The history of the Triticeae is replete with changes in generic concepts, caused by taxonomists' struggle with the task of representing its highly reticulate history within the hierarchical classification system demanded by scientific nomenclature. Disagreement over the criteria used for delimiting taxa is an additional complication. Linnaeus' goal was an easy identification scheme. Subsequent taxonomists sought to improve Linnaeus' scheme by making his genera more 'natural', a vague term encompassing both general similarity and relatedness. In the 1880s Bentham and Hackel published nearly identical treatments of the tribe. These became the standard for the next fifty years. In 1933 Nevski advocated an explicitly evolutionary treatment, including much narrower generic concepts. Several of Nevski's generic concepts were adopted by European taxonomists, but English speaking taxonomists continued to employ Bentham's. In the 1980s, Dewey and Löve proposed that genera in the Triticeae should be determined primarily by genomic constitution. Although not all agree with treating such groups as genera, it has been found productive to interpret data in terms of such groups. This will aid us in understanding the history of the Triticeae and evolutionary processes in general, a more important objective than complete nomenclatural agreement.

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My goals in this overview of the taxonomy of the Triticeae are to provide the basis for a better understanding of contemporary treatments of the tribe. I have taken a historical perspective because understanding where we are now is easier if one understands the past. One obvious historical component to taxonomy lies in scientific nomenclature. The International Code of Botanical Nomenclature (Greuter et al. 1988) ensures that, because Linnaeus named a genus Triticum, there will be a genus named Triticum today. Current concepts of the genus are very different from Linnaeus', but his name is still used. Possibly equally importantly, taxonomy is a discipline in which the human element plays a major role. Because there are no universally accepted criteria for determining which taxonomic treatment is best, subjective judgment plays a significant role. Such judgment is influenced by data, but also by an individual's taxonomic goals and background as well as prevailing taxonomic concepts. There is little likelihood that there will ever be a single, universally accepted, taxonomic treatment of the Triticeae because of its highly reticulate evolutionary history and its low crossing barriers. We need, therefore, to understand why taxonomists can reach different conclusions from the same data and consider ways in which those whose primary need is a stable nomenclatural system can best be satisfied.

Taxonomic philosophies

Taxonomic treatments, whether of biological organisms, physical objects, or ideas, are always about grouping. Entities are placed in groups based on certain criteria. The problem is that plant taxonomists do not agree completely as to what these criteria should be. There is enough agreement that in taxonomically easy groups, no disputes exist, but the Triticeae is not a simple taxonomic group. Much has been written on the different philosophies of biological taxonomy (see, e.g., Davis and Heywood 1973; McNeill 1979a, b; Stevens 1985; Estes and Tyrl 1987; Small 1989). For the purposes of this discussion it is useful to distinguish three approaches: artificial, "natural" (or phenetic), and phylogenetic. Few contemporary taxonomists adhere rigidly to any one position; it is almost impossible to do so in the Triticeae. The problem is that different taxonomists have adopted different intermediate
positions. Nevertheless, it is useful to clarify the extreme positions before considering the positions adopted by individual taxonomists.

Artificial classification

In artificial taxonomic treatments, the goal is simply to provide an easy and reliable means of grouping the organisms that others can use. This permits easy identification of any given organism to the group whose members are similar with respect to the characters used in grouping. There is no guarantee that these groups will be useful in any other way. The criteria for determining the "goodness" of artificial treatments is the ease with which they enable different people to assign objects to the same groups, i.e., to identify the group to which an organism should be assigned. The best example of an artificial treatment is that in *Species Plantarum* (Linnaeus 1733), of which Smith (1807, quoted in Stearn 1960) said, "Its sole aim is to help any one to learn the name and history of an unknown plant in the most easy and certain manner, by first determining its Class and Order in this system; after which its Genus is to be made out by comparing the parts of the fructification with all the generic characters of that Order;... The classes of the Linnaean System... are founded on the number, situation, or proportion of the stamens. The Orders are founded either on the number of the Pistils, or on some circumstance equally easy".

Contemporary examples of this approach to grouping are to be found in popular wildflower books in which species are grouped first by flower color, then by flower shape, and then by inflorescence. The difference between these books and *Species Plantarum* is that authors of wildflower books do not use their groups as a basis for naming the plants involved. This illustrates an important point: there is no essential link between the rules for identifying an organism and the rules for forming the groups that are used to determine that name. Or, putting it differently, the ability to write easy identification keys should not determine what taxa are recognized unless having easily identified taxa is part of one's taxonomic goal.

No contemporary taxonomist emphasizes easy identification as much as Linnaeus, but it is still a consideration for many. Estes and Tyrl (1987, p. 332–333) commented that "The users of our classifications demand, appropriately, a stable system, based on biological reality, in which taxa may be readily recognized. Thus, from our perspective,... there is one additional facet that must be incorporated into the classification as we attempt to reflect biological reality: utility. If we fail to represent biological reality or to produce recognizable entities, then we will have failed to realize the goals of taxonomy in the formulation of systems of classification". Arnow (1987, p. 692) cited the concept that "a genus is composed of taxa universally recognizable [as members of that genus] by a unique cluster of characters" in support of her decision to interpret Elymus broadly (Table 1). An informal comment that indicates a similar attitude is "A genus should be recognizable when driving by at 30 m.p.h."

| Melderis (1978, 1980) | Love (1984, 1986) | Tsvelev (1976, 1989) | Clayton & Renvoize (1986) | Baum (1979) and Baum et al. (1991) | Klo (1987) |
|----------------------|-------------------|---------------------|--------------------------|-----------------------------------|-----------|
| Elymus               | Elymus             | Elymus              | Elymus                    | Elymus                            | Elymus    |
| Anthosachne          | Anthosachne        | Anthosachne         | Anthosachne               | Pseudoroegneria                   | Pseudoroegneria |
| Elytrigia            | Hystrix            | Hystrix             | Hystrix                   | Elytrigia                         | Elytrigia |
| Lophopyrum           | Roegneria          | Australopyrum       | Lophopyrum                | Roegneria                         | Roegneria |
| Pseudoroegneria      | Sitanion           | Elytrigia           | Pseudoroegneria           | Pseudoroegneria                   | Terrellia |
| Roegneria            | Sitanion           | Pascopyrum          | Roegneria                 | Terrellia                         | Elytrigia |
| Sitanion             | Elytrigia          | Thinoopyrum         | Elytrigia                 | Thinoopyrum                       | Thinoopyrm |
| Terrellia            | Elytrigia          | Thinoopyrm          | Pascopyrum                | Pascopyrum                        | Pascopyrm |
| Pascopyrum           | Lophopyrum         | Pascopyrum          | Hystrix                   | Hystrix                           | Hystrix   |
| Thinoopyrum          | Lophopyrum         | Trichopyrum         | Sitanion                  | Sitanion                          | Thinoopyrm |
| Trichopyrum          | Pseudoroegneria    | Hystrix             | Trichopyrum               | Trichopyrum                       | Trichopyrm |
| Australopyrum        | Thinoopyrum        | Sitanion            | [Australopyrum in Agropyron]| Sitanion                          | Thinopyrm |
| Hystrix              | Trichopyrum        | Terrellia           |                          |                                  | Thinopyrm |

Table 1. Alternative treatments of *Elymus* in various contemporary publications. The authors shown recognize the genera shown in **boldface** as including the genera listed immediately below in *italics*. Taxa listed in normal typeface were not discussed by the author(s) concerned.
"Natural" or phenetic classification

Linnaeus' system met the most pressing need of his time, provision of an easy, reproducible method for identifying the large number of species being discovered as a result of the increased interest in geographic and scientific exploration that had begun two centuries earlier. With a system for naming, and hence communicating, about species in place, it became easier to work toward developing a "natural" system. It is difficult to tell now to what extent individual taxonomists used "natural" to mean overall similarity and to what extent descended from a common ancestor. Although Darwin did not publish On the Origin of Species until 1859, it was recognized that "like begets like". In practice, grouping was based on overall similarity, i.e., plants within a group were considered to resemble each other overall more than members of another group. Because the grouping depends entirely on the phenotype, this kind of classification has come to be called phenetic classification. The most noticeable difference between it and artificial classification lies in the manner of choosing characters. In the artificial approach, the characters are chosen in advance of forming the groups. Phenetic classification demands, in theory, that all aspects of the whole plant be examined, including molecular aspects, without preconceived notions as to which aspects are most important. Obviously there are limits as to what any taxonomist can examine. One consequence is that taxonomists need to collaborate with workers in other disciplines in order to obtain a desirable range of characters. It is also difficult to eliminate all preconceived notions as to which characters are important. As the examination continues, however, characters found to be strongly determined by environmental conditions or to show little correlation with other characters are quickly, often subconsciously, discarded or downgraded whereas those that show little response to the environment and high correlation with other characters (with no obvious reason for doing so) are treated as more significant. The resulting groups often have to be described in terms of a combination of characteristics, some of which may not be exhibited by all members of the group. The problem, of course, is deciding how different a taxon can be and still remain a member of the group. Another problem, particularly if the characters holding the taxa together are non-morphological, is preparing morphological identification keys, but this is a different problem from that of preparing the classification in the first place.

In the middle of this century, several methods of numerical data analysis were developed based on the principles of grouping on overall similarity (see, e.g., Sneath and Sokal 1973). As McNeill (1979a) explained, phenetic classification does not necessarily imply numerical data analysis. Such methods can help overcome any tendency to weigh more heavily characters with which one is familiar, has been the first to discover, and/or can detect easily, and can clarify the reasons for proposing a particular classification, but they are not an essential component of phenetic classification.

The primary criterion for evaluating a phenetic classification is, "How well does it summarize the distribution of features not known at the time it was proposed?" Phenetic classifications are called into question when the variation in new characters fail to support their groups; if several new characters agree in suggesting a particular rearrangement, revision of the classification should be seriously considered.

Phylogenetic classification

Recognition of the role of evolution in the differentiation of taxa led to the belief that the members of a taxonomic group should be more closely related to each other than to members of other groups. Such a classification would be phylogenetic in the original, broad interpretation of this term. In practice, it was often assumed that groups based on overall similarity, i.e., groups obtained through phenetic classification, would be good phylogenetic groups; consequently, the incorporation of a phylogenetic point of view initially had little influence on the end results of classification, the taxa recognized. The two approaches will, however, suggest different groupings if the characteristics common to the members of a phenetic group reflect adaptation to similar conditions rather than inheritance from a common ancestor. One's reaction to such a situation indicates one's basic taxonomic philosophy.

In recent years phylogenetic classification has come to mean that it must be possible to reconstruct the phylogenetic history of the taxa from the classification, a more stringent requirement than that just stated. This school of thought is associated with a method of analysis, cladistic analysis, based on principles enunciated by Hennig (1966). More importantly, Hennig pointed out that, if
elucidating phylogenetic history is the goal, it is character state changes, not the character states themselves, that are important. He also suggested that the most probable phylogeny is the one which requires the minimum number of changes to give the combinations of character states found in extant species. Hennig's insights, which form the basis of cladistic analysis, have had a profound effect on taxonomic thinking, but they are based on the presumption that speciation always involves the division of one species into two, never the combination of two species into one. This means that most taxa of the Triticeae cannot be validly included in a cladistic analysis unless all the data considered are obtained from characters that are inherited from only one parent, e.g., characters associated with the mitochondria and chloroplasts. Results of analyses that ignore this are meaningless (KELLOGG 1989; SEBERG 1989).

In an ideal group, all three taxonomic approaches yield identical results. In such a group, no feature would evolve more than once; obvious morphological differences would mark species groups having different ancestors: species, once differentiated, would either not hybridize or would produce completely sterile hybrids; and there would be no polyploidy. The Triticeae does not meet any of these criteria. Consequently, differences in taxonomic philosophy result in evident differences among taxonomists concerning the best taxonomic treatment of the tribe. This, in turn, leads to different names being applied to the same taxon, a situation that is, understandably, frustrating for all those working with the Triticeae, including taxonomists. It is not a new situation. Only five of the genera recognized today have had over 50% of their species described as members of that genus (Table 2). Of these, only *Aegilops*, *Hordeum*, and *Kengyilia* have maintained basically the same interpretation since they were first published, and *Kengyilia*, which was first described in 1990 (YEN and YANG 1990) is likely to undergo substantial change in the near future (BAUM et al. 1991).

There is also considerable disagreement over the appropriate taxonomic treatment of the Triticeae at the specific level. For instance, LÖVE (1984) recognizes 12 subspecies in *E. trachycaulus*, many of which are customarily treated as species (see, e.g. BOWDEN 1965; HITCHCOCK 1969; SCOGGAN 1978). I have restricted this paper to the generic level because species have a limited distribution and are generally unfamiliar to those working elsewhere. Note, however, that although LÖVE (1984, 1986) and CLAYTON and RENVOIZE (1986) differ significantly over the number of genera they recognize (38 and 18, respectively), they are in substantial agreement with respect to the number of species, approx. 350. TSVELEV (1989) recognizes 24 genera and ca 451 species (based on the totals he gave for individual genera).

### Table 2. Number of species first described as members of a given genus (FIRST) and number now recognized in the genus (NOW).

| Genus      | First | Now | Genus      | First | Now |
|------------|-------|-----|------------|-------|-----|
| *Aegilops* | 28    | 31  | *Hordeum*  | 50    | 51  |
| *Agropyron*| 18    | 27  | *Kengyilia*| 2     | 2   |
| *Amblyopyrum* | 0   | 2   | *Leymus*   | 45    | 4   |
| *Australopyrum* | 0  | 4   | *Pascopyrum*| 0    | 1   |
| *Dasypyrum*  | 0     | 3   | *Psathrostachys*| 3  | 12  |
| *Elymus*    | 43    | 123 | *Pseudoroegneria*| 0 | 32  |
| *Elytrigia* | 0     | 13  | *Roegneria*| 71    | 130 |
| *Eremopyrum*| 1     | 12  | *Secale*   | 5     | 5   |
| *Festucopsis* | 0  | 3   | *Tseniatherum*| 0  | 3   |
| *Henrardia* | 1     | 4   | *Thinopyrum*| 1    | 27  |
| *Heteranthelium* | 0 | 1   | *Triticum* | 23    | 27  |
| *Hordelymus*| 0     | 1   |           |       |     |

Taxonomic overview

The formal generic history of the Triticeae starts, of course, with LINNAEUS' (1753) publication of *Species Plantarum*. In this work he recognizes five genera (Table 3) that would now be included in the Triticeae. Not surprisingly, these include the three important cereal genera, *Secale*, *Triticum*, and *Hordeum*. The others were *Aegilops*, a major weed of wheat fields, and *Elymus*. Linnaeus' emphasis on identification is manifest in the separation of *Aegilops* from other members of the tribe. This resulted from his decision to use the number and distribution of the sexual parts as the basis for his classes. *Aegilops* was placed in the Class 23, Polygamy, because it had both unisexual and bisexual flowers whereas the other four genera were placed in Class 3, Triandria because they had (according to Linnaeus) only bisexual flowers.

Examination of Linnaeus' genera reveals further differences between his concepts and ours. His *Elymus* included members of both *Leymus* and *Taeniatherum*; his *Secale*, members of both *Dasypyrum* and *Eremopyrum*; his *Triticum*, members of *Elytrigia* and *Elymus* (those with one
spikelet at a node); his *Aegilops*, a member of another tribe altogether, *Parapholis incurva* (L.) C. E. Hubbard; and *Hordeum*, two species that Löve (1984), Dewey (1984) and I (Barkworth and Dewey 1985) have placed in the segregate genus *Critesion*. Linnaeus also misplaced one species, placing what we now call *Agropyron cristatum* in *Bromus*, where it was anomalous in having sessile spikelets. He subsequently made some adjustments to his original treatment, transferring *Triticum caninum* to *Elymus* (Linnaeus 1755) and recognizing two additional species, *Hordeum bulbosum* (Linnaeus 1756) and *Elymus europaeus* (Linnaeus 1767), a species now included in *Hordelymus*.

The first new genera recognized were all morphologically quite distinct from previously recognized genera in terms of the species known at the time. The first was *Agropyron*, which Gaertner erected in 1770 (Löve 1984) to accommodate two species, *Elymus* and *Hordeum*, and recognizing *Hordelymus* (Linnaeus 1756) from *Elymus* (Linnaeus 1767), a species now included in *Hordelymus*.

The next genus recognized, *Hystrich*, was first published by Humboldt in 1790 as *Asperella*, a name that had already been used (Löve 1984). The genus was initially composed only of *Elymus hystrich* L., a species that has highly reduced glumes but stiff, long-awned lemmas. Like *Agropyron*, *Hystrich* was evidently different from others known at the time. Indeed, both Schreber (1810) and Beauvois (1812) proposed moving *E. hystrich* out of *Elymus* (Löve 1984). Several segregates of *E. hystrich*, the type species, were described (see Löve 1984), in the nineteenth century. The first new species, *Asperella sibirica* Trautv. [= E. asiaticus A. Löve], was not described until 1877.

In 1802, Koeler recognized a third new genus, *Cuitiera*, in which he placed Linnaeus' *Elymus europaeus*. As with *Asperella*, the original generic name has been changed, to *Hordelymus* (Jessen) Harz. Koeler's reason for placing *Elymus europaeus* in a new genus was that it differed from *Elymus* in having three spikelets at each node and from *Hordeum* in having more than one floret per spikelet. Despite the few characters cited for distinguishing *Hordelymus* from *Elymus* and *Hordeum*, the genus is still considered "good". Of course, Koeler may have taken into account other characters in reaching his decision but mentioned only those that would enable others to identify it when it came to publication.

The next genus recognized (excluding those now universally treated as synonyms of earlier genera) was *Elyrigia* Desv., one of those whose treatment varies substantially in recent treatments. Melderis (1978), Arnow (1987), and Dorn (1984) included it in *Elymus*; Löve (1984, 1986) and Dewey (1984) treated it as a genus of approximately seven species; Tsvelev (1976) included

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**Table 3. Current treatment of species of Triticeae mentioned by Linnaeus**

| Linnean genus | Current generic assignment |
|---------------|---------------------------|
| *Elymus*      | *Elymus sibiricus* L., *E. canadensis* L., *E. viriginicus* L., *E. hystrich* L. [added in the addendum]; *E. europaeus* L. [in 1767] *Leymus arenarius* (L.) Hochst., *Taeniatherum capitatum-sectae* (L.) Nevski |
| *Secale*      | *Secale cereale* L., *S. creticum* L. *Dasyxylon villorum* (L.) Candargy *Eremopyrum orientale* (L.) Jaub. & Spach |
| *Hordeum*     | *Hordeum vulgare* L. *Critesion maritimum* (L.) A. Löve, *C. jubatum* (L.) Nevski |
| *Triticum*    | *Triticum aestivum* L., *T. turgidum* L., *T. monococcum* L. *Elyrigia repens* (L.) Nevski *Elymus caninus* (L.) L. [transferred to *Elymus* in 1755] |
| *Aegilops*    | *Aegilops squarrosa* L., *A. caudata* L., *A. triuncialis* L. *Parapholis incurvata* (L.) C. E. Hubbard |
| *Bromus*      | *Agropyron cristatum* (L.) Gaertner [Remaining species included by Linnaeus do not belong in Triticeae].
four of Löve's segregate genera (Pseuderogneria, Lophopyrum, Trichopyrum, Thinopyrum); Jarvie's (in press) interpretation is similar to Tsvelev's but excludes Pseuderogneria. This lack of concordance suggests that Elyrigia is not a particularly distinctive genus, so one might well wonder why Desvaux considered a new genus necessary. The answer appears to lie in considering which species had been recognized in 1810, the year Desvaux published Elyrigia, and in what genera they had been placed. Agropyron at that time still included only A. cristatum, and Eremopyrum triticoides. Most species traditionally included in Agropyron were placed in Triticum and, like Triticum, were not rhizomatous. Two, Agropyron scabrum (R. Br.) Beauv. [≡ Elymus scabrus (R. Br.) A. Löve] and A. pectinatum (Labill.) Beauv. [≡ Australopyrum pectinatum (Labill.) A. Löve] were still included in Festuca, the genus in which they had originally been described by Labilliardiére in 1802 (Löve 1984). Against this background, Desvaux' treatment of the highly rhizomatous species E. repens as so distinct it deserved a new genus does not seem so strange.

What might be considered the first major revision of the tribe was undertaken by Beauvois (1812) as part of his revision of the family. In his introduction, Beauvois claimed that his genera were more natural than those recognized by his predecessors because they were based on characters that were fundamental to the reproduction of the organism whereas those used by his predecessors were often arbitrarily chosen, frequently variable, and sometimes merely negative (i.e., the absence of a feature). Despite Beauvois' claim, his approach was at least partly artificial because he believed that certain parts of the plant should be used to distinguish taxa at particular levels in the hierarchy. This led him to separate Hordeum and Zeoriton (a segregate of Hordeum) from the remainder of the tribe because they had one floret in their spikelets rather than two or more. Unlike Linnaeus, however, he placed Aegilops near other members of the tribe, albeit nearer Secale than Triticum. Beauvois also attached considerable importance to having at least one character constant in all members of a taxon and in having easily recognized taxa. We owe Beauvois the emphasis on number of spikelets at a node in traditional treatments of the tribe for it was he who first expanded Agropyron to include most species of Triticeae with one spikelet at each node (the exceptions being Triticum and Aegilops) and returned Hystrix and Hordelymus to Elymus. Beauvois also stated that there were four good groups within Agropyron which merited generic recognition, but he refrained from proposing them as such because he was already being criticized for creating too many new genera. The four groups differed in whether or not they (a) where rhizomatous, and (b) had awned lemmas. It is just as well he did not propose them formally; none would be accepted today.

In 1819, Rafinesque, a French botanist, who had settled in North America, described two more new genera, Sitanion, based on Elymus elymoides (Rafin.) Sweezey, and Critesion, based on H. jubatum L. Both species had already been described, E. elymoides as Aegilops hystrix Nutt. According to Rafinesque, Sitanion (in which he included only E. elymoides) differed from Elymus in its glumes and lemmas and in being polygamous, i.e., bearing both bisexual and unisexual flowers and Critesion from Hordeum in its involucre [i.e., number of glumes at each node], lemmas, and in being polygamous. His mention of polygamy in both instances suggests that, like Linnaeus, he considered the distribution of sexual organs inherently more important than other characters; alternatively, he may have thought that other botanists would be more readily persuaded of the merits of his genera if they were based on Linnaean characters. Each would be more easily distinguished from its former genus by the combination of long lemma awns and, in the case of Sitanion, the awnlike glumes.

During the next 60 years, several more generic and infrageneric taxa were described (Table 4), but few won widespread acceptance. Four still recognized as genera by at least some taxonomists, are Heteranthelium, Leymus, Roegneria and Eremopyrum, published in 1843, 1848, 1848, and 1851, respectively. By 1880, each of these genera still included only one species. Moreover, as late as 1902 Podpera employed Linnaeus' interpretation of Triticum in describing T. ponticum Podp. [≡ Lophopyrum ponticum (Podp.) A. Löve, Elyrigia pontica (Podp.) Holub, Elymus elongatus subsp. ponticus (Podp.) Melderis] (Löve 1984). Part of the reason new genera were not widely accepted may have been the relatively poor communications available during the nineteenth century. Another factor may have been that many of the genera were published in regional floras that were not always examined by taxonomists working in other regions. But another reason was that many were not well-founded, being based on a single species and a few, albeit highly conspicuous, characters.
Table 4. Year of publication of generic taxa in the Triticeae. Comments on synonymy etc. are provided only as a guide; they should not be regarded as a definitive statement.

| Taxon             | Author            | Date     | Date  | Comment |
|-------------------|-------------------|----------|-------|---------|
| Aegilops          | Linnaeus          | 1753     | 1753  |         |
| Elymus            | Linnaeus          | 1753     | 1753  |         |
| Hordeum           | Linnaeus          | 1753     | 1753  |         |
| Secale            | Linnaeus          | 1753     | 1753  |         |
| Triticum          | Linnaeus          | 1753     | 1753  |         |
| Gramen            | Seguier           | 1754     | 1754  |         |
| Aegeon            | Adanson           | 1763     | 1763  |         |
| Perlaria          | Fabricius         | 1763     | 1763  |         |
| Sitospelos        | Adanson           | 1763     | 1763  |         |
| Agropyron         | J. Gaertner       | 1770     | 1770  |         |
| Spelta            | Wolf              | 1776     | 1776  |         |
| Zocratton         | Wolf              | 1776     | 1776  |         |
| Bromus            | Scopoli           | 1777     | 1777  |         |
| Asperella         | Humboldt          | 1790     | 1790  |         |
| Hystrix           | Moench            | 1794     | 1794  |         |
| Curiera           | Koeler            | 1802     | 1802  |         |
| Elytrigia         | Desvaux           | 1810     | 1810  |         |
| Gymnosstichium    | Schreber          | 1810     | 1810  |         |
| Critestis         | Rafinesque        | 1819     | 1819  |         |
| Sitanion          | Rafinesque        | 1819     | 1819  |         |
| Lepotostrix       | (Dumortier) Dumortier | 1824  | 1868  |         |
| Eremopyron        | (Ledebour) Jaub & Spach | 1829  | 1851  |         |
| Crithiodium       | Link              | 1834     | 1834  |         |
| Gigachillon       | Seidl             | 1836     | 1836  |         |
| Polypantherix     | Nees              | 1838     | 1838  |         |
| Orostachys        | Steudel           | 1841     | 1841  |         |
| Nitiera           | Seringe           | 1842     | 1842  |         |
| Heterausbulium    | Hochstetter       | 1848     | 1848  |         |
| Bracostella       | Godron            | 1844     | 1844  |         |
| Cryptopyrum       | Heynhold          | 1846     | 1846  |         |
| Criho             | E. Meyer          | 1848     | 1848  |         |
| Leymus            | Hochstetter       | 1848     | 1848  |         |
| Roegneria         | C. Koch           | 1848     | 1848  |         |
| Amblyopyrum       | (Jaub. & Spach) Eig | 1850    | 1929  |         |
| Crithopsis        | Jaub. & Spach     | 1851     | 1851  |         |
| Cylindropyrum     | (Jaub. & Spach) A. Löve | 1851  | 1851  |         |
| Gastropyrum       | (Jaub. & Spach) A. Löve | 1851  | 1851  |         |
| Sitopsis          | (Jaub. & Spach) A. Löve | 1851  | 1851  |         |
| Kratizmannia      | Opiz              | 1852     | 1852  |         |
| Antiospum         | (Grisbach) Grenier & Duval | 1852  | 1852  |         |
| Clinemysis        | (Grisbach) Nevski  | 1852     | 1932  |         |
| Secalidium        | Schur             | 1853     | 1853  |         |
| Anthosachne       | Steudel           | 1854     | 1854  |         |
| Crihopyrum        | Steudel           | 1854     | 1854  |         |
| Daspyrum          | (Coss. & T. Durand) T. Durand | 1855  | 1888  |         |
| Pseudoscalagnia   | (Gordon) Degener  | 1856     | 1936  |         |
| Costia            | Willkomm          | 1858     | 1858  |         |
| Stenostachys      | Turecanianow      | 1862     | 1862  |         |
| Hordeleymus       | (Jessen) Harz     | 1863     | 1885  |         |
| Deina             | Atefeld           | 1866     | 1866  |         |
| Haynaldia         | Schur             | 1866     | 1866  |         |
| Gouardia          | Husnot            | 1896     | 1896  |         |
| Frumentum         | Krause            | 1898     | 1898  |         |
| Meusather         | Candargy          | 1901     | 1901  |         |
| Terrellia         | Lunnell           | 1915     | 1915  |         |
| Zeia              | Lunnell           | 1915     | 1915  |         |
| Malacurus         | Nevski            | 1933     | 1933  |         |
| Aneurolepidium    | Nevski            | 1934     | 1934  |         |
| Psathyrostachys   | Nevski            | 1934     | 1934  |         |
| Taeniatherum      | Nevski            | 1934     | 1934  |         |
| Pseudoregeneloria | (Nevski) A. Löve  | 1934     | 1980  |         |
| Festucopsis       | (C. E. Hubbard) Melderis | 1935  | 1978  |         |
| Thinopyrum        | A. Löve           | 1936     | 1980  |         |
| Campeostachys     | Drobov            | 1941     | 1941  |         |
| Semeioostachys    | Drobov            | 1941     | 1941  |         |
| Cockaynea         | Zotov             | 1943     | 1943  |         |
The second significant revision of the genera in the tribe was that presented by Bentham (1882). In his introduction to this work, Bentham states that "The best genera and other groups are usually distinguished by a combination of characters, to each one of which there may be occasional exceptions, . . ." (BENTHAM 1882, p. 21). He was highly critical of many of his predecessors, stating that "... every local botanist considers himself perfectly competent to describe as new species or genera suggested only by comparisons with the few forms known to him from the same limited locality. ... The consequence is that ... the number of bad species and genera of Gramineae with which science has been overwhelmed is appalling" (loc. cit., p. 14). Having criticised others for their restricted knowledge of the family and failure to make original observations, Bentham carefully listed his own qualifications for the task. These included working with grasses from Europe, Hong Kong, Australia, America, southern Europe, the Orient and Africa. He also acknowledged that many of his ideas were based on the work of Munro, a botanist who had worked on the grasses of India and Australia and whose knowledge and judgment Bentham admired. Bentham described the Triticeae as one of the most well-defined tribes in the family and its genera as "mostly very distinct", but his treatment at both levels has now been rejected by most taxonomists. His error at the tribal level lay in the inclusion of genera such as Lepturus R. Br., Nardus L., and Lolium L., all of which have a single terminal spicate inflorescence. He did, however, include most of them in a different subtribe from the two subtribes in which he placed the genera now accepted as constituting the Triticeae. His first triticaceous subtribe included Lolium L. (now excluded from the tribe), Agropyron Gaertner, Secale L., and Triticum L. Bentham's generic interpretations were broad (Table 5). Within Agropyron he recognized two sections, one consisting primarily of perennial species, with widely spaced spikelets, and asymmetric unkeeled glumes; the other mostly of annuals with evidently distichous, closely spaced spikelets, and narrow, symmetric, keeled glumes. The first section included Roegneria, Anthosachne, as well as

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| Taxon       | Author       | Date   | Date | Comment |
|-------------|--------------|--------|------|---------|
| Henrardia   | C. E. Hubbard | 1954   | 1954 |         |
| Australopyrum | (Tzvelev) A. Löve | 1973   | 1984 |         |
| Lophopyrum  | A. Löve      | 1980   | 1980 |         |
| Pascopyrum  | A. Löve      | 1982   | 1982 | synonym of Aegilops |
| Aegilemna   | A. Löve      | 1982   | 1982 | synonym of Aegilops |
| Aegilonearum| A. Löve      | 1982   | 1982 | synonym of Aegilops |
| Aegilopodes | A. Löve      | 1982   | 1982 | synonym of Aegilops |
| Chenanpyrum | A. Löve      | 1982   | 1982 | synonym of Aegilops |
| Comopyrum   | A. Löve      | 1982   | 1982 | synonym of Aegilops |
| Kiharupyrum | A. Löve      | 1982   | 1982 | synonym of Aegilops |
| Orthopygium | A. Löve      | 1982   | 1982 | synonym of Aegilops |
| Patropyrum  | A. Löve      | 1982   | 1982 | synonym of Aegilops |
| Trichopyrum | A. Löve      | 1986   | 1986 |         |
| Kengyilia   | Yen & Yang   | 1990   | 1990 |         |

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Table 5. Comparison of genera recognized by Bentham (1882) and Hackel (1887)

| Bentham       | Hackel          |
|---------------|-----------------|
| AGROPYRON     | AGROPYRON       |
| (Agropyron, Dasypyrum, Eremopyrum) | (Agropyron, Eremopyrum) |
| SECALE        | SECALE          |
| TRITICUM      | TRITICUM        |
| (Triticum, Aegilops) | (Triticum, Aegilops) |
| HORDUEUM      | HORDUEUM        |
| (Hordeum, Criithopsis, Hordelymus) | (Hordeum, Criithopsis, Hordelymus) |
| ELYMUS        | ELYMUS          |
| (Elymus, Sitanion, Leymus) | (Elymus, Sitanion, Leymus) |
| HYSTRIX       | HYSTRIX         |
| HETERANTHELIUM| HETERANTHELIUM  |
Agropyron s. str.; the second, Dasypyrum, and Heteranthelium. In his second triticaceous subtribe, Bentham recognised Hordeum, Elymus, and Hystrix. In Hordeum he recognized three sections, Zeocriton, Critopsis, and Hordeymus. He considered H. vulgare L. and related forms as “luxuriant monstrosities” (p. 133) that did not rate a place in a formal classification, at least, he does not cite them as members of any of his sections. Bentham also recognized three sections in Elymus, each of which had earlier been proposed as genera: Sitanion, Clinelymus, and Psammelymus. According to Bentham, members of Sitanion usually had three-awned glumes; members of Clinelymus (Elymus s. str.) usually had two spikelets at each node and one-awned glumes; and members of Psammelymus (Leymus) frequently had more than two spikelets at a node and the glumes were either unawned or shortly awned.

In 1887, Hackel published a treatment of the Triticaceae as part of Die Natürlichen Pflanzenfamilien. Hackel’s treatment was almost identical to Bentham’s, differing only in recognition of Heteranthelium Hochst. and Haynaldia as distinct genera. In his introductory paragraph Hackel acknowledges having seen Bentham’s paper but this need not mean that he based his treatment largely on Bentham’s work; the two may have reached similar conclusions through correspondence. Whatever the reasons, the effect of having two respected agrostologists come out with very similar treatments was to place a moratorium on new genera that lasted forty years. Moreover, of the 134 species recognised in Löve (1984) that were first published between 1882 and 1932, all but 19 were based on the generic concepts of Bentham and Hackel. Of the exceptions, ten were species of Aegilops published by Eig, Host, and Zhukovsky in 1928 and 1929; five were species that Bentham and Hackel included in the Triticeae by Bentham into two distantly related groups, one with complex starch grains and the other, which corresponds to our current interpretation of the tribe, with simple starch grains. Harz’ work appears to have been ignored by Bentham and Hackel, for which they were criticized by Nevski (1933). Harz’ conclusions were subsequently supported by Holmberg’s (1926) morphological and Avdulov’s (1931) karyological studies. An additional area of disagreement concerning the tribal limits is the position of Brachypodium P. Beauv., which Holmberg (1926), Nevski (1933), and Clayton and Renvoize (1986) included in the Triticaceae. Holmberg’s interpretation of the tribal limits were generally accepted by European taxonomists, but many North American taxonomists followed Hitchcock’s lead (Hitchcock 1935, 1951) in employing Bentham and Hackel’s tribal limits (see, e.g., Munz 1959; Scoggan 1978).

Nevski (1933, 1934) was the first to adopt an explicitly phylogenetic approach to the taxonomy of the Triticaceae. He worked at the herbarium in Leningrad, center of work for the monumental Flora of the U.S.S.R. project and the location where Avdulov (1931) completed his landmark paper, Karyotaxonomic Investigations of the Grass Family. He was clearly influenced both by Avdulov and Komarov’s (1934) ideas on the evolution and phytogeography of the Soviet Union. Nevski included the subtribe Brachypodinae in the Triticaceae, but it is his treatment of subtribe Triticinae that is of interest here. Nevski considered his subtribe to consist of three large groups of genera, in each of which a similar set of evolutionary trends could be observed. These trends included a change from grouped spikelets to solitary spikelets, from tough rachises to disarticulating rachises, and from adaptation to mesic conditions to adaptation to arid conditions. Nevski’s first group, according to current nomenclature, was based on Leymus, which he interpreted as including only L. arenarius (L.) Hochst., L. mollis (Trinius) Pilger, L. villosissimus (Scribner) Pilger, and L. giganteus (Vahl) Pilger. He regarded Aneurolepidium Nevski, which is usually included in Leymus, as being derived
from the ancestor of *Leymus* and showing greater advancement in the form and position of its glumes, its shortly-awned lemmas, and its tolerance of semi-arid conditions. Another evolutionary line led from *Leymus* through *Elytrigia* to *Agropyron*, but an *Agropyron* that differed from Bentham and Hackel's *Agropyron* in the loss of several species to *Roegneria*. Trends he saw in this line were adaptation to the dry continental climate of the eastern Mediterranean Region, development of a caespitose habit, and shortening of overall height and rachis length, reduction of the lateral veins of the glumes, and thickening of the central glume vein.

Nevski considered his second group to have evolved in mesophilic forests or meadows of a Pacific floristic center, all genera in the group being connected with the South American mainland or eastern Asia. The most primitive genera in the group was *Terrella*, a North American segregate of *Elymus*, a very narrowly interpreted *Elymus*, and *Hystrix*. *Roegneria* he saw as a derivative of *Elymus*, differing in its solitary spikelets. The base of Nevski's third group was *Hordeum*, out of which evolved all the annual species, plus *Heteranthelium*, *Hordelymus*, and *Psathyrostachys*. He noted that it was most diverse in the western and central portion of the Mediterranean.

Nevski differed from earlier students of the tribe in the variety of information he considered, stating (freely translated): "I find the foundation of my system not only in morphological data and data of botanical geography, but also in the facts that are gathered on the one hand by cytologists studying in grasses and on the other hand by practical workers studying the economical, practical side. Unfortunately, taxonomic karyology is still in a rudimentary state but there can be no doubt that the data of karyology will acquire tremendous significance in the near future ..." (NEVSKI 1933, p. 24). The difference between Nevski's broad-based approach to the taxonomy of the Triticeae and that of Bentham and Hackel is striking. Bentham talks about using a wide range of characters, but most of his discussion concerns morphology. Nevski devoted much of his 1933 paper to anatomical and geographic data but did not neglect morphology. His discussion of cytology is brief, but few taxonomists outside Leningrad gave any consideration to cytological data at the time. If Nevski were alive today I suspect he would be learning all he could about molecular cytogenetics while continuing to talk with "practical workers".

Nevski recognized five new genera: *Aneurolepidium*, *Malacurus*, *Psathyrostachys*, and *Taeniatherum* in addition to several segregate genera. *Psathyrostachys* and *Taeniatherum* have become generally accepted, but the first two are generally included in *Leymus*. PILGER (1954), however, recognized *Malacurus* as a distinct genus and BAUM (1979) recognized *Aneurolepidium*. Nevski's most controversial genus today seems to be *Roegneria*, which has been recognized by Chinese taxonomists for some time (see, e.g., KENG and CHEN 1963) and more recently by KUO (1987) and BAUM et al. (1991), but Nevski's concept of the genus differed from that being advocated by Baum et al. in its inclusion of all species of *Elymus* sensu Tsvelev with a single spikelet at each node. According to BAUM et al. (1991), *Roegneria* has its greatest diversity in western China, an area that is still poorly known, botanically speaking. As species become better known and characterized, it becomes easier to evaluate alternative treatments. Until this occurs, it is easy to conclude that a group known only from relatively few herbarium specimens should be included within a similar, well-known group. Easy, but not necessarily appropriate.

Although few would disagree with Nevski's perception of evolutionary trends in the Triticeae, few accept his interpretation of phylogenetic relationships within the tribe. Nevski's handicap was that he was unaware of the role polyploidy has played in the tribe's evolution. Elucidation of the genetic structure of the tribe by experimental work was the next phase in its taxonomic history. The landmark studies in this regard were those of Stebbins and his students in California (e.g., STEBBINS and WALTERS 1949; STEBBINS 1956, and references therein) and CHURCH (1958, 1967) in Rhode Island. SNYDER (1950, 1951), one of Stebbins' students, attempted to find out why *Elymus glaucus* Buckl. is such a variable species. He not only observed several natural populations but also made a number of interspecific and intergeneric crosses. He concluded that some of the variation was attributable to the fixation of different genotypes that might be expected in a predominantly selfing species but that part was attributable to introgression from other species and genera. He also noted that different populations differed markedly in their crossability, a point to consider when using crossability from a limited number of plants as a taxonomic criterion. Subsequent students conducted similar experiments, crossing a wide range..."
of species. The results of these studies resulted in Stebbins's comment that, "... a systematic treatment of the tribe Hordeae which will express the true interrelationships of its species must begin by uniting all of the genera into one, ..." (STEBBINS 1956, p. 240).

Stebbins and his students worked primarily with western North American species. CHURCH (1958, 1967) conducted similar studies of E. virginicus L. and its allies in eastern North America and reached similar conclusions concerning its ability to hybridize with other species and genera. Later, COLLINS (1965) and JOZWIK (1966) examined variation in Elymus trachycaulus (Link.) Gould in Montana and Wyoming, respectively. Again, their data suggested that crossing barriers between E. trachycaulus and other species, including some placed in different genera, were low. The net result of these studies was to convince some North American taxonomists that it was pointless trying to construct a phylogenetic taxonomy of the Triticeae so one might as well learn to live with Bentham's treatment even though it now appeared artificial. It was at least easy to use, much easier than Nevski's or even PILGER'S (1954) treatment. About this time, however, CAUDERON (CAUDERON and SAIGNE 1961; CAUDERON 1966, 1968), DEWEY (see references in DEWEY 1984) and others began to develop the wealth of genomic data now available for the tribe.

As the genomic data accumulated, it became evident that they did not support the generic groupings recognized by Bentham and Hackel. It also began to be evident that genomically similar species were often morphologically similar, although not with respect to those characters used by Bentham and Hackel. In 1977, Dewey circulated a manuscript in which he proposed realigning the species occurring in North America according to genomic constitution. There was a strong reaction. Some respondents praised him but asked why he did not go further; others, equally vehemently, told him that only one genus should be recognized. He presented his ideas in 1979 (DEWEY 1982). These were further developed in DEWEY (1984). About the same time, LÖVE (1982) argued for a complete concurrence between genomic constitution and generic boundaries and later (LÖVE 1984) presented a synopsis of the tribe in which this concept was implemented. Because several taxa have never been genomically analysed, some of his generic assignments had to be based on morphological similarity, but similarity in characters that appeared to be reliable indicators of genomic similarity rather than traditional characters.

Despite his emphasis on genomic criteria for generic limits, LÖve was convinced that, "Though we emphasize the genetical or genomic background of our considerations, they could as well be strictly morphologically motivated because when each genomic unit is considered separately and compared to the others, clear morphological discontinuities distinguish [each unit]" (LÖVE 1982). He saw his treatment as phylogenetic in the sense that the members of his genera would have a similar ancestry. Diploids with identical genomic constitution would be monophyletic; allopolyploids with the same genomic constitution might be derived from different hybrids, but the two (or more) parents would come from the same two (or more) genomic groups.

The papers of LÖve and Dewey have had a profound effect on the questions being asked by those engaged in research in the tribe, both taxonomic and otherwise. It has become standard practice for results to be discussed in terms of genomic groups (see, e.g., ZHANG and DVORÁK 1990; SALOMON and LU 1991). As molecular techniques are brought to bear on the implications of genomic similarity for the structure of chromosomes, our understanding of the phylogenetic history of the tribe and our understanding of the interplay between morphological, physiological, and genetic history in the origin of its species can only increase. Nevertheless, it is unlikely that taxonomists will ever be in complete accord as to the best taxonomic treatment of the tribe. This would require agreement on the criteria for grouping and the rank at which different groups should be recognized, decisions that cannot be settled by further study. I consider that all disciplines are best served by grouping on the basis of ancestry, i.e., phylogenetically. Grouping on the basis of overall similarity depends too much on which characters are looked at. Similarly, the value of a "general purpose" classification depends on whose purpose is being considered. In the USA, those oriented towards floristics tend to favor morphologically recognizable genera whereas those involved in plant breeding consider pairing relationships more useful. Favoring phylogenetic classification does not mean ignoring the need for morphological circumscriptions; it does mean that the morphological circumscriptions be written after the groups have been recognized. Linnaeus recognized this principle, stating (in Philosophia Botanica, cited in
Cronquist 1988), "Scias characterem non constuere genus, sed genus charactere". The first task is, therefore, to identify appropriate groups, a task that requires trying to understand evolutionary mechanisms and the significance of the patterns of variation observed in extant members of the tribe. Bentham thought he had the answer, so far as the Triticeae was concerned. Papers such as Zhang and Dvořák (1991) and Petersen (1991) should protect us from a similar overconfidence and encourage us to collaborate so that we can better understand the evolution of this fascinating tribe.

Taxonomy and other disciplines

Elucidating phylogenetic relationships may be the first goal of taxonomists, but we cannot ignore the needs of those for whom a taxonomic classification is important only as it affects nomenclature. Unfortunately, reaching agreement on nomenclature is more difficult than agreeing on phylogeny. Even if everyone agrees on phylogeny, there is the problem of the rank to assign to different groups. Alternatives to the present procedure (or lack of procedure) for determining the best name for individual taxa include application of a rigid set of rules, which would put us back to taxonomy as Linnaeus practiced it; or rule by committee, a cumbersome procedure at best but possibly useful within a company or government agency. I suspect the problem is not as significant as is sometimes made out. In written papers, well-known alternatives to the preferred names can always be cited within parentheses; computer databases can be programmed to translate to a common nomenclatural system. But if a nomenclatural system is to be meaningful, we must learn to accept changes as our understanding increases. At the same time, it behoves those of us who are taxonomists not to make new nomenclatural combinations until we have confidence in the proposal. We should also make a point of explaining why we feel the change is needed even though this is not required by the International Code of Botanical Nomenclature. Of far greater interest are the biological questions that will lead us to an understanding of the evolutionary mechanisms that have led to the tribe's present diversity.

The interaction between taxonomists and others is not limited to the matter of names. Taxonomy is a synthetic discipline, consequently taxonomists need to be able to understand data from a variety of different disciplines. In doing so, they should be alert to the potential limitations in the data and the goals of the other disciplines. For instance, statements that "species X has this property" should be examined to determine how species X was represented in the study. Snyder (1950, 1951) and Church (1958, 1967) demonstrated that the crossability within a population may be highly variable, as can crossability between populations. Data on crossability from a single accession should, therefore, be treated with caution. Even chloroplast DNA, frequently referred to as a conservative molecule, may vary within a species (Rieseberg and Soltis 1991). This variation will not be uncovered unless several specimens are examined. Extensive sampling may not contribute to achievement of the goals of a non-taxonomist, but collaboration may enable both taxonomic and nontaxonomic goals to be met.

There is another aspect of sampling that might, with relatively little effort, enhance the value of a study whose taxonomic aspects are secondary to the main goal. This aspect is sampling design. As Watson and Clifford (1976) pointed out, existing taxonomic treatments should be taken as a guide to sampling. A generalization based on data from four species, each representing a different section in a genus, is a better basis for generalizing about the genus than a sample of four species, all drawn from the same section. Similarly, generalizations based on populations from different regions are likely to be more reliable than those based on the populations from a single region (Tesfaye et al. 1991).

Another concern is the accuracy of the identification of the materials used in a study. All too often, no statement is made as how the material was identified nor where voucher specimens have been deposited. In many instances, there are no voucher specimens. I am not suggesting that the literature is replete with data from misidentified specimens, but most taxonomists know of instances in which, after weeks of work, it was realised that the material being worked with had not been correctly identified. Preparing voucher specimens is not difficult; any taxonomist would be happy to give advice, if necessary. For field collected materials, it merely means that an herbarium specimen is prepared at the time of collection and examined later to check any field identification. If seed are used, some seeds should be grown to maturity so their identity can be verified. Germplasm curators readily admit that maintaining the purity of their accessions is a major concern.
This possibility can be checked by preparing and examining a voucher specimen. In some cases, the possibility that material was misidentified may not be recognized until further studies have shown an old report to be anomalous. If a voucher specimen has been deposited in a herbarium that makes loans, this possibility can be checked long after the original study has been completed.

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