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TAXONOMICAL, CHOROLOGICAL AND KARYOLOGICAL PROBLEMS IN SELECTED REPRESENTATIVES OF THE TRIBE AVENEAE (POACEAE)

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ABSTRACT

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In this paper the author presents a rewiev of hitherto studies carried out on taxonomy, distribution and karyology of 12 genera (including 30 species) of the tribe *Aveneae*. All three subjects were rewieved separately in respect of problems which appear to be interesting or complex. This rewiev is based mainly on the author's own studies, supplemented however by literature, data of various workers. In addition, some general remarks concerning grasses and the tribe *Aveneae* are given.

Keywords: taxonomy, chorology, karyology, Poaceae, Pooideae, Aveneae, Aveninae, Aristaveninae, Alopecurinae

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Taxonómiai, chorológiai és kariológiai problémák az *Aveneae tribusz (Poaceae)* egyes típusaiban

A dolgozatban a szerző alapos áttekintést ad a Pázsitfűfélék ***(Poaceae)*** családjának ***Aveneae*** tribuszáról, különösen kitér a lengyel ill. a közép-európai anyagok vizsgálata során felmerülő rendszertani, elterjedésbeli vonatkozásokra és a kromoszóma-adatok kritikai értékelésére, aktuális helyzetére.

A nemzetközi szakirodalom valamint a saját kutatások összegezésével, a jelen feldolgozásban a következő taxonokra kapunk értékes információkat: ***Aveninae*** szubtribusz: *Avenula planiculmis, A. pratense, A. pubescens, Avena strigosa, Trisetum alpestre, T. flavescens, T. fuscum, T. sibiricum, Ventenata dubia, Koeleria glauca, K. grandis, K. macrantha, K. pyramidalis, Avenella flexuosa, Holcus lanatus, H. mollis, Aira caryophyllea, A. praecox;*

Aristaveninae szubtribusz: *Deschampsia caespitosa, Aristavena setacea;* ***Alopecurinae*** szubtribusz: *Agrostis alpina, A. rupestris, Calamagrostis arundinacea, C. canescens, C. epigeios, C. pseudophragmites, C. stricta, C. varia, C. villosa.*

Az egyes bemutatásokból kitűnik, hogy számos összetett és kétes kérdés nincs kellőképpen megválaszolva. Ilyen pl. rendszertanilag a ***Pooideae*** alcsalád tribusz felosztása, mely egyes szerzőknél 3, míg másoknál 28 egységre (tribuszra) tagolódik. Továbbá, az ***Aveneae*** tribusz 3-8 altribuszra osztható. Nincsenek kellőképpen tisztázva az elterjedési határok, a diverzitási központok. Jól kirajzolódik viszont a három flóraelem körüli csoportosulás: cirkumpoláris (pl. *Calamagrostis stricta*), eurázsiai (pl. *Calamagrostis arundinacea, C. canescens, C. epigeios*) ill. az európai elterjedés (*Calamagrostis varia, C. villosa*). A kromoszóma-szám adatok és általában a kariológiai vizsgálatok arra utalnak, hogy a tribuszon belül három csoport különíthető el. Az elsőhöz azok a taxonok tartoznak, amelyeknél stabil a kromoszóma-szám (pl. *Koeleria glauca, Trisetum alpestre, Agrostis alpina*), a másodikhoz azok a taxonok tartoznak, amelyeknél a populációrendszerek változó kromoszóma-szám összetételt viselnek (pl. *Avenula pratensis, Koeleria macrantha*), a harmadikhoz pedig azok, amelyeknél két-három kromoszóma-szám is ismeretes (pl. *Trisetum flavescens, Koeleria grandis,* stb.). Tekintettel a bemutatott taxonok rendszertani, chorológiai és kariológiai változatosságára, a rokonsági kapcsolatok bonyolultságára, az evolúciós folyamatok különlegességére a további kutatások számos értékes eredményt tartogatnak.

Introduction

The grasses (*Gramineae, Poaceae*) is the large family of flowering plants, though not largest in terms of species and genera, coming after *Compositae*, *Leguminosae*, *Orchidaceae* and *Rubiaceae*. However, the grasses are the most important family on earth in biomass, area covered, diversity of habitats and value to man. Grasses have a wider range of adaptation than any other family of plants. They occur on mountaintops and seashores, in deserts and swamps, in the tropics, in the arctic and antarctic. Grasses live under nearly all conditions where exist soil and moisture. The grasslands occupy a third of the land's surface and a great part of the land area are devoted to crops upon which much of the world's population depends for its food. In addition, grasses are the basis of lawns and playing fields and there are ornamental species among them. You cannot survive at all in a world without grasses.

The grasses occupy a fairly isolated position among *Angiospermae* and *Monocotyledonae*. They posses a distinctive lifeform in which single external and internal structure is counterbalanced by their variability (TSVELEV 1984).

Grass taxonomy traditionally based upon spikelet structure have been the focus of numerous classifications. However, even before 1900 it was evident that a classification based on spikelet features lead to artificial groupings because of parallel evolution of similar spikelets in more than one lineage. In the beginning of 1930s AVDULOV used leaf anatomy, cytology and physiology and correlated them with spikelet structure to construct a system of grasses. In 1950s and later a number of new classification systems have been published including spikelet structure, leaf blade anatomy, cytology, embryo and starch grain structure, and photosynthetic metabolism. Unfortunately, many of the new non-morphological characters proved too indefinitive or contradictory and for this reason are not of much practical diagnostic value (MACFARLANE & WATSON 1982; CLAYTON & RENVOIZE 1986; WATSON & DALLWITZ 1992).

The *Poaceae* comprise 8 000 to 10 000 of species and 600 to 800 genera. In grass taxonomy rather reasonable agreement has been reached at subfamily level, and five major subfamilies can be recognized: *Bambusoideae*, *Arundinoideae*, *Pooideae*, *Chloridoideae* and *Panicoideae*. Some authors accept a small tropical subfamily *Centothecoideae* of ten genera and about 30 species distinctive by its embryo and leaf anatomical characters (CLAYTON & RENVOIZE 1986; WATSON & DALLWITZ 1992; CHAPMAN & PEAT 1992; FREY 1997d). On the other hand, CARO (1982) recognized 13 subfamilies, whereas TSVELEV (1984) at the other extreme - only two.

Subfamily Pooideae

In various systematic treatments of Poaceae the subfamily Pooideae Macfarlane & Watson has received more attention regarding its internal classification than have the others. It is a large group of grasses, mostly temperate in distribution, with always membranous ligules and non-Kranz leaf anatomy typical of species with C3 photosynthesis as well as large chromosomes. The number of tribes ranges from 4 to even 24 (PRAT 1960); in four important recent systems - from 7 to 28 (Table 1).

Tribe Aveneae

According to TŠVELEV (1984) the differences between tribes constituting Pooideae demonstrate gradual transition from a complete set of festucoid to a complete set of panicoid characters. In consequence there are the troubles with providing a precise definition of this tribe, since different genera have been excluded from or included in it. For example, to date there is controversy whether the genus *Agrostis* L. with uniflowered spikelets should be placed in the *Aveneae* or segregated (together with closely related genera) as a tribe of its own, *Agrostideae* (PILGER 1954; MACFARLANE & WATSON 1982; TSVELEV 1984; CLAYTON & RENVOIZE 1986; WATSON & DALLWITZ 1992). Besides, the evidence of the heterogeneity of *Aveneae* is an extensive list of synonyms (CLAYTON & RENVOIZE 1986).

Nevertheless, *Aveneae* Dumort. composed of about 60 genera and about 1000 species has been universally recognized as an outstanding and real taxon in the majority of classifications (PRAT 1960; FREY 1993b). In the opinion of CLAYTON and RENVOIZE (1986) the following diagnostic characters are most important for the tribe: inflorescence panicle (rarely raceme), ligule membranous, spikelets usually laterally compressed, glumes persistent, usually longer than adjacent lemmas and often as long as spikelet, lemmas typically with a dorsal awn, often geniculate with twisted column, endosperm sometimes soft or occasionally liquid. The two last characters suggest the phylogenetic advancement of the tribe.

The number of subtribes recognized within the *Aveneae* is also debatable (Table 2).

The present author accepted tribal classification of the subfamily and generic composition of particular tribes suggested by CLAYTON and RENVOIZE (1986), however a little modified (Fig. 1). Namely, the tribe

Macfarlane & Watson (1982)	Supertribe Triticanae 3 tribes: Triticeae, Brachypodieae, Bromeae Supertribe Poanae 5 tribes: Agrostideae, Aveneae, Meliceae, Seslerieae, Poeae;
Tsvelev (1984)	28 tribes: Oryzeae, Brachypodieae, Bromeae, Aveneae, Phalarideae, Phleeae, Scolochloeae, Poeae, Monermeae, Seslerieae, Brylkinieae, Meliceae, Molinieae, Diarrheneae, Nardeae, Stipeae, Arundineae, Cortaderieae, Danthonieae, Aristideae, Aeluropodeae, Pappophoreae, Cynodonteae, Zoysieae, Arundinelleae, Paniceae, Andropogoneae;
Clayton & Renvoize (1986)	10 tribes: Nardeae, Lygeeae, Stipeae, Poeae, Hainardieae, Meliceae, Brylkinieae, Aveneae, Bromeae, Triticeae;
Dallwitz & Watson (1992)	Supertribe Triticodae 3 tribes: Triticeae, Brachypodieae, Bromeae, Supertribe Poodae 4 tribes: Aveneae, Poeae, Seslerieae, Meliceae.

Table 1. Comparison of four important classifications of the subfamily Pooideae

Pilger (1954)	3 subtribes, 61 genera	Aveninae, Duthieinae, Danthieinae
Holub (1958, cit. after Albers 1980)	5 subtribes, 22 genera	Aveninae,Trisetinae, Ventenatinae, Gaudiniinae, Deschampsiinae
Tsvelev (1984)	8 subtribes, 29 genera	Aveninae,Ventenatinae, Koeleriinae, Airinae, Holcinae, Agrostidinae,Gaudiniinae, Moliinae
Clayton & Renvoize (1986)	4 subtribes, 57 genera	Duthieinae, Aveninae, Phalaridinae Alopecurinae

Table 2. Subdivisions of the tribe Aveneae

Aveneae was supplemented by the fifth subtribe *Aristaveninae* with two genera, *Aristavena* and *Deschampsia* excluded from *Aveninae* sensu Clayton and Renvoize by ALBERS and BUTZIN (1977).

Thus according to the classification accepted by the present author, 12 genera and 30 species discussed here were placed in three subtribes (Table 3). Some of them were discussed considering both their taxonomy, chorology and karyology if these problems appear to be interesting or complex. The others were treated taking into account various arrangements of the issues according to degree of their recognition. All three subjects were rewieved separately as follows: taxonomy, chorology and karyology. This rewiev is based mainly on the author's own studies, supplemented, however, by literature data of various workers.

A review of the genera and species Taxonomy

Subtribe *Aveninae* Presl

Avenula (Dumort.) Dumort.

The genus consists of ca 60 species grouped in several subgenera. Of these, 30 species occur in Europe. They belong to subgenus *Pubavenastrum* (Vierh.) Holub and to the type subgenus which is subsequently divided into two sections, *Avenula* and *Scleravenastrum* (Holub) Holub. *Avenula* is recognized as a distinct genus since 1868, but for a long time its species had usually been included in the genus *Avena* L. The name *Avenula* was for the first time used by DUMORTIER in 1824 for a section of *Trisetum* Pers., and then raised to genus by DUMORTIER himself in 1868 (FREY 1991b and cited literature).

Four species studied by the author (Table 3) are included in section *Avenula* of subgenus *Avenastrum*. Infraspecific variability has been detected in *Avenula pratensis* (L.) Dumort. and *A. planiculmis* (Schrad.) W. Sauer & Chmelitschek. The first species was described by LINNAEUS (1753) as *Avena pratensis*. HOLUB (1961) pointed out the fact that the description by LINNAEUS in part does not refer to the species in its current comprehension. Currently, *A. pratensis* is considered to be much differentiated morphologically and lower taxa within it are distinguished. Additionaly, the question is complicated by the existence of numerous chromosomal races, some of which have a taxonomic value. The variability of *A. pratensis* refers the pubescence of the blades and sheath of the leaves. Two varieties, var. *pratensis* with

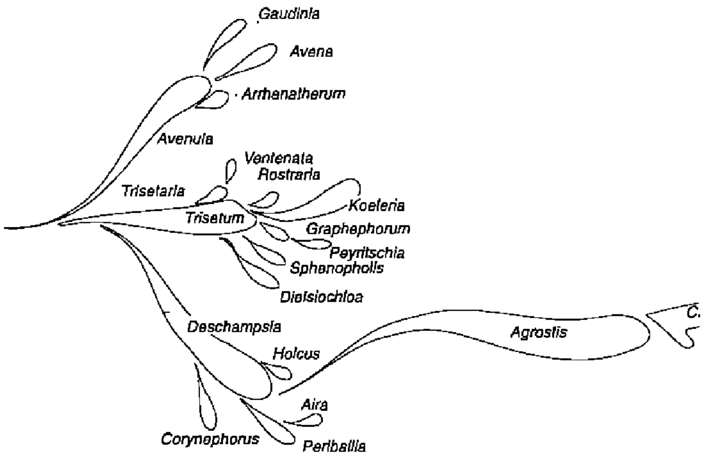

Fig. 1. Relationships in Aveneae Dumort (according to Clayton & Renovize 1986, modified)

basal leaves non pubescent, and var. *hirtifolia* (Podp.) Frey, with basal leaves, or at least the youngest basal leaves pubescent have been distinguished. The second species, was described by SCHRADER in 1806 as *Avena planiculmis*. Although most workers did not recognize any infraspecific taxa within it, the species is little variable with regard to rough and strongly compressed sheaths and culms, shape of the panicle, variegated spikelets, and wide blades, with long, whitish cilia in their lower part. The type, montane variety, var. *planiculmis* and the lowland var. *hispidula* (Zapał.) Frey have been recognized. They differ in the pubescence of the axis and branches of the panicle, present in the former, and absent in the second variety (FREY 1991b and cited literature).

The montane *Avenula versicolor* (Vill.) Lainz is one of the least variable species of the genus and no infraspecific taxa have been distinguished in it. *A. pubescens* (Huds.) Dumort. is greatly variable morphologically, especially with regard to the pubescence, the colour and the length of spikelets and number of veins of the lower glume. However, the infraspecific taxa usually made on the base of the pubescence appear to have no taxonomic value, because this variability is clearly phenotypic so the species should be undivided (FREY 1991b and cited literature).

Avena L.

The genus is composed of ca 25 species. There are several (6-7) cultivated species including *A. sativa*.

Avena strigosa Schreb. is recently placed rather among weedy forms. Together with *A. hispanica* Ard. and *A. nuda* L. constitute an autonomous European group of species included by BAUM (1977) in the section *Agraria* Baum. The taxonomy of *Avena* is usually based on the mode of disarticulation of florets, number of florets in the spikelets, range of size of spikelets, glumes and lemmas and lemma tips. As to the morphological characters *A. strigosa* differs markedly from the other and only rarely may be confused with similar *A. hispanica* and *A. brevis*. The main features distinguishing *A. strigosa* from the remaining species are the structure of lodicules and place of insertion of the awn, however most significant character of the species is lemma tip - bisetulate-biaristate or biaristulate only (MALTSEV 1930; BAUM 1977). Although the species is fairly uniform with respect of its morphology, the pubescence of the lemma is of the special value feature for infraspecific classification, and two varieties have been recognized on that base: var. *glabrescens* (Marquand) Thell., with glabrous lemma and var. *subpilosa* Maltsev having hairs around insertion of the awn. Additional features useful in differentiating of both taxa concern length of the upper glume and aristulae in the second floret in spikelet and size of caryopsis (KORNIAK & FREY 1999 and cited literature).

Trisetum Pers.

The genus includes ca 70 species, 30 of which grouped in four subgenera are known to occur in Europe (CHRTEK 1965; CLAYTON & RENVOIZE 1986).

In numerous publications of the past century, representatives of the genus *Trisetum* had been included in *Avena* L., although the species was established by PERSOON in 1805, but without designation of the type. Since *T. flavescens* is generally considered to be a lectotype of *Trisetum*, VELDKAMP (1983) had proposed to retain it as a conserved type of the genus..

Four species were investigated by the author (Table 3), one of which, *Trisetum flavescens* (L.) P. Beauv., is divided infraspecifically. This species is morphologically most variable species, and number of taxa have been recognized within it including subspecies and varieties. It was divided on the basis of pubescence of the basal sheath and blades, the length and width of the blades, the shape and the length of the panicle, the length of the culm as well as the colour and length of the spikelets. Only two infraspecific taxa have been recorded by the present author differing in the width of the leaves, the structure of the panicle, the colour of spikelets and the length of the ligule, namely var. *flavescens* (frequent in the lowlands and in the mountains) and var. *purpurascens* (DC.) Arcang. (rare in mountains). The remaining three species, *T. alpestre* (Host) P. Beauv., *T. fuscum* (Kit. *ex* Schult.) Schult. and *T. sibiricum* Rupr. are rather little morphologically variable and no lower taxa have been distinguished in them. Growing in mixed stands in the field *T. flavescens* and *T. sibiricum* as well as *T. alpestre* and *T. fuscum* are sometimes confused. However, these are separate and distinct species different in morphology, ecological requirements and chemical characters (phenolic compounds) (FREY 1992, 1996).

Koeleria Pers.

The genus comprises probably more than 50 closely intergrading species. *Koeleria* is considered to be a morphologically and taxonomically complex genus therefore the number of species depends on the taxonomic approach. The systematics of this controversial genus established in 1805 by PERSOON has been studied by a number of the authors. PERSOON (1805) distinguished five species both annual and perennial, CANDOLLE (1813) divided the genus into annuals and perennials, LINK (1827) included all perennials and annuals in two separate genera, *Airochloa* and *Koeleria*, respectively (FREY 1993a and cited literature). DOMIN (1907) proposed to include annuals and perennials in different subgenera (*Lophochloa* and *Airochloa*), whereas HUMPHRIES (1980) includes only perennial species in *Koeleria*, and annual in the separate genus *Lophochloa*. Very interesting system based on cytology and leaf anatomy was proposed by UJHELYI (1961, 1962, 1970, 1972a,b). He divided the genus into 18 equivalent series, looked upon as phylogenetic ranks and particular series embraced species of different degree of ploidy, so it was not hierarchic. *Koeleria* and *Trisetum* are very close related taxa, and in the opinion of TSVELEV (1971, 1984) they exist as separate genera owing but to tradition, because differences between them are inconspicuous.

Four species have been studied by the author (Table 3). Of these, *Koeleria macrantha* (Ledeb.) Schult. is morphologically most variable species for which it is difficult to find any features useful for discrimination of infraspecific taxa. The problem of variability and nomenclature of the species are strongly connected with each other. The three names have been most frequently used: *K. gracilis* Pers., *K. cristata* (L.) Pers. and *K. macrantha* (Ledeb.) Schult. However, the ccorect name is the third one, based on *Aira macrantha* Ledeb., while the other two names proved to be invalid. All attempts to make order in the taxonomy of this species have been not successful. DOMIN (1907) distinguished 169 lower taxa, mostly without taxonomic value. According to HUMPHRIES (1980) *K. macrantha* is the complex of nine species, in which great variability is caused by poliploidy and adaptation to varied ecological conditions. BAJON (1989) basing on morphological, karyological and biochemical features divided this species into two subspecies of various cytotypes from di- to dodecaploids. It seems, this division useful from the practical point of view is fairly risky with regard to the rules of nomenclature and taxonomy. In the opinion of ROBERTSON

Subtribe Aveninae	
Avenula	*planiculmis* (TCK), *pratense* (TCK), *pubescens* (TCK), *versicolor* (TC)
Avena	*strigosa* (TC),
Trisetum	*alpestre* (TCK), *flavescens* (TCK), *fuscum* (TCK), *sibiricum* (TCK)
Ventenata	*dubia* (C),
Koeleria	*glauca* (TC), *grandis* (CK), *macrantha* (TCK), *pyramidata* (C),
Avenella	*flexuosa* (T),
Holcus	*lanatus* (C), *mollis* (C),
Aira	*caryophyllea* (C), *praecox* (C),
Subtribe Aristaveninae	
Deschampsia	*caespitosa* (TK),
Aristavena	*setacea* (TC),
Subtribe Alopecurinae	
Agrostis	*alpina* (TCK), *rupestris* (TCK),
Calamagrostis	*arundinacea* (TC), *canescens* (TC), *epigejos* (TCK), *pseudophragmites* (TC), *stricta* (TCK), *varia* (TC), *villosa* (TC)

Table 3. Subtribes, genera and species of the tribe Aveneae discussed in the present paper (classification according to Clayton & Renvoize 1986, modified). T (taxonomy), C (chorology), K (karyology) - mean which adequate problems have been discussed in relation to particular species.

(1974) *K. macrantha* is a excellent subject of studies on the ecotypic rather than on taxonomic variability. The occurrence of but two varieties have been recognized by the present author. They are different in pubescence. Var. *macrantha* is a frequent taxon characterized by pubescent sheaths and blades, while var. *glabra* Domin is a rare taxon with glabrous sheaths and blades (FREY 1993a and cited literature).

Three other representatives of the species are rather uniform in morphology and no infraspecific taxa have been distinguished in them. Slight morphological differentiation is phenotypic and partially physiological in nature. *Koeleria glauca* (Spreng.) DC. seems to be one of the less variable species of the genus. This species was described in 1801 as *Aira glauca* Spreng., but PERSOON (1805) did not include it among five species originally placed in the genus. It was transferred to *Koeleria* by CANDOLLE (1813). Some nomenclatural rather than taxonomic problems concern *K. grandis* Besser *ex* Gorski and *K. pyramidata* (Lam.) P. Beauv., however, they surely are separate species (FREY 1993a and cited literature; SZELĄG 1995).

Avenella (Bluff. & Fingerh.) Drejer

This small genus includes two or three species. Its separateness as a distinct taxonomical unit has been observed by various authors and at least four names have been simultaneously used: *Aira*, *Deschampsia*, *Lerchenfeldia* and *Avenella*. In contemporary literature *Avenella* has been included most often in the genus *Deschampsia*. The problem does not concern the nomenclature only, but rather correct classification on the base well-defined characters, so it is clear, that the genus has long be the subject of controversy with regard to its (seemingly) obscure systematic position. The name *Avenella* had appeared firstly as a name of section of the *Aira* (BLUFF & FINGERHUTH 1821-1823). In 1838 DREJER distinguished a new genus *Avenella* with one species - *A. flexuosa*. Recent morphological, anatomical, genetic and chemical studies support the former recognition of *Avenella* as a distinct genus and correct name of the type species should be *Avenella flexuosa* (L.) Drejer (FREY 1982, 1999 and cited literature).

Subtribe *Aristaveninae* Albers & Butzin

Deschampsia P. Beauv.

The genus includes about 40 species. It was separated in 1812 by PALISOT de BEAUVOIS. Formerly, species included in the *Deschampsia*, originally belonged to the *Aira* (LINNAEUS 1753). *D. caespitosa* (L.) P. Beauv. is variable species considered rarerly to be an undivided species or (most often) to have subspecies or a few varieties and forms. This great morphological differentiation appears probably as a result of modifying influence of the environment and hitherto distinguished taxa are not clearly genetically deliminated. The infraspecific division was based on characters concerning the plant height, the length and shape of the panicle, the appearance of leaves, the length and colour of spikelets, and the number of flowers in a spikelet. In the studied material two varieties have been distinguished: very common var. *caespitosa* and very rare var. *parviflora* (Thuill.) Richt., differing mainly in respect of the length of spikelets and number of flowers in the spikelet. Var. *parviflora* was described under the name *Aira parviflora* in 1790 by THUILLIER, who stressed the small size of its spikelets. This taxon is most often distinguished as a variety, and more rarely as a subspecies (FREY 1982 and cited literature). According to KAWANO (1963) var. *parviflora* can be regarded as a philogenetically advanced form, in accordance with the general scheme of morphological changes, i.e. a reduction in the number of flowers in a spikelet from 4 through 3 to 2 or 1, and a decrease in spikelet size.

Aristavena Albers & Butzin

The original diagnosis of *Aristavena setacea* was given by HUDSON (1872) who called it *Aira setacea*. Later, however, he considered this species to be a variety of *Aira montana*. HACKEL (1880) included it in the genus *Deschampsia* under the name *D. setacea*. BUSCHMANN (1948) presented a detailed characteristic of the species and verified its systematic position (FREY 1982 and cited literature). ALBERS AND BUTZIN (1977) excluded *D. setacea* from the genus *Deschampsia* and named it *Aristavena setacea* (Huds.) Albers & Butzin, placing it in the subtribe *Aristaveninae*. They stressed the fact that *Aristavena* differs clearly from *Deschampsia*.

Subtribe *Alopecurinae* Dumort.

Agrostis L.

It is one of 10 largest genera of the *Poaceae* and embraces ca 220 species (CLAYTON & RENVOIZE 1986; FREY 1997d). *Agrostis* is considered to be a morphologically complex genus. Different opinions exist with regard to its infrageneric division. The comprehensive reviews of its systematics has been published by BJÖRKMAN (1960) and ROMERO GARCIA *et al.* (1988). The genus was usually divided into groups either without taxonomic rank or into subgenera and sections. The most important basic features for infrageneric division are: structure of lemma, presence or absence of awn, length of palea and lemma/palea ratio. ROMERO GARCIA *et al.* (1988) divided *Agrostis* into subgen. *Agrostis* (with sections *Agrostis*, *Vilfa*, *Aperopsis*) and subgen. *Zingrostis*. The two discussed species (Table 3) were included in the first section of subgen. *Agrostis* (FREY 1997a and cited literature).

Agrostis rupestris All. has often been confused with *A. alpina* Scop. However, in the present author's opinion there is no doubt that they are separate species. Three key characters differing them have been established: length of spikelets (longer in *A. alpina*), panicle branches (almost smooth in *A. rupestris*, aculeolate in *A. alpina*), and upper/lower glume ratio (greater in *A. rupestris*). *A. rupestris* is fairly uniform morphologically. Sometimes the varieties have been distinguihed, e.g. var. *straminea* (with light yellow or light green spikelets) or var. *rupestris* (tetraploid $2n = 28$) and var. *pyrenaica* (diploid $2n = 14$) in which the differences are inconspicuous and refer mainly to anther length (longer in diploids) and stomata (longer in tetraploids). *A. alpina* is one of the least variable species of the genus. Generally no infraspecific taxa have been distinguished within it except var. *aurata* (with light yellow spikelets), probably without taxonomical value (FREY 1997a and cited literature).

Calamagrostis Adans.

The genus belongs to 10 largest genera of *Poaceae* and comprises more than 250 species (CLAYTON & RENVOIZE 1986; FREY 1997d).

The taxonomical problems in *Calamagrostis* are considered to be most difficult in grasses. This complexity is due to extensive interspecific hybridization and polyploidy very often resulting formation of the apomictic complexes, e.g. *C. lapponica*, *C. chalybaea* and *C. purpurea*. Because of considerable morphological variability of the genus the limit between *Calamagrostis* and close related genera (*Agrostis* and *Deyeuxia*) is rather obscure. In numerous infragegeric systems *Calamagrostis* have been divided into subgenera and sections. The hybridization in the *Calamagrostis* is very common and numerous hybrids have been recorded both between species of a single section, and between species of different sections. They are predominantly sterile, but vigorous and steady because of the vegetative reproduction. Their total number in the genus reported by various authors ranged from 15 to 28 (FREY & PASZKO 1999 and cited literature).

The species under discussion (Table 3) have been included in three sections sensu TSVELEV (1965). The species of the *Pseudophragmites* section (*C. epigejos* and *C. pseudophragmites*) are characterized by 3-veined lemma while the species of the sections *Calamagrostis* (*C. villosa* and *C. canescens*) and *Deyeuxia* (*C. stricta*, *C. arundinacea*, *C. varia*) have 5-veined lemmas. The differences between species in particular sections concern first of all: length and place of insertion of the awn, callus hairs, and presence or absence of the prolongation of spikelet rachis (FREY & PASZKO 1999 and cited literature).

Chorology

The representatives of the *Aveneae* typically enough for the majority of grasses with festucoid features are distributed mainly in the temperate zone of the northern (rarely southern) hemisphere and in the mountains in the tropics. They represent three geographical elements (Table 4) (FREY 1993b and cited literature).

Subtribe *Aveninae*

Avenula (Dumort.) Dumort.

The commonest species of the genus *Avenula pubescens* has Eurasiatic, markedly disjunct geographical distribution. In Europe the species extends from the British Isles and northern Spain in the west, eastwards to the Ural, with some isolated and disjunct localities near the Black Sea and in Greece. In Asia it occurs in the montane regions of Central Siberia and northern Mongolia. Besides, the species has been recorded from Iceland and North America as an introduced (FREY 1991b and cited literature).

In Poland *Avenula pubescens* is quite common in the southern and central part of the lowlands becoming fairly rare to the north and in the mountains where it has been recorded from several ranges in the Sudety Mts. and

Circumpolar:	*Koeleria macrantha, Calamagrostis stricta*;
Eurasiatic:	*Koeleria glauca, Trisetum sibiricum, Avenula pubescens, Deschampsia caespitosa, Avenella flexuosa, Calamagrostis arundinacea, C. canescens C. epigejos, C. pseudophragmites*;
European:	*Koeleria gracilis, Trisetum flavescens, T. alpestre, T. fuscum, Avenula planiculmis, A. versicolor, A. pratensis, Ventenata dubia, Avena strigosa Aristavena setacea, Holcus mollis, H. lanatus, Aira caryophyllea, A. praecox, Agrostis rupestris, A. alpina, Calamagrostis varia, C. villosa*

Table 4. The species divided into geographical elements

Carpathians. In the mountains it was firstly found by PAWŁOWSKI (1949), and this locality has been rediscovered almost 30 years later by the present author (FREY 1991b).

According to HOLUB (1977) the distribution of *Avenula pratensis* is still questionable. In his opinion it is a sub-oceanic European species with eastern controversial boundary running from St. Petersburg, through the Baltic countries, the vicinity of Kaliningrad, central Poland, the Czech Republic and Slovakia, to eastern Austria. It does not occur in the eastern Ukraine and Hungary, although SOÓ (1973) reported it from that country. On the other hand, SAUER and CHMELITSCHEK (1976) gave their own interpretation of the range of the species which is similar to that given by MEUSEL *et al.* (1965). The fundamental difference, however, is its absence in the Alps, former Yugoslavia and Romania.

The geographical range of *Avenula planiculmis* is still insufficiently known. It grows, undoubtedly, in the Sudetes and West Carpathians, but it does not occur in the Alps at all. The data concerning its occurrence south of Danube are questionable. It has erroneously been recorded from Austria and Siberia, and data on its distribution in northern Asia Minor are still obscure (FREY 1991b and cited literature). *A. planiculmis* had originally a much broader range subsequently reduced during the Pleistocene glaciations and it survived only in the montane refugia in Central Europe and in Scotland (Isle of Arran) where it has the northernmost locality (SAUER & CHMELITSCHEK 1976). In Poland it has only one documented locality in Tatras given by PAWŁOWSKI (1925), but there are several records in the lowlands restricted, however, to the forelands of the West Carpathians [var. *hispidula* (Zap.) Frey]. Thus, *A. planiculmis* can be included in the group of the so-called entire relics of the West Carpathians origin (FREY 1991b and cited literature).

The typical montane *Avenula versicolor* has its localities in the mountains of the whole Europe including the Pyrenees, Alps, Appenines, Balcan Peninsula mountains and the Carpathians. It does not grow in the British Isles and Scandinavia, and its occurrence in the Caucasus is doubtful (FREY 1991b and cited literature).

Avena L.

Recently, the geographical range of *Avena strigosa* is evidently diminishing and considerable part of the data on its occurrence is probably now of a historical value only. The northern and western boundaries of its distribution are unquestionable, whereas the eastern and partially southern limits are fairly obscure, mainly due to scarcity of herbarium material (Fig. 2). The eastern limit reaches the Ural Mountains, and runs southwards and southwestwards, crossing the south-eastern territories of the former Soviet

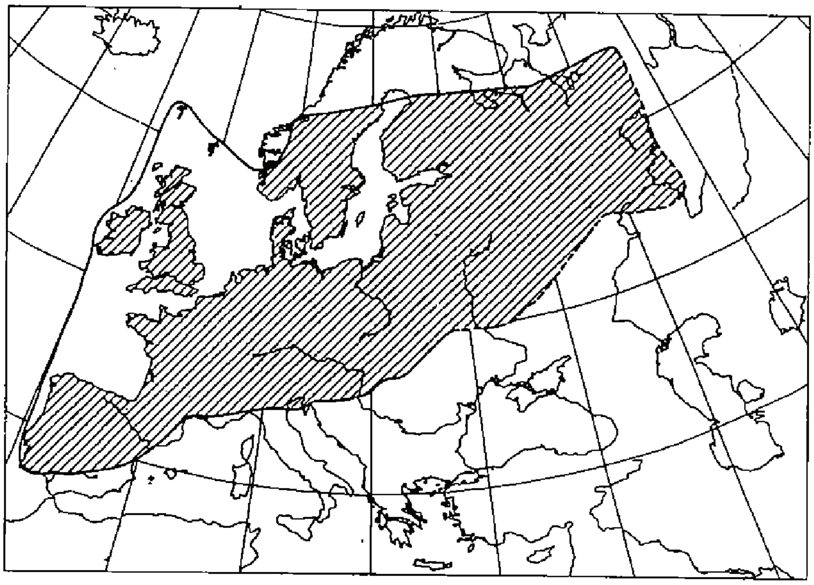

Fig. 2. Distribution of Avena strigosa Schreb. in Europe (according to Frey 1991c)

Union. In the south the occurrence of *A. strigosa* is problematic or doutful in the Crimea, Romania and former Yugoslavia. The boundary of distribution runs probably along the Yugoslavian-Romanian border with Hungary, where the species is certainly known to occur. The information on its occurrence in Hungary was given by NYMAN (1878-1882) and JÁVORKA (1925) and confirmed by the present author on the base of herbarium studies. However, most of the specimens were collected by the end of the 19th and the beginning of the 20th century. According to Dr. Horanszky (University of Budapest - personal communication) the expansiveness of *A. strigosa* has increased in Hungary during the years 1983-1985. The species occurs in the northern Italy whereas it has been absent from the southern part of the country, so the southern limit should approximately run along Po river, to the French border up to the mouth of the Rhône river (FREY 1991c and cited literature).

Trisetum Pers.

The range of *Trisetum flavescens* covers the whole Europe, although it is rare in the Iberian, Balcan and Scandinavian Peninsulas. Its occurrence was noted in the western part of the northern coast of Africa. On the other hand, it is absent in the North (the Faroes, Iceland and Spitsbergen). In North America it was introduced from Europe (FREY 1992 and cited literature). In Poland it occurs frequently in southern and central part of the country, and rarely in the north, especially in the north-eastern regions, where it was confused with *T. sibiricum*. For a long time *T. flavescens* has been unknown from the Tatra Mts. It was recorded only from the foothills of the Tatras (PAWŁOWSKI 1930).

Trisetum sibiricum is widely distributed throughout Asia. It was found also in North America (Alaska). In Europe its occurence is restricted to eastern part of the continent (northern, central and south-western areas of the European part of the former Soviet Union, Poland and probably Yugoslavia and Romania); in south it does not exceed latitude 50OS. In the north-eastern Poland the species reaches western limit of its distribution (FREY 1992 and cited literature).

The two remaining species are montane plants. *Trisetum alpestre* is a typical alpine plant. It has two main centres of distribution in Europe: the Eastern and the Southern Alps and the Carpathians. Besides, two localities are known beyond the limits of distribution - Mt. Cenis (Western Alps) and

Montenegro. In Poland the species occurs in the Tatra Mts. (mainly western part), but it was also observed in the Pieniny Mts. as a relic population, and - unexpectedly - in the Pieniny Klippen Belt - only one locality (FREY 1985). *T. fuscum* is a Carpathian endemic. Two other localities reported from Austria (Tyrol) and Montenegro were not confirmed later. In the Polish Tatra Mts. the species is fairly rare and only 22 localities were found. It is the plant of inconsiderable power of expansion, strongly connected with its habitat and for this reason potentially threatened (FREY 1992 and cited literature).

Ventenata Koeler

Ventenata dubia (Leers) Coss. occurs mainly in the south of Europe. Its geographical range is disjunct and recently diminishing. In the western part of the continent (Portugal and Spain) and in Switzerland and France the species is fairly rare. In Italy it occurs mainly in the northern and central parts of the country. Though *V. dubia* has been found in the central part of Germany, in its eastern part it is considered to be an endangered plants. The species is fairly frequent in Austria and in southern regions of the Czech Republic, Slovakia and Hungary. Its most frequent and most abundant localities has been reported in the Balcan Peninsula (from Slovenia to Bulgaria). Probably its northernmost locality in Europe there is in Belgium. In Poland *V. dubia* was reported from only five localities, unfortunately all of historical value, not confirmed recently (FREY & PASZKO 1998 and cited literature).

Koeleria Pers.

Koeleria glauca has an Eurasiatic geographical distribution from Central Europe (Germany) to Central Asia (environs of the Lake Baikal), between latitudes 450N and 600N. In Europe it is absent from the north (Norway, Finland, Iceland), south (Italy, Greece, Bulgaria) and west (Portugal). It does not also occur in the mountains. In Germany it is considered to be a much endangered species and in former Czechoslovakia it is considered to be a rare species (FREY 1993a and cited literature). According to MEUSEL *et al.* (1965) and STACE (1991) the species is absent from the British Isles, whereas it was recorded from there by HUMPHRIES (1980).

Koeleria macrantha is a circumpolar species occurring mainly in Eurasia and North America. In Asia it is widely distributed in western and central part of the continent. In North America it occurs in Canada and United

States except for south-eastern part of the continent. The species is fairly widespread in the central Europe; it is absent from the Iberian and Scandinavian Peninsulas as well as Azores, Sardinia, Corsica and Sicilia. As a synanthropic plant it has been recorded from Central and South Africa, New Zealand and South America (FREY 1993a and cited literature).

The geographical range of *Koeleria grandis* covers a part of Central and Eastern Europe and in Poland it reaches its western limit. The species is infrequent in the Ukraine, Belorussia, Lithuania, Latvia and Estonia. In Russia it has been recorded in the environs of St. Petersburg and Arkhangelsk (it is uncertain whether the plants from there should be included in this species) and in the east as far as Moscow. However, the eastern limit has not been definitely determined for the reason of lack correct data from the environs of the Russian capital (FREY 1993a and cited literature) (Fig. 3). There are different opinions dealing with the present range of *K. grandis*. SZAFER (1919) is of the opinion, that it is a migratory relic which moved with pine from its Volhynian refuge, where it survived through the glacial epoch, towards

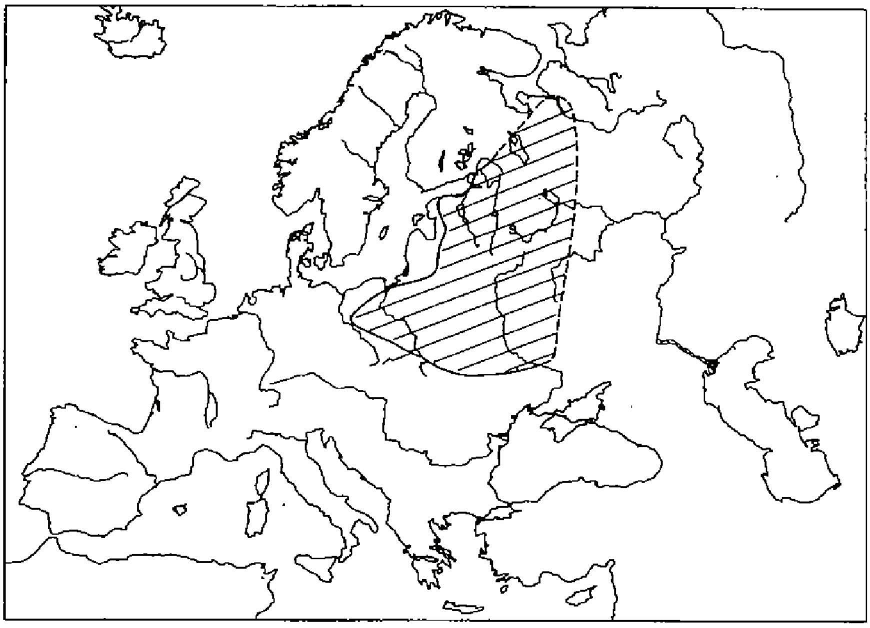

Fig. 3. Distribution of Koeleria grandis Bess. ex Gorski in Europe (accordind to Frey (1993a)

the north as far as Arkhangelsk after retreat of the ice cover. According to TSVELEV (1979) the occurrence of *K. grandis* in the north of Russia and the Baltic region is the result of its hybrid origin, because the species is a hybrid between western *K. pyramidata* and eastern *K. delavignei*. When the subsequent climatic changes wasted northern and north-western populations of both parental species, *K. grandis* as a hybrid with a greater expansion abilities gained a wide distribution range.

Because *Koeleria macrantha* and *K. glauca* are often confused with *K. pyramidata*, its correct geographical range, especially in the east, is still dubious. In the opinion of DOMIN (1907) and ZIMMERMANN (1965) the eastern limit of its range does not exceed beyond Germany. On the other hand, according to HUMPHRIES (1980) and CONERT (1987) *K. pyramidata* reaches farther to the east and its range covers Lithuania, Latvia, Estonia, Belorussia, Poland, Romania, Bulgaria, the Ukraine and the part of Russia. In the course of studies of the present author on the genus *Koeleria* in Poland no material of *K. pyramidata* in Poland were found. However, two years later SZELĄG (1995) gave three localities of this species in the western Poland. It is in accordance with opinions of RACIBORSKI and SZAFER (1919) and SZAFER *et al.* (1953) who reported that this species reaches its north-eastern limit of distribution in the west Poland.

Holcus L.

According to HULTÉN and FRIES (1986) *Holcus lanatus* L. should be included in the group of circumpolar plants, but native for continental part of Europe. The northernmost but synanthropic localities of the species have been reported in Iceland. In the west it reaches the Canary Islands and Azores. Its eastern limit of distribution attains 500E, and southern limit runs along the seashore of the Mediterranean Sea. Outside the European continent it occurs as a synanthropic plant in Southern Africa, Central and South America, eastern and southern Asia as well as in Australia and New Zealand.

The geographical range of *Holcus mollis* L. covers mainly eastern and central Europe. Its northern limit runs along the southern Finland, however in general, it is rare in the countries of the Baltic Sea basin. For example, in Lithuania it was placed in the red book of plants as endangered species. In the south of Europe it is fairly frequent (the Ukraine, the Czech Republic, Romania, Bulgaria and former Yugoslavia) (FREY & KUŻDŻAŁ 1996 and cited literature). The opinions about its occurrence in the Iberian Peninsula, in Italy and Switzerland vary widely. PIGNATTI (1982) and HULTÉN and FRIES (1986) give the species from the whole Italy whereas according to MEUSEL *et al.* (1965) *H. mollis* does not occur in the north-eastern and southern areas of the country. In the Iberian Peninsula PALHINHA (1939) and MEUSEL *et al.* (1965) note it only in the central and northern Portugal, whereas HULTÉN and FRIES (1986) reported the species in the whole country. It is interesting that MEUSEL *et al.* (1965) does not report this species on the large territory of Switzerland, although WELTEN and SUTTER (1982) and HULTÉN and FRIES (1986) give it from there. Both species are rare in the Tatra Mts. and only few localities have been found hitherto in Poland and Slovakia.

Aira L.

Aira praecox L. is a subatlantic species. It occurs in the estern and central Europe, in the British Isles and in the Scandinavian Peninsula (western and northern parts) as well as in the Canary Islands and Azores. The species is very rare in Italy, the Czech Republic and Lithuania where it grows only in the coast of the Baltic Sea. It was not found in the South of Europe. The localities from the Crimea, Greece and Dalmatia are doubtful or erroneous. *A. praecox* has been recorded as an introduced plant in North America and in South Africa (FREY 1994 and cited literature).

The distribution of *Aira caryophyllea* L. is centred on Europe and covers the western, central and southern parts of the continent, ranging from Portugal and Spain throughout France, Switzerland and Italy to Denmark and Germany (in Mecklenburg, Schleswig-Holstein and Saxony it has been placed in the category of endangered species). It occurs also in the British Isles and on southern coast in Sweden (Fig. 4). Data dealing with the occurrence of *A. caryophyllea* in the east are often doubful or erroneous and sometimes even impossible to credit. For this reason the western, northern and southern boundaries of its distribution are clear, but the eastern limit remains undefined. According to the present author the northern part (Poland, Slovakia) of the eastern limit does not extend beyond long. 210E. In central part (Hungary, Croatia) it runs appromaximately south-east, reaching long. 150E. In Hungary it occurs mainly in localities west of the Danube. A single stand in the eastern part of the country has been questionably reported in the

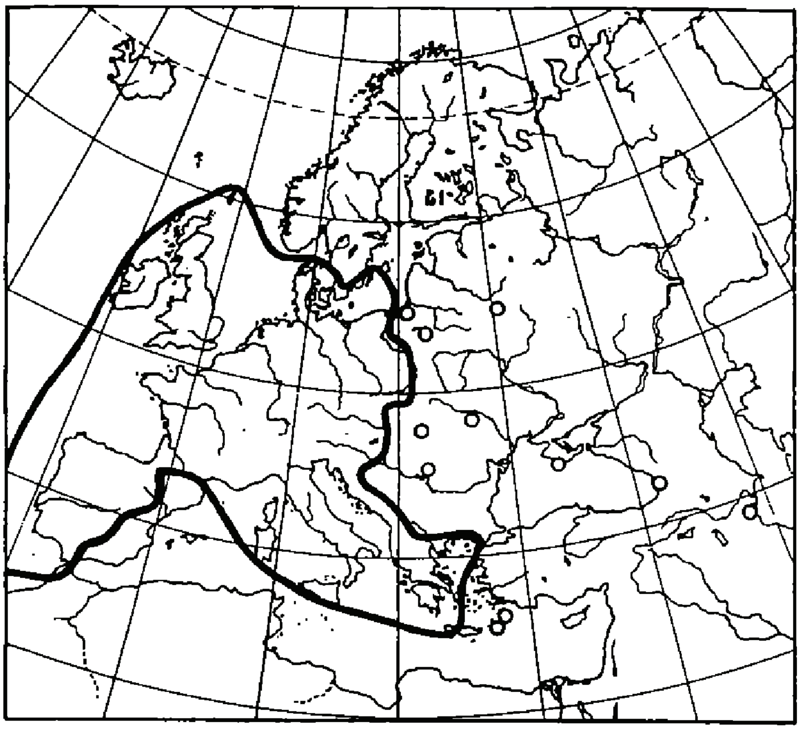

Fig. 4. Distribution of Aira caryophyllea L. in Europe. Open circles – literature records of historical interest (according to Frey 1997b)

vicinity of Debrecen (JÁVORKA 1924; SOÓ 1973). It has not been confirmed recently (Dr. D. Kováts - Budapest, personal communication). In its southern part the eastern limit of the species extends to long. 270E. The localities beyond the undisputed eastern limit are scattered and in the majority of cases, of historical interest only. Within its area of distribution *A. caryophyllea* appears to be scattered and rare near its eastern limit (FREY 1994, 1997b and cited literature).

Subtribe *Aristaveninae*

Aristavena Albers & Butzin

Aristavena setacea occurs along the northern and north-western coast of the European continent, in the British Isles and in the Scandinavian

Peninsula (Skania). The problem of its occurrence in the south-eastern Europe, especially on the territory of Poland, is interesting and obscure. *A. setacea* was reported from there, namely from the Pomerania and Dolny Śląsk (Lower Silesia), in the 19th and in the beginning of 20th century. These localities were often cited by various authors in the botanical literature, however they has been not confirmed by the present author's field searching. The species is now considered to be extinct in Poland and its stands are of the historical interest only. Thus, the southeasternmost, individual localities of this species lying beyond its geographical range should be presently located in the territory of Germany (FREY 1982, 1993c, INGELŐG *et al.* 1993)

Subtribe *Alopecurinae*

Agrostis L.

Agrostis rupestris occurs mainly in the mountains of Central and Southern Europe. There are four main centres of its distribution: the Pyrenees, the Alps (fairly frequent), the Carpathians (frequent) and mountains of the Balkan Peninsula (widely scattered). Minor centres are the mountains of Central Spain, the Massif Central, Šumava Mts. and the Sudetes. MEUSEL *et al.* (1965) claim that *Agrostis rupestris* is distributed in the whole of the Italian Peninsula, whereas PIGNATTI (1982) reported this species in common only in the Italian Alps and rare in the northern part of the Appenines. Most probably its southernmost localities have been recorded in central Italy. Pignatti's opinion was confirmed by the present author's investigations (FREY 1997a and cited literature).

The precise geographical range of *Agrostis alpina* is still not fully known. It occurs in the mountains of Central and Southern Europe: the Alps (frequent), the Pyrenees, the northern part of the Appenines (exclusively in their northern part), the Sudetes, the Carpathians and mountains of the Balkan Peninsula (in all these groups it is rare). The northernmost localities of *A. alpina* are in the eastern Sudetes, but it has not been found in the Karkonosze Mts. (FREY 1997a and cited literature).

Calamagrostis Adans.

The representatives of the genus occur mainly in temperate zones of both hemisperes, exceptionally in colder regions in the North and in the South as well as in tropical mountains (FREY & PASZKO 1999 and cited literature). According to TATEOKA (1974) there are two centres particularly rich in species of *Calamagrostis*, namely the northern part of South America and the south-eastern Asia where most of them are endemic. Although the diploid cytotype has not been detected, it would seem possible to find it in the latter area. This author claims that the genus originated probably in the Palaeocene, or even in Cretaceous on the uplands the paleotropical or paleosubtropical zones. In Eurasia it must have existed at least in the late Miocene period. The species under discussion (Table 3) have mostly Eurasiatic rarely circumpolar and European distribution (Table 4) (FREY & PASZKO 1999).

Karyology

Species under discussion are characteristic by having relatively large chromosomes, with basic chromosome number x = 7. The may be divided into three groups according to their karyological differentiation. First group - species slightly differentiated, which have one chromosome number in the whole area of distribution (e.g. *Koeleria glauca*, *Trisetum sibiricum*, *T. alpestre*, *T. fuscum*, *Agrostis alpina*), the second - species medium differentiated, with two or three chromosome numbers (e.g. *Trisetum flavescens*, *Koeleria grandis*), and the third one - species strongly differentiated, with many chromosome numbers (e.g. *Avenula pratensis*, *Koeleria macrantha*, *Calamagrostis epigejos*). However, the most common numbers are $2n$ = 14 and 28 (FREY 1993b and cited literature).

Avenula (Dumort.) Dumort.

The genus has been infrequently subject to karyological study and there are some species for which chromosome numbers are still unknown. The basic number is x = 7 and the most frequent multiples thereof are $2n$ = 14 and $2n$ = ca 120. Some accessory chromosomes have also been observed.

Avenula pubescens is fairly uniform in respect of karyology and $2n$ = 14 is the most common chromosome number reported by various authors. The different chromosome numbers etablished are $2n$ = 15, 20 and 28. Some accessory chromosomes (2-4) have been noted. In the course of detailed analysis of the karyotype one pair of chromosomes with a median centromere have been observed in which occurred the secondary constriction (FREY 1991b and cited literature).

The counting of the chromosomes of *Avenula pratensis* and *A. planiculmis* is very difficult because of the high number. In the former the commonest number is $2n$ = 126. Quite a few lower and higher chromosome numbers, including $2n$ =

84, 98, 105, 112, 126, 133, ca 136 and 146 havebeen also recorded and described as cytotypes from different mountain ranges in Europe. The accessory chromosomes (1-3) were also observed. The numbers $2n$ = 14, 28 and 42 given for this species are incorrect and concern other species of the genus. In *A. planiculmis* the numbers betwen 120 and 126 were recorded sometimes with two accessory chromosomes (FREY 1991b and cited literature).

Trisetum Pers.

More than a half of the species of the genus were studied with respect to the chromosome number, and a karyological differentiation was noted. The most frequently recorded chromosome numbers are $2n$ = 14, 28, 42 and 56. However the karyological differentiation of particular species is fairly rare. Exceptionally, two or more chromosome numbers have been found in *T. distichophyllum*, *T. flavescens* and *T. spicatum*. For the first time the idiograms of four species were made by the present author and following karyotype formulas were determined according to the terminology given by LEVAN *et al.* (1964-1965): *Trisetum sibiricum* $2n$ = 14; 10 M 4 sm, *T. flavescens* $2n$ = 24; 8 M 14 m 2 sm, *T. alpestre* $2n$ = 14; 6 M 8 m, *T. fuscum* $2n$ = 28; 6 M 22 m. Besides the chromosome number of *T. macrotrichum* (endemic of the East Carpathians) $2n$ = 56 (FREY 1991a, 1992 and cited literature).

The studies of *Trisetum flavescens* karyotype showed two chromosome numbers: $2n$ = 24 and 28. AVDULOV (1931) recognized the tetraploid cytotype $2n$ = 24 as derivate of the cytotype $2n$ = 28 as a result of the loss of two chromosome pairs. According to him the diploid number $2n$ = 12 ought to have existed though, its dicovery is doubtful, because a multiple of the number 6 in the *Poaceae* is very rare. However, the number $2n$ = 12 was detected by SOKOLOVSKAYA and PROBATOVA (1975) in *T. flavescens* var. *parvispiculatum*. The existence of the diploid number shows the tendency towards reducing the basic number in the genus *Trisetum* and AVDULOV (1931) suggests this genus has at least two basic numbers x = 6 and 7. Diploid cytotype is recognized as a putative parental form of *T. flavescens* var. *flavescens* (SOKOLOVSKAYA & PROBATOVA 1975).

Koeleria Pers.

Contrary to *Trisetum* the genus *Koeleria* has been thoroughly karyologically studied, and the chromosome numbers for many, especially for the European, species are already known. *Koeleria* is karyologically differentiated, and in some species (e.g. *K. macrantha*, *K. vallesiana*) a conspicuous diversity in chromosome number has been detected.

In *Koeleria macrantha* a number of chromosome cytotypes has been detected, and the commonest cytotype is $2n = 14$. It occurs in the whole range of the species and has been recorded in many areas in Europe and North America. A more infrequently recorded tetraploid cytotype $2n = 28$ has been found mainly in Europe and in western part of North America, as well as in the Far East and Africa. The higher chromosome numbers $2n = 42$, 56, 70 and 84 have been recorded sporadically in Europe and North America (FREY *et al.* 1977, 1993a and cited literature). There are different opinions whether all ploidy levels refer to one species only or not. In the opinion of UJHELYI (1961) the genuine *K. macrantha* (= *K. gracilis*) is diploid $2n = 14$. BAJON (1989) claims that it includes di-, tetra- and hexaploids. According to SOKOLOVSKAYA and PROBATOVA (1975) a number 14 is characteristic of *K. cristata* subsp. *mongolica,* whereas subsp. *cristata* is tetraploid (28). ROBERTSON (1974) noticed a certain dependence in the occurrence of di- and tetraploids on the respective environment conditions, whereas LOOMAN (1978) who found tetra- and hexaploids and recognized the subspecies of the discussed species, did not notice any correlation between particular taxa, chromosome numbers, and environmental conditions.

The information on karyology of *Koeleria grandis* are ambiguous, and three completely different chromosome numbers were hitherto given: $2n = 56$ (UJHELYI 1962), 14 (KALENICHENKO 1977) and 70 (DMITRIEVA & PARFENOV 1991). It seems, that the occurrence of three chromosome cytotypes within fairly morphologically uniform species is dubious. The results by the present author $2n = 70$ (FREY 1993a) agree with those by DMITRIEVA and PARFENOV (1991), however the karyological differentiation of the species could be confirmed only on the base of comprehensive studies from its whole geographical range.

Deschampsia P. Beauv.

The observation of the karyotype of *Deschampsia caespitosa* showed two pairs of chromosomes with a median centromere, five pairs with submedian, and six pairs with centromere position difficult to define. The commonest and very interesting number $2n = 26$ has been reported from various territories. Besides some other aneuploid and euploid numbers were established, but frequently close to 26, e.g. 24, 25, 27 and 28. Unexpectedly $2n$ = ca 39 was recorded in Canadian material determined as *D. caespitosa* var. *caespitosa*. B-chromosomes (1-7) has also been found in the species (FREY 1982 and cited literature).

According to SOKOLOVSKAYA and PROBATOVA (1979) $x = 13$ is the basic number of probably amphiploid *Deschampsia caespitosa*. On the other hand, KAWANO (1963) is of the opinion that the basic number for the species is probably $x = 7$, in spite of the appearance of the number $2n = 26$ resulted from the loss of one chromosome pair. He claims that in *D. caespitosa* the process of cytological evolution takes place starting with ancestral original forms with $2n = 14$, through duplication to $2n = 28$ forms, then through further reduction (28 to 26) and reduplication (26 to 39 and to 52). This assumption was confirmed by ALBERS (1972) especially with reference to the origin of $2n = 26$ through reduction.

Subtribe *Alopecurinae*

Agrostis L.

Out of 220 species about the half has been studied karyologically. In the northern hemisphere occur all the known diploids and the majority of the tetra- and hexaploids. South of the equator only a few tetra-, hexa-, octo- and decaploids have been recorded. The chromosome numbers in *Agrostis* species are relatively stable. Infraspecific karyological differentiation has been found in a mere 21% of the species reviewed, the remaining being karyologically uniform. Only in several taxonomically complex species, usually widely distributed, has karyological differentiation been observed and a polyploid range from di- to octoploid established. B-chromosomes (1-10) have been found in 17 species (FREY 1997c).

In *Agrostis rupestris* diploid ($2n = 14$) and tetraploid ($2n = 28$) cytotypes have been established, differing in their geographical ranges and taxonomic rank (var. *pyrenaica* and var. *rupestris* respectively). In addition, aneuploid chromosome numbers $2n = 17\text{-}22$ and triploid $2n = 21$ have been detected. Accessory chromosomes (1-3) have been found in di-, tri- and tetraploids as well as in diploid *A. alpina* which is karyologically uniform (FREY 1997a and cited literature).

Calamagrostis Adans

In *Calamagrostis* the great morphological variability accompanies a karyological differentiation. The chromosome numbers reported hitherto range from $2n = 28$ to 140. Most frequent is the tetraploid number (28), a little rarer are hexa- and octoploid numbers (42, 56) and the high numbers (84-140) are very rare. The most karyologically differentiated species are: *C. epigejos* ($2n = 28$, 42, 56, ca 70), *C. inexpansa* (28, 56, 70, 84-105) and *C. purpurea* (28, 42, 56, 84). The very high chromosome numbers has been found in *C. lapponica* (98-112, 91-140, ca 120), *C. stricta* (ca 104, 114, 116, 119, 123, 129), and *C. crassiglumis* (140). B-chromosomes have been reported in many species at various ploidy level (FREY & PASZKO 1999 and cited literature). The diploids are not known, indicating that *Calamagrostis* is quite old genus and polyploidization occurred early in its evolutionary development (HAVENS & HOLLAND 1998).

Final remarks

The present review showed that problems concerning taxonomy, chorology and karyology of discussed representatives of the tribe *Aveneae* are interesting, complex and controversial. It confirmed also, that the placement of these taxa in *Aveneae* is fully justified. Nevertheless, the relationships between members of the tribe, their variability, karyological differentiation and distribution need further, comprehensive, or sometimes, complementary studies.

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