The Impact of Löve and Dewey's Genomic Classification Proposal

M. E. BARKWORTH¹ and R. VON BOTHMER²

¹Intermountain Herbarium, Department of Biology, Utah State University, Logan, Utah, U.S.A. 84322-5305; ²Department of Crop Science, Swedish University of Agricultural Sciences, SE-230 53 Alnarp, Sweden, e-mail: mary@biology.usu.edu

Abstract: The Fifth International Triticeae Symposium was held 21 years after Drs. ASKEL LÖVE and DOUGLAS R. DEWEY independently proposed that generic classification in the *Triticeae* be based on genomic constitution, species containing the same genomes being placed in the same genus. This was a startling proposal, particularly for taxonomists in North America where the existing treatments of the tribe still reflected the proposals made a century earlier by Bentham and Hackel. Although few taxonomists endorsed the principle of genomic circumscription, current generic treatments of the *Triticeae* have been strongly influenced by the wealth of genomic data available. The challenge that faces taxonomists is to determine which, if any, morphological characters or character sets can be used to identify the genomic composition of species in the tribe. The challenges for those engaged in molecular research include elucidating the mechanism that underlies the formation of genomes and understanding the causal relationship of genomic constitution and morphology.

Keywords: *Triticeae*; taxonomy; generic delimitation; genomic classification

In 1984, Löve and Dewey independently proposed that generic classification in the *Triticeae* should be based on genomic constitution (LÖVE 1984; DEWEY 1984), in other words, that species with the same genomic constitution be placed in the same genus. The Fifth International Triticeae Symposium was held 21 years after publication of their papers. This makes the papers "adults" according to the law in some countries. It seemed appropriate to start this symposium with a review of the impact of their recommendation on research in the tribe.

The two papers differed in their focus and taxonomic scope. Löve provided a checklist of the whole tribe that included all the names of which he was aware, together with their place of publication. As he stated in the introduction, many of Löve's decisions were based on existing treatments rather than personal knowledge of the plants involved and in some cases he inferred the genomic

constitution of a species from its customary taxonomic treatment. One may not agree with Löve's taxonomic treatment (i.e. his decisions as to which names represent good taxa and which should be synonyms), but his synopsis is a phenomenal summary of nomenclatural information for the *Triticeae* and is the obvious starting point for an electronic nomenclatural catalogue of the tribe, one of the necessities for development of information on the *Triticeae* in the Global Biodiversity Information Facility (GBIF; <http://www.gbif.org>). The frequently heard statement that the tribe includes about 350 specific or subspecific taxa is based, in large part, on Löve's treatment.

Löve also provided short descriptions of the genera and subgenera, including their chromosome number and genomic constitution. The descriptions were not intended to be comprehensive, nor to serve as the basis for writing keys. KELLOGG (1989) used

them as the starting point for a cladistic analysis of the tribe, but added information from other sources in order to develop an almost complete data matrix. A more serious problem arises from Löve's failure to cite sources for the cytological information included. Such an omission is quite common in floras and checklists. Unfortunately, in at least one case, Löve's omission conceals a lack of supporting evidence: his statement that *Leymus* has an **NsJ** genomic constitution (genomic symbols used in accordance with recommendations of the International Triticeae Consortium, see WANG *et al.* (1994); <http://herbarium.usu.edu/Triticeae/genmsymb.htm>) was based on instinct rather than cytological study (Löve, pers. comm. to DEWEY, circa 1986). His statement was accepted by several individuals, including BARKWORTH *et al.* (1983) and DEWEY (1984). Subsequent work (ZHANG & DVORAK 1991; WANG & JENSEN 1994; ANAMTHAWAT-JÓNSSON & BODVARSDÓTTIR 2001; ØRGAARD & HESLOP-HARRISON 1994a, b) provides no evidence for the presence of the **J** genome; the second genome appears to be a modification of the **Ns** genome. A well-documented online database of cytological information needs to be developed so that, in future, it will be easy to determine for which species the genomic constitution has been determined and by what means.

DEWEY (1984) in paper, *The genomic system of classification as a guide to intergeneric hybridization with the perennial Triticeae*, was restricted to the perennial genera, among which he included *Hordeum*. In it he stated that, because genomic constitution was the best guide to biological and phylogenetic relationships within the *Triticeae*, it should be used for generic delimitation. He discussed the relationships of the genera he recognized based on wide hybridizations and classical analyses of meiosis and cited the papers documenting his statements. He listed the species he knew to be included in each genus, but did not attempt to include species with which he was not familiar. He did not provide morphological descriptions for the genera, nor a complete list of synonyms.

The only difference between Dewey and Löve in their treatment of the perennial *Triticeae* was Löve's recognition of *Lophopyrum*, a genus whose members Dewey included in *Thinopyrum*. This difference reflected a difference in opinion as to whether the genome of *T. elongatum* [= *L. elongatum*] should be designated **J^E** or **E** (WANG 1985; WANG & HSIAO 1989; JAUHAR 1990; WANG *et al.* 1994).

Both Löve and Dewey stated that future work might lead to the necessity of recognizing additional genera. In 1986, Löve published two additional genera: *Trichopyrum* for species having a genomic constitution of **E^eSt** or **E^eE^eSt** and *Psammopyrum* for species with a **LE^e**, **LLE^e**, or **LLE^eE^e** constitution (using designations of Wang *et al.* (1994) that are equivalent to the **JS**, **JJS**, **GJ**, **GGJ**, and **GGJJ**, respectively, used by Löve). Dewey, although aware that *Elymus*, as he and Löve treated it, contained species with at least three different genomic constitutions, was not prepared to publish additional generic names to reflect the different genomic groups. Since he did not accept *Lophopyrum* as distinct from *Thinopyrum*, it is unlikely that he would have accepted *Trichopyrum* and *Psammopyrum*.

Although Löve and Dewey worked completely independently, Löve was well aware of Dewey's work and used it in formulating his ideas. Dewey became aware of Löve's interest after circulating the manuscript of a paper he had presented at a conference held in 1979 (see DEWEY 1982) in which he proposed a more timid version of his later classification. Löve wrote to Dewey, urging him to be more courageous and telling Dewey about his work on the *Conspectus*. Thus, although the two worked independently of each other, they were aware of each other's work when they prepared their manuscripts.

The immediate response of taxonomists to the proposal made by Löve and Dewey that generic circumscription in the *Triticeae* be based on genomic constitution was negative. To understand the response, it is useful to consider the generic treatments in use in 1984. For this purpose, we review the treatment of the tribe in the major floras that were in existence at that time.

Perceptions of the *Triticeae* in 1984

Americas: In 1984, the majority of North American floras based their treatment of the *Triticeae* (which many still called *Hordeae*) on the treatment in HITCHCOCK (1951) which was, in turn, based on BENTHAM (1882) or HACKEL (1887). In other words, *Agropyron* included annual and perennial species with a tough rachis and a single spikelet at each node, species with tough rachises and more than one spikelet at a node being placed in *Elymus*. The one departure from Bentham's treatment involved recognition of the North American genus *Sitanion*, which differs from other species of *Elymus* in hav-

ing disarticulating rachises. In 1956, STEBBINS commented that, genetically speaking, the whole tribe could be treated as a single genus. Despite this, American floras continued to adopt the traditional generic treatment of the tribe (e.g. ROSENGURTT *et al.* 1970; SCOGGAN 1978; BEETLE 1983).

Eurasia: The former Soviet Union followed TSVELEV (1976), whose treatment differed from that of BENTHAM (1882) and HACKEL (1887) in recognizing several additional genera, both annual and perennial, e.g. *Eremopyrum*, *Taeniatherum*, *Elytrigia*, and *Leymus*. *Agropyron* was restricted to *A. cristatum* and its allies (the crested wheat-grasses), the other species Bentham included in *Agropyron* being placed in *Elymus* or *Elytrigia*. The treatment in *Flora Europea* (MELDERIS 1980) was similar to that in TSVELEV (1976) except that *Elytrigia* was included in *Elymus*. Chinese taxonomists (KENG 1965; GUO & WANG 1981) adhered more closely to the treatment advocated by NEVSKI (1934) than that adopted by TSVELEV (1976), placing *Agropyron* species that Tsvelev included in *Elymus* into *Roegneria*.

Where the authors of all the treatments cited did not differ was in basing their generic circumscription primarily on morphological similarity and the relative frequency with which hybrids were formed. Cytological data were considered but not given priority (see, e.g. NEVSKI 1934; MELDERIS 1953, 1978), let alone used to define genera as Löve and Dewey advocated.

It is worth noting that Dewey and Löve were working in the region where the generic treatment had changed least in the century following publication of the global synopses by Bentham and Hackel. In 1978, Dewey circulated a preliminary draft of his generic concepts to several taxonomists in North America (including Barkworth); with few exceptions the response was negative (Dewey, pers. comm. to Barkworth, 1979). The most frequent comment was that the new generic concepts would be difficult to apply in the field. Other comments were that treatments used in other regions of the world were not necessarily better than those in use in North America and that the change would be difficult for people to learn. Taxonomists can be very conservative when it comes to names. Löve's response was one of very few that was positive. It was against this background that the two prepared their papers advocating that genomic constitution should be used to determine generic limits in the *Triticeae*.

Immediate Response

The immediate response of most systematists was negative. Almost all objected to the concept of basing generic delimitation on what was seen as a single character, pairing behavior of chromosomes. This objection reflects a long history of discovering that new characters or approaches, despite their initial promise, have never lived up to their early promise for solving taxonomic problems; exceptions to a generalization are soon discovered. Why should looking at meiotic pairing be different? Löve and Dewey argued that pairing behavior reflected the genetic similarity along the chromosomes and was, therefore, a summary of multiple characters. They knew that, in some instances, pairing is overridden by genes that control pairing but considered such instances exceptional, at least in the *Triticeae*.

Another objection was that, if adopted, the generic affiliation, and hence the name of a species, could not be determined until its genomic constitution had been determined. LÖVE (1984) made it clear that he considered that morphological similarity was usually a reliable indicator of genomic constitution, relying on it to place the many species of which he had no personal knowledge. Indeed, in 1986 he stated (LÖVE 1986, p. 44), "Therefore, the methods of genome analysis based on studies of meiosis in hybrids may be augmented or even replaced by several other more or less subjective procedures. Utilizing either or both herbarium or live material, comparison of descriptions and specimens are sometimes enhanced by a variation of methods ...". Dewey would point out to those who asked the morphological similarity among the taxa that had similar genome constitutions. Both were aware of examples where the correlation between morphology and genomic constitution breaks down. For instance, *Hystrix* is a genus that is distinguished by its lack of glumes. Its type species, *Elymus hystrix*, is an **StH** species (CHURCH 1967) but other species examined appear to be autopolyploids based on the **Ns** genome and either a modification of that genome or a different genome (JENSEN & WANG 1997; ZHANG *et al.* 2002). According to genomic classification, such species belong in *Leymus*. When confronted with such discrepancies between the genomic and morphological data, both Löve and Dewey placed the species concerned on the basis of their genomic constitution. Even if genomic data were only available for one of a recognized group of species, as

was the case with *Hystrix* in 1984, they treated all species of the group in the same way.

Dewey was not always consistent. He knew in 1984 that *Elymus* as he treated it included species with at least three different genomic constitutions, but he considered it premature to name additional genera. Recently, YEN *et al.* (2005) published one of the additional names needed to accommodate the known variation and indicated their intention of publishing another. These names, combined with *Roegneria* (**StY**), *Kengyia* (**StYP**), *Austrolapypum* (**W**), and *Stenostachys* (**HW**), will permit recognition at the generic level of all varied genomic groups that Löve and Dewey included in *Elymus*. What no one has provided so far are good morphological characterizations of the genomically circumscribed taxa and a reliable key to their identification.

In addition to objecting to reliance on a single character for classification, many systematists disagreed with Dewey's statement that genomic constitution was a guide to phylogenetic relationships within the tribe. The objection stems, at least in part, from failure to appreciate that Dewey and Löve used the term phylogeny in the sense that it had had in their academic youth, one that encompassed groups giving rise to groups as well as species to species. One could draw phylogenetic relationships using bubbles, not lines. In that sense, the **StH** species arose from two bubbles, one containing **St** species, the other **H** species. Dewey did not mean to imply that one could tell which **St** species was ancestral to other **St** species, nor to suggest that one could use genomic analysis to determine which **St** and which **H** species had given rise to a particular **StH**. Around 1984, however, the term "phylogeny" was morphing into its current, narrower interpretation that is reflected in the use of lines derived from cladistic analyses, preferably analyses of molecular data, to show phylogenetic relationships.

There is no question that genomic constitution is not, in itself, a guide to phylogenetic relationships in the current sense. Nevertheless, phylogenetic analyses of single genes have consistently shown that diploid species with the same genomic constitution are part of the same lineage or clade; in a few instances, trees based on chloroplast trees have differed from those based on nuclear genes (KELLOGG *et al.* 1996). Interestingly, the species in question have also been regarded as taxonomically puzzling. MASON-GAMER (2004; this volume) has also demonstrated that, at least in *Elymus* (*Elytrigia*)

repens, there may be more genomic diversity within a species than can be detected via traditional meiotic analyses.

What was the reaction of geneticists and plant breeders? In general, such individuals readily adopted Dewey's treatment of the perennials; a few followed Löve. Basing generic delimitation on genomic constitution was appealing for its logical consistency and simplicity. The fact that the new generic boundaries were based on information relevant to breeding undoubtedly added to their appeal. Although it is still not understood how genomic identity is determined, all subsequent methodologies (e.g. DNA sequencing, fluorescent *in situ* hybridization, genomic *in situ* hybridization) have supported their reality. Moreover, many geneticists and plant breeders are only minimally concerned with morphological circumscriptions and field identification of genera.

Within the annual species, Löve's splitting of *Aegilops* was generally rejected, the genus continuing to be interpreted as treated by Linnaeus. It is worth noting that the opposite recommendation, that *Triticum* and *Aegilops* be combined into a single large genus, has also failed to find acceptance despite the strong arguments for such an expansion and its support by some of the major names in taxonomy (e.g. BENTHAM 1882; HACKEL 1887; GREUTER & RECHINGER 1967) and endorsed in this symposium (DE BUSTOS and JOUVE this volume) as well as by YEN *et al.* (2005). This is a reminder that the value of names lies in large part in their stability. So far, the general conclusion seems to be that it is easier for each generation to learn that all polyploid species of *Triticum* include genomes from *Aegilops* than to start referring to the *Aegilops* as members of *Triticum*.

Later responses

To see more clearly whether taxonomic proposals are broadly accepted by taxonomists, one needs to consider floristic treatments, for it is through such treatments that most people acquire taxonomic knowledge and identify plant materials. Table 1 summarizes the treatment of the perennial *Triticeae* in various floras that have been published since 1984, either in print or on the Web. As can be seen, there is still considerable disagreement even among the genera that are widely distributed. Even greater variability would be evident if the floras of other regions (e.g. HUNZIKER & XIFREDA 1986,

Table 1. Treatment of the perennial *Triticeae* in various floras published since 1984

	Flora of New Zealand EDGAR, CONNOR (2000)	<i>Pooideae</i> (<i>Poaceae</i>) in Australia WEILLER <i>et al.</i> (1995)	Grasses of the New World SORENG <i>et al.</i> (2003)	Flora of China (Draft) CHEN & ZHU (2005)	Flora of North America (Draft) BARKWORTH <i>et al.</i> (in prep.)
<i>Agropyron</i>	NA	NA	√	√	√
<i>Australopyrum</i>	√	√	NA	NA	NA
<i>Critesion</i>	√	X	X	X	X
<i>Elymus</i>	√	√	√	√	√
<i>Elytrigia</i>	√	√	X	√	X
<i>Hordeum</i>	NA	√	√	√	√
<i>Hystrix</i>	NA	NA	X	√	X
<i>Kengyilia</i>	NA	NA	NA	√	NA
<i>Leymus</i>	√	NA	√	√	√
<i>Pascopyrum</i>	NA	NA	√	NA	√
<i>Pseudoroegneria</i>	NA	√	√	√	√
<i>Roegneria</i>	NA	NA	NA	X	NA
<i>Sitanion</i>	NA	NA	X	NA	X
<i>Stenostachys</i>	√	X	NA	NA	NA
<i>Thinopyrum</i>	√	√	√	X	√

√ – accepted in publication; NA – not applicable to the region; X – applicable but included in another genus

2000; WELSH *et al.* 2003) and the generic proposals of others (e.g. SEBERG & LINDE-LAURSEN 1996; YEN *et al.* 2005) were included.

And now?

The papers by Dewey and Löve have lead to increased agreement on generic limits within the tribe. The agreement is not complete, but the differences are smaller than they were in 1984. Before the next Symposium in 2011, the taxonomists among us need to focus on developing a species-level treatment of the tribe, because the ability to accurately identify species is critical to all other work. One approach to such a project would be to develop illustrated, multi-entry identification keys using program such as DELTA (DALLWITZ 1980; DALLWITZ *et al.* 1993, 1995, 2000) or Lucid ID (Centre for Bioinformation Technology 2004). Adopting such an approach would develop the data required to determine which, if any, characters, either singly or in combination, are reliable indicators of genomic constitution in the *Triticeae*. Even if no such characters are found, a reliable, illustrated multi-entry key for the identification of species of the *Triticeae*

would be a significant achievement in itself, one that would be welcomed by individuals in many different disciplines.

Despite rejecting the idea that genomic constitution should be used to *define* genera in the *Triticeae*, almost all papers in systematic, cytological, and plant breeding research routinely provide information about the genomic constitution of the species involved. Moreover, determination of the genomic constitution is, as Dewey claimed, an important step in evaluating the breeding potential of any species combination. There have been enormous advances in many fields of research since Dewey and Löve published their papers. A wide array of molecular techniques has permitted considerable progress to be made in understanding the genetic bases for salinity tolerance, root development, and other agronomically important traits. Molecular techniques also make it possible to determine the distribution of genes on the chromosomes in different genomes. We can hope that, eventually, this ability will also enable us to understand the causative difference between genomes and why differences in the location and sequences of homeologous gene sequences result in different

morphologies, even among species with the same genomic constitution.

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