

Review article

Systematics and karyology of the section *Phleum* in the genus *Phleum*

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Abstract. The article presents a concise history of systematic studies on taxa included in the section *Phleum* of the genus *Phleum*. The authors discuss the results of cytotaxonomic studies within the section which have been conducted so far and their importance for studies of phylogeny of particular species. It is suggested that the section should be divided into five species on the basis of karyosystematic criteria considering the karyotype structure as well as localization of heterochromatin in the genome. The question of origin of two polyploid species (*P. commutatum* Gaud. and *P. pratense* L.) is also discussed.

Key words: evolution, heterochromatin, karyotype, *Phleum alpinum*, *Phleum commutatum*, *Phleum nodosum*, *Phleum pratense*, *Phleum rhaeticum*, systematics.

Introduction

The genus *Phleum* (timothy) comprises about 15 species growing mainly within the borders of the Old World. It is usually divided into four small sections (HUMPHRIES 1980, CONERT 1985). However, only some representatives of the section *Phleum* Griseb. are widespread, occur in different climate zones and are of more practical importance. The most important cultivated grass within the section (and also the genus) is *Phleum pratense*, and it arouses the greatest interest of researchers because of both practical and

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theoretical reasons. It is also understandable that the genetic and systematic studies which have been conducted for many years cover other taxa which are in close phylogenetic relationship with *P. pratense*.

Basis for the systematics of the section *Phleum*

Because of a great similarity between taxa constituting the section *Phleum*, their proper identification and determination of the possible phylogenetic relationships between them are difficult. Towards the end of the 19th century, four species forming two separate groups within the section were distinguished: *P. pratense* group (*P. pratense* L. and *P. nodosum* L.) and *P. alpinum* group (*P. alpinum* L. s. str. and *P. alpinum* var. *commutatum* Gaud.). Since differentiation of particular species in a group causes some trouble to taxonomists, and morphological differences between the representatives of the two groups are small, various systematic formulations of the discussed section were suggested. SCHÖRTER (1889) divided it into two coenospecies: *P. pratense* sp. coll. and *P. alpinum* sp. coll. (including respectively: *P. pratense* L. s. str. + *P. pratense* v. *medium* Brugger and *P. alpinum* L. s. str. + *P. alpinum* v. *commutatum* Gaud.), ASCHERSON and GRAEBNER (1899) considered the differences between the two groups to be unimportant and they treated the whole section as a coenospecies *P. pratense* sp. coll., within which they distinguished only two taxa: *P. vulgare* and *P. alpinum*. However, the classic (mainly morphological) criteria, which were used to arrange the systematics did not bring solutions as far as phylogenetic relationships between the taxa which constitute the section are concerned.

In the early 1930s intensive and comprehensive cytotaxonomic studies aiming to determine the alliances between particular taxa were launched. Studies in this field were carried out first by English (GREGOR, SANSOME 1930), then by Swedish researchers (MÜNTZING 1935, 1938, NORDENSKIÖLD 1937, 1941, MÜNTZING, PRAKKEN 1940). It was found that *P. alpinum* var. *commutatum* is tetraploid ($2n=4x=28$), and *P. pratense* is hexaploid ($2n=6x=42$). However, researchers differed in their opinions on the origin of these polyploid forms (cf. JOACHIMIAK, KULA 1993).

An extensive, classical paper on this subject was published by H. NORDENSKIÖLD in 1945. Basing on comprehensive cyto-morphological and experimental studies, the author suggested a clear concept of dividing the section into four species, which differ within groups mainly in the chromosome number (*P. nodosum*, $2n=14 \leftrightarrow P. pratense$, $2n=42$; *P. alpinum*, $2n=14 \leftrightarrow P. com-$

mutatum, $2n=28$). As far as the appearance is concerned, there have been no clear differences so far, which would allow for distinguishing morphologically specimens of *P. pratense* from *P. nodosum* (these taxa differ from each other mainly in size), while *P. alpinum* differs from *P. commutatum* only in the absence of ciliate awns in spikelets (Fig. 1). Contrary to the small morphological differences between *P. pratense* and *P. nodosum* and between *P. alpinum* and *P. commutatum*, the differences in chromosome number seemed to be the most significant to the author.

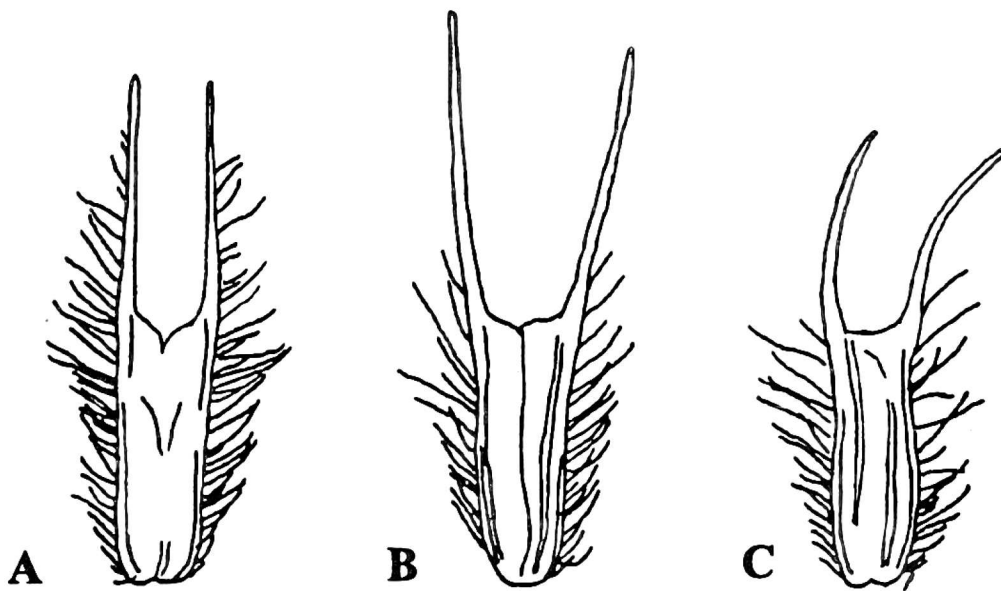


Fig.1. Spikelets of three *Phleum* taxa belonging to the *P. alpinum* group
 A – *Phleum rhaeticum* (Humphries) Rauschert (= *P. alpinum* L.) B – *Phleum commutatum* Gaud., C – *Phleum commutatum*

NORDENSKIÖLD (1945) suggested that phylogenetic relationships between the distinguished species are as follows:

1. The genomes of *P. nodosum* and *P. pratense* are closely homologous. *P. pratense* is the autohexaploid of *P. nodosum*.

2. The diploid *P. alpinum*, though separate from the above-mentioned species, is genetically much closer to them than the tetraploid *P. commutatum*, which is an allotetraploid species of unknown origin.

Experimental studies carried out by the author provided further evidence for autohexaploid origin of *P. pratense* (NORDENSKIÖLD 1949, 1953, 1957, 1960). This has also been confirmed by some other authors (WILTON, KLEBSADEL 1973).

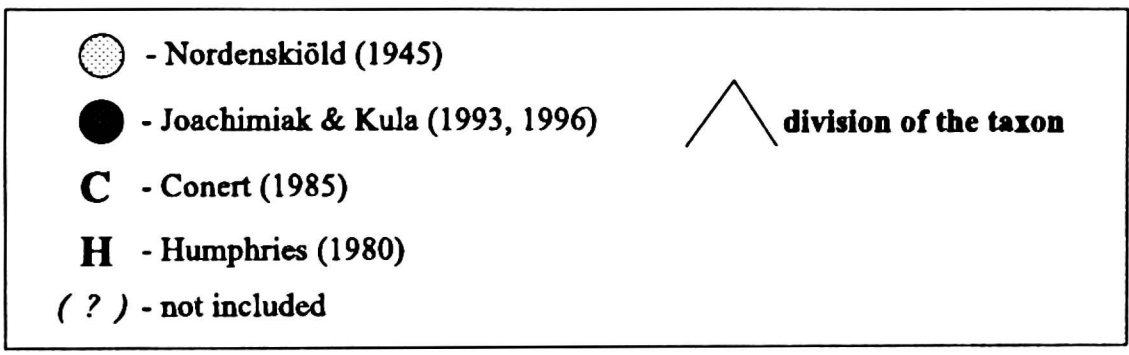
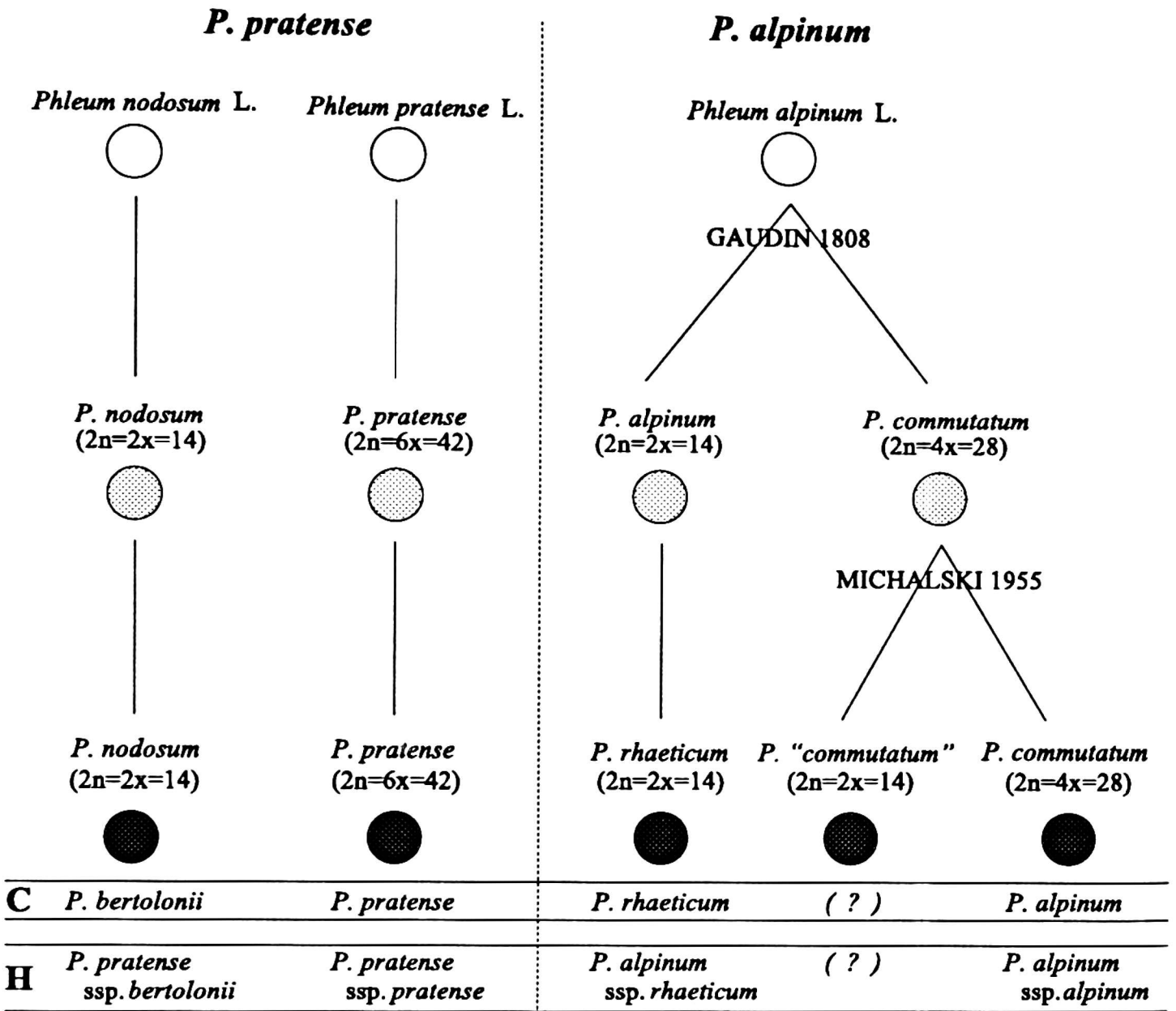


Fig. 2. Systematics of the section *Phleum*

More recent works (HUMPHRIES 1980, CONERT 1985) are substantially based on NORDENSKIÖLDS (1945) proposal, although they acknowledge different taxonomic ranges to the forms constituting it (Fig. 2).

The changes suggested in those works regard mainly the names of some taxa. *Phleum nodosum* L. appears in them as *P. bertolonii* (*P. bertolonii* D.C.

or *P. pratense* subsp. *bertolonii* (D.C.) Bornm.), the diploid *Phleum alpinum* as *P. rhaeticum* (Humphries) Rauschert or *P. alpinum* subsp. *rhaeticum* Humphries, and the tetraploid *Phleum commutatum* as *P. alpinum* L. or *P. alpinum* L. subsp. *alpinum*. In our opinion, the nomenclature suggested by the above-mentioned authors introduces remarkable confusion and may lead to unnecessary misunderstanding. In particular, this regards the specific name *P. alpinum* which, against earlier tradition, was assigned to the tetraploid form (Fig. 2). This is the reason why in the further part of this paper we abandon this specific name, and apart from it we accept the names of species used by NORDENSKIÖLD (1945): *P. pratense* ($2n=6x=42$) and *P. nodosum* ($2n=2x=14$) for the forms from the *P. pratense* group and *P. commutatum* ($2n=4x=28$). For the above-mentioned reasons, for the diploid form ($2n=2x=14$) from the *P. alpinum* group, described by NORDENSKIÖLD as *P. alpinum*, we adopt a more unequivocal name suggested, among others, in CONERT's work (1985): *P. rhaeticum* (Humphries) Rauschert.

Suggested division of the section on the basis of karyosystematic criteria

Now, it seems difficult to accept both the proposed divisions of the *Phleum* section and the conclusions regarding the origin of the polyploid species. Firstly, in 1955 MICHALSKI found in the Tatra Mountains a taxon morphologically corresponding to *P. commutatum*, but having a diploid chromosome number ($2n=2x=14$); secondly, karyotype investigation with the C-banding method (CAI, BULLEN 1991, JOACHIMIAK, KULA 1993) and molecular studies (CAI, BULLEN 1994) suggest allohexaploid origin of *P. pratense*. Particularly the first question seems very important: it disturbs the established picture of the *P. alpinum* group and makes the identification of the taxa occurring within it impossible. The taxon discovered by MICHALSKI (1955), temporarily called by us *P. "commutatum"*, if identified on the basis of the morphology of spikelets, has to be included in *P. commutatum* (Fig. 1); however, if identified on the basis of chromosome number, it has to be included in *P. rhaeticum*. Its origin, systematic position and possible relationships with the two other species in the *P. alpinum* group require a careful explanation. Numerous karyological studies confirm its occurrence not only in the Tatra Mountains, but also in other regions of Europe (FREY et al. 1977, JOACHIMIAK, KULA 1993, 1996, TEPPNER 1980 – for some more recent data).

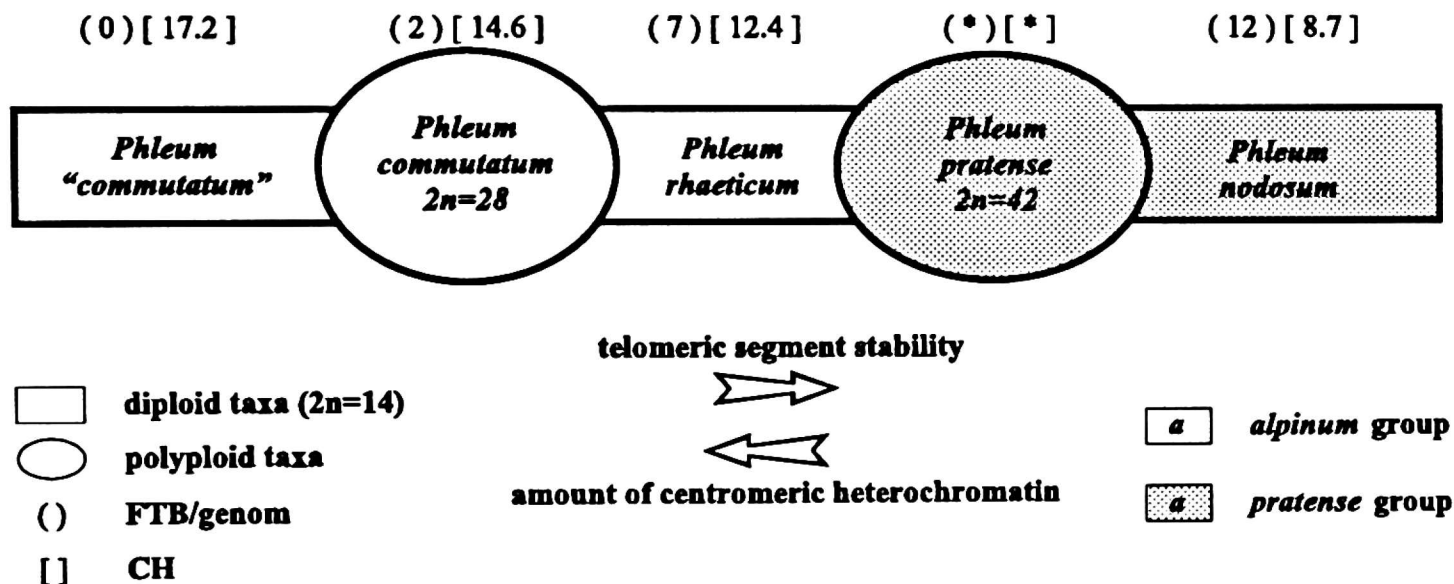
Phleum sect. Phleum

Fig. 3. Evolutionary relationships between five *Phleum* taxa
FTB – number of fixed telomeric bands, CH – amount of centromeric heterochromatin,
(*)[*] – no statistical data from different populations are available

More detailed karyological studies of the section *Phleum* conducted by us (JOACHIMIAK, KULA 1993, 1996) show that there is a possibility of solving the above-mentioned problem on the basis of an advanced analysis of the karyotype. Especially useful in this respect seem to be the data regarding the amount of different fractions of heterochromatin in the genome of particular forms. They indicate the existence of distinct gradients, possibly reflecting the karyotype evolution within the section, which sheds light on both the phylogenetic relationships between the three diploid taxa (*P. commutatum*, *P. rhaeticum* and *P. nodosum*) and the origin of the tetraploid *P. commutatum* and hexaploid *P. pratense* (Fig. 3).

The results suggest allotetraploid origin of *P. commutatum*, which is most probably a hybrid of *P. "commutatum"* and *P. rhaeticum* and allohexaploid origin of *P. pratense*. Since too few specimens of *P. pratense* have been examined so far, we cannot precisely determine the progenitors of this species. But in the light of the already conducted studies it is argued that the *P. pratense* karyotype contains 4 genomes of *P. nodosum* and two genomes of another form. They could be the genomes of *P. rhaeticum*, or the genomes of a so far unidentified diploid taxon, closely related to *P. nodosum*. The latter possibility seems particularly interesting. However, the problem requires further investigation.

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