TAXONOMIC STUDIES IN THE GENUS

POA L. (GRAMINEAE)

J.R. EDMONDSON

Submitted for the degree of Ph.D., 1975.

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STATEMENT.

The accompanying thesis submitted to the University of Leicester for the degree of Doctor of Philosophy, entitled:

"Taxonomic studies in the genus Poa L. (Gramineae)"

is based on work conducted by me in the Department of Botany of the University of Leicester mainly during the period between October 1st, 1970 and September 30th, 1974.

All the work recorded in this thesis is original unless otherwise acknowledged in the text or by references. None of the work has been submitted for another degree in this or any other Univesity.

(Signed) J R Edmondson.

T. G. Tutin

INTRODUCTION

The aim of my study of the genus Poa has been to assemble information on the systematics of the genus which has particular relevence to its classification into sections.

A sectional classification of Poa throughout the world could only be based on a monographic study of the genus as a whole. The number of species of Poa world-wide can be estimated very roughly at 500; it would have been unrealistic to have set out to make detailed observations on all of these, even if material had been available, since the species of Poa in many regions of the world are not yet at all well known and their taxonomy is in a very fluid state. It was therefore decided to confine my research exercise to the European species first of all, later including those species from outside Europe (mainly from western Asia) which were most closely related to the European species and which could be allocated to the sections of Poa which were represented in Europe. By revising the taxonomy of Poa during the preparation of the "Flora Europaea" account of the genus, a sectional classification was produced which was founded on a single person's interpretation of the limits of the species; previous classifications have suffered, among other problems, from the authors' inadequate familiarity with the characteristics of the species which were being classified, particularly where these fell outside the geographical area covered by the flora in question.

The work proceeded through three phases. The first involved becoming familiar with the compendious literature on grasses in general, and Poa in particular, extracting information on the

distribution of the European taxa, their diagnostic features, and their taxonomic limits. Literature which was found to be particularly useful for gaining an entry to the relevent publications on Poa included the Standard and Basic Floras list provided by Flora Europaea; Index Kewensis; Biological Abstracts; Fedorov's compilation of chromosome counts; Metcalfe's 'Anatomy of the Monocotyledons - Gramineae'; and the bibliographies of papers on Poa in Professor Tutin's collection of reprints.

The second phase comprised the task of studying taxonomic characters on the specimens themselves. The choice of characters was determined partly on the basis of the traditional ones used in the Floras which had been consulted, partly through extending the survey of some more recently recognized characters to groups where these had not yet been investigated, and partly by evaluating features which were not previously considered to have systematic importance. Most of the observations made in herbarium material at Leicester were needed in order to survey characters through the genus as a whole which were previously reported as useful in the systematics of certain groups only.

The herbarium of the Botany Department of the University of Leicester contains a medium-sized but reasonably representative collection of European material, as well as a rather large quantity of British material which was of little use to me in my work. To obtain for study a greater number of specimens of the less widely distributed European species, the Poa collection from the herbarium of the Botany Department of the University of Liverpool was obtained on loan, and to fill certain gaps smaller numbers of specimens were borrowed from herbaria at Brussels, Cambridge, Edinburgh, Kiev, London (British Museum, Natural History),

Manchester, Munich, Geneva, Paris and Sofia. In the course of my travels abroad I visited some of these, and other, herbaria and in most cases the plants loaned to me from abroad were selected by me during one of my visits. I visited the following herbaria: Geneva, Istanbul (ISTF, ISTE), Madrid, Munich, Paris, Tehran (IRAN), and Vienna (W). Fuller details of loans, with herbarium abbreviations following the latest edition of Index Herbariorum (ed. Holmgren & Keuken, 1974) are given in appendix 3. The results of this work form the main body of the thesis.

At this stage, I experimented with some new techniques. I had built up a collection of living material of Poa in the Botanic Garden of the University, situated at Oadby; some of the plants were grown from seed sent from various Botanic Gardens, while others were collected either as plants or as seed in the wild by myself and by some of my colleagues and contacts. The availability of fairly large quantities of material of certain species enabled certain techniques to be used which were too demanding or destructive of material to be suitable for use on herbarium specimens. My main experimental project was an investigation of the flavonoid content of leaf extracts, using two-dimensional paper chromatography; as no useful results were obtained from this work, no account of this work will be found in the thesis. I would endorse the views which were expressed by Weimarck (1972), which I can summarize as taking a sceptical view of the value of numerical indices of similarity between sets of chromatographic data (the most usual method of analysis) in providing a measure of the affinities of different taxa. The difficulty of analyzing the flavonoid data was that no level could be found at which there was a sufficient uniformity of content to allow chemically-defined taxa to be recognized.

Comparisons were made at various taxonomic levels; between sections, between species of the same sections, within species (different gatherings) and between different plants grown from seed from a single gathering. While, as might have been expected, the patterns of flavonoids were generally less similar to one another in the first of these categories, no basis for comparison could be established which rested on a fixed range of characters (characters in this instance being equivalent to spots showing identical RF and colour of fluorescence under UV light both before and after having been treated with ammonia fumes). Some of the more frequently occurring flavonoid spots were partially characterized by IR spectoscopy; many of the most variable spots proved to be derivatives of tricin in which different sugar groups were substituted for one another. Since the object of the investigation was to obtain chemotaxonomic data, my wish not to become deeply involved in the chemistry of the substances concerned led to the approach being abandoned.

Towards the end of my period of research, a Mini-SEM scanning electron microscope was acquired by the E.M. section of the School of Biological Sciences. Scanning electron microscopic studies of the surfaces of lemmas and of caryopses were commenced as soon as the instrument's teething troubles had been overcome, and some useful preliminary impressions were obtained from the lemma surfaces though not from the caryopses. The opportunity came too late to be exploited as a means of establishing new characters, but the technique can be recommended as a future topic for an undergraduate project, as both the material and the means are readily available.

The third phase of my work was the preparation of a draft account of the European species of Poa for eventual inclusion in volume 5 of 'Flora Europaea', the Stage I copy of which was produced on October 5th, 1973. After editing, the Stage II ms. was issued

on January 21st, 1974 and at the time of writing the account is in the hands of the regional advisers to the Flora Europaea organization. Since this account forms a statement of my views on the systematics of the European species of Poa, it is appended to my thesis; appendix 1 contains the Flora Europaea account in a form close to that in which it will appear in the Flora, but with the omission of sectional diagnoses (which can be found in chapter 1), ecological statements (which are of very little value in relation to the present work) and biosystematic data (which are presented in chapter 4, table 1). Although I take full responsibility for the account in its present form, it should be noted that this is an edited version of my original work, and has been checked, commented upon and amended by the editorial board of the Flora and by several of its regional advisers.

In the account which follows, chapter 1 contains the main conclusions of my thesis, which proposes a new classification of the European taxa of Poa at the level of sections, and chapter 2 presents additional conclusions regarding taxonomic changes below the sectional level. Chapter 3 gives an account of my conclusions on the question of the treatment of agamospermic and proliferating taxa, a problem peculiar to a relatively small number of angiosperm genera although particularly widespread in the Gramineae. Chapters 4, 5 & 6 contain information on the karyological, morphological and anatomical characters on which the classification of Poa is based. Chapter 7 results from a more detailed study which I carried out on a taxonomically critical group, chapter 8 attempts to give an indication of the patterns of geographical distribution shown by the European species of Poa, and chapter 9 closes the thesis with an indication of possible evolutionary trends which have operated during the diversification of the present-day species of Poa.

I should like to acknowledge my gratitude to Professor Herbert Street for the use of departmental facilities, to Mr Shepherd for space for my living collection at the Botanic Garden, and to Mr Eric Singer and the Botany Department's technical staff, particularly Mr Ted Horwood and Miss Sue Duffey for help in the herbarium.

For financial assistance during my period of research, I am indebted to the Science Research Council for the award of a Research Studentship from 1 October, 1970 to 31 December, 1972 and to my parents for supporting me thereafter. The expenses of my trips abroad in 1971 and 1973 were defrayed in part by financial help from the Godman Trustees of the British Museum (Natural History) and the Bond Fund of the University of Leicester; I am very grateful to them, and to the Vice-Chancellor, for this valued assistance.

For practical help and advice on field-work abroad, and for contributing to the success of the expeditions, I thank Dr Peter Davis, Professor Hüsnü Demiriz, Mr Eskandar Firouz, Dr David French, Miss Alison Gibbins, Dr Fred Harrington, Mr Ian Hedge, Mr Peter Kirchner (H.M. Consul, Ankara), Miss Jennifer Lamond, Mr Oleg Polunin, Dr Derek Scott and Mr George Willcox. My special thanks go to Mr Arthur Chater, for advice on a wide range of taxonomic, bibliographic and plant-collecting matters. For providing material for study, I am grateful for the co-operation of Dr Edmond Bonner, Dr Santiago Castroviejo, Dr James Cullen, Mr Chris Fraser-Jenkins, Dr H. Heine, Mr William Hughes, Dr Bogdan Kuzmanov, Mr Andrew Lauener, Dr André Lawalrée, MR Ion Lungeanu, Prof. Hermann Merxmüller, Mr Oleg Polunin, Prof. Karl Heinz Rechinger and Dr Harald Riedl. My particular thanks go to Mr Philip Brown, for halping me to obtain seed from Botanic Gardens both at home and abroad.

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CHAPTER 1. Supraspecific classification and nomenclature of Poa.

1.1 Taxonomic characters.

These may be defined as "any observable feature or attribute of a plant that can be considered separately and used for the purpose of comparison or interpretation" (Davis & Heywood, 1963, p. 8), i.e. attributes of a class which serve to define that class. These must be distinguished from character states, which are alternative forms of a taxonomic character, i.e. attributes of a class which illustrate the variation within that class. Character states may be expressed quantitatively or qualitatively, according to the type of character. Quantitative character states may be given in numerical terms; qualitative character states are those which are expressed in non-numerical terms. Quantitative character states may be further subdivided according to whether they are exclusive or inclusive. An example of an exclusive quantitative character state is the number of panicle branches at each pseudowhorl of the panicle; a particular panicle may have one, two, three or four panicle branches, but not 1.2 - 3.4 panicle branches. An example of an inclusive quantitative character state is the width of the leaf blade in mm. Finally, an example of a qualitative character is the colour of the anthers.

The borderline between quantitative inclusive states and qualitative states is defined solely by man's ability to express these states in numerical terms; in the case of width, we can; whereas in the case of colour we cannot. Where possible, quantitative exclusive characters are preferred by taxonomists when preparing keys.

Taxonomic characters are in theory applicable at every taxonomic level, since any attribute or feature of an individual

grass specimen is equally an attribute of the species, genus and family to which it is allocated. In practice, different characters are used to distinguish taxa at different levels; the level at which a character state is a constant attribute of a taxon will determine which rank is appropriate. An example concerning Poa, in which a character applies at the generic level but not at the sectional level, is provided by the caryopsis, whose hilum is punctiform in every species and section of Poa examined and which is slit-shaped in the allied genus Festuca.

1.2 Taxonomic categories.

A classificatory unit of unspecified rank is termed a taxon (pl. taxa). A taxonomic category is the particular rank to which a group of taxa of equal status is allocated by the taxonomist. The names available for taxonomic categories between the levels of species and genus, arranged in descending order, are as follows:

genus
subgenus
sectio, section
subsectio, subsection
series
species

This system of categories forms a hierarchy, following the rule that all taxa of a given rank must be included in one or more taxa of the next higher rank.

Because the variation observed in the plants which we study is expressed through choosing particular levels in the taxonomic hierarchy, it follows that different opinions are possible on the correct level to which a particular taxon is to be assigned. The question of choice of rank in turn leads to problems of nomenclature, since according to the International Code of Botanical Nomenclature certain conditions apply if the name of a taxon is to be valid. One of these conditions is that there should not be a valid name

already belonging to the specified taxon at the chosen rank.

The question of the definition of species and subspecies has been amply discussed elsewhere. In a phylogenetic, as opposed to a phenetic, system of classification the species category has an evolutionary significance in that it embraces sterility barriers which have been erected during the process of speciation and which provide criteria for a biological definition of the species. It is not possible to define the higher taxonomic categories in this way, however, and the only practical definitions for such categories as section, subgenus and genus are phenetic ones. These take account of the overall similarity between the various groups which indicates a taxonomic affinity, and do not depend on evolutionary interpretations of relationships. The existence of intersectional hybridization in the Gramineae, and even of intergeneric hybridization in this and other Monocotyledonous families such as the Orchidaceae, in any event detracts from the value of sterility barriers in indicating species limits.

The allocation of a taxon to a given rank is in practice scarcely ever made on the basis of breeding behaviour alone. The widest possible range of characters is studied, and groups are defined on the basis of as many different attributes as possible. Since at the higher taxonomic levels there are fewer available characters, at least in the genus Poa, the taxonomist must rely to some extent on combinations of characters.

Different schools of thought exist on the most appropriate categories into which to subdivide the genus Poa. Few authors employ more than two ranks of the four available between the genus and the species. The rank of series is the most neglected of the four, the rank of subgenus being usually reserved for the major subdivision of the genus into two groups of dioecious and hermaphrodite

species. The least conventional treatment of the classification of Poa is that of Rozhevits (1934), who uses the series as the sole category below that of subgenus, in line with Komarov's dictum, quoted by Bobrov (1972) that the series is to be considered as both a phylogenetic and a morphological category, serving to indicate the "actual course of evolution". In other words, species are to be regarded as geographically defined subunits of the series. This presupposes a pre-Darwinian species concept allowing only for varieties, whereas in western Europe it is customary to employ a polytypic, as opposed to a monotypic, species concept which admits subspecies as the geographically defined subunits of the species. In preparing an account of the European species of Poa, as well as in revising the supraspecific classification of the genus, I have adhered to the polytypic species concept. I regard sections as morphologically defined groups of related species, not as groups of species having a supposed phylogenetic affinity or cousinhood. One may, of course, seek to interpret evolutionary trends in terms of the distribution of different character states among the various sections (see chapter 9). Reluctance to speculate on phylogenetic matters is further encouraged by the demonstration that hybridization may occur in the genus Poa between quite distantly related species, both in the wild (Tutin, 1957) and in cultivation (Almgård, 1960). Much of the evolutionary history of the higher groupings in Poa may be attributable to such processes of allo-polyploidy and intersectional hybridization.

1.3 Previous classification schemes.

Many of the published accounts of the genus Poa include sectional headings, or other indications of the author's opinion on the taxonomic relationships of the species treated. Those accounts which are genuinely fresh approaches to the classification

of the genus have been distinguished from the much larger number of accounts where sectional names taken from an earlier author's treatment are employed, or where a composite classification is produced from several authors' treatments. The following original treatments can be recognized:

a) Ascherson & Graebner (1900). The pioneer classification of European Poa, this account adopts only a few earlier names and is almost comprehensive in its coverage of European species. Although the detailed treatment of species is confined to those occurring in "Mitteleuropa", which includes much of south-east Europe, the work also contains brief references to species which are not formally treated in the Flora, allowing the authors' view on their place within the system of classification to be determined.

b) Rozhevits (1934). This treatment, in one of the earliest volumes of Flora SSSR to be published, adheres closely to the Komarovian principles, the most important of which are the concepts of monotypic species and series as phylogenetic as well as morphological categories. Since no other infrageneric categories are employed (save for subgenera other than subgenus Poa, which are now generally regarded as separate genera), the rank of series might be expected to correspond roughly to the western European polytypic species. In fact, the taxa designated as sections are frequently comparable to those which Rozhevits treats as series, and in some cases his series are even broader than the sections employed in Flora Europaea; in the remaining cases, the series are narrower than conventional sections. Unfortunately, the diagnoses of the series are so often based on superficial characters that they do not even serve to define the groups of species so included, and the account as a whole is sketchy and uncritical.

c) Jirásek (1935a, 1935b). Jirásek is responsible for a number of new subsections which subdivide the larger European sections of Poa. In addition, he 'recombines' Ascherson & Graebner's sections as sections, believing them to have insufficient indication of rank in their place of original publication. It is a debatable point whether the hierarchical system in Ascherson & Graebner's Flora which indicates rank by means of typographical symbols and margin insets is a sufficient indication of rank, the more so since the table explaining the system was printed on the loose-leaf covers of the parts of the Flora as they were issued, which were naturally discarded when the parts were bound together. I prefer to regard the original sections as adequately designated; even if one does not agree with this, one cannot accept the names given by Jirásek as validly published, since they lack the citations of types which are required by the Code of Nomenclature - an error which was finally remedied by Cherepanov (1973).

d) Nannfeldt (1935). Unlike the previous author, Nannfeldt attempts to produce a comprehensive reassessment of Ascherson & Graebner's classification. He points out some of its greatest defects, particularly with regard to sect. Oreinos, which he redefines as a much narrower section containing only three species. The resulting system differs from mine in only one major respect: Nannfeldt groups together sect. Poa and sect. Cenisia into a composite section, Stoloniferae Nannf. This, as also his section Abbreviatae, is nomenclaturally invalid since it is published after Jan. 1st, 1935 and lacks a Latin description or reference to a previously published Latin description.

e) Hermann (1939). His classification is based on that of Ascherson & Graebner, and retains the principal doubtful feature

of that system, the large and heterogeneous sect. Oreinos, as well as making some innovations which have not proved to be lasting. For example, a separate section is erected which contains P. flaccidula, now included in sect. Stenopoa. Hermann is however responsible for one new feature which has been retained, namely sect. Macropoa (based on P. longifolia); the name of this section, having been published without a Latin description, was invalid until Tsvelev (1972) provided a description.

f) Janchen (1955). This classification appears to be the result of an attempt to combine the classifications of Ascherson & Graebner and Jirásek, with certain alterations; it may particularly be criticized for including P. cenisia in a redefined sect. Oreinos.

g) Probatova (1971). This paper has been selected as representative of several by this author, whose classification of the Soviet Far-Eastern species of Poa comes close to fully agreeing with the present arrangement. The only significant difference is that, like Nannfeldt (1935), she unites sect. Cenisia with sect. Poa, the former as sect. Poa subsect. Pratenses, the latter as subsect. Malacanthae.

h) Tsvelev (1972). Although this author had earlier (1964, 1968) adopted a conventional treatment of the classification of Poa, in this paper he makes a radical reappraisal of all previous schemes, arriving at some rather startling conclusions. One of these is that sect. Bolbophorum should not be separated from sect. Poa.

1.4 Sectional synonymy.

For the European species of Poa, the tabulation of seven of the eight classification schemes listed in section 1.3 above, together with the scheme adopted for Flora Europaea, enables a direct comparison to be made of any pair of schemes. The table is arranged in

Edmondson (1975)	Tsvelev (1972)	Probatova (1971)	Janchen (1958)	Hermann (1939)	Nannfeldt (1935)	Rozhevits (1934) (Series throughout)	A. & Gr. (1900)
OCHLOPOA	OCHLOPOA	OCHLOPOA	OCHLOPOA	OCHLOPOA	OCHLOPOA	ANNUAE	OCHLOPOA
annua	annua	annua	annua	annua	annua	annua	annua
infirma	-	-	-	infirma	infirma	-	infirma
supina	=ustulata	-	supina	supina *balearica	=exilis *dimorphantha	supina	supina
COENOPOA	COENOPOA	COENOPOA	PANDEMOS subsect. Triviales	PANDEMOS	TRIVIALES	TRIVIALES p.p.	PANDEMOS
trivialis	trivialis	trivialis	trivialis	trivialis	trivialis	trivialis	trivialis
ssp. trivialis	ssp. trivialis	=	=	=	=	=	=
ssp. silvicola	ssp. silvicola	-	=silvicola	-	=silvicola	=silvicola	=
feratiana	-		-	-	+	-	-
POA	POA p.p.	POA subsect. Pratenses	subsect. Pratenses p.p.		STOLONIFERAE	PRATENSES	
alpigena	P. pratensis	alpigena	-	alpigena	=	alpigena	=
subcaerulea	=ssp. alpigena =ssp. irrigata	subcaerulea	-	-	=	=irrigata	=
pratensis	=ssp. pratensis	pratensis	pratensis	pratensis	pratensis	pratensis	pratensis
angustifolia	=ssp. angustifolia *ssp. colpodea *ssp. rigens	angustifolia	angustifolia	angustifolia	=	angustifolia	=
CENISIA		subsect. Malacanthae	OREINOS subsect. CENISIAE			ARCTICAE	CENISIA
arctica	arctica	arctica	-	-	arctica	arctica	arctica
granitica	*	-	-	-	granitica	-	-
ssp. granitica	-	-	-	-	=	-	-
ssp. disparilis	=deylii	-	-	-	-	-	-
cenisia	-	-	cenisia	cenisia	-	-	cenisia
ssp. sardoa	-	-	-	-	-	-	-
ssp. cenisia	-	-	=	=	-	-	=
ssp. contracta	-	-	-	-	-	-	-
MACROPOA	MACROPOA	MACROPOA		MACROPOA		SIBIRICAE	
longifolia	*	longifolia	-	longifolia	-	longifolia	-
ssp. fagetorum	=fagetorum	-	-	-	-	sibirica	-
sibirica	sibirica *ssp. sibirica *ssp. uralensis	sibirica	-				
HOMALOPOA	HOMALOPOA	HOMALOPOA	HOMALOPOA	HOMALOPOA	HOMALOPOA	TRIVIALES p.p.	HOMALOPOA
chaixii	chaixii	chaixii	chaixii	chaixii	chaixii	chaixii	chaixii
hybrida	hybrida	-	hybrida	hybrida	hybrida	hybrida	hybrida
remota	remota	-	remota	remota	remota	remota	remota
LEPTOPHYLLAE	L		PANDEMOS subsect. Pratenses p.p.	-	-	-	-
stiriaca	-	-	stiriaca				
OREINOS		OREINOS	OREINOS subsect. Laxae	OREINOS p.p.	OREINOS		OREINOS p.p.
flexuosa	-	-		flexuosa	flexuosa	-	flexuosa
laxa	-	laxa	laxa	laxa ssp. laxa +ssp. riphaea	laxa	-	laxa ssp. laxa +ssp. riphaea
pirinica	-	-	-	minor	minor	-	minor
minor	-	-	minor				
TICHOPOA	STENOPOA	TICHOPOA	TICHOPOA	HYLOPOA p.p.	TICHOPOA	STEPPOSAE p.p.	TICHOPOA
compressa	compressa *taurica	compressa	compressa	compressa	compressa	compressa	compressa
STENOPOA		STENOPOA subsect. Nemorales	HYLOPOA subsect. Palustres	LEPTOPOA			HYLOPOA p.p.
flaccidula	-			flaccidula	STENOPOA	PALUSTRES	-
palustris	palustris ssp. =palustris	palustris	palustris	HYLOPOA p.p.	+flaccidula	-	palustris
glauca	glauca	-	subsect. Nemorales	palustris	palustris	palustris	GLAUCOPOA
nemoralis	nemoralis ssp. =nemoralis	nemoralis	nemoralis	glauca ssp. =glauca (+ssp. riphaea)	glauca	glauca	glauca *balbisii
rehmannii	rehmannii	-	-	nemoralis	nemoralis	nemoralis	HYLOPOA
pannonica	-	subsect. Steriles	-	*balbisii	-		nemoralis
ssp. pannonica	-		-	sterilis ssp. =pannonica	-	=podolica	=ssp. nemoralis =ssp. rehmannii
ssp. scabra	-	-	-	=ssp. scabra	-	versicolor	*pannonica
versicolor	versicolor ssp. =versicolor	-	-	=ssp. versicolor	-	STERILES	*podolica
sterilis	sterilis ssp. =sterilis	sterilis	-	=ssp. sterilis	-	sterilis	*scabra
relaxa		-	-	-	-	STEPPOSAE p.p.	*versicolor
ABBREVIATAE		ABBREVIATAE		OREINOS p.p.	ABBREVIATAE	stepposa	*sterilis
abbreviata	abbreviata	abbreviata	-	abbreviata	abbreviata	-	OREINOS p.p.
NANOPOA				trichophylla	SUBBULBOSAE		abbreviatae
trichophylla	-	-	-	BOLBOPOA p.p.	trichophylla	-	trichophylla
BOLBOPHORUM	POA p.p.	ALPINAE	BOLBOPHORUM subsect. Bulbosae	bulbosa	bulbosa	BULBOSAE	BOLBOPHORUM p.p.
bulbosa	bulbosa *ssp. bulbosa	-	bulbosa	=concinna	=concinna	bulbosa	bulbosa
perconcinna	*ssp. vivipara	-	-	OREINOS p.p.	ligulata	-	=concinna
ligulata	-	-	subsect. Alpinae	ligulata	-	-	ligulata
timoleontis	-	-	-	BOLBOPOA p.p.	media	-	timoleontis
media	media	-	pumila	timoleontis	pumila	-	*parnassica
pumila	-	-	molineri	OREINOS p.p.	-	ALPINAE	=ursina
molineri	-	-	badensis	pumila	*thessala	-	OREINOS p.p.
badensis	-	-	alpina	badensis	badensis	-	pumila
alpina	alpina *ssp. alpina	alpina		*bivonae	alpina	alpina	*stricta
+INCERTAE SEDIS	*ssp. vivipara			*parnassica			*thessala
jubata	-	-	-	*thessala			BOLBOPHORUM p.p.
				alpina =ssp. alpina			badensis
				*ssp. fallax			alpina
							*insularis *balearica
				jubata	-	-	jubata

KEY to symbols:
= recognized by the author of the account, but at a different rank to the one currently employed
* synonym of taxon recognized by the author of the account
+ 'incertae sedis'; not included in the section indicated.

chronological order from right to left. The vertical sequence of the sections follows the latest account, necessitating alterations to the sequence adopted by earlier authors.

Sections adopted by the various schemes are listed with their modern equivalents in the following pages.

a) Ascherson & Graebner (1900):

sect. OCHLOPOA A. & Gr.	- unchanged.
sect. PANDEMOS A. & Gr.	= sect. COENOPOA Hyl. sect. POA
sect. CENISIA A. & Gr.	- unchanged.
sect. HOMALOPOA Dumort.	- unchanged.
sect. OREINOS A. & Gr.	= sect. OREINOS A. & Gr. sect. ABBREVIATAE Nannf. sect. NANOPOA J.R.E. sect. BOLBOPHORUM A. & Gr. p.p.
sect. TICHOPOA A. & Gr.	- unchanged.
sect. HYLOPOA A. & Gr.	= sect. STENOPOA Dumort. p.p.
sect. GLAUCOPOA A. & Gr.	= sect. STENOPOA Dumort. p.p.
sect. BOLBOPHORUM A. & Gr.	- largely unchanged; P. pumila transferred here from sect. OREINOS A.&Gr.

Section Macropoa Hermann ex Tsvelev falls outside the scope of this Flora, and sect. Leptophyllae J.R.E. is based on a species which was not yet recognized as such at the time of writing of the Flora.

The greatest defect of Ascherson and Graebner's treatment lies in their large sect. Oreinos, which merits the name 'dustbin section'; the sectional diagnoses are arranged in the form of a key, and the reliance which is placed on single characters such as the number of panicle branches at the lowest whorl of the panicle

leads to unsatisfactory groupings being made. Their sect. Hylopoa is almost synonymous with Dumortier's sect. Stenopoa, which differs only in that it includes P. glauca.

b) Rozhevits (1934):

ser. BULBOSAE Rozhev.	= sect. BOLBOPHORUM A. & Gr. p.p.
ser. ANNUAE Rozhev.	= sect. OCHLOPOA A. & Gr.
ser. NIVICOLAE Rozhev.	- comprises extra-European species only.
ser. SIBIRICAE Rozhev.	= sect. MACROPOA F. Hermann
ser. TRIVIALES Rozhev.	= sect. COENOPOA Hyl.
	sect. HOMALOPOA Dumort.
ser. PRATENSES Rozhev.	= sect. POA
ser. PALUSTRES Rozhev.	= sect. STENOPOA Dumort. p.p.
ser. STEPPOSAE Rozhev.	= sect. TICHOPOA A. & Gr.
	sect. STENOPOA Dumort. p.p.
ser. STERILES Rozhev.	= sect. STENOPOA Dumort. p.p.
ser. LANATIFLORAE Rozhev.	- comprises extra-European species only.
ser. ARCTICAE Rozhev.	= sect. CENISIA A. & Gr.
ser. ALPINAE Rozhev.	= sect. ABBREVIATAE Nannf.
	sect. BOLBOPHORUM A. & Gr. p.p.

ser. DSHUNGARICAE Rozhev., ser. MALACANTHAE Rozhev. and ser. CRASSICULMAE Rozhev. comprise extra-European species only.

Sect. Leptophyllae J.R.E. and sect. Nanopoa J.R.E. fall outside the geographical scope of the Flora SSSR.

The category of series is the lowest supraspecific category, and is not equivalent to the categories of either subsection or section. From the above comparative table, it is evident that Rozhevits' series are generally as broad in scope as are most other authors' sections, with two exceptions; he subdivides sect. Stenopoa into a number of series, and he amalgamates sect. Coenopoa

and sect. Homalopoa into a single series Triviales. The other differences are the result of a broad series concept; sect. Abbreviatae is included in ser. Alpinae, and sect. Tichopoa is included in ser. Stepposae.

c) Nannfeldt (1935):

sect. OCHLOPOA A. & Gr.	- unchanged.
sect. TRIVIALES Nannf.	= sect. COENOPOA Hyl.
sect. STOLONIFERAE Nannf.	= sect. POA, sect. CENISIA A. & Gr.
sect. HOMALOPOA Dumort.	- unchanged.
sect. OREINOS A. & Gr.	- accepted in a narrower circumscription.
sect. TICHOPOA A. & Gr.	- unchanged.
sect. STENOPOA Dumort.	- unchanged. Nannfeldt cites "Lindm." as authority for this section.
sect. ABBREVIATAE Nannf. ex Tsv.	- unchanged.
sect. SUBBULBOSAE Fries ex Andersson	= sect. BOLBOPHORUM A. & Gr.

The species belonging to sections Macropoa F. Hermann, Leptophyllae J.R.E. and Nanopoa J.R.E. are not considered by Nannfeldt. His sections named for the first time - Triviales, Stoloniferae and Abbreviatae, - lack descriptions and citation of types, and are therefore nomenclaturally invalid. Sect. Stoloniferae Nannf. is now regarded as comprising two sections; sect. Triviales Nannf. has been superseded by sect. Coenopoa Hyl. which was validly described in 1953; and sect. Abbreviatae Nannf. ex Tsvelev, which was validated in 1974, and will be provided with a description in a future paper in the series 'Notulae Systematicae ad Floram Europaeam Spectantes'. Sect. Subbulbosae Fries ex Andersson is a possible name for the section now named Bolbophorum A. & Gr., but in my opinion the section does not adequately circumscribe the range of

species now included in sect. Bolbophorum, since it is based on P. alpina and P. bulbosa alone.

d) F. Hermann (1939):

sect. OCHLOPOA A. & Gr.	- unchanged.
sect. PANDEMOS A. & Gr. emend. F. Hermann	= sect. COENOPOA A. & Gr.
	sect. POA
	sect. CENISIA A. & Gr.
sect. MACROPOA F. Hermann	- unchanged.
sect. HOMALOPOA Dumort.	- unchanged.
sect. OREINOS A. & Gr. emend. F. Hermann	= sect. OREINOS A. & Gr. emend. Nannf.
	sect. ABBREVIATAE Nannf.
	sect. NANOPOA J.R.E.
	sect. BOLBOPHORUM A. & Gr. p.p.
sect. HYLOPOA A. & Gr. emend. F. Hermann	= sect. TICHOPOA A. & Gr.
	sect. STENOPOA A. & Gr. p.p.
sect. LEPTOPOA F. Hermann	= sect. STENOPOA A. & Gr. p.p.
sect. BOLBOPOA F. Hermann	= sect. BOLBOPHORUM A. & Gr. p.p.

Hermann attempts to remould some of Ascherson and Graebner's sections in order to make them more workable, but fails to tackle sect. Oreinos and sect. Bolbophorum satisfactorily. He makes no reference to, and appears to have been unaware of, Nannfeldt's contributions to the classification, although he quotes Lindman's (1926) arrangement in Holmberg's 'Skandinaviens Flora'. Since Lindman does not produce any new groupings which have remained to be accepted at the present time, his classification has not been included in table 1.1, but the present equivalents of his sections are as follows:

sect. ANNUAE Lindman	= sect. OCHLOPOA A. & Gr.
sect. PRATENSES Lindman	= sect. COENOPOA Hyl.
	sect. POA

sect. ALPINAE Lindman = sect. CENISIA A. & Gr.
sect. OREINOS Nannf.
sect. BOLBOPHORUM A. & Gr. p.p.

sect. HOMALOPOA Dumort. - unchanged.

sect. TICHOPOA A. & Gr. - unchanged.

sect. STENOPOA Dumort. - unchanged.

sect. ARENARIAE Lindman = sect. BOLBOPHORUM A. & Gr. p.p.

Hermann (1939) evidently based his sect. Bolbopoa on Lindman's sect. Arenariae, since both have the effect of separating the members of sect. Bolbophorum A. & Gr. with bulbous stem bases from those with collars of basal leaf sheaths.

e) Janchen (1955):

sect. OCHLOPOA A. & Gr. - unchanged.

sect. PANDEMOS A. & Gr.

subsect. TRIVIALES (Nannf.) Jirásek = sect. COENOPOA Hyl.

subsect. PRATENSES Jirásek = sect. POA
sect. LEPTOPHYLLAE J.R.E.

sect. OREINOS A. & Gr.

subsect. CENISIAE (A. & Gr.) Janchen = sect. CENISIA A. & Gr.

subsect. LAXAE Jirásek = sect. OREINOS A. & Gr.

sect. HOMALOPOA Dumort. - unchanged.

sect. TICHOPOA A. & Gr, - unchanged.

sect. HYLOPOA A. & Gr.

subsect. PALUSTRES Janchen = sect. STENOPOA Dumort. p.p.

subsect. NEMORALES Janchen = sect. STENOPOA Dumort. p.p.

sect. BOLBOPHORUM A. & Gr.

subsect. BULBOSAE Jirásek = sect. BOLBOPHORUM A. & Gr. p.p.

subsect. ALPINAE Janchen = sect. BOLBOPHORUM A. & Gr. p.p.

Janchen's classification does not include sect. Macropoa F. Hermann,

sect. Abbreviatae Nannf. or sect. Nanopoa J.R.E., as these fall outside the geographical area covered by the Flora. His subsectional classification is closely modelled upon that of Jirásek (1934, 1935) but while some of Jirásek's epithets are taken up, other subsections are re-named afresh by Janchen. The following list gives those subsections of Janchen's which appear to be identical with those of Jirásek's classification:

sect. OREINOS subsect. CENISIAE Janchen = subsect. GRANITICAE Jirásek

sect. HYLOPOA subsect. NEMORALES Janchen = subsect. BREVILIGULATAE Jirásek

subsect. PALUSTRES Janchen = subsect. LONGILIGULATAE Jirásek

sect. BOLBOPHORUM subsect. ALPINAE Janchen = subsect. CAESPITOSAE Jirásek

Janchen does not indicate the authorship of the taxa employed in his classification; where these are identical with those of Jirásek I have used Jirásek's name as author, and elsewhere I have assumed that Janchen is the author.

f) Probatova (1971):

sect. OCHLOPOA A. & Gr. - unchanged.

sect. COENOPOA Hyl. - unchanged.

sect. POA

subsect. PRATENSES Jirásek = sect. POA

subsect. MALACANTHAE Probatova = sect. CENISIA A. & Gr.

sect. MACROPOA F. Hermann - unchanged.

sect. HOMALOPOA Dumort. - unchanged.

sect. OREINOS A. & Gr. - unchanged.

sect. TICHOPOA A. & Gr. - unchanged.

sect. STENOPOA Dumort.

subsect. NEMORALES Probatova = sect. STENOPOA Dumort. p.p.

subsect. STERILES Probatova = sect. STENOPOA Dumort. p.p.

sect. ABBREVIATAE Nannf.(ined.) - unchanged.

sect. ALPINAE Hegetschw. = sect. BOLBOPHORUM

Sect. Leptophyllae nobis J.R.E. and sect. Nanopoa nobis J.R.E. are not included in the classification, as the species involved are not known in the area covered by Probatova's paper.

The high level of agreement between Probatova's system and the present one is all the more remarkable for the fact that an entirely different geographical area is covered by each classification.

g) Tsvelev (1972):

sect. OCHLOPOA A. & Gr.	- unchanged.
sect. COENOPOA Hyl.	- unchanged.
sect. POA	= sect. POA
	sect. CENISIA A. & Gr.
	sect. BOLBOPHORUM A. & Gr.
sect. MACROPOA F. Hermann	- unchanged.
sect. HOMALOPOA Dumort.	- unchanged.
sect. STENOPOA Dumort.	= sect. TICHOPOA A. & Gr.
	sect. STENOPOA Dumort.
sect. ABBREVIATAE Nannf. ex Tsv.	- unchanged.

Sect. Leptophyllae nobis J.R.E., Oreinos A. & Gr. and Nanopoa nobis J.R.E. are not included in the classification; in the case of sect. Leptophyllae and sect. Nanopoa, the taxa fall outside the geographical range of the paper, while in the case of sect. Oreinos, Tsvelev appears to have overlooked the occurrence of P. laxa in the Ukraine. The most unusual aspect of this classification is the very broad view of sect. Poa, which is taken by Tsvelev to include both sect. Cenisia and sect. Bolbophorum. In my opinion, this drastic amalgamation is not supported by the evidence either from morphological, anatomical or karyological sources.

1.5 Nomenclatural considerations.

In establishing the correct names for the European sections of *Poa*, not only must the sections be adequately circumscribed, but they must also be named in accordance with the International Rules of Botanical Nomenclature (11th edition, Seattle Congress 1968; F.A. Stafleu et al., 1972). It is regrettable that so little attention has hitherto been paid to this matter, since strict observance of the Code is a prerequisite of a stable future nomenclature.

Provisions of the code having a direct bearing on the naming of European sections of *Poa* are as follows (they have been paraphrased for brevity):

Article 7.

The type of a name of a taxon is determined from the description accompanying its first valid publication. (Articles 32 to 45 define 'valid publication').

Article 11.

The correct name for any taxon from the rank of family to the rank of genus inclusive is the earliest legitimate name at that rank. This is known as the 'rule of priority'.

Below the rank of genus, the correct name is the combination of the generic (or specific) name with the earliest legitimate epithet at that rank (but see article 22).

The principle of priority is limited, in Spermatophyta, to 1st May, 1753 (Article 13).

Article 21.

The name of a subdivision of a genus is a combination of a generic name and a subdivisional epithet connected by a term (e.g. 'section') denoting its rank.

Article 22.

The subgenus and section (but not subsection or lower subdivision) which includes the type species of the genus bears the generic name unaltered as its epithet, without citation of the author's name.

Article 35.

A new name published on or after 1st January, 1953 without a clear indication of rank of the taxon concerned is not validly published.

For such names published before that date, the choice made by the first author who assigned a definite rank to the taxon concerned is to be followed.

Article 36.

In order to be validly published, a name of a new taxon published on or after 1st January, 1935 must be accompanied by a Latin description or diagnosis or by a reference to a previously published Latin description or diagnosis of the taxon.

Article 37.

Publication on or after 1st January, 1958 of the name of a new taxon of the rank of family or below is valid only when the nomenclatural type is indicated.

Some of the particular cases where the choice of a name for a section of Poa was determined by an article of the Code are given below.

a) The type of Poa sect. Tichopoa A. & Gr. is P. compressa, since although the type species was not indicated by the authors, the description of the section clearly indicates that the section is based on that species (Article 7).

b) The correct name for the section first proposed as sect.

Triviales Nannf. is sect. Coenopoa Hyl. Nannfeldt (1935) failed to provide a Latin diagnosis or description, contrary to Article 36; the provision of the second part of Article 35 would also apply even if a description had been provided, since the rank of the group is not specifically stated (although Nannfeldt clearly had the rank of section in mind). Since Hylander (1953) produced a different name for the section, together with a diagnosis in Latin which validated the name, his name stands.

c) The correct name for sect. Bolbophorum A. & Gr. is a rather tricky question, since there is an earlier name (sect. Subbulbosae Fries ex Andersson) which is a possible candidate for the sectional name, and was adopted by Nannfeldt (1935) in preference to sect. Bolbophorum. Ascherson & Graebner's name, published in 1900, did not require a Latin diagnosis (Article 35). It was, however, necessary for its rank to be explicitly stated. The rank of the various taxa in Ascherson & Graebner's flora was indicated by means of a typographical convention of symbols and indentations, which was explained on the fly-leaf of the unbound parts of the Flora. Although Jirásek (1935) was considered by some authors to have 'validated' Ascherson & Graebner's name, which they cite as sect. Bolbophorum(A. & Gr.) Jirásek, e.g. Tsvelev (1968), this is not necessary as 'Bolbophorum' had already been designated as a section by its original authors. The earlier name, sect. Subbulbosae Fries ex Andersson, was applied only to P. alpina and P. bulbosa and does not adequately circumscribe the group. Sect. Alpinae Hegetschw., another earlier excluded name, has an even narrower circumscription.

d) The name Poa sect. Pandemos A. & Gr. is illegitimate, since according to Article 22 the name of the section containing the type species of the genus (P. pratensis) shall be the same as that of the genus, i.e. Poa sect. Poa.

e) The names of sect. Abbreviatae Nannf. and sect. Macropoa F. Hermann were invalid when published, since as they were published after January 1st, 1935 a Latin diagnosis is required. In the latter case, Tsvelev provided a Latin diagnosis (albeit a very brief one) in 1972, while in the former case he did not recognize the section until 1974, in his paper published immediately prior to the appearance of the Flora of the European Part of the USSR.

Adherence to Recommendation 73C (b) of the Code requires that certain changes be made in the orthography of specific names consisting of the genitive form of a person's name:

P. fontquerii should read P. fontqueri;

P. molinerii should read P. molineri;

P. rehmanni should read P. rehmannii.

Article 73 also requires that the letter i is to be replaced by a letter j when occupying the position of a consonant. This results in only one change of spelling of an epithet of a European species: P. iubata should read P. jubata.

1.6 Characters employed in sectional diagnoses.

The diagnosis of a section should ideally contain those characters whose states in the section concerned best serve to distinguish it from species of other sections. Single characters occasionally permit sections to be recognized without further reference to additional characters, but more commonly one is obliged to employ combinations of more than one character. A sectional description, on the other hand, would contain (in addition to such characters) those characters in which the section concerned has a characteristic state, or for which they are a constant attribute, but which may also occur in some or all of the other sections of the genus and which are thus of little value in the diagnosis of the section. For this reason, characters are used in a description which can be observed throughout the range of species. Since no useful purpose would be served by including such non-diagnostic

characters, the following list is a much abbreviated selection of the full range of available characters, which are described in greater detail in chapter 5.

1. Life form of the plant.

The great majority of species of *Poa* are perennial. Among the European species, the annual habit is peculiar to *P. annua* and *P. infirma* (sect. Ochlopoa) and to the unplaced species *P. jubata*. Elsewhere, annual species are quite rare; most fall into the two related sections Ochlopoa A. & Gr. and Diversipoa V. Jirásek, (Bor, 1948; Chrtek & Jirásek, 1962).

2. Presence or absence of rhizomes and stolons.

One of the most fundamental components of the growth-form of the grass, the rhizome/stolon system for achieving vegetative spread involves specialized shoots whose presence or absence forms one of the main criteria used in dividing the genus into sections. Rhizomes are defined as underground shoots (which in *Poa* are of determinate growth), while stolons are epigeal shoots which periodically root at the nodes.

3. Compactness of the tussock.

This character is difficult to quantify, being a function of the degree of branching and new shoot production ("tillering") at the base of the stem; the overall appearance of the tussock is also influenced by the rhizome/stolon system, if present.

4. Orientation of the new shoots.

Innovations - new shoots arising at the base of the stem - may arise extravaginally or intravaginally. In the former, the shoots arise from buds subtended only by a specialized bladeless sheath or cataphyll (Vickery, 1970, p. 152); in the latter, the shoot buds are enclosed within blade-bearing leaf sheaths, which are more or less imbricated at the base of the stem and typically (sect. Bolbophorum) decay to leave a fibrous collar sheathing the

lower part of the stem. Since the cataphylls are caducous, the type of shoot innovation is easily observed in mature specimens.

5. Angle of ascent and size of stem base.

Though the stem base is usually proportionate in size to the rest of the plant, it becomes bulbous-thickened in a few species of sect. Bolbophorum, and is strongly compressed in sect. Homalopoa. The angle at which the stem arises from the rootstock is important in distinguishing sect. Genisia from sect. Poa. In sect. Genisia, the stem arises at only a small angle from the horizontal at first, subsequently curving upwards; 'geniculate-ascendent' is a phrase sometimes employed in describing this character state, though more properly this should only be used when describing a stem which turns through a prominent angle at one of the lower nodes, e.g. in some forms of P. compressa. In sect. Poa, the stem arises more or less vertically from the apex of the rhizome.

6. Width of leaf blade.

This character varies over a very wide range, section Homalopoa having the broadest leaves, and section Nanopoa the narrowest. The range of leaf-widths within individual sections is much narrower, however, and provides one of the most easily observed quantitative sectional characters.

7. Degree of folding of leaf blade.

The blade may be flat or folded at the keel, or channelled (inrolled). This character is most easily observed in transverse sections of the leaf blade, and is discussed in more detail in the introduction to chapter 6.

8. Type of apex of leaf blade.

Two alternative states of this character are recorded; in practice there is some gradation between the one and the other.

In the first, the leaf blade tapers only very slightly in width from base to tip before narrowing abruptly into a cucullate or 'boat-shaped' apex. In the second, the blade tapers gradually before terminating in an acute point (finely cucullate if closely observed). If the latter state occurs, it is necessary to measure leaf blade widths at the base of the blade, for comparative purposes.

9. Length of ligule.

This character sometimes varies between basal and cauline leaves; for this reason, unless specially stated, comparisons are made between ligules of the uppermost stem leaves, where this feature is more easily observed.

10. Type of apex of ligule.

The type of apex is a useful diagnostic feature, although it is partially correlated with the previous character: very short ligules (under 1 mm) are almost invariably truncate, while longer ligules may be truncate, rounded or finely pointed, and species with ligules over 5 mm in length usually have a finely pointed ligule with an acute apex. Longer ligules also tend to become lacerated.

11. Scabridity of the stem below the panicle.

The stem is usually smooth below the panicle; in most of the few species with cauline aculeoli, these are confined to the upper part.

12. Shape of the stem in cross-section.

Except for two species - *P. compressa* and *P. rehmannii* - all the European species of *Poa* have a stem which is more or less terete in cross-section, though as mentioned in (5) above the base of the stem is strongly compressed in sect. Homalopoa.

13. Shape of the panicle branches in cross-section.

The panicle branches are usually terete; where they are sulcate, a useful diagnostic feature is provided either for the sections: Abbreviatae, Nanopoa; or for the species of sect. Oreinos: P. flexuosa, P. laxa.

14. Scabridity of panicle branches.

Aculeoli may be entirely absent, or if present their density may vary over a wide range. Several sections of Poa in Europe are distinguished by having species with smooth panicle-branches.

15. Number of florets in each spikelet.

This character is of only marginal utility at the level of the sections. Since the range of numbers is small - rarely less than two, rarely more than six - and intraspecific variation so large, this character is chiefly noted when describing sect. Bolbophorum, in which several species commonly have up to ten florets in a single spikelet.

16. Indumentum of the veins and inter-vein surfaces of the lemma.

The lemma may be completely glabrous, or may bear hairs on the veins and/or on the abaxial surface between the veins. The hairs on the veins are generally rather long and silky, whereas those which clothe the inter-vein surfaces are usually shorter and are more or less adpressed.

17. Wool on the callus at the base of the lemma.

The amount of wool, if present, varies so greatly that its quantity is of little value as a diagnostic character. Absence of wool, on the other hand, is a useful sectional attribute.

18. Palea keel dentition and indumentum.

Whereas unicellular hairs and aculeoli are not generally considered as aspects of a single character, this distinction breaks down when considering the palea keels. They may be aculeolate

along their whole length, or the teeth may be replaced for a varying distance from the base by unicellular hairs. In sect. Ochlopoa, these hairs extend the full length of the palea keels.

19. Anther length.

Though this is potentially a very useful character for distinguishing species, insufficient data has been obtained to allow full use to be made of it in the sectional diagnoses. Sect. Macropoa has anthers up to 3.7 mm in length, and this figure is unlikely to be exceeded in any other European species; at the other end of the scale, sect. Abbreviata is distinguished by its very short anthers (0.6 - 0.8 mm in length).

1.7 Sectional diagnoses.

In the diagnoses which follow, certain abbreviations are used. 'Leaves' stands for leaf blades; measurements of the ligule refer to its length; 'marginal veins' of the lemma refers to the outer pair of lateral (submarginal) veins.

POA subgenus POA.

Sect. OCHLOPOA A. & Gr., Syn. Mitteleur. Fl. 2: 387 (1900).

Annual or perennial, loosely or very loosely tufted; innovations extravaginal, shoots erect to procumbent, plant sometimes shortly rhizomatous. Leaves flat, 1 - 3 mm wide, abruptly contracted at the apex; ligule 1 - 1.5 mm, truncate. Stem smooth, slightly compressed. Panicle branches terete, smooth. Spikelets with 3 - 6 florets. Lemma hairy only on the marginal veins, not lanate at base. Palea keels ciliate along their whole length. Anthers 0.2 - 2.5 mm long. Type: P. annua L.

Sect. COENOPOA Hyl., Botaniska Notiser 3: 354 (1953).

Perennial, with a short rhizome, stoloniferous, loosely tufted; innovations extravaginal, shoots geniculate-ascendent to erect. Leaves 1 - 4.5 mm wide, flat, tapering gradually to the apex; ligule 3 - 10 mm, acute. Stem smooth, terete. Panicle branches terete, densely scabrid.

Spikelets with 1 - 4 florets. Lemma hairy on the keel, glabrous on the marginal veins; not or sparsely lanate at base. Palea keels aculeolate. Type: P. trivialis L.

Sect. POA.

Perennial, rhizomatous, loosely to densely tufted; innovations extravaginal, shoots arising vertically from the stem base. Leaves flat to folded, 0.8 - 4 mm wide, tapering gradually to, or abruptly contracted at, the apex; ligule 0.5 - 1 (-3) mm, rounded to truncate. Stem smooth, terete. Panicle branches terete, sparsely scabrid. Spikelets with 3 - 5 florets. Lemma hairy on the keel and marginal veins, copiously lanate at the base. Palea keels aculeolate, or ciliate in lower half. Anthers 1.4 - 2 mm long. Type: P. pratensis L.

Sect. CENISIA A. & Gr., Syn. Mitteleur. Fl. 2: 404 (1900).

Perennial, rhizomatous, loosely to moderately densely tufted; innovations extravaginal, shoots arising at first obliquely from the base, then curving upwards. Leaves flat, 1 - 5 mm wide, abruptly contracted at the apex; ligule 1.5 - 9 mm, acute to rounded. Stem smooth, terete. Panicle branches terete, sparsely to densely scabrid. Spikelets with 2 - 5 florets. Lemma hairy on the keel and marginal veins, moderately lanate at the base. Palea keels aculeolate, or ciliate in lower half. Anthers 1.5 - 2.4 mm long. Type: P. cenisia All.

Sect. MACROPOA F. Hermann, Hercynia 2: 457, 459 (1939) ex Tsvelev, Nov. Sist. Vyssh. Rast. 9: 49 (1972).

Perennial, rhizomatous, densely tufted; both types of innovations present. Stem base stout, shoots arising obliquely at first. Leaves 1 - 5 mm wide, tapering gradually to the apex; ligule 1 - 2 mm, obtuse. Stem smooth, terete. Panicle branches terete, weakly scabrid. Spikelets with 2 - 5 florets. Lemma glabrous, not lanate at the base. Palea keels aculeolate. Anthers 1.5 - 3.7 mm long. Type.: P. longifolia Trin.

Sect. HOMALOPOA Dumort., Obs. gram. belg. 110, 113 (1823).

Perennial, lacking rhizomes, with or without short stolons; densely tufted, innovations extravaginal. Stem base stout, strongly compressed, enclosed by folded leaf-sheaths. Leaves flat to folded, 4 - 15 mm wide, tapering gradually to the apex or abruptly contracted at the apex; ligule 1 - 5 mm, rounded to truncate. Stem smooth, somewhat compressed in lower half. Panicle branches terete, sparsely to densely scabrid. Lemma glabrous, or hairy only on the keel, lanate or not at the base. Palea keels aculeolate. Type: P. chaixii Vill.

Sect. LEPTOPHYLLAE mihi, ined.

Perennial, shortly stoloniferous, lacking rhizomes; densely tufted, innovations extravaginal. Stem base slender, erect, with numerous non-flowering shoots. Leaves strongly folded, 0.2 - 0.3 mm wide, abruptly contracted at the apex; ligule 1 - 2 mm, rounded. Stem smooth, rather rigid. Panicle branches sulcate, densely scabrid. Lemma sparsely hairy on the keel and marginal veins, very sparsely lanate at the base. Palea keels weakly aculeolate. Type: P. stiriaca Fritsch & Hayek ex Dörfler.

Sect. OREINOS A. & Gr., Syn. Mitteleur. Fl. 2: 400 (1900) emend. Nannf., Symb. Bot. Upsal. 5: 21, 29 (1935).

Perennial, without rhizomes; loosely to densely tufted, innovations extravaginal. Stem base slender. Leaves flat to folded, 0.2 - 2.5 mm wide, tapering gradually to the apex; ligule 0.5 - 3.5 mm, acute to truncate. Stem smooth, terete. Panicle branches terete or sulcate, smooth (in our species*). Lemma hairy on the keel and marginal veins, lanate at the base. Palea keels aculeolate or

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*NOTE: Poa scopulorum Butters & Abbe, Rhodora 49: 16 (1947), assigned by its authors to sect. Oreinos A. & Gr., has panicle branches which range from being smooth to being strongly scabrid.

ciliate in lower half. Anthers 0.6 - 1.7 mm. Type: P. laxa Haenke.

Sect. TICHOPOA A. & Gr., Syn. Mitteleur. Fl. 2: 419 (1900).

Perennial, rhizomatous; very loosely tufted, innovations extravaginal. Stem base geniculate-ascendent. Leaves flat, 3 - 5 mm wide, tapering at first gradually then rather abruptly to the apex; ligule 1 - 3 mm, rounded to truncate. Stem smooth, strongly compressed in upper part. Panicle branches terete, moderately scabrid. Spikelets with 2 - 8 florets. Lemma glabrous or (less commonly) shortly appressed-hairy on the keel and marginal veins, lanate at the base. Palea keels aculeolate. Anthers 1 - 1.2 mm long. Type: P. compressa L.

Sect. STENOPOA Dumort., Agrost. belg. 111 (1827).

Perennial, lacking rhizomes, loosely to densely tufted; innovations extravaginal. Leaves flat to somewhat convolute, 1 - 3 mm wide, tapering more or less gradually to the apex; ligule 0 - 3.5 mm, acute to truncate or obsolete. Stem terete or compressed above, smooth to densely scabrid. Panicle branches terete, scabrid. Spikelets with 2 - 5 florets. Lemma hairy on the keel and marginal veins, or appressed-hairy between the veins, not or sparsely (rarely copiously) lanate at the base. Palea keels aculeolate or ciliate in lower half. Type: P. nemoralis L.

Sect. ABBREVIATAE Nannf., Symbol. Bot. Upsal. 5: 25, 29 (1935) (sine descriptione Latino) ex Tsv., Nov. Sist. vys. r. 11: 30 (1974).

Perennial, lacking rhizomes, densely tufted; innovations intravaginal, stem base with numerous non-flowering shoots. Leaves folded, 1 - 2.5 mm, abruptly contracted at the apex; ligule 0.5 - 1 mm, rounded. Stem terete, smooth or verrucose above, uppermost leaf-blade appressed to the stem. Panicle branches sulcate, smooth or verrucose. Spikelets with 3 - 5 florets.

Lemma glabrous, or shortly appressed-hairy on surface, not lanate at the base. Palea keels aculeolate in upper part. Anthers 0.6 - 0.8 mm long. Type: P. abbreviata R.Br.

Sect. NANOPOA mihi, ined.

Perennial, lacking rhizomes, densely pulvinate; innovations intravaginal. Leaves setaceous, convolute, 0.3 - 0.5 mm wide, apex finely tapering; ligule 1.5 - 2 mm, acute. Stem and panicle branches terete, smooth. Spikelets with 2 - 3 florets. Lemma glabrous, apex obtuse, scarcely folded at the keel, not lanate at the base; palea keels aculeolate. Type: P. trichophylla Heldr. & Sart. ex Boiss.

Sect. BOLBOPHORUM A. & Gr., Syn. Mitteleur. Fl. 2: 391 (1900).

Perennial, lacking rhizomes, loosely to densely tufted; innovations intravaginal. Stem bulbous-swollen at the base, or base clothed with the fibrous remains of leaf sheaths which form a collar. Leaves 0.5 - 4.5 mm wide, flat to folded, usually abruptly contracted at the apex, but in some species tapering more gradually to the apex; ligule 1 - 6 mm, acute to truncate. Stem smooth, terete. Panicle branches smooth to densely scabrid, terete. Spikelets with 2 - 10 florets. Lemma hairy on the keel and marginal veins, sometimes also shortly appressed-hairy on surface, not or sparsely lanate at the base. Palea keels aculeolate, or ciliate in lower half. Anthers 1 - 2 mm long. Type: P. alpina L.

CHAPTER 2. Taxonomic changes below the level of section.

2.1 Scope.

During the preparation of the account of the European species of *Poa*, certain nomenclatural changes were found to be necessary. Details of these alterations are presented briefly in this chapter; it forms the basis for a paper in the series 'Notulae Systematicae ad Floram Europaeam spectantes' in which the sectional names used in chapter 1 are also validated.

2.2 Changes in taxonomic rank.

a) *P. cenisia* All. subsp. *sardoa* Schmid, Viert. Naturf. Ges. Zürich *78*: 239 (1933).

Type: "perdas crapias am Gennargentu" (Sardinia), Schmid s.n., 22.7.1927.

Syn.: *P. fontqueri* Br.-Bl., Comm. Stat. Int. Géobot. Médit. Alp. *87*: 220 (1945), *syn. nov.*

It is necessary to apply this little-known subspecific epithet to the *P. cenisia* subspecies which occurs in Corsica, Sardinia and the Pyrenees. Braun-Blanquet (1945) makes no reference to the earlier paper, and while he later recorded *P. cenisia* (sub *P. fontqueri*) from Corsica (Braun-Blanquet, 1947) he must still have been unaware of Schmid's record from Sardinia.

This subspecies shows a preference throughout its range for schistose, gneissic and granitic soils, in contrast to subsp. *cenisia* which occupies more or less calcareous habitats.

b) *P. longifolia* Trin. subsp. *fagetorum* mihi, *stat. nov.*

Basionym: *P. fagetorum* P. Smirnov, Byull. Mosk. o-va isp. prir., otdel. biologii, *58*: 57 (1953) ex Smirnov, ibid. *90*: 96 (1965).

Type: "montes Babugan Tauriae. Fagetum schistosum infra aelam Gursufiensem prope pag. Gursuf", P. Smirnov s.n., 29.5.1951.

This subspecies is believed to be endemic to Krym (Crimea). According to Smirnov (1965), whose paper includes a full description of the taxon with illustrations, it occurs in the upper zone of the Crimean beechwoods at an altitude of from 900 m to 1200 m.

The type subspecies, P. longifolia subsp. longifolia, was known until recently only from the Caucasus and Pontus mountains. Its range is now known to extend into NE Iraq (Bor, 1970) and along the Zagros mountains of western Iran (M. Vahedi, personal communication).

2.3 A nomen novum.

P. perconcinna mihi, ined.

Syn.: P. concinna Gaudin, Agrost. Helv. 196 (1811) non R.Br.

Unfortunately, the plant known familiarly as P. concinna must be provided with a new name, as its present one is a later homonym of P. concinna R.Br., Flora Nov. Holl. 180 (1810). Article 64 of the International Code of Botanical Nomenclature (Stafleu et al., 1972) requires that the later name be rejected, even though Robert Brown's name is no longer current (being regarded as a synonym of Eragrostis concinna).

This was the second occasion on which this species was found to have an illegitimate name. The first was in 1805, when Lamarck & De Candolle named it P. molineri in Fl. Fr. 3: 65 non P. molineri Balbis (1801).

Before naming the species afresh, a search was made for a validly published epithet to replace the illegitimate name. Since P. carniolica Hladnik ex L. Reichenbach & H.G. Reichenbach fil., Ic. Fl. Germ. et Helv. 1: 34, tab. 81 fig. 1618 (1834) was cited by Ascherson & Graebner (1900) as a possible synonym of P. concinna Gaud., its prior claims were first considered. An examination of the illustration cited led me to the conclusion that the figure does not

satisfactorily match P. concinna Gaud. Indeed, it is set alongside a figure of P. concinna Gaud., indicating that the authors did not consider the two to be synonymous. In my opinion, P. carniolica Hład. ex Reich. & Reich. fil. must be referred to P. bulbosa, and a new name must be provided for P. concinna Gaud.

2.4 Species relegated to synonymy.

In addition to the taxonomic changes presented above, a number of species have been reduced to synonymy or have been relegated from an intermediate position as subspecies etc. Also included in this list are some cases where the synonymy has previously been confused.

P. alpina L. subsp. fallax F. Hermann pro parte (European material) = P. pumila.

P. alpina L. subsp. xerophila Br.-Bl. = P. molineri.

P. biebersteinii Poyarkova = P. sterilis.

P. x breazensis Nyárády = P. granitica subsp. disparilis.

P. carniolica Hład. ex Reich. & Reich. fil. = P. bulbosa.

P. crassipes Domin ex Šourek = P. molineri.

P. hypanica Prokudin = P. nemoralis.

P. lapponica Prokudin = P. nemoralis.

P. membranacea (Boiss.) C. Vicioso = P. ligulata.

P. petschorica Rozhevits = P. arctica.

P. pinegensis Rozhevits = P. pratensis.

P. pinetorum Klokov = P. palustris.

P. podolica Błocki ex Ascherson & Graebner = P. pannonica.

P. polonica Błocki = P. versicolor.

P. tanfiljewii Rozhevits = P. palustris.

P. thessala Boiss. & Orph.	=	P. pumila.
P. tolmatschewii Rozhevits	=	?P. arctica.
P. turfosa Litw.	=	P. pratensis.
P. volhynensis Klokov	=	P. palustris.

2.5 Treatment of hybrids.

Two types of naturally occurring hybrids can be distinguished on the basis of the taxonomic relationship between their parents:

a) intrasectional hybrids; hybrids between two species of the same section.

b) intersectional hybrids; hybrids between two species of different sections.

A further distinction can be made between hybrids arising facultatively between parents which grow together and which remain capable of introgression with the parents, and 'stabilized' hybrids which have become genetically isolated by means of the apomictic breeding system and which reproduce themselves (often by means of proliferous inflorescence propagules) without regard to further hybridization of the parents. A 'stabilized' hybrid is most easily recognized when it has a geographical distribution, or even an ecological preference, which extends beyond the range of one or both of its parent species.

Table 2.1 show examples of the four possible types of hybrid. Poa annua has become stabilized as an allotetraploid and has a sexual breeding system, and is therefore treated as a full species without the hybrid sign (X). Several other species of Poa may well be of allopolyploid origin; this has not yet been demonstrated experimentally.

In the absence of experimental evidence, it is difficult to establish workable criteria for accepting or rejecting putative hybrids. The following list contains the hybrids which I regard

as reasonably likely on the basis of the available evidence: P. hartzii Gandoger, P. herjedalica H.Sm., P. jemtlandica (Almq.) K. Richter, P. nannfeldtii Jir., P. nobilis Skalińska, P. pawlowskii Jirásek, P. taurica Poyarkova and the un-named hybrid between P. hybrida and P. chaixii (Hess, Landolt & Hirzel, 1967). Their putative parents, distribution, and stabilized/unstabilized and inter/intrasectional status are set out in table 2.2 .

A much larger number of names occur in the literature for which evidence of hybrid status is flimsy or non-existent. Where I have been able to examine type material or authentic material named by the author, conclusions have sometimes been drawn as to the suspected identity of the taxa concerned. Other cases exist where a hybrid has been described without being given a hybrid epithet. Table 2.3 lists these so-called hybrids, both named and un-named.

Numerous hybrids have been produced artificially: see, for example, the papers of Almgård (1960), Brittingham (1941) and Tutin (1957). Tutin demonstrated that the hypothesis of an allo-tetraploid origin for P. annua was supported by the evidence of artificial crosses between its putative parents, P. infirma and P. supina, as well as of back-crosses between the artificial and the natural 'P. annua' and the parent species.

The suggestion is sometimes made that whole sections of the genus Poa may be of hybrid origin; evidence in support of this suggestion, as applied to sect. Poa, was obtained by Kiellander (1942) who obtained segregate plants resembling P. trivialis from sets of twins produced by the double reduction of P. pratensis. Almgård (1960) indicates that P. pratensis may have a genome in common with P. hybrida, whereas Åkerberg & Nygren (1959) propose P. trivialis x P. alpina vel aff. as the origin of P. pratensis.

TABLE 2.1 Types of naturally occurring hybrids.

	INTERSECTIONAL	INTRASECTIONAL
UNSTABILIZED	P. x herjedalica H.Sm.	P. x pawlowskii V.Jirásek
	P. alpigena, sect. Poa	P. chaixii, sect. Homalopoa
	x	x
	P. alpina, sect. Bolbophorum	P. remota, sect. Homalopoa
STABILIZED	P. x jemtlandica (Almq.) K. Richter	P. annua L.
	P. flexuosa, sect. Oreinos	P. infirma, sect. Ochlopoa
	x	x
	P. alpina, sect. Bolbophorum	P. supina, sect. Ochlopoa

TABLE 2.2 Accepted interspecific hybrids.

NAME	PUTATIVE PARENTS nos.- see appendix 1	LOCATION	Stabilized/ Unstabilized	INTER/ INTRASECTL.
P. x hartzii Gdgr.	26 x 33	Sb, Greenland	Stabilized	Intersectional
P. x herjedalica H.Sm.	16 x 43	Fe No Su	Unstabilized	Intersectional
P. x jemtlandica (Almq.) K. Richter	19 x 43	Br No Su	Stabilized	Intersectional
P. x nannfeldtii Jirásek	1 x 3	Cz Ge He No Su	Unstabilized	Intrasectional
P. x nobilis Skalińska	11 x 43	Po	?Stabilized	Intersectional
P. x pawlowskii Jirásek	15 x 17	Cz	Unstabilized	Intrasectional
P. x taurica Poyarkova	23 x 31	Rs(K)	Unstabilized	Intersectional
un-named (Hess et al, 1970)	15 x 16	He	Unstabilized	Intrasectional

TABLE 2.3 Insufficiently well-established names for interspecific hybrids; un-named hybrid combinations.

NAME	PUTATIVE PARENTS	SUSPECTED IDENTITY	DISTRIBUTION
P. x breazensis Nyár.	8 x 11	11b	Cz Rm
P. x complanata Schur) - P. x schuri Jsk.)	8 x 23	-	- (Ga Rm (Cz He
P. x custurae Nyár.	12c x 20	12c, 20, 39	Rm
P. x czernjajevii Prokudin	1 x 8	-	Rs(W)
P. x figertii Gerh.	23 x 27	-	Cz Ga Ge He
P. x insolita Nyár.	12 x 20 x 39 (sic)	12c, 20, 39	Rm
P. x jurassica Chrtek & Jirásek	26 x 27	26	He
P. x lepusnica Nyár.	12c x 39	-	Rm
P. x mataniae Nyár.	20 x 39	-	Rm
P. x ronnigeri	22 x 43	41	Au
P. x sabauda Beauv.	?	-	Ga
P. x sanionis A. & Gr.	4 x 8	?4	Cz Ga Ge Ho
P. x sclerocalamos Facch.	26 x 43	-	Au It
P. x stricta Lindeb.	10 x 20	10	Su

UN-NAMED HYBRID COMBINATIONS:

Rothmaler (1963)	4 x 23	Ge
Åkerberg (1942)	8 x 25	Su
Hess et al. (1970)	8 x 26	He
Åkerberg (1942)	8 x 27	Su
Rothmaler (1963)	8 x 43	Ge
Hess et al. (1970)	8 x 43	He
Hiitonen (1933)	9 x 27	Fe
Lid 1963	10 x 43	Su
Rothmaler (1963)	23 x 25	Ge
Rothmaler (1963)	25 x 27	Ge

CHAPTER 3. The problem of choosing a taxonomic rank for the members of agamic complexes.

3.1 Species or microspecies?

The taxonomist who approaches the study of a group such as the genus Poa, which includes species with a normal sexual mode of reproduction and 'species' with more than one type of agamic breeding system, is faced with the task of reconciling two fundamentally different types of variation. There is clearly a need to adapt the species definition which normally serves among sexual groups. This is necessary in order to avoid having to rely on the criterion of the degree of reproductive isolation between taxa. Such a criterion is evidently inapplicable to plants with an apomictic mode of reproduction, whether agamospermic or involving vegetative proliferation.

In other groups having apomictic breeding systems, this has led to a number of proposals for a specialized terminology to be used in cases where apomixis has caused abnormal patterns of variation. The problem is compounded in Poa in two ways: the agamic mode of reproduction is not confined to a specific group or taxonomic category, but is spread throughout the genus; and the facultative nature of apomixis in Poa permits plants to retain a capability to produce an occasional sexually-formed caryopsis, thus exchanging hereditary material. Fortunately, in the genus Poa taxonomists have been less assiduous in giving specific names to every apomictic variant than, for example, in Taraxacum, Hieracium or Alchemilla. Such taxonomic efforts to study variation patterns within 'species' such as P. arctica and P. bulbosa were aimed at achieving a varietal nomenclature.

Some of the earliest work which attempted to redefine the species concept in the light of what is now known as ecotypic variability

was that of Turesson (1922a, 1922b, 1925). He defined the ecospecies as a group of plants comprising one or more ecotypes whose members are able to interchange their genes without detriment to the offspring. Clausen et al. (1944, 1945) were able to strengthen this definition, as a result of their work on ecotypic differentiation studied through transplant experiments, by showing that it had a factual basis in a wide range of species in different families of flowering plants.

The importance of such work to the question of assigning rank to apomictic taxa is that it stressed the establishment of proof of the capability to exchange hereditary material as the basis of a species definition, rather than requiring that it be shown that such exchanges were occurring in nature. In the case of ecotypes, it was recognized that morphological differences between ecotypes were maintained through the operation of ecological barriers rather than genetical barriers to free gene exchange.

Different apomictic clones of certain species of *Poa* have often been treated as if there was an ecotypic relationship between them. Since the barriers to free gene exchange are primarily genetical, not ecological, it is impermissible to use the term 'ecotype' to describe them. Turesson (1926), recognizing this, proposed a series of terms applicable to such entities in his study of proliferous *Festuca ovina*. This resulted in a trinomial nomenclature, the third epithet being designated as the amphiapomict (aapm) epithet. The same author later used the term agmospecies when discussing apomictic taxa within the *Alchemilla vulgaris* aggregate. The terms 'agmospecies' and 'amphiapomict' are regarded by Turesson (1943) as having a formal taxonomic status, the term 'microspecies' being reserved as a general name for such entities.

An alternative way of naming microspecies by means of tertiary epithets was suggested by Babcock & Stebbins (1938), who added names

designated 'formae apomicticae' to the binary names of their apomictic species. Gustafsson (1947) reverted to using Turesson's term microspecies, proposing that it should be employed for such tertiary epithets as were felt to be necessary for an adequate documentation of the apomictic variants of a species. This view received recent support from Jauhar & Joshi (1970), who believe that such variants would best be given an independent status from the varietal status permitted by the International Code of Botanical nomenclature (Stafleu et al., 1972).

The Code itself makes no recommendations regarding the treatment of apomictic complexes; the only relevent statement is (Article 24) that the name of an infraspecific taxon is formed by the name of the species and an infraspecific epithet connected by a term denoting its rank.

Jauhar & Joshi's recommendations are not, in my view, suitable for the apomictic groups in the genus Poa. The available data on chromosome numbers is sufficient to indicate those groups where excessive varietal fission has occurred on account of apomixis, even where the type of breeding system has not been determined experimentally (see chapter 4). This is in any case evident from the proliferation of varietal names in the literature of certain groups (Nannfeldt, 1940; Jirásek, 1964). These 'varieties' differ from the 'microspecies' of such groups as Alchemilla in that the exchange of genetical material is not entirely ruled out by the mainly agamospermous breeding system found in Poa sect. Poa, for example. It is probably for this reason that two different types of agamic complex can be found and recognized:

a) groups of variants with a particular range of ecological tolerances, exhibiting a common range of adaptation to such conditions, and capable of being treated taxonomically in a similar manner to

amphimictic species (but frequently treated as subspecies or varieties of a 'circle-species'), e.g. the groups known as P. pratensis, P. subcaerulea, P. angustifolia and P. alpigena which are adapted to meadows, marshes and flushes, dry grassland and wall-tops, and arctic conditions respectively.

b) hybrids stabilized through apomixis, and taxa suspected of having a hybrid origin on account of being taxonomically intermediate between two species, often of different sections (e.g. P. x hartzii, P. x jemtlandica). These should be distinguished from amphimictic species of allopolyploid origin such as P. annua, which have preserved a sexual breeding system by means of the doubling of their chromosome numbers and which behave like any other amphimictic species.

The members of group (a) which are subsequently found to have a hybrid origin may be maintained without nomenclatural disturbance, other than the addition of a hybrid sign (x) when being transferred to group (b).

Tsvelev (1966) approaches this problem from the point of view that a treatment is possible which recognizes the geographical race as the primary unit, and which is treated as a monotypic species according to the Komarovian species-concept (Komarov, 1902) whether or not the unit is stabilized through apomixis. Whereas this argument leads to the conclusion that apomictic 'eco-geographical entities' should not be treated as subspecies of a polytypical species, i.e. a species with several types, in line with the doctrine of Komarov, Tsvelev suggests that groups which on closer investigation are found to be related through hybridization with or without accompanying polyploidy are best grouped under a single binary name: e.g. Poa agg. annua L. including the species P. annua, P. infirma and P. supina. I believe that this is a gross distortion of systematic relationships which widens even further the gap between

the theoretical concept of the species and its recognition in practice; it should be noted that Tsvelev noes not adopt his own proposals in his later accounts of Poa.

3.2 The taxonomic treatment of proliferous grasses.

Plants in which the flower or inflorescence proliferates are often described as 'viviparous'; this term is best confined to its original meaning, i.e. the bringing forth of the young alive, or in the sense in which it is applied to grasses, producing seeds which germinate while still attached to the parent plant. In a proliferous grass, the spikelets undergo modification to produce a plantlet or bulbil; in Poa, the lemma is the organ principally involved.

Proliferation of the inflorescence is reported from a number of species of angiosperms scattered through a wide range of families. The phenomenon is extremely rare, however, except in the Gramineae. It is by no means the only means of vegetative reproduction; apart from specialized shoots - rhizomes and stolons - the bulbous stem bases of P. bulbosa, P. sinaica and P. timoleontis may act as freely dispersed vegetative propagules under particular environmental conditions. The production of units of dispersal from the tissues of the spikelet has probably arisen through evolutionary selection for two reasons:

a) the reproductive organs are relatively sensitive to conditions of environmental stress during their periods of differentiation;

b) the height at which the propagules are borne and released favours their dispersal.

Proliferation is known in several genera of the Festucoideae: Agrostis, Deschampsia, Festuca and Poa. It is also reported from Zea (Eyster, 1931). Poa has by far the largest number of species in which proliferation is recorded. The following list, probably

incomplete, gives the names of those species and hybrids recorded in the literature as having proliferous forms:

P. alpigena (Fr.) Lindm.	P. hispidula Vasey
P. alpina L.	P. x jemtlandica (Almq.) Richter
P. arctica R.Br.	P. komarovii Rozhev.
P. bulbosa L.	P. labillardieri Steudel
P. costiniana Vickery	P. lanata Scribn. & Merr.
P. gunnii Vickery	P. malacantha Komarov
P. x herjedalica H.Sm.	P. x nobilis Skalińska
P. hiemata Vickery	P. stenantha Trinius

P. timoleontis Boiss. & Heldr.

P. macroglossa Hack. is now regarded as synonymous with proliferous P. timoleontis (Feinbrun, 1940) and P. eigii Fein. is likewise a proliferous form of P. bulbosa (Heyn, 1972).

Proliferation appears to offer a reproductive strategy to otherwise sterile intersectional hybrids: P. x herjedalica, P. x jemtlandica and P. x nobilis are known only in the proliferous state.

The traditional treatment of 'viviparous' grasses has been to give them varietal status (Linnaeus, 1753, p. 67). This view was reiterated by Wycherley (1953) in a discussion of the taxonomic status of proliferous "races" in Festuca, Deschampsia and Poa. Though his account introduces some taxonomic changes in the first two genera, his treatment of Poa is conventional, the two proliferous British taxa being treated thus:

P. alpina L. var. vivipara L.

P. bulbosa L. var. vivipara Koel.

A rather different view was presented by Tsvelev (1972). He makes new combinations in Poa pratensis, P. alpina and P. bulbosa in order to treat the proliferous taxa as subspecies:

P. pratensis L. subsp. colpodea (Th. Fries) Tsvelev;

Basionym: P. stricta Lindeb. subsp. colpodea Th. Fries.

P. alpina L. subsp. vivipara (L.) Tsvelev;

Basionym: P. alpina L. var. vivipara L.

P. bulbosa L. subsp. crispa (Thuill.) Tsvelev;

Basionym: P. crispa Thuill., syn. P. bulbosa L. var. vivipara Koel.

Koeler's epithet (1802) is rejected in favour of Thuillier's earlier epithet (1791). Tsvelev's use of the category of subspecies for these proliferous taxa is a marked deviation from customary usage. There is, of course, a tendency on the part of those wishing to support the 'geographical-morphological' species concept (Bobrov, 1972) to cast suspicion on the rank of subspecies. Bobrov presents the argument for a monotypic species concept in terms which seem to me to be very questionable. He poses the question, "to where does a species vanish if it is said to 'fall' into subspecies?", a technique of argument reminiscent of the mediaeval arguments for and against the existence of God, and also maintains that since the 'genetic race' should be considered as the primary unit for investigation, the western European usage of the category of species is based on faulty reasoning. Seen, in this light, the use of the rank of subspecies has some bearing on the question of which approach to adopt, but to use the subspecies category for proliferous variants introduces a further area of disagreement between Soviet and Western approaches, which in my view only hinders the process of improving the classification of grasses.

Tsvelev presents three arguments for the choice of category: a) the proliferous 'subspecies' do not tend to change into non-proliferous 'subspecies' either under natural conditions or over long periods of cultivation.

b) the distribution of related proliferous and non-proliferous 'subspecies' is partially allopatric, and this lack of coincidence has historical causes.

c) there are differences in chromosome number between the subspecies, and in some cases they are of hybrid origin.

(a) Foreman (1971) concluded from a study of clones of P. alpina grown in a phytotron under various combinations of conditions of day-length, temperature and light intensity that there is a strong inherent tendency to produce a non-proliferous inflorescence, but that proliferation occurs under conditions which are marginally favourable to growth. The fact that prolifery is induced in non-proliferous plants through exposure to an abnormal environment is now widely recognized.

(b) The two taxa of each species may indeed have different geographical distributions in the USSR, but in Europe as a whole there is only a relatively minor difference between the ranges of the proliferous and non-proliferous taxa. In the case of P. bulbosa, it has been suggested that the plants native to the British Isles lack the capacity for transformation into proliferous forms under adverse conditions, and that proliferous material collected in Britain has therefore been introduced. Further work needs to be done in comparing the micro-distribution of proliferous and non-proliferous plants.

(c) The chromosome number of a particular clone may well be important in determining whether or not the particular plants have the capacity to produce a proliferous (or normal) inflorescence. However, a comparison of the published chromosome counts stated to have been taken from plants with proliferous inflorescences suggests that the differences are due to the large number of possible counts

and the relatively few recorded chromosome numbers, rather than genuine and consistent differences between plants with certain chromosome numbers.

These considerations lead to the conclusion that proliferous plants are deserving of at most varietal status, though much more work needs to be done if the nature of the control of proliferation is to be discovered.

3.3 The nature of the proliferous spikelet.

The general form of the proliferous spikelet differs only slightly from that of a normal spikelet. Varying degrees of modification occur; in a typical case, a normal pair of glumes subtend a rhachilla on the first segment of which is borne an abaxial proliferous blade which substitutes for the lemma. Facing the blade in the position normally occupied by the palea is a more normal lemma, which may or may not enclose functional or rudimentary stamens and ovary. The second segment of the rhachilla, jointed at its junction with the first, bears a similar arrangement of scales. A third unit may complete the spikelet, depending upon the species, or it may be replaced by a rudimentary lemma. Sometimes (notably in P. bulbosa) the proliferous blades may be swollen at the base, so that the propagule takes on the form of a bulbil; in general, however, the term 'plantlet' is preferred to the term 'bulbil', as the latter gives an impression of being bulbous which is not true of the majority of proliferous taxa.

In some proliferous taxa, e.g. P. x nobilis Skalińska, the first floret is normal, subsequent lemmas undergoing transformation.

The evidence provided by the structure of the proliferous spikelet suggests that the lemma, when modified, takes on the structure of a vegetative leaf. Parallel studies on the developmental

biology of Stipa (Maze et al., 1971, 1972) have come to an exactly similar conclusion. They suggest that the homology of the lemma and the leaf is probably the result of a floral organ acquiring the characteristics of a vegetative organ, rather than having evolved directly from a vegetative leaf. The floral parts, and their homology with vegetative organs, are discussed in more detail in chapter 5.

CHAPTER 4. Chromosome numbers and breeding systems.

4.1 Introduction

The information published on the chromosome numbers of species of *Poa* has recently been brought together in the massive compilation edited by A.A. Fedorov (1969), which assembles the available data up to the end of 1967. Additional counts have been obtained from R.J. Moore's cumulation of the Indices to Plant Chromosome Numbers for the years 1967 to 1971 inclusive, updating Fedorov's work to the end of 1971. Later publications have been included where these have come to my attention. Finally, counts have been obtained from material grown in Leicester (see appendix 4); details of the technique employed in making chromosome squashes are provided in appendix 2. The technical difficulties in making satisfactory preparations are considerable; I give strong endorsement to the view expressed by Flovik (1938, p. 307), that "as a rule *Poa* is a most unsuitable object for detailed cytological investigation, for even a simple determination of the number of chromosomes is often impossible". Nevertheless, it has proved possible to make comparative karyotype studies in a few groups: see for example the work of Nannfeldt (1937b), T.K. Koshy (1968) and M.K. Ahmed et al. (1972).

The bulk of the published data on chromosome numbers of *Poa* falls into one of two categories: occasional counts of a few species of *Poa*, obtained during a general investigation of the karyology of the flora of an area or region; and detailed investigations, on a population by population basis, of particular species often with a view to providing a full account of the range of numbers of chromosomes in an aneuploid species.

Table 4.1 sets out the available published data on chromosome

numbers in the European sections of Poa. Species and subspecies of Poa known to occur in Europe have been listed separately from non-European species where there is reason to believe that the latter belong to the sections of Poa which occur in Europe. In the case of species from the Himalayas and from the Soviet Far East, I have generally accepted the sectional placement of the author of the most recent revision (e.g. Bor, 1948; Probatova, 1971). On the basis of their ranges of chromosome numbers, the sections have been grouped into five categories according to the levels of polyploidy of their constituent species. Levels of polyploidy (abbr. to 'ploidy levels') refer to chromosome numbers which are exact multiples of the basic number, which in Poa is 7. Irregular numbers are termed aneuploids; odd- and even-numbered multiples, or euploids, can also be known by a term based on the Greek root of the number of sets of sevem chromosomes present. The range of numbers in Poa includes diploids (2n = 14), triploids (2n = 21), tetraploids (2n = 28), pentaploids (2n = 35), hexaploids (2n = 42), heptaploids (2n = 49), octaploids (2n = 56), nonaploids (2n = 63) and dekaploids (2n = 70). 'High-aneuploids' have an irregular number that in general is greater than 49; 'mid-aneuploids' span a rather lower range of numbers: 21-49.

4.2 Apomixis and polyploidy.

Maheshwari (1950) defined apomixis as the substitution for sexual reproduction (amphimixis) of an asexual process, i.e. one which does not involve nuclear fusion. Of the four classes of apomixis recognized by Maheshwari, only two occur in Poa:

a) recurrent apomixis, in which the embryo sac arises either from an archesporial cell or from some other part of the nucellus. No meiotic reduction occurs, and the embryo is formed either from the unreduced egg (diploid parthenogenesis) or from some other

cell of the gametophyte (diploid apogamy);

b) production of vegetative propagules by proliferation of the inflorescence. The taxonomic implications of the second type of asexual reproduction have been discussed in the previous chapter.

The distinction between embryos derived from the archesporial cell and those developing from some other cell of the nucellus is somewhat artificial, as Maheshwari points out. Since no meiosis takes place, and no genetical recombination of genes can therefore occur, the genotype of the cells involved is uniform. Work on the type of apomixis in Poa has led to a very detailed knowledge of the processes involved; nevertheless, this is of little taxonomic importance. The most crucial consideration in the apomictic process is that meiosis is not eliminated by apospory - merely by-passed - so that the failure of the aposporic embryo-sac to develop leaves the way open for sexual reproduction to occur. Apomixis is thus facultative; the plants retain the facility for out-crossing, and this residual ability leads to a much greater level of complexity of patterns of variation than would be the case if all plants were strictly asexual in their mode of reproduction. Hybrids formed from an occasional event of out-crossing can reproduce asexually in the same way as their parent(s); in the event of their becoming stabilized in this way, they may extend their area of distribution and behave in every way as normal plants not of hybrid origin (save for their mode of reproduction).

Although no direct link exists between apomixis and polyploidy, it is nevertheless true that in Poa apomixis is known from polyploids and conversely those diploids which have been studied have been found to reproduce sexually. Some polyploids (mostly tetraploids) are known to be amphimictic, but the majority of polyploids, along with the species which have aneuploid chromosome numbers, are very likely to

reproduce apomictically. Since any pair of plants sufficiently closely related not to be reproductively incompatible may produce 'normal' offspring, whatever the chromosome number of each parent may be, the stock of aneuploid clones is constantly being augmented.

4.3 History of breeding system investigations in Poa.

Much of the pioneer work on apomixis in grasses was carried out on two species of Poa: P. pratensis and P. alpina. The existence of a much larger number of species showing apomixis was not recognized until later. Even today, the necessary experimental work has not yet been undertaken in more than a small proportion of the species suspected of reproducing apomictically.

Müntzing (1933) concluded, from an examination of the aneuploid chromosome numbers of the Poa pratensis group, that their constancy could best be explained by apomixis. Kiellander (1935, 1937) came to similar conclusions with P. palustris.

The evidence of embryological studies was available within the next ten or so years. Håkansson (1943), in his pioneering work on the development of the embryo-sac in P. alpina, showed for the first time that the apomictic embryo developed from an unreduced egg originating from an embryo sac which had itself developed from sporophytic tissue. Independently, Khristov (1942) achieved similar results with P. pratensis, discussing the related problems of polyploidy, apomixis and polyembryony.

As Müntzing had suggested (1933), non-proliferating florets of a largely proliferous clone of P. bulbosa studied by Nikolov & Georgiev (1959) were shown to have preserved normalysexual reproduction in some cases. Later, Georgiev (1961) suggested some correlations between environmental factors and the frequency of apomixis, and

Khristov & Nikolov (1962) found both sexual and aposporous embryo-sacs in a polyploid strain of P. pratensis.

These results showed beyond reasonable doubt that apomixis was the explanation for the existence of constant aneuploid strains, as had been predicted by Müntzing. Application of these peculiar breeding characteristics to plant breeding soon became widepread, since it allowed a way of producing hybrids between quite distantly related strains without the usual breeding system breakdown at meiosis, and subsequent sterility, through inability of the chromosomes from the different parents to pair. Cloning of desirable strains could be achieved simply by allowing the selected plants to reproduce themselves, producing progeny showing great similarity with the mother plant: see, for example, the paper of Almgård (1960). The separation of hybrids became feasible, since even when only a low percentage of hybrid offspring was produced, they could be detected easily by the way in which they differed from the highly uniform apomictic offspring. A summary of these applications is given by Clausen (1961).

4.4 Taxonomic consequences of the incidence of apomixis.

It has long been recognized that certain species of Poa are morphologically extremely variable. The discovery of apomixis provided an elegant explanation of why some species should be so much more variable than others. Further than this, however, these insights into breeding behaviour did not lead to any clarification of the taxonomy of the groups involved; rather, it has led to a reluctance to tackle the naming of entities within these groups, and disagreements over the taxonomic rank to be accorded them (see chapter 3). However, the role of inter-group hybridization as a possible source of new species was recognized, and certain species were re-evaluated as inter-sectional hybrids (Holmen, 1962).

Apomictic progeny can also be distinguished from those arising sexually (and having a mixed biotype), according to uniformity of certain morphological features (Miroshnichenko, 1964). Using P. nemoralis and P. glauca (sect. Stenopoa) and P. pratensis (sect. Poa) certain differences were used to select plants of the two types, allowing their rates of development at an early stage to be studied.

Although the embryological evidence for apomixis in polyploid plant species was available from the start, the causal relationship between polyploidy and apomixis was only established quite recently (Khokhlov, 1965). The early work of Thomas (1940) indicated that while Rubus species of allopolyploid origin are amphimictic, those which were autoploids were also apomictic in their mode of reproduction. Zhirov (1967) had studied the inheritance of diplospory, and in his second paper (1968) quoted Thomas's work, observing that the opposite tendency was most often found in Poa - i.e. apomixis is more characteristic of allopolyploids. Zhirov had produced 'polyhaploid' plants of P. palustris from plants with 42 chromosomes, which had in turn been produced by self-pollination of a 28-chromosome plant, where an unreduced ovum had been fertilized by a reduced male nucleus. The advantage of studying such a 'polyhaploid' is that it allows the third set of chromosomes to pair, or not to pair, with the first two sets according to whether they are or are not homologous. If the degree of homology is low, a high proportion of bivalents and univalents would be expected at meiosis; if high, a number of trivalents would be expected. Zhirov proved statistically that the proportions of univalents, bivalents and trivalents observed corresponded to the theoretical proportions to be expected in the case of an autopolyploid.

The taxonomic interest of Zhirov's conclusions is that they confirm the possibility that species in which apomixis is detected are not necessarily allopolyploids (Gustafsson, 1947). Since the triploids reported to have been found in a population of P. minor (Nygren, 1956) may have arisen naturally in the same way as the triploid P. pratensis plant produced artificially by Zhirov (1968), the possibility of P. minor being autopolyploid can not be ruled out.

One of the least remarked-upon features of the range of chromosome numbers in Poa is that it includes quite a large number of diploid species. Whereas some polyploid species have recorded diploid counts, this has only happened where there are closely related diploid species with which they might have been confused. The great majority of the diploid species are not now known to have polyploid numbers, i.e. they are exclusively diploid; furthermore, they tend to fall into a relatively small number of taxonomic groups. Since the incidence of diploid numbers in the Gramineae as a whole is quite low (Nannfeldt, 1937b) the relatively high incidence of diploid species in Poa is an interesting phenomenon. It is probably true to say that the capacity of species of Poa to retain their reproductive capabilities in the short term through apomixis may nevertheless put them at a long-term selective disadvantage, and that the existence of relatively large numbers of diploid species in this evolutionarily ancient group testifies to the long-term selective advantage of retaining an amphimictic breeding system.

4.5 Chromosome number categories.

As this account is primarily directed towards the sectional level of the taxonomic hierarchy, chromosome numbers of individual species are not discussed here in detail. In most cases, suitable comments have been provided by the authors of the chromosome counts. With the exception of the exclusively diploid species, the number of species of Poa with only one known chromosome number is quite

small, and will doubtless be further reduced as the genus becomes karyologically better known. Only four European species remain entirely unknown from the point of view of their chromosome numbers: P. feratiana (sect. Coenopoa), P. flaccidula (sect. Stenopoa), P. jubata (sect. incogn.) and P. pirinica (sect. Oreinos).

With a degree of generalization, five categories can be defined into which the European sections of Poa can be placed. It is not suggested that to place two sections into one such category is to imply that they are thereby taxonomically related; rather, it enables the range of chromosome numbers in each category to be discussed, with comments which to some extent hold true for each of the sections placed within that category. In descending order of size (total number of species in each category), these are specified as follows:

CATEGORY A: sections containing species with numbers ranging from diploid to mid-aneuploid*;

CATEGORY B: sections containing species with numbers from tetraploid upwards, including high-aneuploids**;

CATEGORY C: sections containing diploid and tetraploid species;

CATEGORY D : sections containing species with numbers ranging from tetraploid to octaploid;

CATEGORY E: sections containing exclusively diploid species.

As explained in 4.1 above, the terms 'diploid', 'tetraploid' etc. assume a base-number of n = 7. There seems to be no reason to question this assumption, as the genus shares this base-number with the closely related genera Bellardiochloa Chiovenda and Festuca L., and indeed the number is one of the most frequent base-numbers in the subfamily Festucoideae as a whole.

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*, ** Note: the definition of 'mid-' and 'high-aneuploid' can be stated loosely as being in the range 21 - 49 and 49 upwards respectively.

Category A. Chromosome numbers ranging from diploid to mid-aneuploid.

Sect. Bolbophorum and sect. Stenopoa, the two largest sections in Europe, belong to this category. Despite the similarity between the overall range of numbers of the two sections, the distribution of the numbers among the species of the two sections is very dissimilar. Whereas sect. Stenopoa has only one diploid species, sect. Bolbophorum consists mainly of diploids.

Taking sect. Bolbophorum first, aneuploidy is confined to the two most widely distributed and variable species, P. alpina and P. bulbosa. Of the other species, only two are aneuploid to any extent, and both of these are non-European species: P. elbrussica and P. sinaica, the latter sometimes considered conspecific with P. bulbosa and the former possibly a form of P. alpina. All the other species are diploid, only P. badensis among them having additional chromosome numbers. P. media, counted for the first time at Leicester, proved to be a diploid, and the only published count for P. ligulata at the time of writing, that of Kupfer (1968), was confirmed.

The accuracy of the identification of at least some of the material on which Nygren's (1962) counts of 'P. concinna', now P. perconcinna, are based must be questioned. Doubts arise for the following reasons: firstly, Nygren evidently confused the species with P. molineri to the extent that he copied Buschmann's distribution map of P. molineri when mapping the various species counted; compare his map with that of Buschmann (1942). It seems probable that Nygren mistook Buschmann's P. molineri Balbis for P. molineri Lam. & DC., which is a synonym of P. perconcinna. Secondly, the illustration of a series of plants named as P. perconcinna leads me to believe that the seeds supplied to Nygren were of P. molineri. The appearance of the plants is inconsistent with the habit of P. perconcinna in the wild, although the possibility that the material was true

P. perconcinna which had become markedly modified as a result of cultivation cannot be ruled out.

The diploid assemblage within sect. Bolbophorum is interesting from an evolutionary point of view. A consideration of the probable direction of evolutionary trends (see chapter 9) suggests that these species are xeromorphic derivatives of a more mesophilic diploid ancestor (it follows that the ancestor must be diploid, since polyploidy is not normally reversible). On karyological grounds, P. alpina must be considered a possible ancestor, since diploid counts have been recorded for this species from various localities in western Eurasia (N. Africa - Atlas mts., Carpathian mts., and the Caucasus mts.) though on morphological grounds there are reasons for believing that P. alpina itself is quite highly evolved. P. bulbosa seems to have differentiated independently and at an earlier stage in the evolution of the group, since both its present-day distribution and likely centre of origin suggest a long period of independent existence. It appears to be of recent appearance in the Mediterranean region, and an Irano-Turanian origin can be postulated.

Proliferous plants of P. bulbosa are sometimes diploids; hence we must note that polyploidy is not an essential pre-requisite of proliferation (unless Guinochet's count was based on P. perconcinna, which is not known in the proliferous state).

P. ligulata and P. timoleontis form a vicarious species-pair. Both are diploid, and whereas proliferous plants of the former species are unknown the latter has a well-documented proliferous tendency (proliferous specimens have frequently been named P. macroglossa Hackel, reduced to synonymy with P. timoleontis by Feinbrun (1940)). In view of the evidence that P. bulbosa can occur as a proliferous diploid, the proliferation of P. timoleontis is not necessarily indicative of polyploidy. However, so far as is known none of the counts of P. timoleontis is based on proliferous material.

The geographical distribution of proliferous plants of P. timoleontis is insufficiently known, but appears to be concentrated in the south-eastern part of the range of the species, in southern Turkey and northern Syria.

The occurrence of B-chromosomes at meiosis in most of the diploid species of sect. Bolbophorum has been fully documented: Müntzing & Nygren (1955); Nygren (1955, 1957, 1962). In an anther squash preparation, I found B-chromosomes in a mitotic figure of P. media (see App. 4). The count of 2n = 14 + 2B is of no particular interest, except that it was observed in somatic tissue.

P. badensis, known both as a diploid and a tetraploid (together with a triploid, which in view of the fact that some of the seed used by Nygren was of garden origin could have resulted from the hybridization of the two chromosomal strains), is interesting in that it has a correlation between the size of its anthers and the ploidy of the plant concerned, (Nygren, 1962). This paper also reports chiasma frequencies for the various species studied, and it is interesting to note that the chiasma frequencies of P. pumila and P. molineri are very similar, providing an additional indication of their close relationship to one another.

As there are no published counts of P. media, my two determinations appear to be the first to be made for this species. Both were made from plants grown from seed of wild origin; the first was a plant grown in Leicester Botanic Garden by Mr Philip Brown from seed collected in the wild; whereas the second was made on a plant grown from a caryopsis recovered from a herbarium specimen collected in 1963 by P.W. Ball and Arthur Chater. This incidentally provides an indication of the potential longevity of Poa caryopses, since the seeds were stored for nine years on a presed and dried specimen which had been treated with an alcoholic solution of mercuric chloride

as preservative.

P. pumila is the last species of the exclusively diploid group to be mentioned. Morphologically it appears to show clinal variation, since the southernmost examples show the most strongly xeromorphic features. My count of P. pumila is the only one since those of Nygren (1962). Nygren's earlier statement (1957, p. 490) that P. timoleontis is a "very primitive member of the sect. Bolbophorum" on which is based the supposition that the supernumerary chromosomes must have originated a very long time ago, must be questioned. The morphological characters of P. pumila, P. molineri, P. ligulata and P. timoleontis are those of specialized xerophilic derivatives (Achtarov, 1939); see also chapter 9.

The remaining species of sect. Bolbophorum are P. alpina and P. bulbosa. Though mainly apomictic in their system of breeding, their limited capability for sexual reproduction confers evolutionary flexibility on the assemblage. Their chromosome numbers seldom exceed 50 (with the notable exception of a count of P. alpina from the Himalayas) and numbers close to those which are multiples of seven are frequent, suggesting that those strains which are regular even-numbered polyploids are better adapted (though this conclusion is based on only limited material). The frequency of apomixis in P. alpina probably varies with the ecological conditions (Heyn, 1972). It is interesting to note that the places where diploid P. alpina has been detected are those which are centres of diversity of d endemic species of Poa: the Carpathian mts, the Caucasus mts, and the Pamirs. The present diversity of aneuploid numbers, especially in the Arctic and subarctic, suggests an invasive tendency in P. alpina and this is no doubt favoured by asexual means of reproduction which confer the maximum degree of fitness for present-day conditions at the

expense of longer-term flexibility through the retention of genetic diversity.

Some of the more puzzling variants of P. alpina, e.g. subsp. insularis from the mountains of Sicily and Greece, and subsp. fallax F. Hermann from Anatolia, particularly need investigation of their chromosome numbers, since this would provide valuable extra evidence for the assessment of their taxonomic status.

Sect. Stenopoa

By contrast with sect. Bolbophorum, the range of chromosome numbers of the members of sect. Stenopoa is less well known. Almost every species so far counted shows a different range of numbers. The European species of the group are particularly interesting in that aneuploidy is the exception rather than the rule, despite the fact that several are known to have apomictic breeding systems (Håkansson, 1943). Only P. glauca has a significant number of aneuploid counts recorded; occasional aneuploid counts are found in other species of the section, but there appears to be a tendency for chromosome numbers to be at the even-numbered ploidy levels.

P. rehmannii, with 2n = 14, is the only known diploid belonging to this section from either within or outside Europe. Further confirmatory counts would be desirable, as only one determination has so far been made. The diploid chromosome number lends support to my view that P. rehmannii is specifically distinct from P. nemoralis. The restricted distribution of this species allows it to be regarded as one of the 'Balkan relicts' (though their distribution extends a little way beyond the Balkan peninsula as defined in Flora Europaea) which are characterized by their narrowly defined chorology, their lack of close relatives, their montane habitats and (where data is available) their diploid chromosome numbers. Other members of this

informal group in the genus Poa are P. stiriaca (sect. Leptophyllae), P. pirinica (sect. Oreinos) and P. trichophylla (sect. Nanopoa). While historical factors must have been important in favouring the survival of such an assemblage of taxonomically isolated species in the area over what has probably been a geologically lengthy period of time, these are not yet well understood; see Kuzmanov (1969).

P. palustris is nearly always tetraploid. Zhirov (1968) has demonstrated that his material of the species is autotetraploid. This is consistent with Serebryakova's conclusions (1965, fig. 7) on the probable evolutionary relationships between the members of sect. Stenopoa, deduced from a study of the development of the different types of growth-form found in this section. Further work on the two ecologically distinct types found by Serebryakova would be interesting, in view of the evidence that the hydrophytic habitat is a secondary one occupied by a specialized derivative of the loosely tufted meadow form of the species.

Most counts of P. nemoralis are at the hexaploid level. Insufficient data exists to establish any correlation between the ploidy level and the varieties which exist in P. nemoralis, though it has been suggested by Hooper, in an annotation of herbarium material, that British material found to be octaploid was referable to subsp. montana Hooper, ined. (syn. P. nemoralis L. var. montana Gaud.), a glaucous form of the species. It is possible that Hooper has mistaken material of P. glauca, under the name P. balfouri, for P. nemoralis. Further work is necessary on the dividing line between P. nemoralis and P. glauca.

It remains an open question as to whether P. nemoralis is autotetraploid or allotetraploid in origin. The virtual absence of odd-numbered multiples of seven in the range of counts suggests that the species is not prone to forming chromosomal 'hybrids' between the different ploidy levels. The apomictic nature of the

breeding system (Håkansson, 1943) by no means excludes this possibility.

The existence of hybrids between P. nemoralis and other species has long been a matter of speculation. Tsvelev (1972), in his account of Poa in the European part of the USSR, suggests that some of the regional variants of P. nemoralis in the Carpathian and Ural mts. and in Lappland, to which he accords the rank of subspecies, may have arisen through hybridization between P. nemoralis and P. glauca. He postulates a similar origin for some subspecies of P. palustris. The great variability shown by both P. nemoralis and P. palustris is attributed to an historical process whereby their predecessors migrated from their supposed 'ancestral home' in the montane deciduous 'Turgai' forest belt (P. nemoralis) and the subalpine belt of the southern part of the coniferous 'Taiga' forest (P. palustris). Towards the end of the Miocene period, as a result of the continentalization of the climate, Tsvelev supposes that the lowlands became colonized first by the Turgai and then by the Taiga type of forest, with the more stable elements in the former remaining behind to hybridize with related species of the latter grouping, to survive in the mixed forests of the Pliocene period.

There is no factual evidence to support this rather interesting speculation; indeed, some of the available evidence tends to contradict it. Serebryakova's study of the evolution of growth form types agrees with this proposal in identifying P. nemoralis as the closest living relative of the ancestral type, but disagrees in portraying P. palustris as a derivative of P. nemoralis, with some quite convincing evidence to support her view.

The agreement between this scheme and that of Tsvelev on a fundamental point - the fact that the section as a whole has had mesophilic ancestors - permits the conclusion to be drawn that it has been the mesophilic members of the section which occupy habitats

at the present day which resemble those occupied by the ancestral species, whatever the alterations in chromosome number and breeding behaviour. This in turn leads to the realization that P. rehmanni is probably a primitive member of the section, despite its apparently numerous differences from the remaining members.

P. glauca has a wide range of chromosome numbers, of which the hexaploid and octaploid levels are best represented. The 8n, 9n± and 10n± are generally of a more northerly distribution. Although this range of numbers is symptomatic of an apomictic breeding system (Hakansson, 1943) the trend towards asexual reproduction, which favours survival in northerly climates, has not reached the stage of producing a proliferous inflorescence. The closely related P. bryophila Trin. occuring in Vrangeli island, a very northerly arctic land-mass in north-east Asia, has been counted and found to be 2n = 63, i.e. nonaploid. Zhukova (1965) suggests that this is indicative of allopolyploidy, which had already been postulated by Tsvelev (1964). Other non-European species are largely tetraploid and hexaploid; the N. American vicariad of P. nemoralis, P. interior Rydberg, has a similar range of chromosome numbers to that of its Eurasian relative, although fewer determinations have so far been made.

The available counts for P. sterilis and its European allies indicate that they are probably centred upon the tetraploid and hexaploid levels, although the unreliability of the identifications of the material on which the counts were made renders the information useless at the level of species. More precise information is available for the non-European members of the group, which are tetraploid, hexaploid and octaploid.

CATEGORY B. Numbers ranging from tetraploid upwards and including high-aneuploids.

The remarks made above on the role of polyploidy in the development of apomictic breeding systems are equally applicable to the species of this category. Two features distinguish the sections allocated to this category to those mentioned previously; the first is the absence of diploid members, and the second is that the level of ploidy attained among the species with aneuploid chromosome numbers often exceeds dekaploid. Nygren (1950) reports a count of 2n = 127 for P. alpigena, which is just over 18-ploid, and Löve & Löve (1952) record 21-ploid P. subcaerulea. These numbers by no means constitute the upper limit of chromosome numbers in the genus Poa; Hair (1968) records 2n = c. 266 for P. litorosa Cheeseman from New Zealand, a 38-ploid.

The absence of diploid members of the two sections in this category - sect. Cenisia and sect. Poa - is significant. In order to postulate that the original mechanism which raised the chromosome numbers of the ancestors of the present day species was through hybridization of diploids followed by doubling of chromosome numbers of the hybrids, or alternatively to postulate autotetraploids arising from diploids, one must look outside the sections for suitable diploid ancestors (with the possible exception of P. kolymensis Tsvelev from the Soviet Far East). This leads to the conclusion that hybridization between members of different sections is likely to have played a significant part in the ancestry of the present-day species.

The chromosome numbers of the members of the two sections are reasonably well documented. In the case of sect. Poa, much of the information has emerged as a result of genetical studies of the mechanisms of apomixis, whereas in the case of sect. Cenisia the emphasis has been on purely karyological studies.

Sect. Poa contains only four European species; its greatest

number of species occurs in eastern Asia. The four European species are very widely distributed; they are partly sympatric, but occupy different habitat types within the same geographical region. They form one of the most taxonomically critical groups within the genus Poa, and are sometimes treated as subspecies of a single, polymorphic species (Tsvelev, 1974). P. pratensis has the largest number of different chromosome numbers, but all four species have a wide range of counts.

There are several explanations of the success of apomictic polyploidy as a breeding strategy in sect. Poa; it is sometimes suggested that the section as a whole is of polyphyletic origin, having resulted from a series of events of intersectional hybridization followed by polyploidy and consequent apomixis. It seems doubtful whether the origin of the group will ever be traced to such an event, or whether light will be thrown on the relationship between the members of sect. Poa and such closely-related sections as sect. Cenisia, which include species with a similar breeding strategy and equally high degree of variability (P. arctica and P. granitica). New techniques, such as serology, may help to clarify these problems. It seems likely, however, that if the explanation of the group's origin is to be satisfactory, ancestral forms within the group must be sought; this may prove unproductive, since the offspring of a cross between such taxa would tend to supplant them by means of their greater fitness.

The means by which the high degree of variability is maintained are summarized by Clausen (1961), who describes the mechanism by which biotypic exchange takes place - occasional caryopses are produced sexually - without prejudice to the principal mechanism for apomictic seed production. Useful adaptations are thereby retained along with a degree of heterozygosity, and large numbers of highly uniform offspring are produced (as in the case of sexual inbreeding).

From the chromosome data, little can be added to the picture of P. angustifolia as a relatively xeromorphic assemblage of

ecotypes which is sometimes relegated to the rank of subspecies within an enlarged P. pratensis. The highest ploidy level attained (11-ploid) is rather lower than in other species of the section in Europe.

P. subcaerulea, more familiar under the name P. irrigata, comprises a subarctic and flush-dwelling group of ecotypes, usually regarded as specifically distinct on account of the rather specialized taxonomic features and habitat of the plants. Although this species has the highest recorded chromosome number of perhaps any Eurasian species of Poa, its range of numbers is generally similar to those of the other species of the section.

P. alpigena has a more exclusively arctic distribution than the previous species, and with its large number of high-aneuploid chromosome counts is no exception to the general pattern. It has one unusual characteristic: of the species of sect. Poa, it is the only one in Europe to show proliferation of the inflorescence.

Among the non-European species which can be assigned to this section with confidence, there is a similar range of aneuploid numbers. P. malacantha Komarov is similar to P. alpigena in having proliferous forms; it, and many of the other Far-Eastern species of the section, are assigned by Probatova (1971) to a separate subsection Malacanthae of the section Poa. P. kolymensis Rozhev., assigned by Sokolovskaya & Probatova (1973) to sect. Poa, is diploid; its sectional position, like that of the other far-east Asian species, requires confirmation.

Sect. Cenisia differs karyologically from sect. Poa in several respects. Its European species include two with high-aneuploid series of chromosome numbers, but in these species proliferation is a common occurrence. The third species, P. cenisia, has three geographically well-defined subspecies only two of which have so far been investigated

karyologically.

Tsvelev (1972) justifies the inclusion of sect. Cenisia in a much more broadly-defined sect. Poa partly on karyological grounds. Sect. Bolbophorum, which is represented in the European part of the Soviet Union by only three species (P. alpina, P. bulbosa and P. media) is likewise included in sect. Poa. He notes that there is some similarity between rhizomatous and caespitose species in the Far East such as P. platyantha Kom. and P. malacantha Kom. and the Central Asiatic species P. smirnovii Rozhev. and P. lipskyi Rozhev. with the members of sect. Cenisia, and suggests that these species form a link between sect. Bolbophorum and sect. Poa. While it is true that the presence or absence of rhizomes is not universally applicable as a sectional character, this is insufficient reason for combining two very dissimilar sections. The case for including sect. Cenisia in sect. Poa is somewhat stronger, since the growth-forms of the members of the two sections are similar and the two sections are evidently closely related. Tsvelev also suggests an 'inter-sectional hybrid' origin for the members of sect. Cenisia; putative parents are given as a diploid caespitose ancestor of sect. Bolbophorum, and an unknown, probably extinct, member of sect. Arctopoa (Griseb.) Tsvelev, a section unknown in Europe and including such long-rhizomatous species as P. eminens Presl (2n = 28, 42) and P. subfastigiata Trin. (2n = 42). Tsvelev also mentions P. tibetica Munro ex Stapf as a member of sect. Arctopoa; I prefer to regard it as a member of sect. Cenisia. It is possible that sect. Arctopoa and sect. Cenisia should be united.

P. cenisia is unusual in having only tetraploid and octaploid numbers recorded. The possibility that this indicates autoploidy causing a doubling of a tetraploid to give an octaploid is not so far ruled out, but many more counts need to be made, particularly of the eastern subspecies contracta (incl. P. psychrophila Boiss.

described from the mountains of western Anatolia). The recent count of 2n = 49 from the French alps appears to indicate the presence of hexaploids, as the only reasonable explanation for the occurrence of a 7-ploid strain is that a cross has occurred between a 6-ploid and an 8-ploid parent. Autopolyploidy is not ruled out as an explanation of the origin of the octaploid plants.

Of the aneuploid species of Poa, P. granitica has the most limited distribution. This fact indicates that the species is probably of recent origin. The status of proliferous plants described by Skalińska (1955) as P. nobilis is uncertain; the taxon is treated in the Flora Europaea account as an intersectional hybrid between P. granitica and P. alpina, following the suggestion of the author; however, the possibility that P. granitica itself has proliferous forms cannot be ruled out.

The karyological evidence supports the separation of P. arctica from P. cenisia, in which it has sometimes been included as a subspecies. It has a circumpolar arctic distribution, it is morphologically extremely variable, and has a range of aneuploid chromosome numbers similar to that of P. granitica. Proliferous forms are known.

CATEGORY C. Species with diploid and tetraploid chromosome numbers.

Three sections fall into this category: sect. Coenopoa, sect. Macropoa and sect. Ochlopoa.

Sect. Macropoa is centred upon the Caucasus mts. While all its species extend outside Europe, only two occur in the extreme east of Europe. The limits of the species in the Caucasus are not well understood; my count of 2n = 14 was performed on material named as P. iberica Fisch. & Mey., which was almost identical in cultivation with some plants of P. longifolia supplied from the

same source. I therefore regard the two species as synonymous, though they are sometimes regarded as distinct (Khramtsova, 1965). P. longifolia sensu lato occurs in the Caucasus and Transcaucasus mts, in the Pontus mts. of NE Turkey, and in NE Iraq and western Iran. An endemic subspecies, subsp. fagetorum, occurs in Krym. Chromosome numbers of the latter are not available, but the type subspecies has several published counts indicating that it is tetraploid.

A natural intersectional hybrid is recorded from NE Turkey between P. diversifolia (another member of sect. Macropoa) and P. chaixii; the collector, B. Balansa, named it P. controversa (in Pl. d'Orient 1866). In my opinion, Balansa has mistaken a plant of P. longifolia (which occupies an intermediate position between P. diversifolia (Boiss. & Bal.) Hackel and sect. Homalopoa) for a hybrid between the two sections. Nevertheless, the intriguing possibility is raised that P. longifolia s.l. may have arisen through just such a hybridization. Karyological examination of the whole group would therefore promise to be extremely rewarding.

The most northerly member of the section, P. sibirica, is more widely distributed in the boreal/subarctic zone of northern Asia, and only enters a small portion of E Europe. Plants named as subsp. uralensis by Tsvelev (1972) need to be investigated karyologically, if his suggestion is to be confirmed that they have arisen when populations of P. hybrida in the Ural mts. were 'swallowed' by P. sibirica migrating westwards.

The chromosome numbers of the members of sect. Macropoa indicate that a normal sexual breeding system is present. Their readiness to hybridize confirms this impression (Almgård, 1960) but further work is needed to confirm this.

Sect. Coenopoa contains two European species, only one of which is widely distributed. This species, P. trivialis, has been

counted frequently, and both diploid and tetraploid numbers are recorded; the latter category is less frequent. In most cases the possibility cannot be ruled out that the material counted was subsp. silvicola, which occurs in southern Europe. Only one count is specifically mentioned for this subspecies, indicating that it is diploid.

Mehra & Sunder (1959) record a count of 2n = 56 in P. trivialis from the Himalayas. This count has been excluded, on the grounds that the species is undoubtedly introduced to the area (Bor, 1948 p. 68) and may therefore be of agricultural origin.

P. feratiana, a seldom-collected species which is confined to the Pyrenees and NW Spain, has not been investigated karyologically.

Sect. Ochlopoa is centred upon the Himalayas, where it has several endemic species. Two of its three European species have relatively restricted distributions, while the third, P. annua, is cosmopolitan. The eastern extent of P. supina, one of the parents of P. annua according to Tutin (1957), is not clear as according to Fröhner (1968) it is replaced in central Asia by P. ustulata Fröhner. Some doubt has been raised by Koshi (1968) as to the generally accepted story of the origin of P. annua (Nannfeldt, 1937b). P. infirma and P. supina, both diploids, are said to have hybridized; the hybrid plants then became tetraploids by a process of allopolyploidy, regaining thereby the ability to reproduce sexually. Koshi showed that the karyotype of P. annua examined by him was not consistent with this explanation, as the karyotypes of P. infirma and P. supina did not add up to the karyotype of P. annua. The possibility that Koshi's material was atypical, or incorrectly named, or that P. annua is of polyphyletic origin, is consistent with that explanation. Another possibility is that the karyotypes of P. infirma or P. supina are heterogeneous.

The chromosome numbers of the non-European species of sect. Ochlopoa are mainly tetraploid; one species, P. nepalensis Wallich, is diploid. Some of these species - notably those described from north Africa such as P. maroccana - may well be synonymous with P. annua. Plants matching P. maroccana Nannf. have been recorded from S. Spain; the characters by which they are said to differ from P. annua are in my opinion not conclusive, in view of the variability shown by P. annua, (Scholz, 1968). P. pentapolitana, described by Scholz in 1971 from material collected in the vicinity of plants of P. annua, may well turn out to be a back-cross between P. annua and P. infirma.

CATEGORY D. Species with tetraploid to octaploid chromosome numbers.

This category includes three sections of Poa in Europe, two containing only a single species each, and one containing four European and at least three non-European species. Sect. Abbreviatae is distantly related to sect. Bolbophorum; sect. Oreinos is taxonomically isolated; and sect. Tichopoa is quite close to sect. Stenopoa.

Sect. Abbreviatae has a circumpolar Arctic distribution. Its sole European species, P. abbreviata, has been counted at various longitudes; three agree on its being hexaploid, one count is tetraploid, and two authors record higher figures. I have not been able to determine the origin of the material counted by Sokolovskaya (1955); in the case of Flovik's counts from Svalbard, it is possible that material of the intersectional hybrid P. x hartzii was mistaken for true P. abbreviata. Holmen (1952) expresses doubts regarding Flovik's counts (1938, 1940) for this species. Still, counts for this species higher than hexaploid cannot be ruled out.

Sect. Oreinos, with four European species, has been the subject of a special study by Nygren (1955). Two Soviet Far-Eastern species, P. leptocoma Trin. and P. paucispicula Scribn. & Merr., are also included in this section, which has at least one North American member, P. fernaldiana Nannf. The distribution pattern is therefore highly disjunct, an unusual pattern in the genus Poa.

The narrowly endemic species of SW Bulgaria, P. pirinica Stoj. and Acht., has no published chromosome counts.

P. minor and P. laxa are tetraploid. Nygren's counts included one of 2n = 21 for P. laxa; this need not be taken as indicating the presence of an undiscovered diploid race, since plants with a triploid number could have arisen in other ways, e.g. by the fertilization of an unreduced egg by a reduced male gamete (see Zhirov, 1968).

P. flexuosa is hexaploid. Nygren reports that pollen formation in this species is poor, but his embryological study (Nygren, 1950) showed that it was sexual and not, as one might expect in an arctic-subarctic species, apomictic.

The extra-European distribution of P. laxa is not known; it is recorded in the Flora Europaea account as endemic to Europe, but its occurrence in Greenland should not be ruled out as improbable.

The non-European members of sect. Oreinos are mainly hexaploids; one count of 2n = 28 is recorded for P. paucispicula Scribn. & Merr.

P. laxa is very variable in the Carpathian mts., and a special investigation of the species in that area would be interesting. The possibility of further undiscovered species of sect. Oreinos existing in the mountains of south-east Europe should be considered.

P. compressa, the only member of sect. Tichopoa, has rather a wide range of chromosome numbers. Munz's report of diploid P. compressa from California should be treated with caution, since the species is

undoubtedly introduced into that region. With that exception, its chromosome numbers range from tetraploid to octaploid.

The occasional aneuploid counts recorded stress that the allocation of sect. Tichopoa to this category, rather than to category A, is arbitrary. Despite its rhizomatous habit, P. compressa is quite closely related to sect. Stenopoa, and has sometimes been included in it. Its breeding system is apomictic (Nygren, 1953; Almgård, 1960).

CATEGORY E. Diploid species.

Three sections fall into this category; two are monotypic, and the third has three species.

Sect. Leptophyllae, with its single species P. stiriaca, was karyologically unknown until counted at Leicester. It was previously included in sect. Poa, on account of the superficial similarity between P. stiriaca and P. angustifolia. Its distinctive morphological characters (see chapter 5), and the characteristic anatomical features of the leaf-blade, serve amply to distinguish it as a separate section; the diploid chromosome number is an additional item of support for this view.

Sect. Nanopoa, containing P. trichophylla, is also newly erected. P. trichophylla is almost certainly the most isolated, species, from the taxonomic point of view, of all the European species. Authors' views have varied considerably on the question of its closest affinities; Ascherson & Graebner (1900) included it in their ill-defined sect. Oreinos, Nannfeldt (1935) excluded it along with several other species, placing it instead in sect. Subbulbosae (synonymous with sect. Bolbophorum), whereas Hermann (1939) redefined sect. Oreinos in a rather wider sense than Nannfeldt, to include P. trichophylla. Subsequently, the species has been overlooked.

The third section in this category, sect. Homalopoa, contains three diploid species. P. hybrida is normally sexual (Almgård, 1960) and the same can be assumed to be true of P. chaixii and P. remota.

Outside Europe, these members of the section extend into the Caucasus mts. and Pontus mts. According to Probatova (1969), who made a study of some far-eastern Asiatic species showing a similarity with sect. Homalopoa, P. radula and P. ussuriensis show a strong affinity with the section. Like P. remota, P. radula inhabits damp forests; this species is also mentioned by Tsvelev (1972) as a possible link between the rhizomatous and caespitose sections. However, the chromosome counts published for these two species indicate that P. ussuriensis is tetraploid and that P. radula is hexaploid, suggesting the need for further study.

The ability of members of sect. Homalopoa to form hybrids is well known. Naturally occurring hybrids have been reported for a number of different pairs of parents (see chapter 2); of these, P. x pawlowskii Jirásek is well-known in the Czechoslovakian Tatra mts., and a hybrid between P. chaixii and P. nemoralis has recently been detected in Britain (C.A. Stace, verbal communication).

Almgård (1960) gives an account of a programme of artificially produced hybrids between P. longifolia and members of sect. Homalopoa. These are produced readily.

Tsvelev (1972) suggests that the species P. ussuriensis Rozhev. may have originated from a cross between P. remota and P. acroleuca Steudel. This, and many other such reports, need to be investigated through the use of new techniques such as serology, and by the examination of pairing behaviour of chromosomes at meiosis in artificially produced hybrids, if relationships are to be firmly established.

4.6 The correlation between chromosome numbers and geographical areas.

Polyploidy is significant not only in relation to its influence

on the type of breeding system of the plant, but also in connection with the adaptive significance of the type of breeding system, and hence on the geographical area colonized by the species.

There has been a particular interest in the adaptive significance of polyploidy in relation to arctic conditions, and much of the early attention paid to polyploidy neglected its importance in determining the reproductive strategy which is a characteristic of plants with high chromosome numbers. In high latitudes, the shortness of the growing season requires great economy of production of reproductive structures. The ability to replicate successful genotypes asexually, avoiding the normal process of genetical recombination, is of considerable selective value.

The occurrence of species with high chromosome numbers ('high-aneuploids') in the territories used in Flora Europaea gives an approximate indication of the extent to which polyploid taxa with irregular breeding systems are distributed in Europe. Map 4.1 shows the absolute number of species in each territorial unit; since the number of species of Poa is smaller in some of the most northerly areas, the difference between these areas and those of southern Europe is even greater than the map indicates.

For comparative purposes, the incidence of diploid species in the Flora Europaea territories is also mapped (map 4.2). Here, the relative richness of diploid species in the mountains of Central and Southern Europe is clearly indicated.

4.6.1 Distribution of high-aneuploids in Europe.

The results show, not surprisingly, that high-aneuploids are richest in the arctic and boreal regions. The importance of the arctic-alpine disjunction is also indicated, since territories with a mainly lowland flora in the northern half of Europe (Da, Hb, Ho, Po, Rs(B)) have a lower score than those with more mountainous terrain

such as Br. The main areas from which high-aneuploids are entirely absent (Az, Bl) or almost absent (e.g. Cr, Si) are islands with a maritime-Mediterranean climate. The low score achieved by Al and Be probably can be attributed to the under-recording of P. angustifolia as well as to their southerly situation and low relief respectively.

The territories with two or three species in this category are of little interest, since the presence of P. pratensis and P. angustifolia in most of the territories of Europe accounts for the high frequency of occurrence of this pair of numbers.

Comparison of these crude data with similar data for other groups is not possible at present, since in most grass genera no account has yet been compiled for Flora Europaea in which there are forty or more species occupying such a wide range of natural habitats as the genus Poa. It is interesting to note, however, that the genus Puccinellia, whose habitat preferences are almost nowhere the same as those of Poa, appears to have the reverse of the type of distribution of ploidy types shown by the species of Poa. The arctic members of the genus include almost all the diploid species, whereas in the Mediterranean region the incidence of polyploids is highest.

4.6.2 Distribution of diploid species in Europe.

The centre of abundance of diploids lies in the north-east corner of the Adriatic Sea; Au and Ju have the highest scores. Italy and Romania also achieve high ratings, presumably on account of their combination of alpine and Mediterranean habitats, in the case of Italy, and Carpathian and Black Sea coastal habitats, in the case of Romania. South-west Europe attracts only a small score, while the nil score of Krym underlines the fact that as a mountainous area it is peculiarly poor in species of Poa. Hu scores a relatively low number of diploid species, since it lacks montane habitats. Northern Europe, as is to be expected, has the lowest scores.

TABLE 4.1 Chromosome numbers in the European sections of Poa.

Note: European and non-European species are listed separately; both are arranged in alphabetical order. For the purpose of discussion they are allocated to categories A to E as follows (for explanation see text):

Section	Category	Section	Category
ABBREVIATAE	D.	NANOPOA	E.
BOLBOPHORUM	A.	OCHLOPOA	C.
CENISIA	B.	OREINOS	D.
COENOPOA	C.	POA	B.
HOMALOPOA	E.	STENOPOA	A.
LEPTOPHYLLAE	E.	TICHOPOA	D.
MACROPOA	C.		

Sect. ABBREVIATAE

a) European species:

P. abbreviata

28	*S & S 1960	USSR	Franz Josef Land: Tikhaya.
42	Holmen 1952	N. Greenland	Peary Land.
42	Jörgensen et al. 1958	Greenland.	
c. 42	Mosquin & Hayley 1966	Canadian Arctic.	
42	Zhukova et al. 1973	USSR	Far East: Vrangely island.

doubtful (referable to P. x hartzii?):

70	Sokolovskaya 1955	USSR	Arctic.
c. 76	Flovik 1938, 1940	Sb	Isfjorden.

b) Non-European species:

P. pseudoabbreviata Rozhev.

14	*S & P 1973	USSR	Far East: Yakutskaya ASSR.

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*Note: the following pairs of authors' names are abbreviated as follows: S & P = Sokolovskaya & Probatova;

S & S = Sokolovskaya & Strelkova.

Sect. BOLBOPHORUM

a) European species:

P. alpina

14	S & S 1938, 1940	USSR Caucasus mts.
14	Quézel 1957	Morocco Atlas mts.
14	Timpko 1964	USSR Caucasus: mt. Elbrus.
14, 22	Skalińska 1952	Po W. Tatra mts.
14, 32, 34	S & S 1940	USSR Caucasus mts.
22-23, 26, 28, 33, 34, 35	Skalińska 1950	Po Tatra mts., Pieniny mts.
22, 26, 33	Skalińska et al. 1957	Po Tatra mts.
22, 23, 24, 25, 31	Håkansson 1943	He
22-32, 33, 35, 38	Müntzing 1932	
21 - 64	Müntzing 1940	He
28	Böcher & Larsen 1950	W. Greenland, 67° N.
32, 33, 39, 42	Bowden 1961	Alaska; Canada: Alberta, Manitoba.
32 - 34	Avdulov 1928, 1931	ex hort. bot.?
32, 39	Hedberg 1958	Br Scotland.
33 - 46	Knaben 1966, K. & Engelskjön 1967	No Near Oslo; inner Oslofjord.
34, 42	S & S 1948a	USSR Siberia: Altai mts.
35	Johnson & Packer 1968	Alaska Ogotruk creek.
35	Gadella & Kliphuis 1970	Ga Alpes, Haute Savoie.
35, 42	Tutin, unpubl. (herb. LTR)	Br Scotland: Coire amt Sneachda;
42	Stählin 1929	He Graubunden, Preda.
42	S & S 1938	USSR Pamir mts.
42	Sokolovskaya 1955	USSR Arctic.
42	S & S 1960	USSR Arctic: Khibiny.
42	Löve & Ritchie 1966	Canada Manitoba: Churchill.
42	Taylor & Brockman 1966	Canada Alberta.
42, 44 + 4 fragments	Flovik 1938, 1940	Sb Isfjorden.
44	Müntzing & Müntzing 1971	Su Koster islands.
c. 48	Böcher 1938	Fa
63	Mehra & Sunder 1959	Kashmir Tangmarg.

P. badensis

14	Nygren 1956	Au Mödling near Baden.
14	Bakšay 1956	Hu
14 + 2-8 B	Müntzing & Nygren 1956	He Ardez; Ga Hautes Alpes; Au Innsbrück.
14	Majovsky et al. 1970	Cz Slovakia: Muranska planina.

P. badensis (ctd.)

14, 18	Holub et al. 1971	Cz	Topolčany, Rožnava, Kosiče.
14, 21, 28	Nygren 1962	Au Cz Ga Ge Hu	
28	Armstrong 1937		

P. bulbosa

14	Guinochet 1943		
21	Fernandes & Queiros 1969	Lu	Coimbra.
21, 50	Mehra & Remanandam 1973	India	W. Himalayas.
28	Armstrong 1937	USSR	
28	Litardière 1949	Ga Co	
28	Tutin (Löve & Löve 1961)	It	
28	Strid 1971	Al	Kruj.
28, 42	Tarnavschi 1948	Rm	
28, 42	Petrova 1973	USSR	
28, 45	Åkerberg 1942		
c. 36, c. 43, c. 45, c. 46, c. 50	Heyn 1971	Israel	Jerusalem.
39	Skalińska et al. 1957	Po	Nida valley, Skorocice gorge.
42	Skalińska et al. 1961	Po	Grochow, Rembertow near Warsaw.
42	Hartung 1946	USA	N. Dakota: Dickinson.

P. ligulata

14	Küpfer 1968	Hs	Sierra Nevada, Mulhacen.
14	Edmondson, unpubl.	Hs	Sierra Nevada, Veleta road.

P. media

14 + 28	Kozhukharov & Kuzmanov 1970	Bu	Pirin Planina,
14 + 0-28 ?16	Edmondson, unpubl.	Ju	(see appendix 2)

P. molineri

14	Müntzing & Nygren 1955	He	Engadine valley, Ardez.
14	Nygren 1955	He	Engadine valley, Ardez.
14	Nygren 1962	He	Engadine valley, Ardez.

P. perconcinna

14	Nygren 1962	Bu	Klisura near Sofia;
		Ga	Hautes Alpes: St. Veran, Savoie: St. Jean de Marianne;
		He	Valais; Sion.

P. pumila

14	Nygren 1962	Au	Karnten: Grossglockner, Leitertal.
14	Edmondson (unpublished)	Ju	(see appendix 2)

P. timoleontis

14	Nygren 1957	Ju	Makedonija: Topalka gorge, near Skopje.

b) Non-European species:

P. elbrussica Timpko

35	Timpko 1964	USSR	Caucasus: mt. Elbrus.

P. sinaica Steudel

c. 40 - c. 58	Heyn 1962	Israel.	

Sect. CENISIA

A) European species:

P. arctica

36	Löve, Löve & Kapoor 1971	USA	Rocky mts.
38, c. 56, c. 68, c. 75	Nannfeldt 1940	No	Dovre mts., Knutsho, Kvernbekkho.
39 - 92	Nygren 1950		
42, 56, 62, 70, 70 - 74	Zhukova 1968	USSR	Far East: Chutotka peninsula, Vrangeli island.
56	Flovik 1938, 1940	Sb	Isfjorden.
56	Holmen 1952	N. Greenland: Peary Land.	
56	Jörgensen et al. 1958	Greenland.	
56	S & P 1968	USSR	Far East: Koryakskiĭ range.
56, 60	Zhukova 1969	USSR	Far East: Anyuiskoe mts.
56, 63, 70, c. 75, 82, 85, 86, 106	Bowden 1960	Canadian Arctic.	
c. 66, c. 67, c. 68	Hedberg 1967		
70	Armstrong 1937		
70+	Zhukova & Tikhanova 1971	USSR	Chukotka peninsula
70 - 72	S & S 1960	Rs(N)	Kolguev island.
72	S & S 1941	Rs(N)	Kolguev island.
72	Sokolovskaya 1955	USSR	Arctic.
76	Löve & Löve 1956		
c. 72, 80 ± 10	Mosquin & Hayley 1966	Canada	Arctic.

P. cenisia

subsp. cenisia

28, 50 - 52, 50 - 55	Favarger 1959	Ga	Val d'Emagny;
		Ge	Mortheys, Freiburger Alpen;
		He	Glarus, Gumen.
49	Bajon & Greber 1971	Ga	Isère: massif du Taillefer.

subsp. sardoa

56	Contandriopoulos 1962	Co	Monte Rotondo.
56	Favarger & Huynh 1964	Ga	Pyrénées, Pic Peric.
c. 56	Küpfer & Favarger 1967	Ga/Hs	Pyrénées.
c. 56	Favarger & Küpfer 1968	Ga/Hs	Pyrénées, Pic Péric.

P. granitica

48 - 56	Hadač, Haškova 1956	Cz	Tatra mts.
64, 67, 71, 72, 94	Skalińska et al. 1957	Po	Tatra mts.
c. 80	Skalińska 1950	Po	Tatra mts.

B) Non-European species:

P. tibetica Munro ex Stapf

42	S & S 1938	USSR	Altai mts.
42	S & S 1939	USSR	Pamir mts.
42	S & S 1948a	USSR	Altai mts.

Sect. COENOPOA

P. trivialis

14	Avdulov 1928	Ex hort. bot.	
14	Tischler 1934	Ex hort. bot.	
14	Armstrong 1937		
14	Nannfeldt 1937c		
14	S & S 1939	USSR	Pamir mts.
14	S & S 1940	USSR	Caucasus mts.
14	Åkerberg 1942	No	
14	Löve & Löve 1942a		
14 + 0-5 B	Bosemark 1957	Su	Skane, Västergötland.
14	Skalińska et al. 1957	Po	Tatra mts., Olczyska valley.
14	Bowden 1961	Canada	Nova Scotia.
14	Taylor & Mulligan 1968	Canada	Queen Charlotte islands.
14	Tombal 1968		
14	S & P 1968	USSR	Far East.

14	Fernandes & Queiros 1969	Lu	Porto, Baleia.
14	Pohl & Davidse 1971	Costa Rica	
14	S & P 1973	USSR	Far East: Kuril archipelago, Shikotan island.
14, 28	Guinochet 1943		
28	Tateoka 1954	Japan	
28	Kozuharov & Kuzmanov 1970	Bu	

subsp. silvicola

14	Khristov & Terziiski 1968	Bu	Sevlievo, Chamkoria.

Sect. HOMALOPOA

P. chaixii

14	Avdulov 1928, 1931	-	Ex hort. bot.
14	Stählin 1929	-	Ex hort. bot.
14	Nannfeldt 1937b	Su	Uppsala Bot. Garden, spont.
14	Kiellander in Löve & Löve 1942		
14	Clausen et al. 1944		
14	Skalińska et al. 1961	Po	
14	Miziandy & Frey 1973	Po	W. Zieszczady mts.

P. hybrida

14	Favarger 1959	He	Creux du Van.

P. remota

14	Nannfeldt in Löve & Löve 1942	Su	
14	Holub et al. 1972	Cz	SW Bohemia, mt. Sumava; C. Slovakia.
14	Edmondson, unpublished	Su	(see appendix 2)

Sect. LEPTOPHYLLAE

P. stiriaca

14	Edmondson, unpublished	Seed of garden origin (see appendix 2), originally collected in Cz (Slovakia).

Sect. MACROPOA

a) European species.

P. longifolia

14	Edmondson, unpublished	Seed of garden origin (see appendix 2), originally collected in USSR (Caucasus) under the name P. iberica.

P. longifolia (ctd.)

28	S & S 1940	USSR Caucasus mts.
28	S & S 1948b	USSR Caucasus mts.

Doubtful (seed of unknown origin):

42	Almgård 1960
43	Hartung 1946
44	Clausen et al. 1944

P. sibirica

14	Zhukova 1968	USSR Far East: N. Yakutia.
14	Zhukova 1969	USSR Far East: Anguiskoe foothills.
14	S & P 1973	USSR Far East: Kamchatka peninsula.
28	S & S 1938	USSR Siberia: Altai mts.
28	S & S 1940	USSR Siberia: Altai mts.
28	S & S 1948a	USSR Siberia: Altai mts.

b) Non-European species:

P. bucharica Rozhev.

14	Grif 1965	USSR Tadjikistan: Anzob pass.

Sect. NANOPOA

P. trichophylla

14	Edmondson, unpublished	Gr Mt. Parnassos (see appendix 2)

Sect. OCHLOPOA

a) European species:

P. annua

28	Avdulov 1928	
28	Kattermann 1930	
28	Armstrong 1937	
28	Nannfeldt 1937b, 1938	Su various localities; USSR: N. Caucasus.
28	S & S 1940	USSR Caucasus mts.
28	Parodi 1946	Argentina Buenos Aires.
28	Heiser & Whittaker 1948	USA California.
28	S & S 1948b	USSR Caucasus mts.
28	Polyá 1949	Hu
28	Tateoka 1954	Japan

P. annua (ctd.)

28	Tutin 1954	
28	Löve & Löve 1956b	
28	Tutin 1957	Br Leicester.
28	Jörgensen et al. 1958	Greenland
28	Sokolovskaya 1960a	USSR Far East: Sakhalin island.
28	Bowden 1961	Canada
28	Diers 1961	Peru
28	Beaman et al. 1962	Mexico
28	Chen & Hsu 1962	Taiwan
28	Gadella & Kliphuis 1963	Ho Oost Voorne.
28	Gould & Soderstrom 1974	Ceylon Uva province.

Doubtful: 14 Mehra & Sunder 1969 India Kashmir: Gulmarg.
14 Ellis, Calder & Lee 1970 Australia

P. infirma

14	Nannfeldt 1937c	Jordan, Amman; Algeria, Oran; Israel.
14	Tutin 1957	Ga Jersey island: St. Brelade's Bay.

P. supina

14	Nannfeldt 1937c	Su various localities.
14	Tutin 1957	He Graubunden, Alp Trida near Samaun.

b) Non-European species:

P. acroleuca Steudel

28	Tateoka 1953	Japan
28	Hsu 1971	Taiwan

P. dimorphantha Murbeck

28 Nannfeldt 1937a

P. maroccana Nannfeldt

28 Nannfeldt 1938

P. nepalensis Wallich

14	Mehra & Sunder 1969	India Simla: Matiana.

P. rivulorum Maire & Trabut

28 Nannfeldt 1938

P. stapfiana Bor

28	Mehra & Sunder 1969	Kashmir Tangmarg.

Sect. OREINOS

a) European species:

P. flexuosa

42 Nygren 1950

42 Love (unpublished, quoted by Skalińska et al. 1957) Is

P. laxa

21	Nygren 1956	He	Gotthard pass.
28	Nygren 1956	He	Furkel, Grimsa, Bernina pass.
28	Skalińska 1954	Po	Tatra mts.
28	Hadač & Haskova 1956	Cz	Tatra mts.
28	Skalińska et al. 1957	Po	Sudetic mts., Tatra mts.

P. minor

28 Nygren 1956 He Samnaun, Grigna, Bernina pass.

b) Non-European species:

P. fernaldiana Nannfeldt

42	Nygren 1956	Canada	Québec: Gaspé peninsula.
c. 42	Bowden 1961	USA	New York state.
42	Löve & Löve 1964	USA	Mt. Washington.
42	Löve & Löve 1966	USA	Mt. Washington.

P. leptocoma Trinius

42	Bowden 1961		
42	S & P 1968	USSR	Far East: Kamchatka peninsula.
42	S & P 1973	USSR	Far East: Kamchatka peninsula.

P. paucispicula Scribner & Merrill

28	Zhukova 1965a	USSR	Far East: Chukotka peninsula.
42	Zhukova 1968	USSR	Far East: Chukotka peninsula, Alyermagtyn; Kuekvun'.
42	S & P 1973	USSR	Far East: Koryakskiĭ range.

sect. POA

a) European species:

P. alpigena

28 - 127 Nygren 1950

35	Holmen 1952	N. Greenland: Peary Land.	
37	Johnson & Packer 1968	NW Alaska: Ogotruk creek.	

42, 51, c. 77, 84

P. alpigena (ctd.)

42, 51, c. 77, 84 Flovik 1938, 1940 Sb Isfjorden.
56 Sokolovskaya 1955 USSR Arctic.
56 S & S 1960 USSR Arctic: Khibiny.
56 S & S 1962
56 Zhukova 1965 USSR Far East: Chukotka peninsula.
56 Zhukova 1967 USSR Far East
56 Zhukova 1968 USSR Far East
c. 65, c. 67 Mosquin & Hayley 1966 Canadian Arctic.
c. 68, c. 73, c. 74, 76 Hartung 1946 Su Abisko.
70 S & P 1973 USSR Far East: Koryakskiĭ range.
70 - 72 S & P 1968 USSR Far East: Kamchatka peninsula.
74 Clausen et al. 1944
76 Grun 1955 Su Abisko.
84 S & S 1941 Rs(N) Kolguev island.

P. angustifolia

46 - 72 Love & Love 1956
56 Mehra & Sunder 1959 Kashmir: Gulmarg.
c. 56 Sokolovskaya 1960 USSR Far East: Sakhalin island.
56, 63 - 64 S & P 1968 USSR Far East.

P. pratensis sensu lato.

Note: in most cases it is impossible to know whether the counts listed below refer to P. pratensis sensu stricto, or to one or other of the other species (P. angustifolia, P. subcaerulea) which are sometimes considered conspecific. However, where a reference appears under two or more species of the section, it may be assumed that the count of P. pratensis refers to the species in its narrow circumscription.

25 - 49 Åkerberg 1936
28, 42, 44, 56, c. 66, 67, 70, 74, c. 78, c. 82, 84, 86, 88, c. 124 Bowden 1961 Canada, Alaska.
28, 56, 70 Avdulov 1931
35 + 4B Jörgensen et al. 1958 Greenland.
36 Müntzing 1940
36 - 85 Müntzing 1932c
38 - 96 Juhl 1952 Ge Schleschwig Holstein.

P. pratensis (ctd.)

41 - 64	Brown 1939	USA
42	Almgård 1960	Su
47 - 95	Åkerberg 1936	
49 - 80	Hartung 1946	USA - various localities.
50, 51, 54	Hartung 1946	Su Svalov.
c. 66	Hartung 1946	Turkey.
66, 70	Hartung 1946	No Valdres.
70	Hartung 1946	Canada Athabasca.
76	Hartung 1946	Su Landskrona.
56, 64, 78	Hartung 1946	China Manchuria.
50 - 78	Löve & Löve 1956	Is
53 - 92	Nissen 1950	No South-east Norway.
56	Delay 1947	
56	S & S 1948a	USSR Altai mts.
56	Tateoka 1953	Japan.
56	Sokolovskaya 1955	USSR Arctic.
56	Sokolovskaya 1960a	USSR Far East: Sakhalin island.
56, 70	S & S 1939	USSR Pamir mts.
56, 70	S & S 1940	USSR Caucasus mts.
56, c. 70	S & P 1968	USSR Far East: Sakhalin island; Kamchatka peninsula.
56, c. 70	S & P 1973	USSR Far East: Koryakskiĭ range; Kuriĭl archipelago, Itutup isl.
c. 60	Zhukova & Tikhanova 1971	USSR Far East: Chukotsky peninsula.
64	Mehra & Sunder 1959	Kashmir Tangmarg.
66, 67 + f.	Rancken 1934	Fe
68 - 70, 74	Clausen et al, 1944	USA
68, 75, 76, 84, 106	Grun 1955	USA
70	Nakajima 1933	Japan
70	Sokolovskaya 1963	USSR Far East: Kamchatka peninsula.
70, 78, 91	Löve & Löve 1942a	Is, Su.
72	Sokolovskaya 1965	USSR
74, c. 78, c. 80	Skalińska et al. 1957	Po Tatra mts.
84	Taylor & Mulligan 1968	Canada Queen Charlotte island.
90	Fernandes & Queiros 1968	Lu Ovar, near Ria.
c. 95	Böcher & Larsen 1950	W. Greenland, head of Sondre Stromfjord.
98	Khristov & Nikolov 1962	Bu

P. subcaerulea

38 - 117	Löve & Löve 1956	Is
82 - 147	Löve 1952	Is - various localities.
84 - 101	Åkerberg 1942	

b) Non-European species:

P. eminens C.Presl.

28	Sokolovskaya 1960	USSR Far East: Sakhalin island.
c. 28	Hedberg 1967	North America.
28, 42	S & P 1968	USSR Far East: Sakhalin island, Kamchatka penins., Koryakskiĭ range.
42	Bowden 1961	
42	Sokolovskaya 1963	USSR Far East: Kamchatka peninsula.
42	Sokolovskaya 1968	USSR Far East: Koryakskiĭ range.
42	S & P 1973	USSR Far East: Sakhalin island; Koryakskiĭ range; Kuril archipelago, Shikotan island.
62	Zhukova et al. 1973	USSR Far East: Chukotka peninsula.

P. jaunsariensis Bor

28	Mehra & Sunder 1959	Kashmir Khilanmarg.

P. macrocalyx Trautv. & Meyer

42, 56, 56 - 59, 70	S & P 1973	USSR Far East: Karyakskiĭ range; Sakhalin island; Kuril archipelago: Iturup island.
42, 63, c. 70, 84	Tateoka 1974	Japan Hokkaido.
49, 63 - 64, c. 70	S & P 1968	USSR Far East: Koryakskiĭ range; Sakhalin island.
c. 70	Sokolovskaya 1960	

P. malacantha Komarov

42, 62, 70, 70+	Zhukova 1968	USSR Far East: Kolyma mts.; Vrangely island; Chukotka peninsula.
56	Sokolovskaya 1968	USSR Far East: Koryakskiĭ range.
56	Zhukova 1969	USSR Far East: Chukotka peninsula.
56	Zhukova & Tikhanova 1971	USSR: Far East: Anadyric mts.
56, c. 70, c. 80	S & P 1968	USSR Far East: Kamchatka peninsula, Sakhalin island, Koryakskiĭ range.
63	Zhukova et al. 1973	USSR Far East: Chukotka peninsula.
c. 64, 70 - 72, c. 80	S & P 1973	USSR Far East: Petropavlovsk; Koryakskiĭ range; Kamchatka peninsula.

P. platyantha Komarov

P. platyantha Komarov

42, 70 - 72 S & P 1968 USSR Far East: Kamchatka peninsula.

64. 70 - 72, 84 S & P 1973 USSR Far East: Kamchatka peninsula, Koryakskiĭ range.

c. 70 Sokolovskaya 1963 USSR Far East: Kamchatka peninsula.

P. pruinosa Korotky

28 S & S 1939, 1940 USSR Pamir mts, Caucasus mts.

P. sachalinensis (Koidz.) Honda

42 S & P 1973 USSR Far East: Sakhalin island.

5 42, 56, 63 - 64 S & P 1968 USSR Far East: Sakhalin island.

P. subfastigiata Trinius

42 S & P 1968 USSR Far East: Vladivostok.

42 S & P 1973 USSR Far East: Vladivostok.

P. sublanata Reverd.

56, c. 70 S & P 1968 USSR Far East: Kamchatka peninsula, Koryakskiĭ range, Sakhalin island.

P. tatewakiana Ohwi

42 S & P 1973 USSR Far East: Kuril archipelago, Shikotan and Iturup islands.

Sect. STENOPOA

A) European species:

P. glauca

42 Stählin 1929

42 Maude 1939

42 Delay 1947

42 Hedberg 1958 Br Scotland.

42 Löve & Löve 1966 USA Mt. Washington.

42 Zhukova & Plieva 1973 USSR Far East: Primorskiĭ mts.

42, 47, 50, 56, 60, 70 Kiellander in Löve & Löve 1942 Su

42, c. 48, 56 Zhukova 1969 USSR Far East, various localities.

42, c. 49, 56 S & P 1968 USSR Far East: Sakhalin island, Koryakskiĭ range.

42, 49, 56, 62 Löve & Löve 1956 Is

42, 50, 56 Zhukova 1968 USSR Far East: various localities.

42, 50, 56, 64, 65, 70, 75, 78 Bowden 1961 Canada, Alaska.

42, 56 S & P 1973 USSR Far East: Koryakskiĭ range, Kamchatka peninsula.

P. glauca (ctd.)

44, c. 48, 56	Knaben & Engelskjön 1967	No Hindseter, Visdalen, Kongsvoll, Junkerdal, Duotavarre etc.
45	Kattermann 1930	
56	Holmen 1952	N. Greenland: Peary Land.
56	Zhukova 1965b	USSR Far East: Vrangeli island.
56	Sokolovskaya 1968	USSR Far East: Koryakskiĭ land.
56	Zhukova et al. 1973	USSR Far East: Vrangeli island.
54 - 56	Laane 1967	No East Finnmark.
56, 70	Jörgensen et al. 1958	Greenland.
62	Zhukova et al. 1973	USSR Far East: Chukotka peninsula.
63	Love & Love 1948	Is
63	Böcher & Larsen 1950	W. Greenland; head of Sondre Stromfjord.
65	Akerberg 1942	Su
c. 70	Hedberg 1967	Canada
70	Avdulov 1928	Ex hort. bot.
70	Sørensen & Westergaard (in Love & Love 1948)	E. Greenland.
70 - 72	Flovik 1938, 1940	Sb Isfjorden.

P. nemoralis

28	Avdulov 1928, 1931	Ex hort. bot.
28	S & S 1940, 1948b	USSR Caucasus mts.
28	Skalińska et al. 1957	Cz Belan Tatra: Tatry Bielskie.
28, 42	Åkerberg 1942	Ex hort. bot.
28, 42	Löve & Löve 1942b	
33	Guinochet 1943	Ga
35	Tateoka 1956	Japan.
42	Stählin 1929	
42	Armstrong 1937	
42	Böcher & Larsen 1950	SW. Greenland; Arsukfjord, Gronnedal.
42	Löve & Löve 1956	Is
42	Jörgensen et al. 1958	Greenland.
42	Gadella & Kliphuis 1963	Ho Linburg.
42	Sokolovskaya 1963	USSR Kamchatka peninsula.
42	Hooper (in Löve & Löve 1961)	Br Scotland.
42	S & P 1968	USSR Kamchatka peninsula, Koryakskiĭ range.
42	Fernandes & Queiros 1969	Lu: near Braganca.
c. 50	S & P 1973	USSR Far East: Kuril archipelago, Iturup.
c. 56	Hooper (in Love & Love 1961)	Br Scotland.
56	Mehra & Sunder 1959	Kashmir Gulmarg.

P. palustris

18	Kiellander 1942	Su
21	Kiellander 1935, 1937	Su
28	Avdulov 1928	
28	Armstrong 1937	
28	Hartung 1946	USA Montana; China : Harbin.
28	Sokolovskaya 1955	USSR Arctic.
28	Sokolovskaya 1963	USSR Far East: Kamchatka peninsula.
28	Zhirov 1968	Novosibirsk.
28	S & P 1968	USSR Far East: Kamchatka peninsula, Sakhalin island.
28	S & P 1973	USSR Far East: Kuril archipelago, Iturup.
28, 29, 30, 42	Kiellander (in Love & Love 1942)	Su
28, 30, 32	Bowden 1961	Canada.

P. pannonica subsp. scabra

42	Armstrong 1937	

P. rehmannii

14	Lungeanu 1972	Rm Cheile Bicazului.

P. sterilis sensu lato

Note: since the provenance of the material on which these counts were based is not known, these counts may relate to plants which are now known as P. pannonica or P. versicolor.

28	Stählin 1929	
42	Armstrong 1937	

P. sterilis sensu stricto

42	S & S 1939, 1940	USSR Pamir mts, Caucasus mts.
56	Mehra & Sunder 1959	Kashmir Gulmarg.

b) Non-European species:

P. albertii Regel

42	S & S 1939, 1940	USSR Pamir mts, Caucasus mts.

P. bryophila Trinius

63	Zhukova 1965b	USSR Far East: Vrangeli island.

P. interior Rydberg

28 Hartung 1946 USA Wyoming.

28, 34, 42, 56 Bowden 1961 Canada, Alaska.

42 Löve & Ritchie 1966 Canada Manitoba: Tulibi lake.

P. litwinowiana Ovcz.

42 S & S 1939, 1940 USSR Pamir mts.

P. ochotensis Trinius

28 Hartung 1946

28 Tateoka 1954

28 S & P 1968 USSR Far East: maritime province, Lake Khanka.

28 S & P 1973 USSR Far East: maritime province, Vladivostok.

P. pseudattenuata Prob.

42, c. 56 S & P 1973 USSR Far East: Sakhalin island.

P. pseudonemoralis Skvortsov

42 S & P 1968 USSR Far East: maritime province, Suputin.

42 S & P 1973 USSR Far East: near Vladivostok.

The following Afro-alpine species appear to come close to section Stenopoa (though further work is needed):

P. leptoclada Hocsht. ex A. Rich.

42 Tateoka 1965a Kenya Mt. Kilimanjaro.

42, 28 Hedberg 1957

P. schimperiana Hochst. ex A Rich.

42 Tateoka 1965a Kenya Mt. Kilimanjaro.

Sect. TICHOPOA

P. compressa

35, 39, 50, 56 Munz 1959 (see also below) USA California.

35, 42, 49 Åkerberg 1942

36 Polyá 1950 Hu Cott. Hajdú-Bihar: Mikepércs.

42 Avdulov 1931

42 Turesson 1938

42 Brittingham 1941

42 Guinochet 1943

42 Hartung 1946 USA California, S. Dakota, Wyoming.

<u>P. compressa</u> (ctd.)

42	Delay 1947	
42	Polyl 1950	[illegible]
42	Almgård 1960	
42	S & P 1973	USSR Far East: Kuril archipelago, Iturup island; maritime province, Vladivostok.
42, 50	Grun 1955	USA California; Turkey Corum.
42, 56	Armstrong 1937	
45, 49, 56	Löve & Löve 1948	
50	Clausen et al. 1944	
56	Stählin 1929	

Doubtful:

14 Munz 1959 (see also above): California.

CHAPTER 5. MORPHOLOGICAL CHARACTERS.

5.1 Introduction

Morphological characters have been used to characterize the taxa of Poa since before the time of Linnaeus. It is consequently more difficult to approach the study of such characters without harbouring preconceived notions of the importance of particular characters. The way towards an improved classification of the genus, particularly at the sectional level, lies through the elimination of the bias introduced by the indiscriminate use of these 'traditional' characters and the judicious introduction of new characters after evaluation of their relative merits.

When herbarium specimens of Poa are being studied, one's observations are limited to characters of those parts of the plant which are present in the particular specimen and which have been preserved in a state which allows them to be observed critically; for this reason, if for no other, growth-form data have been largely overlooked. Similarly, when seedling characters prove to have taxonomically useful features, their use is none the less impractical in situations where a general account of taxonomic characters is required, since in practice they may only be observed under experimental conditions.

Most of the most useful characters used to classify the species and sections of Poa may nevertheless be observed easily in a well-collected herbarium specimen. If comparisons are to be made between plants at a similar developmental stage (which is more important for floral characters) it is desirable that observations be made on fully-developed spikelets which are at or a little past anthesis.

Unfortunately, a large number of the grass specimens I have examined fall short of the ideal, and many are defective in other respects: the specimens are incomplete, usually lacking the stem base and rhizome or other underground parts; they are collected at too early (or too late) a stage in the flowering process; or they have been inadequately pressed and dried. It is a common fault of otherwise well-collected specimens that they have been obtained far too early, or too late, in the flowering season, as if it were unimportant whether or not the grass was in flower at the time of collection. One of the less fortunate results of the variation in times of collection in relation to the time of anthesis has been the introduction of spurious characters whose states reflect different stages in the development and maturation of the spikelet, rather than intrinsic taxonomic differences.

A particularly revealing example is provided by the groups Pachyneurae and Leptoneurae. These are informal taxonomic groupings whose rank is not specified, but which lies above that of section and below that of subgenus. Döll (1834) and Ascherson (1864), the authors of these taxa, unwisely based them on a single character - the prominence of the intermediate nerve in the lemma - as a means of subdividing the genus conveniently. The Leptoneurae Döll include sects. Ochlopoa, Bolbophorum and Oreinos, which contain early-flowering species having a relatively short growing season. The Pachyneurae Ascherson include sects. Homalopoa and Poa, which flower later in the summer and whose panicles remain in a 'collectable' condition for much longer; not surprisingly, these are the species which are characterized by their distinct intermediate nerves. The dangers of relying on this character were pointed out by von Oettingen (1925).

A limited number of observations of features of the grass seedling, noted during germination experiments, suggest that they

may provide characters of systematic value. The difficulty of observing these characters in a general context prevents them from serving any diagnostic purpose, except where seedlings are being studied. These characters indubitably show similarities with those of the mature plant, except for the coleoptile which soon disappears. Seedling-stage characters include the length of the coleoptile at maturity (i.e. immediately before the first seedling leaf breaks through); the number of seedling leaves produced at the time when the first lateral shoot is formed; the number of initial coleorhizae sent out (usually two); and the cross-sectional shape of the leaf. This, and the degree of folding of the leaf-blade, appear to be quite closely related to the corresponding characters of the mature leaf-blade.

Since most descriptive work on the genus Poa has been subject to the restrictions imposed in the production of Floras, there has been a natural tendency on the part of authors to restrict their accounts of characters to those which they regard as having paramount systematic value. Unfortunately, authors' views on which characters to include are extremely varied; taxonomists wishing to put forward a new classification are tempted to justify their novel ideas by recourse to a new character or set of characters whose distribution coincides with the new limits of the taxa which he puts forward. This effect has the natural result of causing certain more traditional characters whose distribution corresponds less satisfactorily with the new scheme to be neglected. Another subjective effect which leads to the misuse of information on characters is the tendency of Flora-writers holding less original views to copy from previous works rather uncritically, repeating their errors and not infrequently introducing additional ones.

Both these effects have been recognised by taxonomists developing the technique of numerical taxonomy, since the selection as well as the coding of characters plays such a vitally important part in the numerical-taxonomic process (see Sokal & Sneath, 1973). In a non-numerical study, however, different criteria for the selection of characters are adopted. The question of the treatment of variation is often approached in such a vague manner by traditional taxonomists that the inadequacy of such an approach is a major justification for the adoption of numerical methods (Gilmartin, 1974). The criteria which are adopted for choosing the characters which are discussed in this chapter ought therefore to be explicitly stated:

a) Variation between taxa should exceed variation within taxa. This requirement is usually referred to by the writers or editors of keys and diagnoses as 'workability'; a character 'works' if it can be used to distinguish two groups effectively, i.e. with a minimum overlap.

b) The character should be able to be observed without the use of special preparative techniques. The most notable groups of characters excluded by this criterion are the anatomical and karyological characters, which are described in chapters 4 and 6. Though some prior preparation is needed if the micro-characters of the floret are to be observed with clarity, these are not excluded on these grounds since most can be observed in dried material under favourable conditions with a good binocular microscope.

c) A character is not selected on account of its <u>a priori</u> importance, but because its different states distinguish groups which have been recognised on the basis of all the available evidence (Cronquist, 1968, p. 10). In practice, characters are selected by a process of

grouping taxa according to the maximum number of attributes in common, successively refining the diagnoses of the groups so formed by re-examining the characters of the individual taxa which make up such groups. This process is termed 'backtracking' by Davis & Heywood (1963, p. 273). It involves the application of both positive and negative feedback. An analogous method, followed during the refinement of phytosociological tables in plant ecology, has been termed the 'method of successive approximation'. The latter word is to be taken in its most literal sense of attempting to place the most similar entities (taxa or species-lists) next to one another.

5.2 Growth-form.

The taxonomic significance of the growth-form of grasses in general, and of Poa in particular, has been recognized only recently. Although historically the presence or absence of rhizomes has been seen to have systematic value, some less obvious characters associated with the growth-form of the plant have been largely overlooked. The types of shoots produced by grasses in general are described by Suvorova (1961), and the role played by changes in the growth-form through changes in the mode of shoot formation is the theme of a book by Serebryakova (1971_1). In an earlier paper (1965) she describes how the mode of shoot formation in Poa, particularly in sect. Stenopoa, could be related to the evolution of the group in reponse to changes in environmental conditions; see also chapter 9.1 for a fuller account of the evolutionary trends. The growth-forms of the Central European species of Poa are described by Muhlberg (1965), who classifies them into several different types but who does not comment on the systematic importance of the groupings. A more detailed account of the stem base of Poa and

the mode of shoot formation, particularly with regard to the differences between species with intravaginal and extravaginal shoots, is provided by Vickery (1970) whose account, in English, provides the basis for the terminology which I propose to follow.

5.2.1 Compactness of the tussock.

Since the habit of the grass plant depends not only on the qualitative nature of the shoots, but also on their relative abundance and other factors, the overall appearance of the tussock can vary within quite wide limits. The extent to which the stems and non-flowering shoots are aggregated is difficult to quantify; subjective categories used in Flora accounts suffer from imprecision of terminology. For the purpose of the Flora Europaea account, I propose five categories:

a) stems more or less isolated; e.g. *P. compressa*, *P. jubata*.

b) plant loosely caespitose; e.g. *P. cenisia*, *P. nemoralis*.

c) plant moderately densely caespitose; e.g. *P. versicolor*.

d) plant densely caespitose; e.g. *P. stiriaca*, *P. ligulata*.

e) plant extremely densely tufted, tussock pulviniform; e.g. *P. trichophylla*.

Since in practice species vary to a greater or lesser extent in the density of the tussock, table 5.1 attempts to give an indication of the relative compactness in the European species and sections.

5.2.2 The rootstock; shoot formation.

The subterranean part of the plant at the base of the stem, from which the separate shoots arise which collectively form the grass tussock, is termed the rootstock. It is a rather

TABLE 5.1 Compactness of the tussock.

Species no.	Extremely loosely tufted, stems more or less isolated	Loosely tufted	Moderately densely tufted	Densely tufted	Extremely densely tufted, plants forming cushions
1.	P. annua				
2.	P. infirma				
3.	P. supina				
4.		P. trivialis			
5.		P. feratiana			
6.		P. alpigena			
7.	P. subcaerulea				
8.			P. pratensis		
9.				P. angustifolia	
10.		P. arctica			
11.		P. granitica			
12.		P. cenisia			
13.		P. longifolia			
14.		P. sibirica			
15.				P. chaixii	
16.				P. hybrida	
17.				P. remota	
18.				P. stiriaca	
19.	P. flexuosa				
20.		P. laxa			
21.				P. pirinica	
22.			P. minor		

TABLE 5.1 (continued)

Species no.	Extremely loosely tufted, stems more or less isolated	Loosely tufted	Moderately densely tufted	Densely tufted	Extremely densely tufted, plants forming cushions
23.	P. compressa				
24.		P. flaccidula			
25.		P. palustris			
26.				P. glauca	
27.		P. nemoralis			
28.		P. rehmannii			
29.			P. pannonica		
30.			P. versicolor		
31.				P. sterilis	
32.				P. relaxa	
33.				P. abbreviata	
34.					P. trichophylla
35.			P. bulbosa		
36.				P. perconcinna	
37.				P. ligulata	
38.				P. timoleontis	
39.		P. media			
40.			P. pumila		
41.			P. molineri		
42.			P. badensis		
43.		P. alpina			
44.	P. jubata				

short, highly contracted structure from which the fibrous adventitious roots develop. In caespitose species lacking both rhizomes and stolons, only shoots which develop into flowering stems and non-flowering leafy offsets occur on the rootstock. In rhizomatous species, some buds on the rootstock develop underground into rhizomatous shoots. In stoloniferous species, the shoots arise near the surface and develop above the ground, rooting at the nodes which contact the soil.

Four different types of shoot can thus be recognized:

a) rhizomatous shoots;

b) stoloniferous shoots;

c) non-flowering leafy offsets;

d) flowering stems.

Category (d) includes shoots giving rise to a proliferous inflorescence, although this is not strictly a 'flowering' stem.

Tables 5.2, 5.3 and 5.4 illustrate the distribution of the first three types of shoot in the European sections of Poa. Almost every species has a proportion of non-flowering shoots; some consist of potentially flowering shoots which fail to develop properly, usually because of the shortness of the growing season. Table 5.4 distinguishes those sections where non-flowering leafy offsets are a consistent feature of the growth-form of one or more of their constituent species.

5.2.3 Penetration of the sheaths by new shoots: see table 5.5 .

A distinction can be made between shoots which become enclosed by the sheaths of leaves which surround the stem node at which they arise (intravaginal) and shoots which break through the sheaths (extravaginal). Species with intravaginal shoots tend

to be densely caespitose, since the enclosure of the shoots within the surrounding leaf-sheaths leads to their being bunched together. Species with rhizomes are by definition extravaginal, since the rhizomatous shoot must break through a leaf-sheath below ground level in order to develop a subterranean innovation. Intravaginal shoots in rhizomatous species are not excluded, but in fact occur only in sect. Macropoa.

Extravaginal shoots are associated with specialized bladeless leaf sheaths, termed cataphylls by Vickery (1970, p. 152). These consist of a short enveloping scale with a rounded apex which encloses part of the stem base. Since rhizomatous species are among those with the most primitive characteristics, it is thought that the extravaginal state is evolutionarily more primitive than the intravaginal state, although this interpretation requires that leaves bearing blades which enclose the intravaginal shoots be regarded as neotonous.

5.2.4 The moniliform rhizome.

This condition, in which the rhizome is rather fleshy and swollen but is constricted regularly so that it bears a resemblance to a string of beads, is very rare in the Gramineae in general and in the genus *Poa* in particular. It is a characteristic feature of *P. trivialis* subsp. *silvicola*, but is absent from the type subspecies. The restricted occurrence of this feature detracts from its systematic value; it would appear to be either an adaptation to dry conditions, promoting aestivation by storing water or food, or an organ of perennation. Two other grasses with varieties showing this feature are *Phleum pratense* var. *nodosum* and *Avena elatior* var. *tuberosa* (Hermann, 1939); the latter is now known as *Arrhenatherum elatius*.

TABLES 5.2, 5.3 & 5.4:

Sections numbered as follows;

1. Ochlopoa	5. Macropoa	9. Tichopoa
2. Coenopoa	6. Homalopoa	10. Stenopoa
3. Poa	7. Leptophyllae	11. Abbreviatae
4. Cenisia	8. Oreinos	12. Nanopoa
		13. Bolbophorum

TABLE 5.2 Distribution of rhizomatous species.

1.	2.	3.	4.	5.	6.	7.	8.	9.	10.	11.	12.	13.
(*)	*	*	*	*				*				

Note: * denotes an attribute of all the species comprising the section;

(*) indicates an attribute of some, but not all, species.

TABLE 5.3 Distribution of stoloniferous species.

1.	2.	3.	4.	5.	6.	7.	8.	9.	10.	11.	12.	13.
(*)	*				(*)	*						

TABLE 5.4 Distribution of species with conspicuous non-flowering leafy offsets.

1.	2.	3.	4.	5.	6.	7.	8.	9.	10.	11.	12.	13.
		(*)	(*)							*	*	*

Note: leafy offsets comprise two distinct types. In sects. 3. and 4., these are distichously leafy and are not closely associated with the flowering stems. In sects. 11. 12. and 13. they arise intravaginally and hence occupy a central position in the tussock.

5.3 The roots.

The fibrous adventitious roots of Poa, which are relatively uniform in texture, are frequently missing from herbarium specimens. Their colour varies from whitish to brownish when dry. Their length and thickness varies greatly according to habitat conditions; when cultivated in garden soil, most species have a dense mat of roots within a radius of about 20 to 30 cm from the stem base.

Their taxonomic usefulness was well summarized by Bor (1948): "The dense fibrous shallow roots of the species of Poa vary so much in appearance and size in response to habitat conditions that no reliance can be placed upon them for diagnostic purposes". Their anatomical structure, on the other hand, exhibits some useful features; see chapter 6.3 (Chrtek & Jirásek, 1965a).

5.4 The stem base.

The form of the stem base is primarily determined by the type of innovation. In certain species the stem base takes on a distinctive appearance which not only aids recognition of the species in non-flowering material, but also provides additional taxonomic characters which may be used in keys and diagnoses. Some of these variations are described below:

a) While most of the rhizomatous sections of Poa have a stem base which rises more or less abruptly from the rootstock at the apex of the rhizome (e.g. sects. Macropoa, Poa and Tichopoa) sect. Cenisia may be recognized easily by the manner in which the shoots curve upwards from the apex of the rhizome, so that the stem is markedly inclined near the base.

b) In most sections of Poa, the stem base is not markedly compressed. The members of sect. Homalopoa stand out, therefore,

not only by their rather large size but also by the distinctly two-edged appearance of the base of the stem which is caused by the flattened bases of the leaf sheaths which surround it.
The stem of P. rehmannii (sect. Stenopoa) is distinctly compressed along most of its length, thereby resembling the more familiar P. compressa, where the upper part of the stem is strongly compressed.

c) Sect. Macropoa is peculiar in having heavy brownish or purplish anthocyanin deposits in the somewhat thickened sheaths which clothe the stem base.

d) Sect. Bolbophorum is immediately recognizable on account of its stem base, which in most species is clothed with the rather fibrous remains of imbricated leaf sheaths to such an extent that a collar of whitish tissue is formed. These decaying fibrous sheaths perform a protective function, allowing new shoots to develop intravaginally and to grow up within the collar of sheaths without immediate exposure to dry conditions.

Three European species of this section, however, have become even more highly adapted to dry conditions; in P. bulbosa, P. perconcinna and P. timoleontis the imbricated sheaths at the base of the stem have become bulbous in shape (the latter species less than the two former). This adaptation serves two related purposes: as a means of perennation, and as a means of aestivation. In addition, under certain conditions the bulbous stem bases may even serve as units of dispersal.

Some authors (e.g. Hermann, 1939) utilise this character to effect a separation of P. bulbosa and its allies from the remaining species of sect. Bolbophorum which have cylindrically

thickened stem bases. In my view this separation cannot be maintained; the bulbous-thickened stem base has clearly arisen quite recently as a modification of the cylindrically thickened stem base in response to increasingly arid conditions, while the other diagnostic features of sect. Bolbophorum have remained unaltered.

5.5 The stem.

The basic structure of the grass plant consists of a series of interlocking units comprising that portion of the stem which lies between two successive nodes, together with the attached leaf sheath and blade. The leaf sheath arises at the apex of the internode, while new shoots and/or adventitious roots arise from buds at the basal node of the unit: see fig.

Asa Gray (1879) coined the term 'phytomer' to apply to such a unit, though the original inspiration for the concept of plant structure being based on a series of repeating units belongs to Goethe (1817).

In the genus Poa successive phytomers are arranged so that the leaf blade alternates up the stem, giving a more or less distichous arrangement of leaves. The proportions of the constituent parts of the phytomer are almost infinitely variable; for example, this has the effect of varying the proportions of leaves to sheaths on the stem, and also determines the degree of imbrication of leaf sheaths at the stem base. Likewise, the rhizome consists of a series of phytomers whose elongated 'stem' internodes and reduced leaf sheaths taking the form of scales impart its characteristic form. Even the arrangement of floral scales in the spikelet may be interpreted as a series of phytomers, though here they are so profoundly modified that the underlying structure is wholly masked.

There are relatively few morphological characters of the stem which have any value in the diagnosis of sections of Poa. Such features as the relative leafiness of the stem and the final height attained by the flowering shoots are evidently related to the lengths and number of the constituent phytomers, but for practical purposes only the height of the plant can be employed as a quantitative character.

The tendency of the members of sect. Bolbophorum to be leafy only at the base of the stem is related to the shortening of the lowest internodes, leading to the imbrication of the basal leaf sheaths. This state is most pronounced in sects. Abbreviatae, Bolbophorum, Leptophyllae, Nanopoa and Oreinos, is less noticeable in sects. Cenisia, Homalopoa, Macropoa, Ochlopoa and Poa and is least pronounced in sects. Coenopoa, Stenopoa and Tichopoa, in which the stem is normally leafy to above half-way up.

A character which is of some diagnostic value in separating two closely related species in sect. Stenopoa, P. pannonica and P. versicolor, varies according to whether the uppermost stem node (at the base of the top stem internode which terminates at the base of the panicle) is enclosed within the uppermost sheath or is exposed above it. In P. versicolor the node is concealed by the sheath of the leaf below, while in P. pannonica the node is generally expsed. In the remaining members of sect. Stenopoa the node is generally exserted, though often only very shortly so. The sections whose leaves are mostly basal, e.g. sect. Bolbophorum, sect. Leptophyllae and sect. Nanopoa, also have a conspicuously exserted uppermost node. Other sections with a more leafy stem, e.g. sect. Ochlopoa, are

quite different, the uppermost stem node being enclosed not only by the uppermost leaf sheath but also by the one below. Since sect. Ochlopoa is believed to have the largest number of evolutionarily primitive characteristics, this would imply that a reduction in the relative lengths of the leaf sheaths, leading to the exposure of the uppermost node, is a more advanced characteristic in the genus Poa.

The uppermost part of the stem is generally terete and smooth. In P. compressa and P. rehmannii it is compressed, providing a useful diagnostic feature both for sect. Tichopoa and for P. rehmannii in contrast to the remaining species of sect. Stenopoa.

In some members of sect. Stenopoa and sect. Poa, as well as in certain specimens of P. abbreviata (sect. Abbreviatae), the stem is aculeolate. Since the upper part of the stem is closely associated with the panicle branches, this feature might be expected to show a positive correlation with the scabridity of the panicle branches. However, the two characters vary independently; see table 5.6 .

5.6 The leaf.

Taxonomic characters of the parts of the leaf are among the most useful of the vegetative features of the grass plant. Partly because these vary over such a wide range, and partly because they are relatively easy to observe and to quantify, considerable reliance is placed upon them.

5.6.1 Colour and surface texture.

Although not easily described, the colour of the leaves (both sheaths and blades) often provides the taxonomist with a rapid visual check on the identity of a species. Certain sections are recognizable at a glance by their soft, almost translucent, pale green colour, e.g. sect. Ochlopoa and sect. Coenopoa. Others are a much darker green, e.g. sect. Poa. These differences are less

TABLE 5.5 Distribution of innovation types.

Note: sections are numbered as in tables 5.2 to 5.4

1.	2.	3.	4.	5.	6.	7.	8.	9.	10.	11.	12.	13.
E	E	E	E	I/E	E	E	E	E	E	I	I	I

E = intravaginal shoots

I = extravaginal shoots

TABLE 5.6 Distribution of aculeoli on stem and panicle branches.

	PANICLE BRANCHES SMOOTH	PANICLE BRANCHES SCABROUS
STEM SMOOTH ABOVE	Ochlopoa Genisia (part) Homalopoa (part) Oreinos Nanopoa Bolbophorum (part) Abbreviatae (part)	Coenopoa Genisia (part) *Homalopoa (part) Macropoa Tichopoa Bolbophorum (part) Poa (part) Stenopoa (part)
STEM SCABROUS ABOVE	*Abbreviatae (part)	Stenopoa (part) Poa (part)

Note: * indicates sections with anomalous aculeoli; these are blunt-tipped and are scarcely rough to the touch.

apparent in dried material.

The surface texture of certain species is often described as 'glaucous'. This is usually taken to mean that the plant is a blue-green colour and that the surface has a waxy, non-reflective coating. Species noted for the latter characteristic include P. glauca, P. flaccidula and several members of sect. Bolbophorum. However, only P. glauca has a pronounced blue-green colour, even when dry, the remaining species obtaining their 'glaucous' appearance from the surface texture rather than the underlying colour. For this reason, the term glaucous must be used with a good deal of caution.

5.6.2 The leaf sheath.

The majority of European species of Poa have a rather undifferentiated leaf sheath. Only when the sheaths provide positional characters (e.g. 5.4(d) above) can these species be distinguished by features of the sheath. However, in sect. Homalopoa the strongly folded sheaths are diagnostic for the section. Poa rehmannii (sect. Stenopoa) has a sheath of singular structure, with a raised keel which forms a sharp ridge running down the stem on the side furthest from the leaf blade. The ligule and apex of the sheath of the leaf below are themselves slightly folded in order to accommodate the ridge of the sheath above.

The sheath may be scabrid or smooth on the external surface. The presence of aculeoli is strongly correlated with their presence on the margins of the leaf blade.

5.6.3 The ligule.

Although great reliance is often placed on the ligule for diagnostic purposes in floristic accounts of the genus Poa, either

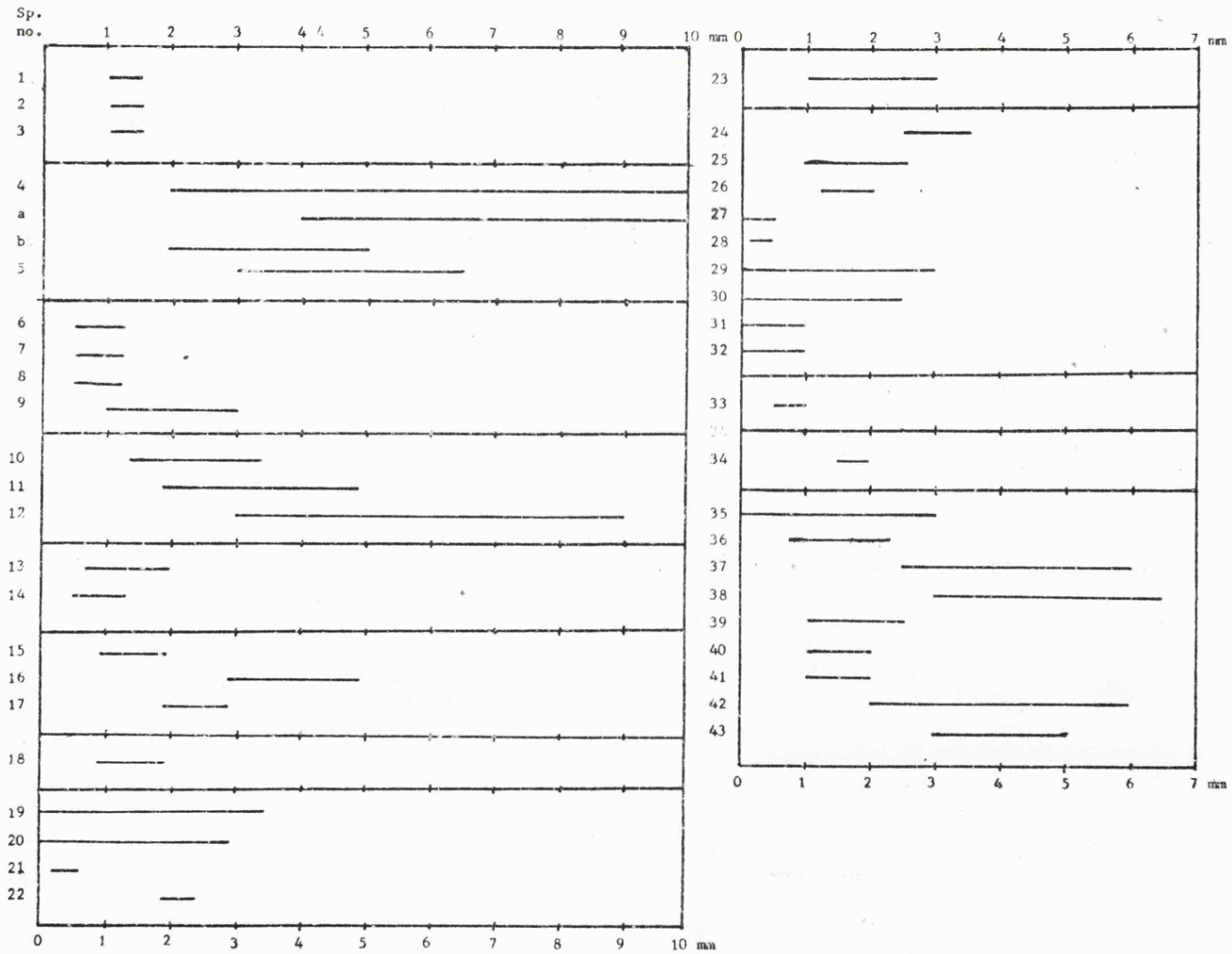

Table 5.7 Length of ligule of uppermost stem leaf.

as an attribute of sections or for distinguishing particular species, the ligule is not in fact as dependable as is often implied from the reliance placed upon it by various authors. In particular, ligule length measurements should be treated with especial caution, and care must be taken to differentiate between characteristics of ligules of basal leaves and those of the ligules of the stem leaves, which often vary markedly and sometimes consistently. With these provisos, the ligule may be considered as one of the most useful organs providing several valuable taxonomic characters; this role is rather surprising in view of the fact that the functional significance of variations in the shape and size of the ligule is rather obscure.

a) Length. Table 5.7 is extracted from the Flora Europaea account of the European species of Poa, and the information is therefore rather generalized; it nevertheless shows the wide range of variation covered by the character of ligule length, and demonstrates that differences in length are often of more value in separating related species than in characterizing particular sections. To avoid masking overall differences by taking account of variation between basal leaves and stem leaves, the latter are usually studied for comparative purposes. In sect. Bolbophorum, however, the short and more or less truncate ligule of the basal leaves serves to distinguish P. alpina from P. badensis, in which the ligule is longer and has a rounded apex.

In making overall comparisons of ligule lengths, allowance must be made for the fact that variations in overall size cause changes in terminology such that a 'short' ligule of P. chaixii that is truncate and is 1 - 2 mm in length is proportionately far smaller

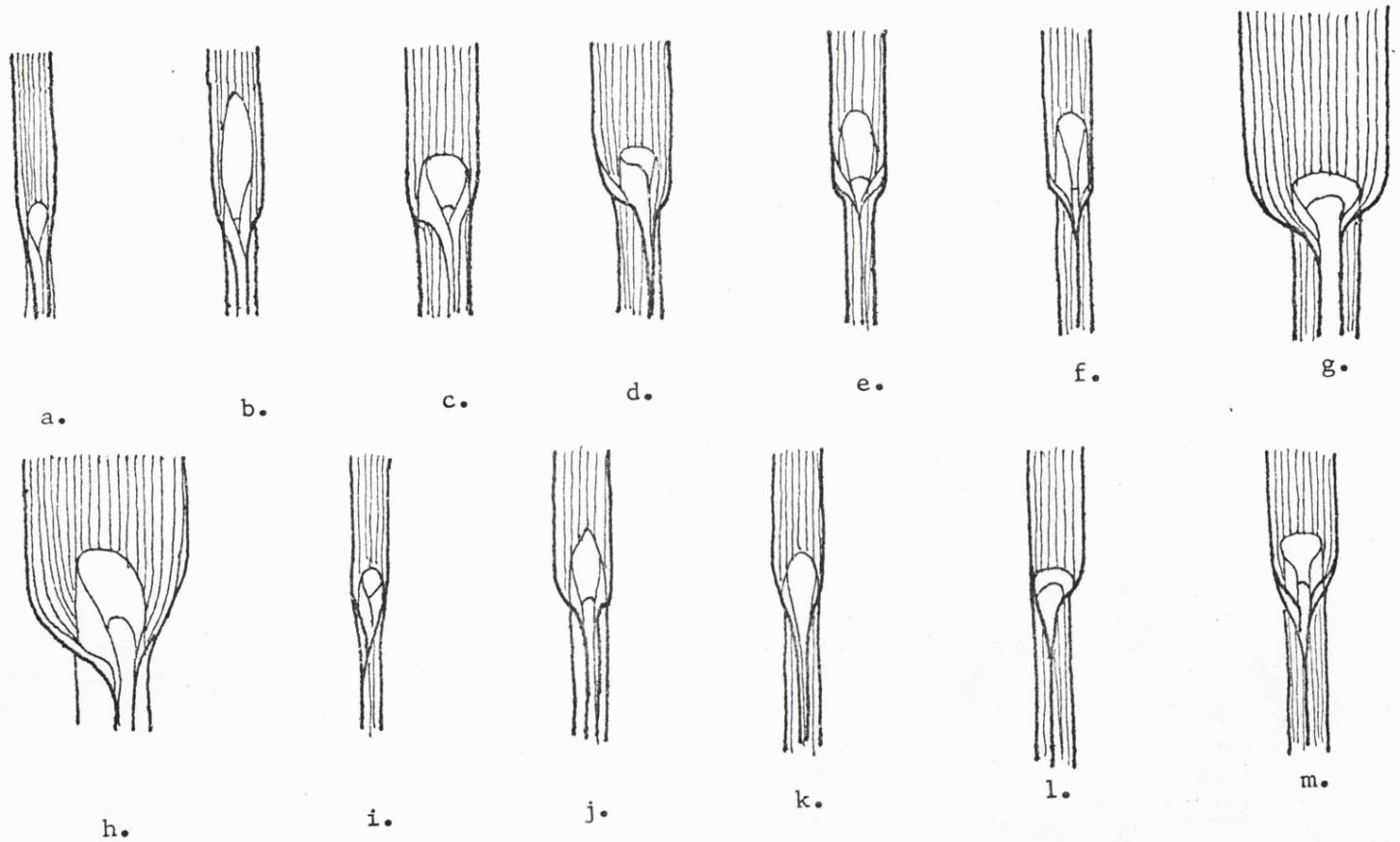

Fig. 1. Variation in shape of ligule apex. (After Hylander, 1953b, p. 112)

a. OCHLOPOA: P. annua b. COENOPOA: P. trivialis c. POA: P. alpigena d. POA: P. pratensis e. CENISIA: P. arctica

f. OREINOS: P. flexuosa g. HOMALOPOA: P. chaixii h. HOMALOPOA: P. remota i. TICHOPOA: P. compressa

j. STENOPOA: P. palustris k. STENOPOA: P. glauca l. STENOPOA: P. nemoralis m. BOLBOPHORUM: P. alpina.

than the prominent milky-white ligule of P. trichophylla, whose length lies in a similar range (1.5 - 2 mm). Further discussion of the influence of scale effects may be found in a paper by Tutin (1963).

b) Shape of apex. Figure 1 illustrates the range of variation of this character, which encompasses all shapes from finely tapering apices coming to an acute point at one extreme to truncate apices at the other. In addition, longer ligules show a tendency to become lacerated or eroded into an irregular or jagged margin; this feature is most noticeable in P. granitica. The shape of the ligule apex is particularly useful in distinguishing certain species; it is less valuable as a sectional attribute, though the following sectional differences should be noted:

Sect. Genisia usually has long, finely tapering ligules with an acute apex, while the related sect. Poa has short, usually truncate ligules which are generally under 1 mm in length (except P. angustifolia).

Sect. Abbreviatae is unusual in having a short (0.5 - 1 mm) ligule which however is rounded, not truncate, at the apex.

Sect. Nanopoa, together with some species belonging to sect. Bolbophorum, has finely tapering milky-white ligules which contrast strongly in colour with the wiry dark-green leaves.

c) Indumentum. The ligule is normally glabrous. However, in sect. Poa the presence of hairs on the abaxial surface of the ligule, which is tomentose in P. subcaerulea, distinguishes that species from the other members of the critical P. pratensis group of species, in which the ligule is glabrous or nearly so.

5.6.4 The leaf blade.

Several of the characters associated with the leaf blade are more fully documented in chapter 6, which describes leaf anatomy. It remains here to mention the characters of leaf length, leaf width, and the type of apex of the leaf.

a) Length. As a diagnostic character at the sectional level, the leaf length may be generally disregarded, since it can vary so greatly both within and between species (where it often has diagnostic value) as well as within and between populations of the same species (where it is a component of ecotypic variation); as we even find much variation in leaf length in a single plant, the difficulties of using this character are enormous. In certain sections where the leaf length is exceptionally great (or small) in relation to the size of the plants concerned, measurements of leaf length can help to give a quantitative expression to differences which are easily seen but less easily formulated. Leaf lengths are particularly useful in the following sections:

Sect. Leptophyllae; leaves (10-) 30 - 40 cm.

Sect. Nanopoa; leaves 1 - 2 cm.

Sect. Bolbophorum; leaf lengths are of some value in distinguishing the various species, and are generally rather short in relation to the size of the plant. Table 5.8 illustrates the range of leaf lengths in sect. Bolbophorum.

b) Width. Whereas variations in leaf width conform more precisely to sectional limits, and are used more widely for diagnostic purposes, this character is of greatest value in distinguishing different species. Overall variation in the European species of Poa is very wide; at one extreme, in sect. Nanopoa, the leaves of P. trichophylla range from 0.3 - 0.5 mm in width, while at the other extreme, in

sect. Homalopoa, where the leaves are commonly 5 - 10 mm wide, they occasionally reach 15 mm in P. chaixii. Few, if any, other quantitative characters in Poa vary by factors as great as 12 times to 20 times. Table 5.8 sets out leaf widths in the European species of Poa.

c) Type of apex. The boat-shaped apex is a characteristic of the genus Poa as a whole, and it may therefore seem surprising that this character should be useful in sectional diagnoses. However, where in some sections and species the leaf blade tapers gradually to the apex, the extreme tip nevertheless shows a cucullate point. In sect. Homalopoa, P. hybrida has the gradually tapering leaf, while P. chaixii and P. remota have an abruptly narrowed leaf apex. The tapering leaf blade is also a characteristic of sect. Poa, in which only P. alpigena has the boat-shaped apex type. It is also encountered in sect. Stenopoa, where it is especially typical of P. glauca and to a lesser extent also of P. nemoralis. It is less apparent in the species of sect. Stenopoa which have narrow leaves, but may be regarded as a diagnostic feature of the section. Table 5.9 illustrates the occurrence of this character.

5.7 The panicle.

A panicle has been defined as 'a branched racemose inflorescence' (Clapham, Tutin & Warburg, 1962, Glossary). In the strictest sense, therefore, the inflorescence of Poa is not a true panicle. It is generally understood that when the term is applied to grasses, it refers to a branched inflorescence in which the individual spikelets are grouped on branches which appear to arise in whorls. Since the groups of panicle branches alternate up the panicle, the term 'pseudowhorl' is sometimes preferred; more loosely, the different

TABLE 5.9 Shape of leaf blade towards the apex.

BLADE GRADUALLY NARROWED TO THE APEX	BLADE ABRUPTLY CONTRACTED AT THE APEX
Coenopoa	Ochlopoa
Poa (part)	Poa (part)
Macropoa	Cenisia
Homalopoa (part)	Homalopoa (part)
Oreinos	Leptophyllae
Tichopoa	Abbreviata
Stenopoa	Bolbophorum
Nanopoa	

TABLE 5.10 Number of branches at each lower node of panicle.

Ochlopoa	2	*Oreinos	1 - 2 (-3)
Coenopoa	2 - 5 (-9)	Tichopoa	1 - 3
Poa	2 - 5	Stenopoa	2 - 5 (-11)
Cenisia	2 - 5	**Abbreviatae	1 - 2
Macropoa	2 - 3	Nanopoa	1 - 2
Homalopoa	5	Bolbophorum	1 - 2 (-3)
**Leptophyllae	3 - 5		

** Sections with sulcate panicle branches

* Sections with sulcate or terete panicle branches.

levels at which branching occurs are referred to as nodes. This should not be taken to suggest an analogy with the nodes of the stem.

The typical panicle consists of an ovoid or pyramidal arrangement of branches, the number of branches at each node generally being largest at the base of the panicle. Although the number of branches at each lower node appears to be determinate, at least in those species where the number is 5 or fewer, there is a tendency for the number to be reduced in response to environmental conditions which adversely affect the development of the panicle. For this reason, Fiori's division of the genus into two groups, 'Paucirameae' and 'Multirameae' is unsatisfactory, although the number of branches is sometimes of diagnostic value, e.g. in distinguishing P. alpigena and P. subcaerulea from P. pratensis and P. angustifolia; the former pair of species has two branches at the lowest node, while the latter pair has from three to five branches.

In taxa with two or three branches at the lowest node, the branches are usually of similar length and bear a relatively large number of spikelets. Where from five to seven or more branches are present at the lowest node, the additional branches are shorter and are inclined away from the horizontal plane, with fewer spikelets borne on each branch. The reduction in number of branches at the lowest node may correspond to an evolutionary trend: see chapter 9.

Panicle shapes may be expressed either as outline forms, using a two-dimensional terminology, or as solid objects, using three-dimensional terms. Since the solid terminology employed in the Flora Europaea account uses some terms whose meaning is open to different interpretations, table 5.11 sets out to give both the two-dimensional equivalents of the terms used and some further explanatory notes on possible ambiguities.

5.8 Panicle branches.

The relative lengths of the panicle branches contributes to the overall appearance of the panicle and to its three-dimensional shape. In addition, the vestiture and cross-sectional shape of the panicle branches provide features of considerable diagnostic importance at the sectional level. The sections which have smooth branches and those which have aculeolate branches have already been distinguished in table 5.6; it should be noted that in sect. Abbreviatae, where the panicle branches are generally quoted as being smooth, verrucose protuberances resembling the bases of aculeoli but lacking their long-drawn-out points are sometimes present. It is possible that this character state has been acquired through introgressive hybridization with P. glauca, the hybrid with P. abbreviata being widely distributed and known as P. x hartzii Gdgr.

The panicle branches are normally terete. In four European species of Poa they are sulcate. Since two of these species each form the type of a monotypic section, this character provides a valuable diagnostic feature (see table 5.10). In the case of the other two species, the character state helps P. flexuosa and P. laxa to be distinguished from the other species of sect. Oreinos, P. minor and P. pirinica, which have terete panicle branches.

5.9 The spikelet.

Leaving aside for the moment the component parts of the spikelet, the spikelet as a whole provides a few characters of diagnostic value at the sectional level, but these have traditionally been given little importance in the overall scheme of classification. These are the colour of the spikelet, its outline shape, and the number

of florets per spikelet. An additional feature of the spikelet is its tendency in certain species to proliferate into vegetative bulbils or plantlets: see chapter 3.

a) Colour. Apart from the greenish colour produced by the photosynthetic pigments, a number of species have supplementary pigments in the parts of the lemma exposed to the light as well as in the glumes. The most conspicuous pigments are the purple or violet anthocyanins; their admixture with other pigments produces a wide range of colours ranging from a pale straw through various shades of purples and browns to a deep, almost black, violet colour. Chemically, these pigments are a complex mixture of anthocyanins and other types of flavonoid pigments, but it is customary to refer always to 'anthocyanins' since these are probably the most abundant class of pigment in the spikelet. Table 5.12 lists those species and sections having a particularly notable concentration of pigments in the spikelet. Almost without exception, those species with the strongest colouration of the spikelet are alpine (montane) in distribution, and conversely those sections which lack species with any conspicuous colouration are distributed largely in lowland areas. It is therefore evident that exposure to strong light irradiation is accompanied by heavy pigment deposition purely as a protective measure, which if it occurs in response to an external stimulus rather than through selection of pigment-rich strains may not be taxonomically significant.

b) Outline shape of the spikelet. Though this is often characteristic of particular species to a taxonomist with a trained eye, the lack of a satisfactory terminology for describing spikelet shapes with sufficient precision prevents any wide use being made of this character for diagnostic purposes. An example of a figure showing

TABLE 5.11 3-D panicle shapes and their 2-D equivalents.

PYRAMIDAL	=	TRIANGULAR; a near-equilateral triangle
CONICAL	=	TRIANGULAR; an isosceles triangle having a relatively narrow base
OVOID	=	OVATE; egg-shaped, widest point below the middle
ELLIPSOID	=	ELLIPTICAL; widest point at the middle
OBLONG	=	OBLONG; this term may be used in either sense
ELONGATE-OVOID	=	LANCEOLATE; widest point below the middle
SPIKE-LIKE	=	LINEAR; this term is preferred to 'spicate' since this remains a panicle.

TABLE 5.12 Sections with species having conspicuous anthocyanin pigmentation

OCHLOPOA: P. supina

CENISIA: P. arctica)
P. granitica) - strongly violet-tinged
subsp. granitica

P. granitica)
subsp. disparilis)
P. cenisia) - bronze, golden or violet-tinged

OREINOS: P. pirinica - strongly violet-tinged

P. flexuosa)
P. laxa) - less strongly violet-tinged
P. minor)

ABBREVIATAE: P. abbreviata NANOPOA: P. trichophylla

BOLBOPHORUM: P. bulbosa, P. ligulata, P. media, P. molineri, and P. pumila - always quite strongly violet-tinged

P. badensis and P. perconcinna - greenish, never violet-tinged.

a range of spikelet shapes is to be found in Lid (1963), p. 113, fig. 49.

c) Number of florets per spikelet. Though the number of florets varies considerably within individual species as well as within and between sections, it has diagnostic value in several cases. One of the merits of this character is that it is expressed in discrete quantitative values; there are few other discontinuous quantitative characters in use in the classification of Poa.

Since the number of species in Europe is a rather small sample of the available range of variation of this character, and since the information is easily extracted from a Flora account, a more broadly-based sample of the frequency of occurrence of the different numbers of florets per spikelet was obtained from Flora SSSR, ed. V.L. Komarov (vol. 2, 1934). Fig. 2 presents a graph showing the number of times a particular number of florets occurs in 107 species from the USSR, together with four species from the area covered by Flora Europaea which extend the range of the graph over eight florets per spikelet (the maximum recorded in Flora SSSR) to nine and ten florets per spikelet. The curve is a skew one, with the maximum score standing at three florets and with species with four and five florets both more numerous than those with two. Those with six, seven and eight are likewise more numerous than those with one floret. The implication of these results is that selection against a reduction in the number of florets per spikelet is stronger than selection against an increase in the number of florets from the median position.

The spikelet axis is commonly terminated by an empty lemma or pair of lemmas greatly reduced in size. These are not counted for the purpose of assessing the total number of florets per spikelet.

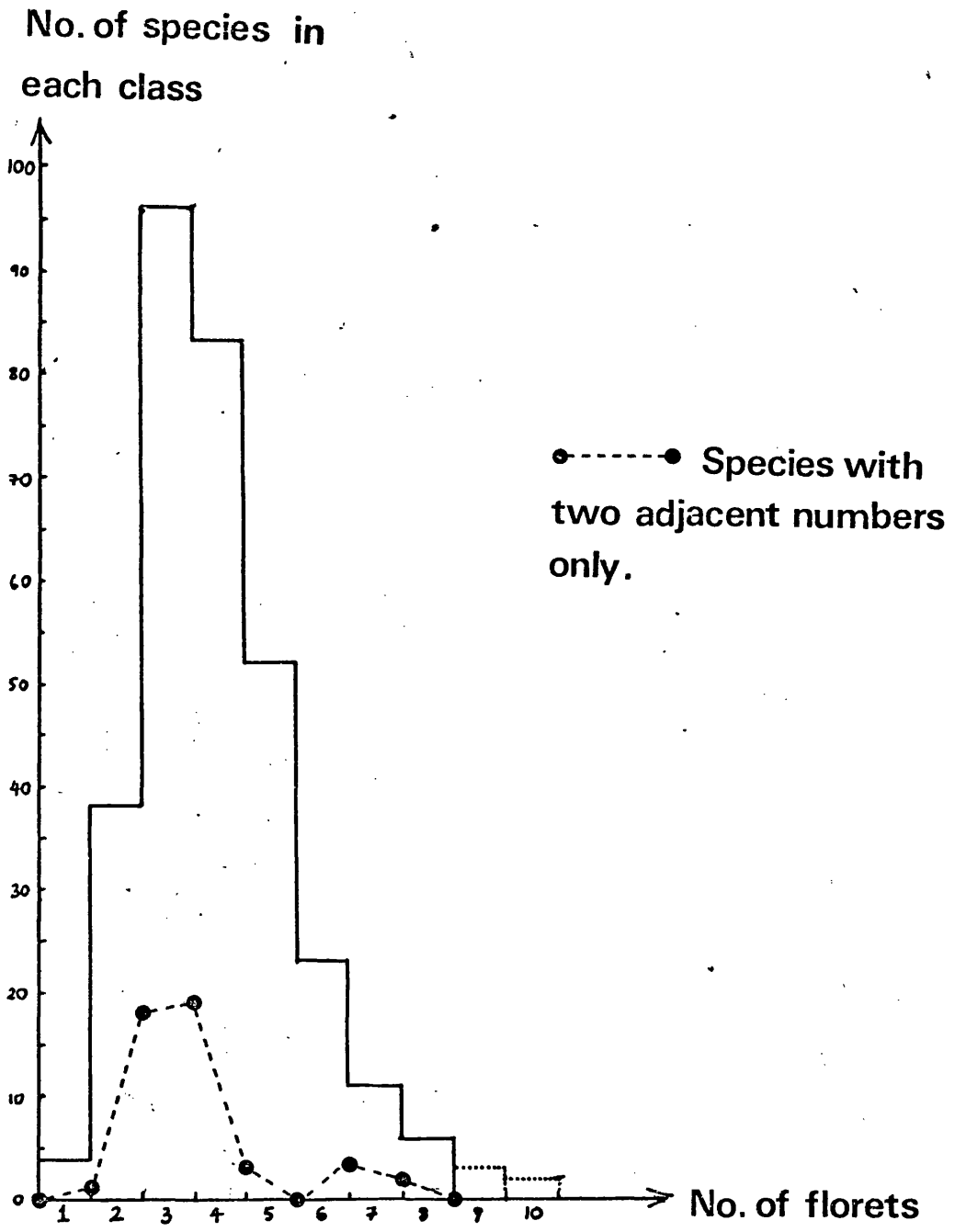

Fig. 2. Number of florets in each spikelet – 107 species from Fl. SSSR —— plus 4 species from Flora Europaea .....

5.10 The glumes

In the genus Poa each spikelet always has two glumes, divisible into a lower and an upper glume, on account of a small separation between them. This must be closely observed if the diagnostic differences between the lower and upper glume are to be correctly noted. The lower glume sometimes equals the upper glume in size, but more often it is shorter and narrower than the upper; this feature is most marked in P. nemoralis.

In addition to a vascular bundle in the keel of each glume, there are normally two lateral veins which anastomose above, the vascular trace rejoining the keel. The lower glume sometimes lacks lateral veins; this is often noted in poorly-developed spikelets, and only in sect. Ochlopoa is the feature sufficiently constant to be of diagnostic value.

The members of sect. Coenopoa and Homalopoa are noted for their particularly slender glumes, which are narrower than those of the remaining European sections of Poa: see fig. 3).

The glume is normally strongly folded at the keel. P. trichophylla is notable for its weakly folded glumes and lemma which are reminiscent of those of a Festuca. With the exception of this species, the character affords a useful and rapid means of distinguishing Poa and Festuca.

The keels of the glumes may be aculeolate or smooth. The presence or absence of aculeoli is not normally of diagnostic value. In P. badensis, however, it has been demonstrated by Nygren (1962) that the size of the aculeoli is correlated with the level of ploidy. The hooks are large and well-developed in the tetraploid, whereas in the diploid they are relatively small and slender.

The lateral veins of the glumes are always glabrous. The abaxial

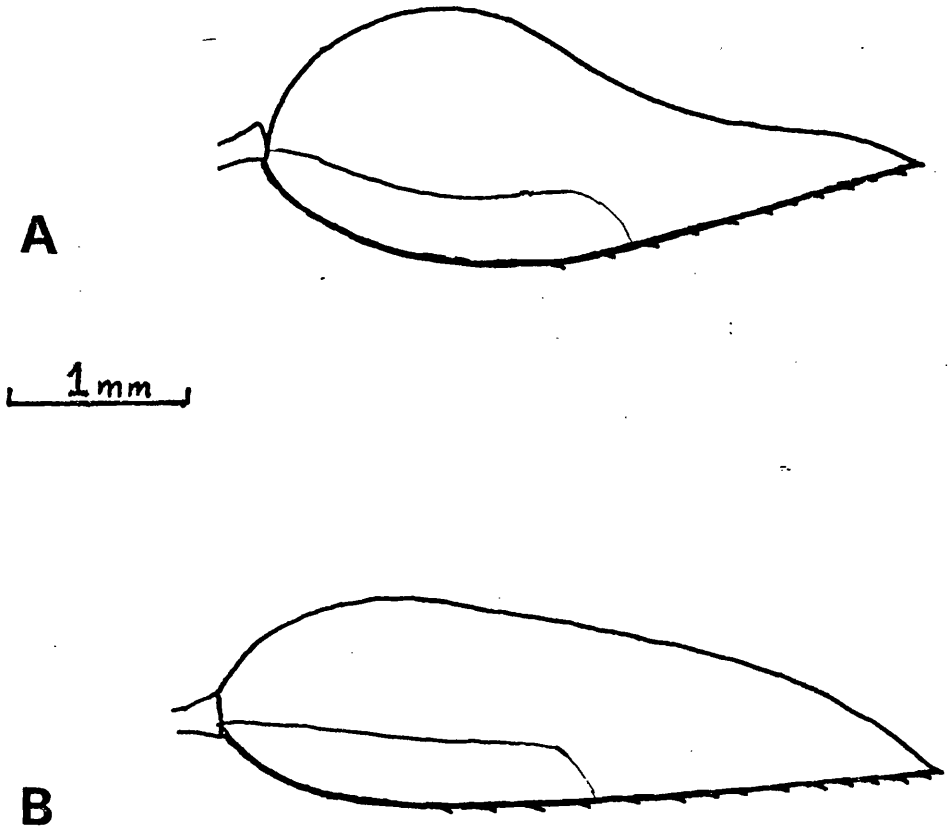

Fig. 3. Shape of lower glume.

A: Sect. Bolbophorum

B: Sect. Homalopoa

surface of the lemma bears papillae formed through the protrusion of the silica-cells in the short cells of the epidermis. These are visible under the light microscope only as points of light surrounded by refraction fringes (particularly when a mountant consisting of a solution of water in phenol is employed). Under the S.E.M., however, these are revealed to be verrucose knobs with a very regular domed structure. A comparison of the size and shape of these papillae may afford valuable new characters in the taxonomy of the genus and perhaps also in the Gramineae as a whole; the S.E.M. instrument became available in Leicester too late for me to start to survey this character through the whole genus.

The tissue of the glume is multiseriate in section towards the middle, its opacity being due to a layer of photosynthetic or pigmented cells sandwiched between the outer and inner epidermes. Towards the margin the glume becomes hyaline as it is reduced to a single layer of epidermal cells with conspicuously wavy margins. The apex of the glume may be slightly apiculate, but there is no awn. It is rare for the tip of the lowest glume to reach or to exceed the tip of the lowest lemma.

The shape of the glumes is important in that it contributes to the general form of the spikelet. It is difficult to express in words, since both the margins and the keel describe inward and outward curves, and the whole has a folded three-dimensional structure. Bor (1948, p. 795) uses the terms "awl-shaped", "ovate", "lanceolate" and "elliptic-acute" to describe the shape of the glumes when flattened. Vickery (1970, p. 156) notes that in the Australian species the variations in shape are too great to be reliable as characters for separating different species, or groups of species.

Since the glumes subtend the spikelet axis or rhachilla on which the individual florets are borne, they may be regarded as equivalent to sterile bracts (Arber, 1934). Developmentally they are clearly leaf-like in initiation and early development (Sattler, 1967).

5.11 The lemma.

The number of lemmas per spikelet is not always exactly the same as the number of florets, since the spikelet axis is frequently terminated by an empty lemma. With this exception, the lemma normally encloses the remaining floral organs: palea, lodicules, callus, androecium and gynoecium.

The lemma is keeled, and possesses five nerves. The vascularization is complex: the primary vascular bundle occupies the keel, and of the four lateral bundles two occupy a submarginal position to midway, or a little further, up the lemma. The two lateral bundles which occupy the intermediate position normally extend only about a third of the way up the lemma, and are less distinct than the submarginal nerves.

The length of the lowest lemma almost always exceeds that of the glumes, and with the added length of the first segment of the rhachilla it projects some way beyond the apex of the glumes. The anatomy of the lemma is very similar to that of the glumes; the blade is hyaline towards the margins, while near the keel its opacity is caused by the interposition of several layers of pigmented or photosynthetic cells between the inner and outer epidermis. Shining silica cells are often visible, even under a low-power hand lens, and the keel is frequently aculeolate, especially in the upper half.

The lemma probably did not evolve directly from a leaf, but probably acquired its present leaf-like structure as a result of

a floral organ adopting the features of a vegetative organ (Maze, 1971).

5.11.1 Indumentum.

Unlike the glumes, the lemma is rarely glabrous. In the great majority of sections the keel and submarginal nerves are pilose, with fine straight hairs which stand out from the surface. The exceptions to this state are few:

a) species and sections with a completely glabrous lemma:

- the whole of sect. Macropoa;
- sect. Nanopoa;
- sect. Abbreviatae (surface of lemma adpressed-hairy);
- P. feratiana (sect. Coenopoa), which distinguishes it from P. trivialis which is pilose on the nerves;
- P. chaixii (sect. Homalopoa), which distinguishes it from P. hybrida and P. remota which are glabrous on the submarginal nerves and hairy only on the keel;
- P. compressa (sect. Tichopoa) is sometimes hairy on the keel and marginal nerves, and sometimes glabrous.

b) species glabrous on the keel and hairy on submarginal nerves only:

- P. supina (sect. Ochlopoa);
- P. hybrida and P. remota (sect. Homalopoa).

c) species with adpressed hairs clothing the surface of the lemma, usually only in the lower half:

- P. arctica (sect. Genisia);
- P. flaccidula (sect. Stenopoa);
- P. abbreviata (sect. Abbreviatae), lemma otherwise glabrous;
- P. molineri and P. alpina (sect. Bolbophorum).

Table 5.13 sets out the indumentum characters of the lemma for each European species of Poa, together with data on the relative

lengths of the lower and upper glumes. Glumes given as 'equal' or 'subequal' in the Flora Europaea account are classed as equal; glumes which are evidently unequal in length are classed as unequal, whether or not they are similar in width.

The hairs on the nerves of the lemma are straight or almost so in nearly all the European species of Poa. P. granitica is very distinct in having wavy, crinkled hairs on the nerves of the lemma in its subsp. granitica, which help to distinguish it from subsp. disparilis (the more southerly subspecies) which has short straight hairs on the keel and marginal nerves.

5.11.2 Types of apex of hairs on the lemma.

The shape of the apex of the hairs occurring on the keel and marginal nerves of the lemma is very varied, ranging from a finely tapering acute apex at one extreme to a club-shaped apex at the other, (see fig. 4). These differences were first reported by Chrtek & Jirásek (1962b) who also presented some conclusions regarding their systematic importance.

Of the sections with three or more European species, only sect. Poa is not heterogeneous for this character. Of the two sections in which I have made a close study of this character, sect. Bolbophorum shows a narrower range of variation, while sect. Stenopoa contains species with all four types of apex, some species exhibiting more than one type but with most showing a preponderance of a particular type of apex. Study of a wider range of material has tended to negate the conclusions of Chrtek & Jirásek regarding the occurrence of the different types of apex in sect. Stenopoa, but in sect. Bolbophorum the differences between my own observations and those of Chrtek & Jirásek are only slight. Where they tend to record club-shaped apices for most of

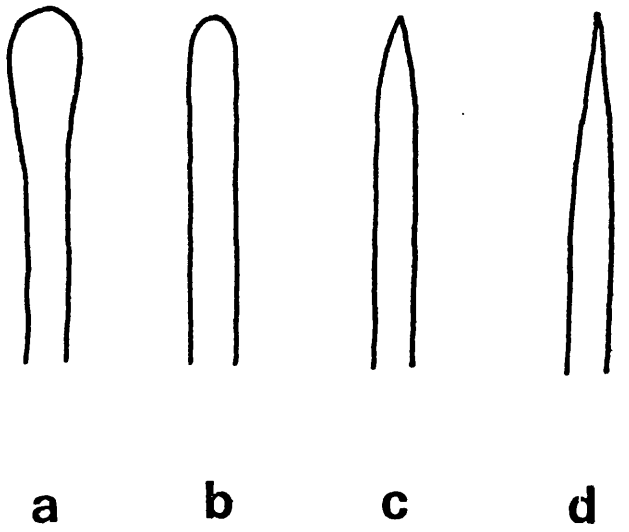

Fig. 4. Types of lemma hair apex.

a: club-shaped

b: rounded

c: ogival

d: acute (after Chrtek & Jirásek, 1965 b)

the members of sect. Bolbophorum, I found mainly the blunt type of apex, with one notable exception: a specimen of P. ligulata from the Atlas mountains in northern Morocco (herb. LTR) proved to have the acute-tipped hair type.

In sect. Oreinos, this character affords a useful separation between P. flexuosa and P. pirinica on the one hand, with hairs with acute apices, and P. minor on the other hand, with club-shaped apices, P. laxa occupying an intermediate position since its hairs have apices which vary in shape from rounded to ogival*.

The character also permits P. arctica (hairs acute-tipped) to be distinguished from the remaining members of sect. Genisia, in which the hairs have rounded tips.

Sections other than monotypic sections in which all species have the same type of apex are as follows:
sect. Ochlopoa: hairs uniformly with club-shaped tips;
sect. Poa: hairs uniformly with rounded tips.

This character does not apply to P. feratiana (sect. Coenopoa) or to the members of sect. Macropoa, Abbreviatae and Nanopoa in which the nerves of the lemma are glabrous.

The distribution of the different types of apex is indicated in table 5.13.

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*NOTE: the term 'ogival' is derived from the word 'ogive', which denotes a Gothic window; the shape resembles that of the apex of such a window. The absence of a term to describe a shape which resembles the apex both of a Gothic window and of some types of rocket nose cone has been a handicap to taxonomists; the first application of 'ogive' known to me was in Cavillier's (1911) monograph of the genus Doronicum, where the term 'ogive-conique' is used in describing a type of hair which occurs on the stems and leaves.

TABLE 5.13 Relative glume length and lemma indumentum in the European species of Poa

Species numbered as in Appendix 1.

KEY: Glumes equal (E) or unequal (U); lemma nerves hairy (H) or glabrous (.); surface adpressed hairy (H) or glabrous (.); hairs on submarginal nerves with club-shaped (A) rounded (B) ogival (C) or acute (D) tips.

	1.	2.	3.	4.	5.	6.	7.	8.	9.	10.	11.	12.	13.	14.	15.	16.	17.	18.	19.	20.	21.	22.
Glumes E/U	U	U	U	E	E	E	E	U	U	U	E	E	U	U	U	U	E		E	E	E	E
Lemma H/. on keel	H	H	.	H	.	H	H	H	H	H	H	H	.	.	.	H	H	H	H	H	H	H
on submarginal nerves	H	H	H	H	.	H	H	H	H	H	H	H	.	.	.	.	.	H	H	H	H	H
on surface	.	.	.	.	.	.	.	.	.	H	.	.	.	.	.	.	.	.	.	.	.	.
Hair tips A/B/C/D (sec. Chrtek & Jir.) (my observations)	A	A	A	A/B	-	C	C	C	C	D	B	B	-	-(A)	B(C)	C	C	D	D	B/C	D	A

	23.	24.	25.	26.	27.	28.	29.	30.	31.	32.	33.	34.	35.	36.	37.	38.	39.	40.	41.	42.	43.	44.
Glumes E/U	E	E	E	E	U	U	E	E	E	E	E	U	E	E	U	U	U	E	E	U	U	U
Lemma H/. on keel	H/.	H	H	H	H	H	H	H	H	H	.	.	H	H	H	H	H	H	H	H	H	H
on submarginal nerves	H/.	H	H	H	H	H	H	H	H	H	.	.	H	H	H	H	H	H	H	H	H	H
Hair tips A/B/C/D (sec. Chrtek & Jir.)	B/D	B	B	D(B)	B/D	D	B/D	B/C	B	-	D	-	B	A	BD	A	B	A	A	A	A	A
(my observations)							(see chapter 7)					B	B	A	ABD	A	B	B	B	A	B	
Lemma H/. on surface	.	H	.	.	.	.	.	.	.	.	H	.	.	.	.	.	.	.	H	.	H	.

5.12 The palea

Of the various scales which make up the spikelet, the palea is the only two-keeled structure. Partially enclosed by the lemma, the palea consists of a thin layer of hyaline cells folded inwards at the keels and supported by vascular strands which run almost to the apex. The palea is broadest at its middle, and is often notched at the tip. Since it is concealed within the spikelet, it is normally lacking in anthocyanin colouration, but is well provided with silica-cells in the short cells of the epidermis, particularly in the lower half. In addition, sparse to tangled unicellular hairs occur on the abaxial surface of the palea in a few species. (The term 'abaxial' is intended to refer to the floret axis rather than to the axis of the spikelet; owing to the orientation of the palea in relation to its accompanying lemma, the 'abaxial' surface of the palea is in fact closest to the rhachilla).

The keels of the palea are provided with aculeoli either throughout their length or towards the apex only, in which case they are gradually replaced towards the base by unicellular hairs.

The shape of the palea is sometimes mentioned in descriptions, but since it varies so greatly depending on the age of the spikelet it is of no diagnostic value.

The palea is considered by some authors (Arber, 1934; Bor, 1948, p. 797) to be homologous with the bracteole which subtends the flower, but this hypothesis is by no means universally accepted; developmental studies (Maze et al., 1971), while confirming that it is foliar in origin, do not supply a definitive answer to the question of whether it should be regarded as a prophyll or as a bracteole. Stebbins, in Youngner & McKell (1972, p. 4) bases his conclusions on the evidence of the genus Streptochaeta, an anomalous

grass on account of the peculiar structure of the palea, which consists of two single-keeled units. Stebbins develops the argument originally presented by Schuster (1910) that the palea represents two of the three outer tepals of a trimerous flower, the third tepal having disappeared and the two-keeled palea having formed through the fusion of the two remaining tepals.

The indumentum of the palea provides one of the most useful diagnostic features within the spikelet. Von Oettingen (1925) gave the first account of the variation shown by the European species of Poa in the indumentum of the keels of the palea, and proposed four groups:

a) Pilosae. Keels ciliate along their whole length.

b) Semipilosae. Keels ciliate in the lower half, the hairs gradually becoming shorter towards the middle and being replaced by aculeoli in the upper half.

c) Dentatae. Keels bearing several rows of aculeoli.

d) Pectinatae. Keels bearing a single row of aculeoli.

Von Oettingen's distinction between species with one row, and those with more than one row, of aculeoli is in practice difficult or impossible to make. For example, P. compressa is placed in the group Pectinatae, though as pointed out by Bor (1948, p. 798) it fails to qualify exclusively for either this group or for the group Dentatae, since the aculeoli can occur in either one or several rows. Taking categories (c) and (d) together, however, these contrast with categories (a) and (b) to provide taxonomically meaningful distinctions.

The only European section falling exclusively into the Pilosae group is sect. Ochlopoa, in which the palea is ciliate for most of its length. P. jubata, a species whose taxonomic position

is uncertain, is probably best placed in this group, since its palea keels are ciliate from the base to about two-thirds of their length. The only other European species which belongs here is P. pirinica (sect. Oreinos) , in which the palea keels are only sparsely ciliate for most of their length.

The species grouped in the Semipilosae belong to a wider range of sections. My detailed study of palea keel indumentum in the P. sterilis group showed that in several cases specimens were found to have a few hairs near the base of the palea but to be aculeolate along most of the length of the keels; two categories were therefore established within the Semipilosae group.

Sections containing semipilose species are: sect. Abbreviatae; sect. Bolbophorum; sect. Cenisia; sect. Poa; and sect. Stenopoa. All of these except sect. Abbreviatae also contain dentate/pectinate species. Poa abbreviata is anomalous in that the palea is almost glabrous in the lower half, having a few hairs below and with aculeoli in the upper third only.

Sections containing exclusively dentate/pectinate species are: sect. Coenopoa; sect. Homalopoa; sect. Leptophyllae; sect. Macropoa; sect. Nanopoa; and sect. Tichopoa.

The only places where variations in palea keel indumentum are taxonomically significant at or below the species level are in sections having both semipilose and dentate/pectinate species, (Chrtek & Rejzlova, 1971).
In sect. Cenisia, P. cenisia subsp. cenisia and subsp. contracta have aculeolate palea keels, whereas most examples of subsp. sardoa have semipilose keels (although some have aculeolate keels). Also in sect. Cenisia, P. arctica has both types of palea keel indumentum, while P. granitica appears to have consistently semipilose palea keels. In sect. Bolbophorum, P. badensis, P. ligulata and P. timoleontis

show only the aculeolate palea keel type, P. bulbosa, P. molineri, P. perconcinna and P. pumila show both types of indumentum, and P. media, P. alpina (except subsp. insularis (Parl.) Hayek) are apparently always provided with ciliate palea keels.

The surface of that part of the palea which lies between the keels is typically glabrous. Some species of Stenopoa are notable for having sparse to dense tangled uniseriate hairs on the palea surface, and although none of the European species of Poa appears to have an aculeolate palea surface, according to Bor (1948, p. 832) this is a conspicuous feature of P. wardiana which is a species described by him and occurring in Assam.

5.13 The callus.

At the base of each floret there is a pad of tissue upon which the constituent parts of the floret are placed, and which attaches them to the articulation of the rhachilla. During the dissection of the floret, it usually remains attached to the lemma, so that its principal feature - the long, flexuous hairs which hang from the base of the floret - is often recorded as a character of the base of the lemma. The occurrence of 'basal wool' is recorded in the Flora Europaea account in the form "lemma.....lanate at base", but this should be understood to be strictly a reference to a character of the callus.

Table 5.14 presents the three categories of section which can be distinguished on account of the callus wool character: those in which wool is invariably present; those in which it may be present or absent; and those in which wool does not occur. It is apparent that the absence of wool is of more importance than its presence, since in some sections (e.g. sect. Stenopoa) the amount varies so widely even within individual species; see chapter 7.

TABLE 5.14 Occurrence of flexuous hairs (wool) on the callus.

a) Sections in which the callus is not lanate:

OCHLOPOA	MACROPOA
ABBREVIATAE	NANOPOA

b) Sections in which the callus is either lanate or not lanate:

COENOPOA	HOMALOPOA
STENOPOA	BOLBOPHORUM

c) Sections in which the callus is lanate:

POA	CENISIA
LEPTOPHYLLAE	OREINOS
TICHOPOA	

TABLE 5.15 Range of anther lengths in the European sections of Poa.

OCHLOPOA	0.2 - 2.5 mm	MACROPOA	1.5 - 3.7 mm
COENOPOA	c. 1.4 mm	HOMALOPOA	
POA	1.4 - 2.0 mm	STENOPOA	
CENISIA	1.5 - 2.4 mm	ABBREVIATAE	0.6 - 0.8 mm
LEPTOPHYLLAE		NANOPOA	
OREINOS	0.6 - 1.7 mm	BOLBOPHORUM	1.0 - 2.0 mm
TICHOPOA	1.0 - 1.2 mm		

Note: anthers measured when mature but undehisced.

The most noticeable feature of sections in which copious wool is present is that the seeds tend to adhere to one another even when separated from the spikelets; the wool thus appears to function as a binding agent which ensures intensive rather than extensive seed dispersal. It may also be an adaptation which favours animal dispersal, since seeds with copious wool adhere to fur and clothing. It may even aid wind dispersal to a slight degree.

5.14 The rhachilla.

The axis of the spikelet consists of a slender, terete stalk divisible into separate segments which break up at the time of seed dispersal. The lowest segment of the rhachilla is the shortest, and connects the lowest floret to the apex of the panicle branch between the glumes. Subsequent segments, which link the first and subsequent florets, are longer and since each segment disarticulates at its apex the individual units of dispersal are provided with a hook. It is these segments of the rhachilla which provide information which can be of systematic value.

Rhachilla indumentum shows great variation. Single-celled hairs, aculeoli and verrucose papillae may each be present, singly or in combination, in varying quantities. Difficulties in observing these features in dried herbarium material without special preparation present problems, and only sect. Stenopoa has been studied in detail. A fuller account is given in chapter 7.

5.15 The lodicules.

No characters are apparent which permit the lodicules to be regarded as having any systematic value. Their two-lobed structure is almost constant within the genus, and their sole function appears to be to facilitate the exsertion of the anthers

and stigma at anthesis, by swelling at the base and forcing the lemma and palea apart.

5.16 The gynoecium.

The ovary in Poa contains a single ovule and has two feathery styles. These have been examined in different species in case some differences might be discovered, but none was observed. The sole aberrant feature noted during the dissection of around 250 spikelets was in a specimen of P. pumila (herb. LTR) which in one floret had an ovary which contained two ovules.

At maturity, the caryopsis is narrowly ellipsoid, with a basal, punctiform hilum. By having this type of hilum, the species of Poa may be distinguished from those of the genus Festuca, in which the hilum takes the form of a slit.

In view of the fact that Poa trichophylla is atypical in having channelled, rather than folded, glumes and lemmas, a feature which normally belongs only to species of Festuca within the two genera, a check was made on the type of hilum in ripe caryopses of a specimen collected by O. Polunin (no. 11221, herb. LTR) and it was found to have the normal punctiform type of hilum.

The caryopsis is not normally dispersed naked; the lemma, palea and callus, together with the segment of the rachilla above the callus, usually remain attached and are dispersed as a unit.

5.17 The androecium

There are three stamens in each floret of Poa, and except where anthers are absent (as for example in the dioecious species of Poa subgenus Dioicopoa) this number is apparently constant. The length of the anthers not only varies over a wide range, but also provides usually reliable diagnostic features at the sectional level as well as at the level of species. Table 5.15 sets out the range of anther lengths in the European sections of Poa. In certain

sections, notably in sect. Ochlopoa, the length of the anthers provides a useful way of distinguishing the different species, since it varies by a factor of up to ten between P. infirma, which has very short anthers, and P. supina, whose anthers are several times as long as broad.

Sect. Abbreviatae is also noted for its very short (0.6 - 0.8 mm) anthers, and in sect. Macropoa the anthers are exceptionally long (up to 3.7 mm). In general, the length of the anthers in most sections of Poa ranges from 1.0 to 2.5 mm.

The length of the anthers is normally measured for comparative purposes in material that is mature but undehisced. At anthesis, the loculi of the anther separate from one another except at the middle, where the filament is attached (medifixed), and become X-shaped.

It is possible that where more than one ploidy level exists in a given species, the size of the anthers is correlated with the level of ploidy. In P. badensis, it was shown by Nygren (1962) that the anthers were larger in tetraploid specimens than in diploid specimens. However, there are relatively few species of Poa with both diploid and tetraploid chromosome races (see chapter 4), and there is so far no evidence that these differences may be seen at higher levels of ploidy.

Fig. 5. Diagram of 'exploded' spikelet.

To close this chapter, a diagram of the constituent parts of the spikelet is provided (fig. 5). Fig. 6 shows the spikelet prior to dissection. The material used was a flowering specimen of Poa alpina L.

KEY:

a) Apex of panicle branch.

b) Lower glume.

KEY to fig. 5 (continued):

c) Upper glume.

d) Lowest segment of rhachilla.

e) Lowest lemma, i.e. lemma of first floret.

f) Lowest palea, i.e. palea of first floret.

g) Segment of rhachilla which separates the first and second florets.

h) Lemma of second floret (subsequent parts omitted).

i) Androecium and gynoecium; lodicules.

Note: when dissecting the spikelet, the constituent parts are normally placed on the microscope slide in the sequence adopted in the figure; this arrangement allows, for example, the differences between the lower and upper glume to be noted without referring to the undissected spikelet. For further details of the technique used when dissecting the spikelet, see appendix 2.

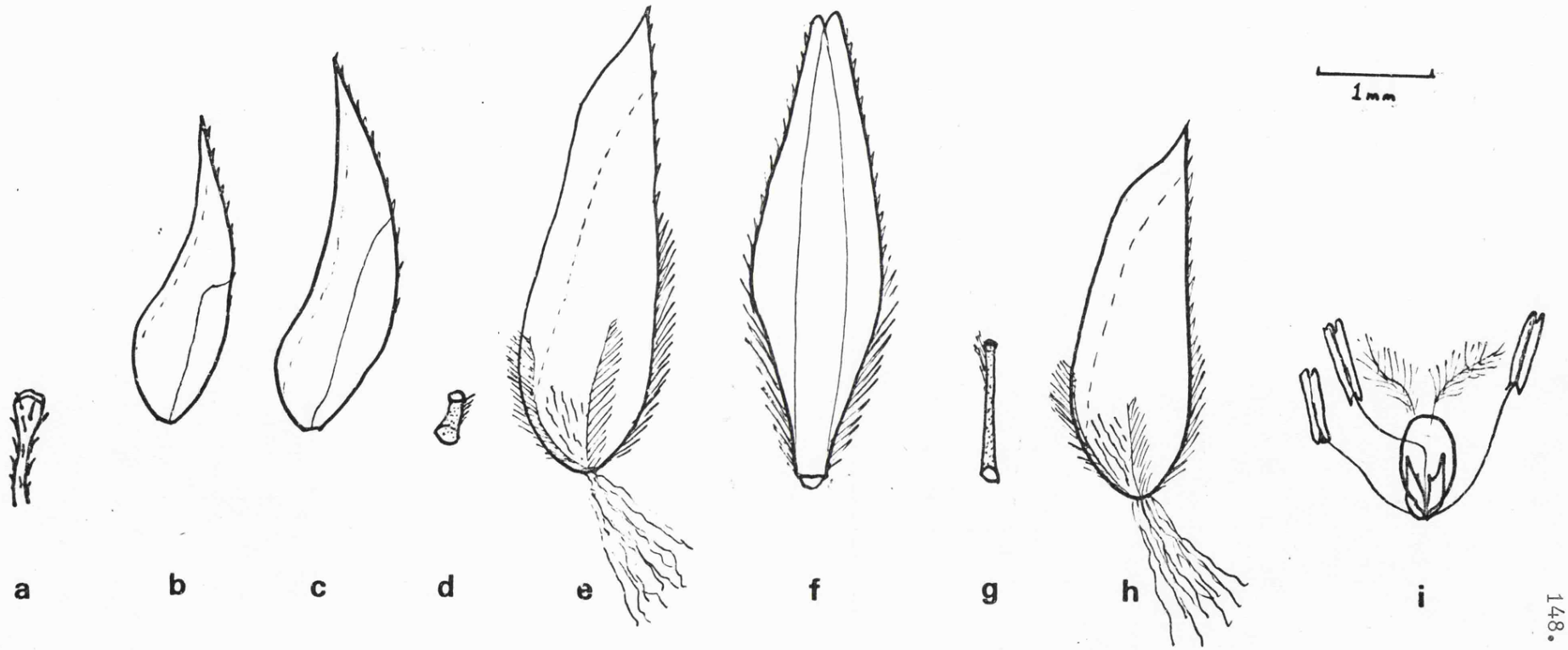


FIG. 5. 'Exploded' spikelet of Poa alpina. Key: pp. 146 – 147.

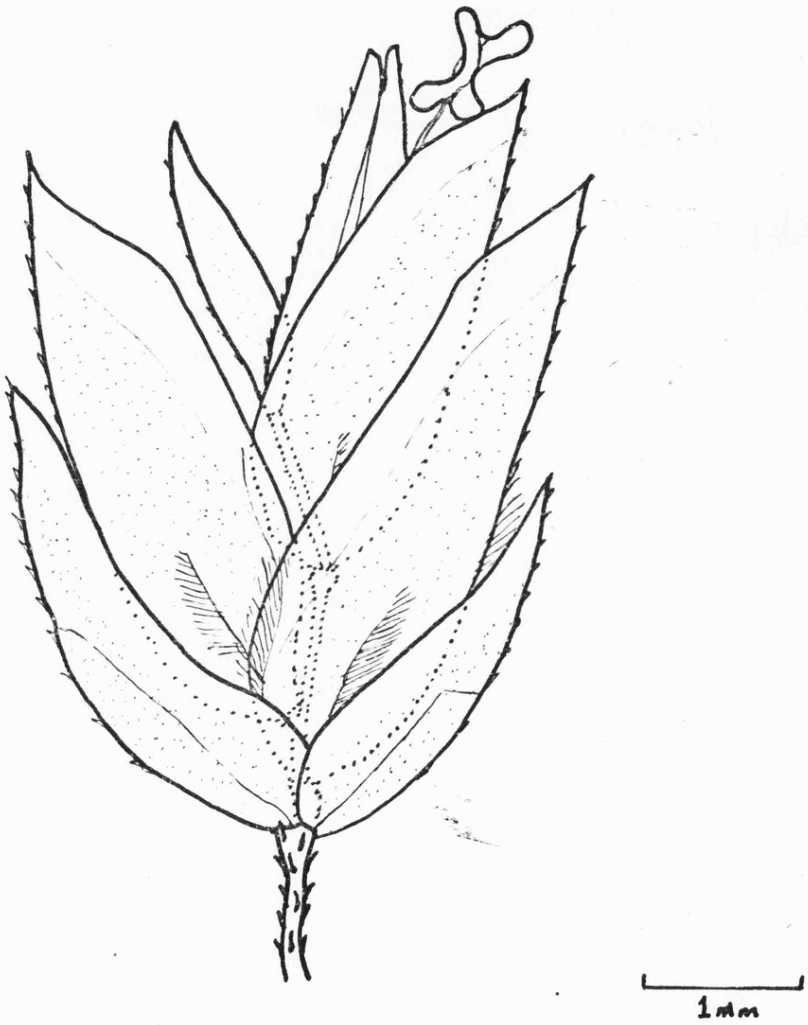


FIG. 6. Spikelet of Poa alpina.

CHAPTER 6. Anatomical structure.

6.1 Introduction.

In studies of the anatomical structure of grasses, the most useful features for taxonomic purposes are found in the anatomy of the leaf blade. There is only limited information on the anatomy of the stem, which appears to have little taxonomic value. The only recent comparative data on the anatomy of the root is that of Chrtek & Jirásek (1965a). The panicle, spikelets and constituent floral parts do not appear to have been studied.

The preparative techniques used in studying anatomical features are described in appendix 2.

6.2 Leaf anatomy.

Metcalfe's first volume of the "Anatomy of the Monocotyledons" (1960) gives an account of the structure of the abaxial epidermis and transverse section of the lamina in three species of *Poa*. He also abstracted information from the literature on a further 19 species of *Poa*, including thirteen species which occur in Europe. While these abstracts are a useful source of comparative data expressed with a uniform terminology, I have preferred to draw upon the original sources where possible.

A list of sources used is given in table 6.1, with a key to the European species mentioned in these accounts. I have not seen the paper by Lewton-Brain (1904), which according to Metcalfe (1960) refers to *P. alpina*, *P. annua*, *P. compressa*, *P. nemoralis*, *P. pratensis* and *P. trivialis*.

Duval-Jouve (1875) published the first information on the leaf anatomy of *Poa*. Lohauss (1905) gave the most complete account prior to Metcalfe's compilation, and unlike Metcalfe he illustrated the leaf sections of most of the species examined. Realization of

the taxonomic usefulness of anatomical data came later; anatomical information was included in certain studies of small taxonomic groups (Nannfeldt, 1935; Jirásek, 1935c; Buschmann, 1942; Timpko, 1964; Smirnov, 1965), and overall surveys of the species of Poa were produced for Czechoslovakia (Vukolov, 1929) and the Ukraine (Konstantinova, 1960; Poyarkova, 1966).

Owing perhaps to the unsatisfactory nature of the existing classification of Poa in the earlier part of the century, there had been little attempt to utilise anatomical criteria for diagnostic purposes. Vukolov (1929), however, categorized the different types of sclerenchyma distribution (fig. 7). Poyarkova used these to define two main classes of anatomical types; the existence of these classes has been confirmed by my own work, but I believe it to be more important to characterize the leaf anatomy of the taxonomic sections recognized on other grounds, thereby enhancing our knowledge of the range of characteristic features of the sections, than to produce an independent classification of anatomical types which is of less systematic value.

The two classes of anatomical types recognized by Poyarkova are listed in table 6.2, and are distinguished as follows: in class A type III sclerenchyma predominates, while in class B the larger veins have type I or type II sclerenchyma, and the smaller veins are accompanied by type V or VI. Sect. Stenopoa cannot be allocated to either class, since some species (P. sterilis and P. versicolor) fall into class A, whereas others (P. palustris, P. glauca etc.) fall into class B.

This is by no means the only diagnostic feature available; other important characters include the shape of the blade in transverse section, the form of the keel, the size and degree of

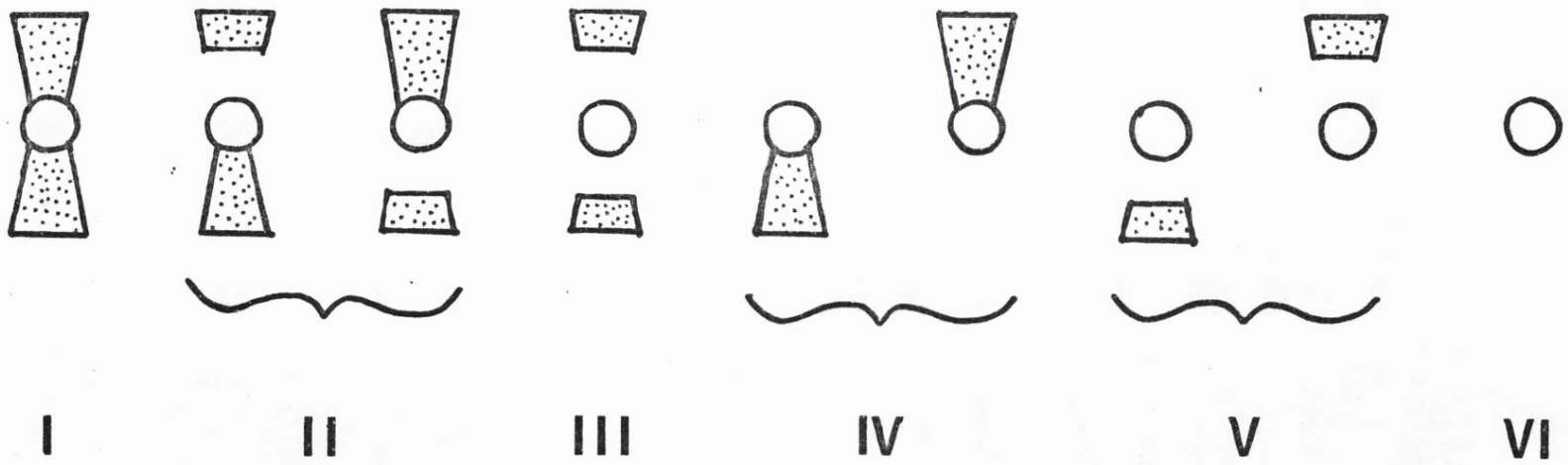


FIG. 7. Types of sclerenchyma distribution in Poa. After Vukolov (1929).

See text (p. 151) for explanation.

TABLE 6.1 Literature sources of anatomical data.

Key: A. Unpublished data from my original work.

B. Duval-Jouve (1875).

C. Lohauss (1905).

D. Vukolov (1929).

E. Jirásek (1935c).

F. Nannfeldt (1935).

G. Mecenović (1939).

H. Buschmann (1942).

I. Bobrov (1955).

J. Metcalfe (1960); original observations only.

K. Konstantinova (1960).

L. Timpko (1964).

M. Smirnov (1965).

N. Poyarkova (1966).

Sect. OCHLOPOA		Sect. MACROPOA	
P. annua	I	P. longifolia	C, M
Sect. COENOPOA		P. sibirica	A
P. trivialis	A, N	Sect. HOMALOPOA	
Sect. POA		P. chaixii	A
P. alpigena	A	P. remota	C
P. angustifolia	C, K, N	Sect. LEPTOPHYLLAE	
P. pratensis	C, K, N	P. stiriaca	A, G
Sect. CENISIA		Sect. OREINOS	
P. granitica	N	P. laxa	C, F
		P. minor	H

(continued)

TABLE 6.1 (ctd.)

Sect. TICHOPOA		Sect. ABBREVIATAE	
P. compressa	A, C, K, N	*P. abbreviata*	F
Sect. STENOPOA		Sect. BOLBOPHORUM	
P. flaccidula	C	*P. alpina*	A, C, H, L
P. glauca	A, J	*P. badensis*	A, C, E, H
P. palustris	A, N	*P. bulbosa*	A, N
P. nemoralis	K	*P. media*	H
P. pannonica	A, C	*P. molineri*	H
P. sterilis	A, K, N	*P. pumila*	A
P. versicolor	A, N		

TABLE 6.2 Classes of sclerenchyma distribution

Class A.	Class B.
OCHLOPOA	POA
COENOPOA	CENISIA
OREINOS	MACROPOA
STENOPOA pro parte	HOMALOPOA
BOLBOPHORUM	LEPTOPHYLLAE
	TICHOPOA
	STENOPOA pro parte
(type III sclerenchyma predominates)	(types I & II sclerenchyma on main veins, types V & VI on smaller veins)

submergence of the bulliform cells, and the type of sclerenchyma bundle in the midrib.

The subdivision of the genus along these lines does not reveal any previously known relationships. Both classes include both primitive and advanced taxa, and while class B embraces those sections which have particularly broad leaf-blades (e.g. sects. Poa, Macropoa and Homalopoa) it also includes narrow-leaved sections such as sect. Heptophyllae.

Not all the recent papers touching on leaf anatomy in Poa have been linked to taxonomic studies. Bobrov (1955) describes changes in leaf histology caused by smog in the Los Angeles region of California, USA, and Slade (1970) reports the effect of shade and/or gibberellin treatments on cell elongation in P. alpina. The commissural veins, which are not normally apparent in transverse sections of the leaf, but which are seen readily if the whole leaf-blade is cleared, can be used as markers enabling the mean length of cells to be estimated. While the number of cells between successive commissural veins remains constant, their length varies in response to different treatments.

6.2.1 Terminology

Metcalfe's terminology has been used as the basis for the descriptions which follow (6.2.2). Certain expressions have been given a quantitative basis which is more precise than that used by Metcalfe, and the anatomical features are given a different emphasis; for example, the characters of the bundle-sheath cells were found to have no systematic value, since in every case they consisted of a complete inner sheath and an incomplete outer sheath with larger adaxial cells; they are therefore not mentioned further.

Transverse sections of the leaf blade were taken near the base for comparative purposes; measurements of leaf blade width are thus

taken as maximum values. Flag leaves, and other cauline leaves with special characteristics, were not included although they often vary in width, degree of folding etc. compared with the basal leaves.

Width of leaf blade:

Very narrow	- under 0.5 mm
Narrow	- 0.5 - 2 mm
Moderately broad	- 2 - 5 mm
Broad	- 5 - 12 mm
Very broad	- over 12 mm

Degree of folding of leaf blade:

Flat	- adaxial faces 160° - 180°

(Note: this term is not inconsistent with blades with furrows between the veins, nor does it imply the absence of a keel)

Channelled	- adaxial faces 90° - 160°
Folded	- adaxial faces under 90°, but not parallel with each other
Strongly folded	- faces more or less parallel
Inrolled	- as 'folded', but faces not flat but concave
Convolute	- strongly inrolled, so that the edges meet or overlap.

The term 'bulliform cells' is reserved for those cells of the adaxial epidermis which adjoin the midrib of the blade, i.e. occupying a hinge-cell position. In Poa, these cells do not appear to have a motor function. Other groups of enlarged epidermal cells which resemble the bulliform cells, and which may occur between the vascular strands of the leaf blade, are said to be 'epidermal cells swollen intercostally'.

The terms 'keel' and 'midrib' refer to the protrusions on the abaxial and adaxial surfaces of the blade respectively.

Metcalfe uses the term 'prickle-hairs' for structures defined as "robust sharply but shortly pointed structures with swollen bases",

which makes it clear that this term is identical in meaning with the term 'aculeolus' (pl. 'aculeoli'), which I prefer as in its adjectival form 'aculeolate' it is more concise, and is used in this sense in Flora Europaea. These teeth are found not only on the surfaces and margins of the leaf blade (mainly above vascular bundles), but also on the stem and leaf sheaths, panicle branches, keels of the glumes and lemmas, and particularly along the keels of the paleas.

Vascular bundles are differentiated as 'primary' and 'subsidiary', in order that the ratio of the largest class of bundles to smaller bundles can be expressed. The bundle at the centre of the blade, within the keel and midrib, is not included in this category, since as principal vascular bundle it has features peculiar to itself.

Sclerenchyma bundles are differentiated as 'girders' and 'strands'; the former link the vascular bundles to the epidermis; the latter are attached only to the epidermis.

6.2.2 Sectional descriptions.

In view of the limited range of material studied, the characters described cannot be regarded as essentially diagnostic for every member of the section, but rather as typical of those members of the section which have been studied. As is noted in several of the descriptions, there are considerable internal similarities between the members of a section; unless, as in sect. Oreinos, the external appearance of the leaf blade differs greatly in one species (P. pirinica) from that of the other members of the section, the descriptions are usually essentially the same.

Sect. ABBREVIATAE

Description based on Nannfeldt's account of P. abbreviata.

Leaf blade narrow, strongly folded, with an inconspicuous keel. Vascular bundles few; in addition to the principal bundle, there is

a single primary bundle and two secondary bundles in each limb of the blade (giving a ratio of 1:2). Sclerenchyma present in modest strands within the keel and margins; the primary bundles have a strand, flattened into a ribbon, abaxially and a few cells adaxially. Leaf surfaces are rather smooth; the epidermal cells are apparently highly cuticularized, especially abaxially (an adaptation to be expected in a high-arctic species). The bulliform cells form a narrow zone.

Sect. BOLBOPHORUM

The range of habitats occupied by the members of this section being particularly wide, there is a correspondingly large degree of anatomical variability. Features common to all members of the group include: the margin of the leaf often appears cartilaginous, owing to the thickness of the submarginal sclerenchyma strands; there are relatively large zones of bulliform cells, often visible as 'tram-lines' on the adaxial surface in fresh material; the strands of sclerenchyma above and below the vascular bundles do not connect them to the epidermis; and the keel is rounded, and contains a relatively large strand of sclerenchyma, by contrast with the midrib which is usually indistinct and with little or no sclerenchyma.

The leaf blade ranges in width from narrow to moderately broad, and may be flat, channelled or folded. The keel is rounded, is wide in relation to its depth, and has a large strand of sclerenchyma.

The ratio of lateral bundles is usually 1:1, except in the species with the narrowest leaves such as P. bulbosa in which it approaches 1:2. Sclerenchyma is well developed, especially abaxially, and takes the form of lenticular strands lying just below the epidermis. The rounded margins of the blade are provided with a thick layer of sclerenchyma.

The epidermis consists of rather large cells. The bulliform cells

are well-developed, but not indented, and consist of cells which are ovate to elongate-pyriform in outline.

Sect. CENISIA

This section has been little studied anatomically. Living material of P. cenisia was not available, since although seed was obtained and grown it proved to have been wrongly named.

The range of size of the leaf blade is similar to that of sect. Poa; the blade is moderately broad (except in P. angustifolia) in both sections, flat or channelled. Poyarkova (1965) describes the keel of P. granitica as triangular, since its outline resembles a triangle but has a rounded apex. Her illustration omits the lateral portions of the blade; the keel has a moderate bundle of sclerenchyma and well-developed bulliform cells, the middle cells having a more or less oblong outline shape.

Sect. COENOPOA

The leaf blade is moderately broad, flat to channelled. The keel is pronounced, with a well-developed bundle of sclerenchyma. The ratio of lateral bundles is in the range from 1:3 to 1:4. The bundles have abaxial and adaxial strands of sclerenchyma. The abaxial strands tend to project a little from the surface, whereas the adaxial strands to not project. Both surfaces are smooth. The acutely tapered margin is rounded at the extreme apex. The epidermal cells of the adaxial surface are small and regular. Those of the abaxial surface are swollen intercostally. The bulliform cells are small and more or less isodiametric.

Sect. HOMALOPOA

The anatomical structure of the leaf blade in this section is very similar to that of sect. Macropoa. Both sections are characterized by the presence of heavy abaxial girders of sclerenchyma of trapezoidal or oblong outline associated with the primary veins.

The principal features of sect. Homalopoa of diagnostic value are the pronounced keel, the very well-developed bulliform cells, and the tapering section of the margin of the blade, which terminates in an acute apex.

The leaf blade is broad to very broad, and may be flat, channelled or folded. The keel is prominent, and comes to an acute apex. It contains a rather small strand of sclerenchyma; the midrib lacks sclerenchyma.

The ratio of lateral bundles varies from around 1:3 to 1:4. The smaller secondary veins are only sparsely provided with strands of sclerenchyma, which may become enlarged into girders on the abaxial sides of the larger veins. The primary veins have heavy girders of abaxial sclerenchyma, the girders having an oblong to triangular outline. There is also a slender adaxial strand. The surfaces of the leaf blade are more or less flat, though the adaxial surface may be slightly furrowed above the veins. The margins, as mentioned above, are acute.

The epidermal cells are of medium size. The bulliform cells are large, with an elongate oblong outline. In one preparation of P. chaixii the left-hand and right-hand zones of cells joined across the centre of the midrib.

Sect. LEPTOPHYLLAE

The distinctive leaf anatomical structure of P. stiriaca provides strong support for the view that its earlier inclusion in sect. Poa was erroneous. Mecenović (1939) stated the traditional view of the systematic position of P. stiriaca, and illustrated the leaf anatomy. He appears to have been insufficiently aware of the anatomical characteristics of sect. Poa, however, and perhaps placed undue emphasis on the supposedly rhizomatous growth-form of P. stiriaca.

The leaf blade is very narrow, but not disproportionately thick

in relation to its length. The blade is strongly folded, so that the adaxial surfaces almost meet. The outline of the abaxial surface is that of a smooth, almost elliptical, curve; the bulliform cells are sunken and the midrib is strongly convex, but there is no distinct keel.

Since the veins in the middle portion of each limb of the blade are at least as large as the vein under the midrib, no comparison is possible in the normal way of the ratio of primary and subsidiary veins: see fig. 8 . The sclerenchyma is very well developed. There is a reniform strand of sclerenchyma in the position normally associated with the keel, while the midrib lacks sclerenchyma. The principal lateral veins have proportionately smaller abaxial trapezoidal girders, and small adaxial girders of more or less oblong outline. The secondary veins lack sclerenchyma. The margins of the blade have an outline similar to the prow of a boat, and contain a thick U-shaped strand of sclerenchyma.

The more or less flat adaxial surfaces exhibit the peculiar indumentum characteristic of a number of southern hemisphere species of Poa (Vickery, 1970), but unknown in other European species of Poa. The hairs are rather stiff, with slightly rounded tips, and arise intercostally from the epidermis. Aculeoli, by contrast, almost always occur only above the veins. Similar hairs, with acute tips, are observed on the adaxial leaf surface of P. colensoi from New Zealand; see fig. 9. Fig. 10 gives a comparable drawing of P. stiriaca.

The bulliform cells are small and more or less isodiametric, differing little from the other cells of the adaxial epidermis. They are recessed in a deep groove which allows the blade to adopt its strongly folded shape.

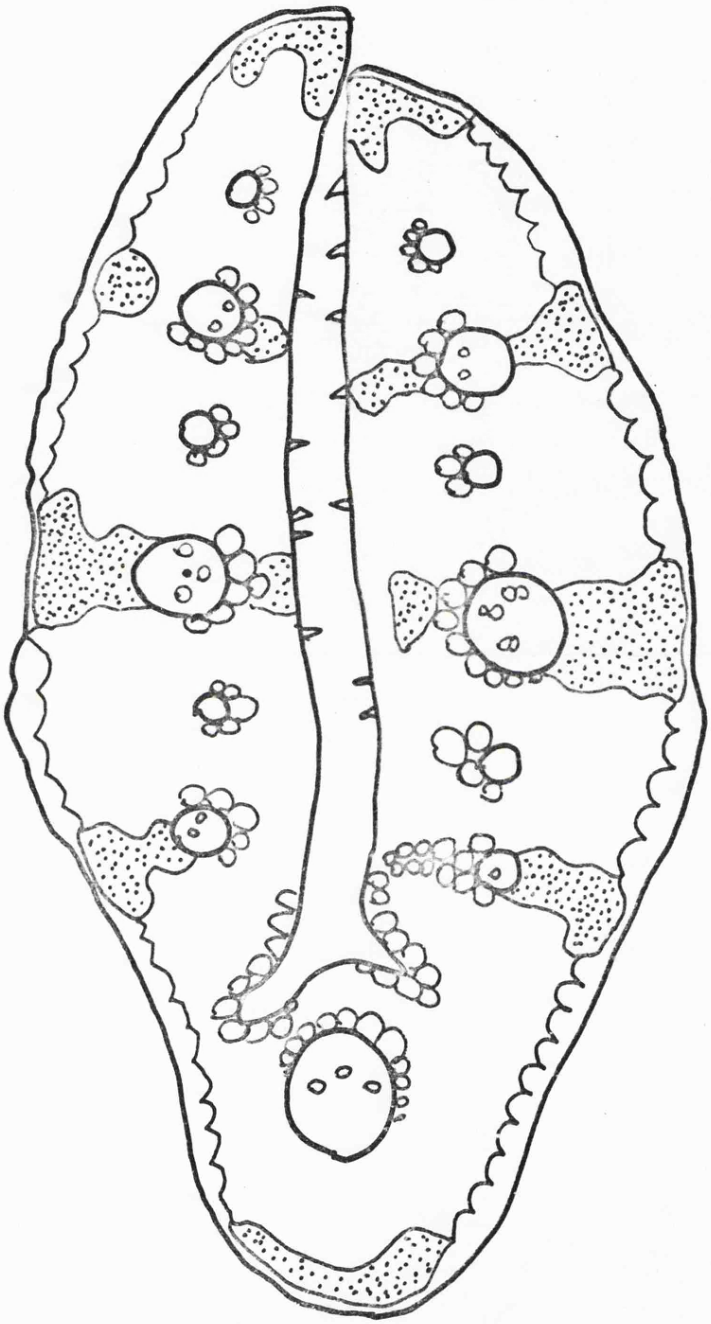


FIG. 8. Transverse section of leaf blade of Poa stiriaca.

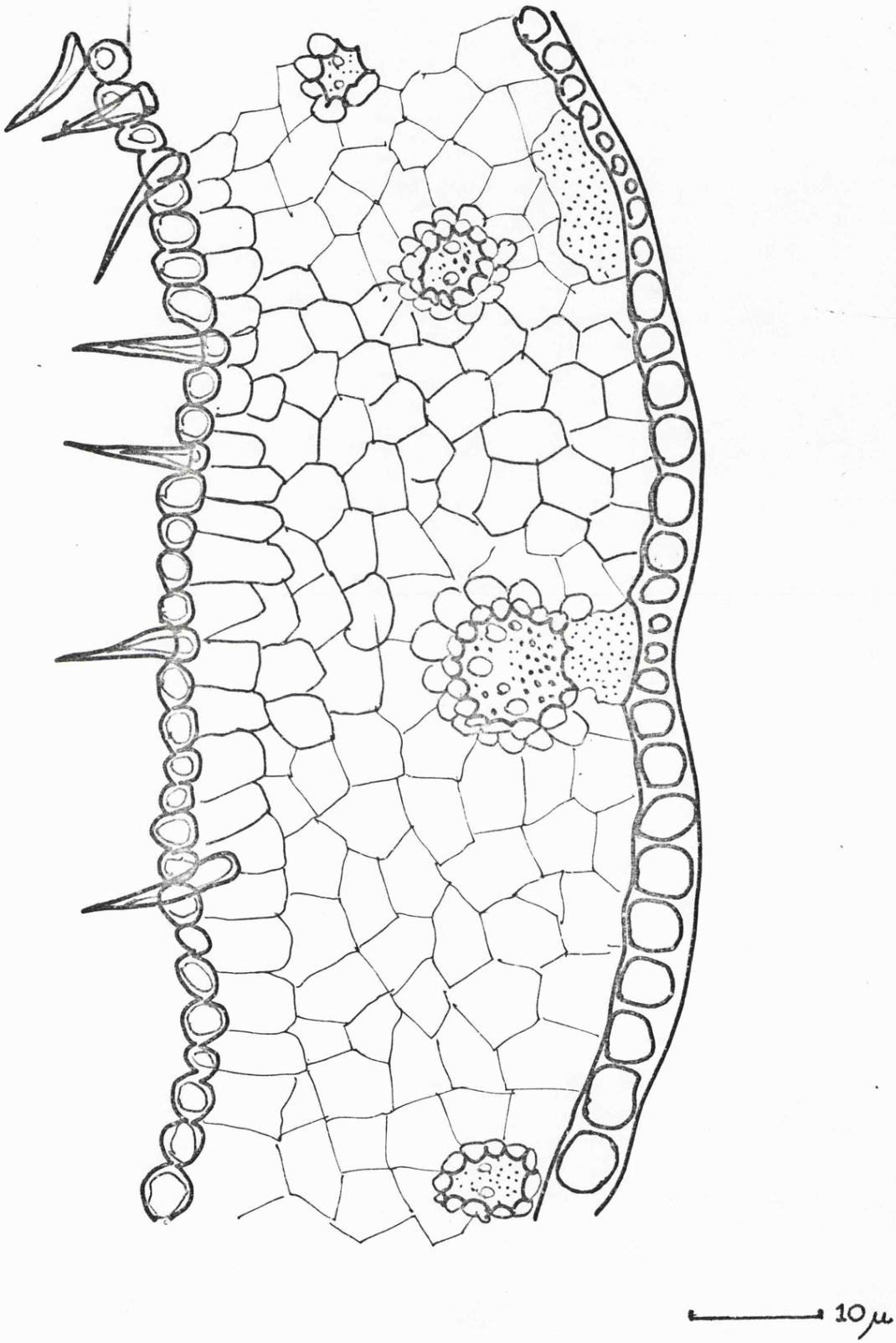


FIG. 9. Anatomy of leaf blade of Poa colensoi.

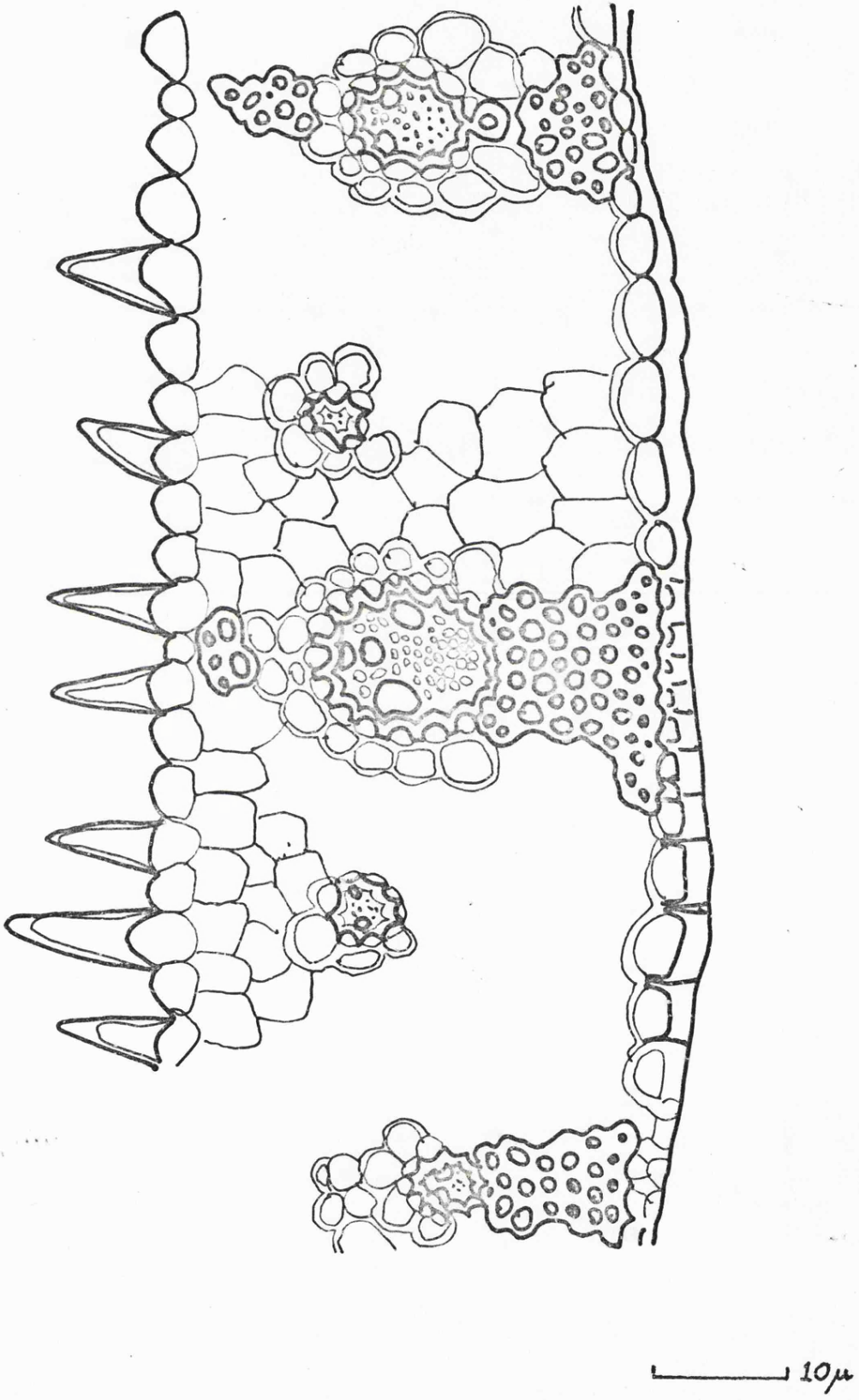


FIG. 10. Anatomy of leaf blade of Poa stiriaca.

Sect. MACROPOA

Two subspecies of P. longifolia, with slightly different anatomical features, are described by Lohauss (1905) and Smirnov (1965). Their data has been supplemented by my own observations on P. sibirica.

The section as a whole has a distinctive anatomical structure, due to the considerable development of abaxial girders of sclerenchyma, trapezoidal in section, linking the larger bundles to the epidermis. In this feature it resembles sect. Homalopoa, which can however be distinguished on anatomical grounds by its much more sharply pointed keel.

The leaf blade is moderately broad, flat to channelled, with a rounded keel and midrib. There is little or no sclerenchyma within the midrib, and the principal vein is connected to a trapezoidal girder of sclerenchyma within the keel.

The ratio of lateral bundles is 1:1, with smaller subsidiary bundles almost entirely absent. The bundles are linked to the abaxial epidermis by trapezoidal girders of sclerenchyma. The adaxial epidermis has a strand of sclerenchyma of circular to oblong cross-section connecting the surface to a line of colourless cells with a similar appearance to those of the outer bundle sheath.

Smirnov suggests that these linking cells may be water-conducting; this would seem to be unlikely, except perhaps by simple diffusion.

The epidermal cells are small, with a relatively thick wall on the outside surface. The bulliform cells are elongate-ovoid in outline, forming a rather narrow though deep zone. The abaxial surface is also grooved at points opposite the bulliform cells, accentuating the 'waist' between the limbs of the blade and its middle portion.

The anatomical structure of P. longifolia subsp. fagetorum differs in certain ways from the generalized description given above.

The principal difference is that it has more or less equal girders of sclerenchyma on both abaxial and adaxial surfaces. The leaf blade is thinner, without an air space in the mesophyll, and is folded rather than channelled.

Sect. OCHLOPOA

The leaf blade is narrow to moderately broad, and is flat. The keel is prominent, subacute to rounded, projecting as a rather narrow ridge, and has a small strand of sclerenchyma. The midrib is flat, and lacks sclerenchyma.

Small strands of sclerenchyma are present adaxially and abaxially, adjacent to the primary bundles. The secondary bundles generally lack sclerenchyma. The ratio of lateral bundles is approximately 1:3.

Both surfaces are more or less smooth and flat; the epidermal cells are quite large. The bulliform cells are few, isodiametric in shape, and form a narrow band on each side of the midrib. The margin of the leaf blade is obtuse, and contains a very small strand of sclerenchyma.

Sect. OREINOS

I have not found it possible to study leaf sections in members of this section, owing to lack of living material and the difficulty of reconstituting dried specimens. The following description is based on the accounts of P. minor and P. laxa in Buschmann (1942), Lohauss (1905) and Nannfeldt (1935).

The leaf blade is thin, narrow or very narrow, and is more or less inrolled. The keel is not large, but is rounded and projecting, whereas the midrib is flat. The principal vein is only sparsely provided with sclerenchyma strands; in P. minor they occur only abaxially, while in P. laxa the strands occur on both surfaces.

The ratio of lateral bundles approaches 1:1; the details of the drawings are insufficient to allow a precise figure to be obtained.

The sclerenchyma occurs as thin strands above and below the primary veins in both species. The limbs of the blade are thin, and taper to a rounded margin containing a thin strand of sclerenchyma.

The adaxial surface is more or less flat; the abaxial surface bulges slightly around the primary veins. The epidermis consists mainly of small isodiametric cells, but in P. laxa they become a little swollen intercostally. The bulliform cells are quite large in the middle of the zone, and range from isodiametric to elongate in outline.

Sect. POA

With the exception of P. angustifolia, the members of this section have moderately broad leaf blades, channelled, with a modest rounded keel. The adaxial and abaxial surfaces are more or less flat, but the adaxial surface may be furrowed above the larger veins.

The ratio of lateral bundles ranges from 1:1 to 1:3. The sclerenchyma is very well developed, linking the adaxial and abaxial surfaces to all but the smallest subsidiary veins with I-shaped girders which are especially thick on the abaxial surface. The strand of sclerenchyma in the keel does not, however, connect with the principal vein. The margin is obtuse, and contains a substantial sclerenchyma strand.

The epidermal cells are moderately large and isodiametric. Those above the zone of sclerenchyma adjacent to the lateral veins are, however, considerably smaller. The bulliform cells are prominent, those in the middle of the zone having a pear-shaped outline.

The anatomical structure of P. angustifolia differs quantitatively rather than qualitatively from the above description. The leaf-blade is much narrower, channelled to folded, but with a similarly small keel. The leaf surfaces are nearly flat; the ratio of lateral bundles

is approximately 1:2. The sclerenchyma is well-developed, especially abaxially, with girders linking the veins to both surfaces; the margins of the blade are obtuse. The epidermal cells are of moderate size. The bulliform cells, while well-developed, tend to occupy a narrower zone; the middle cells are again pear-shaped in outline. These quantitative differences are to be expected in a relatively xerophilic member of a predominantly mesophilic section.

Sect. STENOPOA

Though this section is one of the two largest sections of Poa in Europe, with nine species, the anatomical differences between the species are very minor. All have rather thin, narrow leaves, which are usually flat to channelled or sometimes inrolled; all have quite prominent rounded keels. The keel is narrow in relation to its height, except in P. nemoralis where it is rather less slender. Bundles of sclerenchyma occupy both midrib and keel, the midrib having a particularly large strand or girder in P. sterilis; most species have girders of sclerenchyma, but P. flaccidula is notable for its strands. The ratio of lateral bundles varies between 1:1 and 1:2. Sclerenchyma is quite well developed on both sides, the primary veins being associated with girders, usually of lenticular outline, and the secondary veins having strands both above and below. Owing to the relatively large size of the vascular bundles in relation to the total thickness of the leaf blade, the relative quantity of sclerenchyma is however less than in other sections with sclerenchyma girders such as sect. Homalopoa. The abaxial surface may be flat, e.g. in P. flaccidula, or ridged, e.g. P. sterilis. The adaxial surface is generally more undulate, raised (and usually aculeolate) above the veins and grooved between them. The blade terminates abruptly in a rounded margin containing a small strand of sclerenchyma.

The epidermal cells are generally of medium size, but are usually

interrupted above and below the veins. The bulliform cells form a rather narrow zone and are scarcely indented (except in P. sterilis, where they occupy a distinct groove).

Sect. TICHOPOA

The leaf anatomy of P. compressa is similar to that which is found in sect. Stenopoa, to which this section is quite closely allied. The anatomy of a putative intersectional hybrid - P. x taurica - is described in Poyarkova (1966), but since it does not help to characterize the sections from which its parents are drawn, it has been omitted from the account.

The leaf blade is moderately broad, flat to channelled, with a prominent, obtuse, keel. The midrib is slightly convex. The ratio of lateral bundles ranges from 1:2 to 1:3. The sclerenchyma is rather poorly developed, except for a rather substantial strand in the keel. Only a few strands approach the veins on the adaxial side; there is a larger quantity of sclerenchyma abaxially, with girders forming narrow pillars connected to the veins. The surfaces are more or less flat and smooth on both sides. The leaf margin is obtuse, and contains a small triangular strand of sclerenchyma. The epidermal cells are relatively large, with the walls of those on the abaxial surface somewhat thickened. The bulliform cells occupy a deep U-shaped channel, and are more or less ovate in outline.

6.3 Epidermal characteristics.

Epidermal characters mentioned above are those which are evident in transverse section. Further features are revealed by epidermal strips; these failed to provide any additional characters for the sectional descriptions.

A generalized description of the epidermis in Poa is given below. Various problems stand in the way of achieving useful results from

epidermal strips. One must take account of the differences between the adaxial and abaxial surfaces, and between the parts of the epidermis which are above and between the veins; the tendency of short-cells, prickles and stomata to replace one another must be allowed for; and some means of quantifying such characters as the degree of sinuosity of the longitudinal walls of the long-cells must be found.

For this reason, only a generalized description of the epidermis is practicable. The unspecialized cells of the epidermis are of two basic types: short-cells and long-cells. The two types usually alternate in longitudinal rows or 'files'. In general the cells become specialized in different ways according to whether the row of cells is supracostal or intercostal.

Over the vascular bundles, the epidermal cells are differentiated in three ways. Stomata are absent from this region; the long-cells become narrower, but are not significantly reduced in length; and the short-cells are transformed either into aculeoli (prickles) or into pairs of silica-cells and cork-cells. The region also usually contains silica bodies which are longitudinally elongate and have sinuate outlines, or occasionally are dumb-bell shaped (Blackman, 1971, p. 773, fig. 12).

Between the vascular bundles, undifferentiated short-cells are much rarer. They are normally transformed into stomata, with either dome-shaped or parallel-sided subsidiary cells. Paired silica-cells and cork-cells are also found, together with incompletely differentiated versions of these cells. Micro-hairs are generally absent from European species of Poa, but the hairs on the adaxial intercostal surface of the leaf of P. stiriaca form the one exception to this rule.

6.4 Stem anatomy.

Metcalfe's pessimistic remarks on the usefulness of anatomical characters of the stem (1960, pp. xxxi - xxxii) apply very aptly

to the situation in Poa. The difficulties of making a comparison between the anatomical structure at different levels of the stem, as well as of comparing different species and sections, are so great that they render the characters almost useless. Only the non-anatomical features of the stem, such as the compressed stem of sect. Tichopoa, and the tendency of the stem to become scabrid towards the apex in sect. Stenopoa, are of practical diagnostic value.

There does appear to be a correlation between the increase in scabridity towards the stem apex in sect. Stenopoa, and the fusion of the bands of sclerenchyma into a single continuous zone which encloses lenticular strands of chlorenchyma. This tendency is illustrated in sections taken at various levels of the stem of P. glauca (fig. 11). The changes in the distribution of vascular bundles are relatively minor; subsidiary bundles tend to disappear towards the apex. The chlorenchymatous layer also becomes thinner upwards, before becoming broken up into discrete lenticular strands. The central cylinder of parenchyma tends to become larger in proportion to the total thickness of the stem as the apex is approached.

Differences between P. glauca and P. nemoralis are of three types:

	P. glauca	P. nemoralis
a) outline shape	angular towards apex	terete along whole length
b) secondary v.b.s	accompanied by many sclerenchyma strands	accompanied by few or no sclerenchyma strands
c) main scl. girders	indented	not or slightly indented.

The illustrations of sections of the culm in Konstantinova (1960) and Şerbănescu (1969) are of little value, since the height at which they are made is not specified. The following conclusions have been arrived at: the illustration of the stem section of P. sterilis (Konstantinova) was probably cut at a low level, since the chlorenchyma

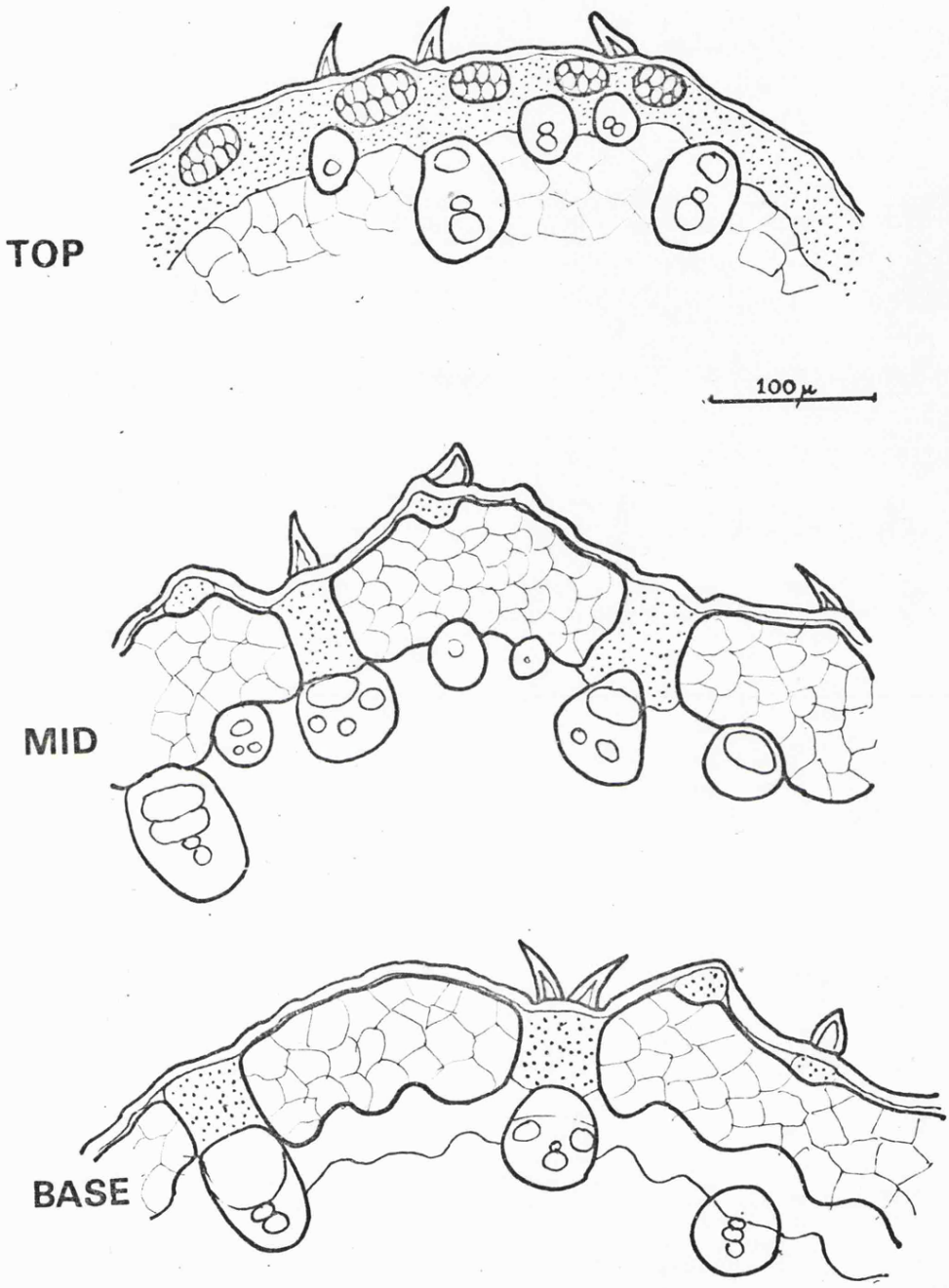
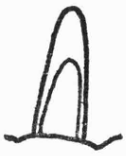


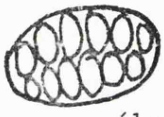
Fig.11. Anatomical structure of the stem of Poa glauca – transverse sections taken at various levels.

Epidermis

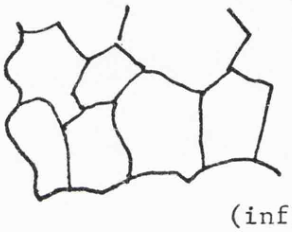


Blunt-tipped prickle-hair (P. stiriaca)

Aculeoli (acute-tipped prickle-hairs)

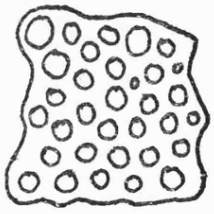


Chlorenchyma (lenticular strands)



Chlorenchyma (infilling or mesophyll)

Sclerenchyma



Sclerenchyma

Vascular bundle

Inner and outer bundle-sheath

KEY to figures 8, 9, 10 & 11.

is shown in discrete lenticular strands. A comparison of the illustration of the stem anatomy of P. palustris (Şerbănescu) with the sections of the stem of P. glauca (fig.11) suggests that in P. palustris the lenticular strands of chlorenchyma become exposed towards the surface before merging laterally. The illustrations of P. trivialis and P. silvicola (= P. trivialis subsp. silvicola) appear to show that the primary vascular bundles are more deeply sunk into the central parenchymatous cylinder in the former subspecies. Another paper by Şerbănescu (1968) illustrates transverse sections of the stems of P. sterilis and P. stepposa (= P. relaxa). It would seem that P. sterilis has rather wider bands of chlorenchyma in the upper part of the stem, whereas P. relaxa has a larger number of separate bands of chlorenchyma.

6.5 Root anatomy.

The type of wall thickening of the endodermal cells of the root is of systematic value. This surprisingly cryptic character was explored by Chrtek & Jirásek (1965a), who found that the distribution of the different types of thickening came close to agreeing with the sectional divisions of the genus. Since their data were not taken into account by me until I had already revised the classification of the group, this agreement is all the more striking.

Other grass genera were also investigated by Chrtek & Jirásek. The genus Festuca shows U-shaped thickening throughout. Buschmann's opinion that Bellardiochloa should be included in Poa (Buschmann, 1952) is not supported by the evidence of the root endodermal cell thickening (Friendenfelt, 1904; Coutzen, 1906), since it also has U-shaped thickening. Table 6.3 sets out the four types of thickening which are observed in Poa. It has not been possible to add to this information.

TABLE 6.3 Types of root endodermal cell thickening.

(i) Cells U-thickened:	Sect. OREINOS (*P. laxa*)
(ii) Cells O-thickened:	Sect. OCHLOPOA (*P. annua*, *P. supina*)
	Sect. POA (*P. pratensis*)
	Sect. STENOPOA (*P. nemoralis*, *P. glauca*, *P. palustris*, *P. sterilis*)
	Sect. TICHOPOA (*P. compressa*)
(iii) Cells radially elongate:	
	Sect. HOMALOPOA (*P. chaixii*, *P. remota*)
(iv) Cells intermediate between U- and O-thickened:	
	Sect. BOLBOPHORUM (*P. alpina*, *P. badensis*, *P. bulbosa*, *P. molineri*)
	Sect. CENISIA (*P. cenisia*)

The results of the study of root endodermal cell thickening allow two main conclusions to be drawn. Firstly, sect. Homalopoa and sect. Oreinos, already regarded as taxonomically rather isolated from the other European sections of Poa, each have a well-defined type of thickening. In view of the fact that sect. Homalopoa is generally regarded as quite closely related to sect. Macropoa, the members of which (P. sibirica, P. longifolia) were not studied by Chrtek & Jirásek, an investigation of these species would be interesting. Secondly, the sections with O-shaped thickening mostly have a lowland distribution in Europe; those with the intermediate type are largely distributed in montane habitats. An ecological correspondance is therefore suggested.

6.6 Anatomical evidence in relation to classification.

Anatomical characters are not normally employed in keys for the identification of species or other groups, since specialized preparative procedures are needed to reveal them. There are a few exceptions to this statement in the floristic literature; for example, Ghişa & Beldie (1972) in volume XII of the Flora of Romania refer to the size of the lumen in sclerenchyma cells in the members of sect. Bolbophorum. Buschmann (1942) refers to the width of the 'cartilaginous margin' of the members of the same group's leaves; this character is the same as the width of the marginal band of sclerenchyma revealed in transverse sections.

There is agreement between the distribution of a number of anatomical characters and the sectional divisions of the genus, which demonstrates that anatomical variation occurs in parallel with morphological variation. The anatomical features of the species studied are sufficiently varied to allow the use of these characters in allocating non-European species to European

sections, but since not all species occurring in Europe have been studied anatomically up to the present time, the account of anatomical features found to date may need to be modified to take account of these species. Further work also needs to be done on the anatomically unknown or less-known groups: sect. Oreinos, sect. Genisia and sect. Nanopoa in particular. Where subsectional divisions may offer themselves, particularly in the larger sections such as sect. Stenopoa, anatomical characters may help to define them. Finally, the anatomical characters of the panicle and spikelet parts offers a completely untouched field of potentially useful taxonomic characters.

CHAPTER 7. Evaluation of taxonomic characters within part of section Stenopoa.

7.1 Purpose of studying the 'P. sterilis group' in detail.

Sect. Stenopoa is one of the two largest sections of Poa in Europe, and probably contains the greatest number of species on a world-wide basis compared to sect. Bolbophorum (with an equal number of species in Europe) or to any other non-European groupings.

Sections, like taxa of other rank, vary in the characters used to define them; variation in the species of which they are made up is equally an attribute of the sections to which they belong. In the classification of sect. Stenopoa, we therefore come across a problem which is analogous to the problems posed by a highly variable species. As in the case of such a species, where the choice of different infraspecific categories is influenced by the type of variation encountered, there is a similar range of 'infra-sectional' categories - subsections, series, and species - from which the taxonomist may choose the rank appropriate to the variation within the section. The group of species associated with P. sterilis lends itself to such a study, where the distribution of all the potentially useful characters can be evaluated.

During my revision of the European Poae, one of the most tricky problems was the naming of material from SE Europe which came under the general name of P. sterilis. The initial purpose of this study was thus to reconcile conflicting treatments in the different Floras; to test the characters used for distinguishing the various taxa; and then to identify the available material. The work provided an insight into the variability of some of the characters used, and if the results of the study are rather negative, this only points out the inadequacies of an orthodox approach to the study of such groups.

7.2 Systematic and nomenclatural survey.

In 1753, Linnaeus described P. nemoralis, and in 1759 his Systema Naturae contained the description of a related species, P. palustris. This pair of species formed the basis of sect. Stenopoa Dumortier (1823), although another species now included in this section had been described earlier: P. glauca Vahl (1790).

The date of discovery of the P. sterilis group can be taken as 1808, when F.A.M. von Bieberstein described P. sterilis in his Flora taurico-caucasica. The presence of similar forms in dry sub-Mediterranean habitats in the coastal areas of Ukraine was recognized only recently. The next species to be named was Besser's P. versicolor from upper Podolia, "prope Jaorlik". This locality cannot be traced; the type material was collected by D. Andrzeiowski, part of whose herbarium came to rest in herb. Kiev (KW). Enquiries made to that herbarium failed to locate the type material of P. versicolor, the exact identity of which is crucial to the nomenclature of the western members of the group.

Later accounts of members of the P. sterilis group can be divided into two main parts: accounts of the flora of central Asia* (by Russian authors) and of south-west Asia (by N.L. Bor); and floristic accounts of various territories in south-east Europe, e.g. Kit. in Steudel (1941), Kerner (1864), Błocki (1865, 1887), Ascherson & Graebner (1900).

The work on the grasses of south-west and Central Asia* has largely been undertaken as part of the preparation of a Flora; for this reason, there is no single taxonomic treatment covering the whole area of distribution of the group (from the Pamir and Altai

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*Note: "Central Asia" is used here to mean Soviet Central Asia, i.e. srednii Aziya (lit. "middle Asia").

mountains in the east to Anatolia and Iran in the south-west and the southern Ural mountains in the north-west). Flora SSSR vol. 2, 1934, in which the account of Poa was prepared by R. Yu. Rozhevits, is very unsatisfactory since its descriptions are extremely sketchy and uncritical, and its key does not work. The most satisfactory modern accounts are those of Bor (1970) and Tsvelev (1968).

Following the early discoveries in south-east Europe, plants similar to those described from the Caucasus mts. and from Krym sub P. sterilis were collected in the Transcaucasus mts. of what is now part of eastern Turkey. Trautvetter named these P. araratica. The two species have since been greatly confused, and though both species are stated by Bor (1970) to extend from Turkey to Kashmir, my impression of material under these two names is that plants from Turkey, Iran and Afghanistan form a single polymorphic complex and P. araratica is much more restricted in its distribution: mt. Ararat (now called Ağri Dağ) and Suphan Dağ. Neither matches the material from the northern Caucasus and Krym (true P. sterilis); a new name therefore appears to be required for the widespread taxon in the Anatolian-Iranian-Afghan-Kashmir region. It has not proved possible to locate such a name, since first the material from central Asia must be included in the study.

P. attenuata, another species closely related to this group, was described in 1835 by Trinius from plants collected in the Altai mts. Its limits are not agreed upon; Tsvelev (1968) gives its distribution as extending from Dzhungaria and western Siberia to Sinkiang, northern Mongolia and China, with P. dahurica Trin. and P. botryoides Trin. in synonymy. An earlier revision of the same group (Pazii, 1962) came to the conclusion that much of the material named as P. attenuata from central Asia was in fact to be regarded as P. litwinowiana Ovcz. and P. relaxa Ovcz. Further

difficulties are encountered owing to errors in the typification of P. litwinowiana Ovcz; it appears (Tsvelev, 1968) that the type of P. albertii Regel is now regarded as identical with the material later described as P. litwinowiana; P. albertii therefore becomes the correct name for this group.

Evidently much of the nomenclatural fluidity results from differing interpretations of the degree of variability of the taxa of the P. sterilis group. Typification of the original names clearly becomes important.

The nomenclatural history of the south-east European members of the P. sterilis group has suffered from similar problems: misidentification of material, differing interpretations of the distribution of taxa, and an inadequate appreciation of the variability of the group (and the plasticity of phenotypes). In addition, the tendency of collectors to specialize in certain well-known localities has led to a concentration of specimens from these sites in all the main European herbaria.

My treatment recognizes five taxa from Europe; of these, four are treated as species, and one species is divided into two subspecies. These are: P. sterilis (Krym, Caucasus); P. relaxa (syn.: P. stepposa (Kryl.) Rozhev.); P. versicolor Bess.; and P. pannonica Kern., subsp. pannonica and subsp. scabra (Kit.) Soó. The distribution of the two subspecies of P. pannonica is not yet fully worked out, as neither records from Floras, nor the distributions given in various papers (e.g. Şerbănescu, 1968; Dihoru, 1968) can be relied upon. Specimens which I have examined from various herbaria, particularly those at BM, BR, E and K, have permitted me to draw up a tentative distribution map of the taxa which occur outside the USSR: see map 7.1 (p. 206).

7.3 Comparison of published treatments of the P. sterilis group with the system adopted for Flora Europaea.

Ascherson & Graebner (1900) recognize four main subdivisions of the 'group species' P. sterilis which are in broad agreement with my treatment regarding the delimitation of the taxa, but which differ over the choice of rank. Table 7.1 lists the equivalents, along with the synonyms cited by Ascherson & Graebner. Their treatment is least satisfactory where it confuses P. scabra Kit. with P. sterilis Bieb.; nevertheless the measure of agreement between the two treatments is quite large. By first equating P. scabra and P. sterilis and then realising that Crimean material does not match material from Hungary and Romania, Ascherson & Graebner turn a complete circle; it is surprising that Poyarkova (1965) should regard P. biebersteinii as worthy of specific rank, in view of its history as a 'subspecies of a subspecies'.

The great variability shown by P. sterilis in the Crimea was recognized by Prokudin (in Vul'f, 1951) in a note under that species in Flora Kryma vol. 1 (part 4):

"P. sterilis Bieb. Distribution: Crimean-Caucasian Endemic species. Crimean material of this species appears heterogeneous. Considerable variation in separate characters was observed. Thus, besides specimens in which the stem is scabrid along its whole length, one encounters specimens with almost smooth culms. The width of the leaves and the degree of divergence of them from the stem is also very variable. One can observe differences in the pubescence of the rhachilla (from thickly pilose to almost glabrous). In a series of specimens a pronounced united tuft of hair was observed at the base of the lemma (in typical specimens of P. sterilis the lemma lacks a woolly tuft of hairs at the base) and some other variation of

characters occurs. It is interesting to note that above all, the bulk of the specimens with characters different from those of the typical P. sterilis occur on limestone in mountain pastures. On the whole one can distinguish specimens from yaylas* in the south through lesser scabridity of the culm, broader leaves, an almost glabrous rhachilla, clumps of wool at the base of the lemma, and certain other characters."

I have examined a sheet of P. sterilis which appears to bear a label in Bieberstein's hand, and which may therefore be a co-type or isotype (herb. CGE) with the following characters: the culm is scarcely scabrid; the panicle attains 5.5 cm in length; the panicle branches are in pairs (to three together at most); and the spikelets are relatively wide at the middle, with 2 (-3) florets. As in the original description, there is little or no ligule. In habit the plant resembles specimens of P. versicolor from Romania (Dobrogea) under the name P. romanica Prodan, which is of short stature and has numerous cauline leaves.

It appears from the additional material of P. sterilis which I have examined, that the 'type (?) specimen' is not typical of Crimean populations of this species. For possible clarification, I turned to Grossheim's Flora Kavkaza (1928), ed. 2, vol. 1, p. 254; The characters used to separate P. sterilis (in the northern Ciscaucasus) from P. araratica (in the southern Transcaucasus) are as follows:

Dichotomy 18 of key:

18. Panicle short, 3 - 5 cm long, 5 - 10 mm wide, strongly compressed. Spikelets 5 mm long, not widening towards the apex

..... 16. P. araratica

--. Panicle 6 - 14 cm long, scarcely compressed. Spikelets

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*Note: 'yayla' = upland, usually summer, pasture; a Turkish word.

TABLE 7.1 Ascherson & Graebner's treatment of the P. sterilis group.

P. sterilis Bieb. - "ligule elongate, acute"

A. (?subsp.?) eusterilis A. & Gr. = P. pannonica subsp. scabra (Kit.) Soó

(a)- 'race' scabra (Kit.) A. & Gr. = " " "

B. (?subsp.?) Biebersteinii A. & Gr.= P. sterilis Bieb.

syn.: P. aspera Pall. non Gaud. syn.: P. biebersteinii (A. & Gr.) Poyark.

C. (?subsp.?) pannonica (Kern.) A. & Gr. = P. pannonica subsp. pannonica

syn.: P. pannonica Kern.
P. podolica Błocki

D. (?subsp.?) versicolor (Bess.) A. & Gr. = P. versicolor Bess.

syn.: P. versicolor Bess.
P. rupestris Bieb. ex C.A. Meyer
P. sterilis (b) versicolor (Bess.) Richter

5 - 6 mm long, widening towards the apex .....P. sterilis. The openness of the spikelet, i.e. whether or not it widens towards the apex, is bound to be associated with anthesis, and no reliance can therefore be placed on such a character. Whether or not the panicle is strongly compressed is unlikely to be visible in a pressed specimen; the tendency for paired panicle-branches to alternate at 180° to one another is in any case noticeable in species with short, stiff panicle branches. Taxonomic characters affording a separation between the two species must evidently be sought in the vegetative features of the plant, as emphasized by Bor (1948, pp. 63 - 64). I concluded that the description of P. sterilis provided by the original author, and the diagnosis in Flora Kavkaza, are insufficient as a basis for deciding whether the P. sterilis group in the Crimea and the Caucasus should be treated as one, two or three species.

Hayek (1932) recognizes two species in the Balkan peninsula: P. pannonica and P. sterilis. Table 7.2, which extracts the descriptions of the two species as circumscribed by Hayek, is presented in the original Latin in order not to detract from the precision of the original language. If the two descriptions seem remarkably similar, this should not be surprising if it is accepted that both are based on material which I refer to P. versicolor. P. versicolor does not appear anywhere in Hayek's Prodromus, either as a synonym of an accepted species or in the index. In overlooking this species, it appears that Hayek has referred material to two different species on the basis of the number of panicle branches at each of the pseudowhorls of the panicle (the character used in the synoptic key). This has led to much later confusion among collectors attempting to name their material using Hayek's key.

TABLE 7.2 Comparison of descriptions of P. sterilis and P. pannonica sensu Hayek.

P. PANNONICA	P. STERILIS
Perennes, caespitosa, interdum stolonifera	Perennes, caespitosa, saepe stolonifera
Culmi erecti, ad 40 cm alti, scabriusculi	Culmi erecti, rigiduli, ad 40 cm alti, scabriusculi
Folia anguste linearia 1 - 2 mm lata, cum vaginis scabriuscula, supremum vagina sua brevius	Folia anguste linearia 1 - 2 mm lata, cum vaginis scabrida, supremum vagina sua parum brevius vel sublongius
Ligula elongata, acuta	Ligula elongata
Panicula diffusa, multispiculata, ramis elongatis erectopatulis infimis subquinis	Panicula oblonga, densa, multispiculata, ramis scabridis erectis infimis plerumque binis
Spiculae ovato-lanceolatae, 3 - 4 florae	Spiculae ovato-lanceolata, 3 - 4 florae
Glumae lanceolatae, acutae, 4 mm longae	Glumae lanceolatae, acutae, 3 - 4 mm longae
Glumella lanceolata acuta, viridis	Glumella lanceolata, acuta, viridis, ante marginem scariosum saepe linea violascente notata, carina et margine sparse pilosa.
In subalpinis	In subalpinis
Epirus.	Macedonia.

In addition to the single record of Hayek's from Epirus, various other gatherings from the southern part of the Balkan peninsula can be matched to P. versicolor:

Al: Alston & Sandwith no. 2706 (herb. BM);

Gr: Sintenis & Bornmüller no. 953 (1891); Hagion Oros, mt. Athos (Herb. E);

Ju: Edmondson no. 182; Šar Planina above Tetovo (Herb. LTR); McCallum Webster nos. 4056a and 4069a (herb. BM).

The critical part of the original description refers to a large patent-nodding ("subnutans") panicle, violet variegation of the spikelet, and finely scabrid stems and leaf sheaths. These characters enable P. pannonica to be distinguished from P. versicolor, since in P. pannonica the panicle is more or less stiffly erect, the spikelets are not normally variegated, and the stem is much more densely scabrid, especially below the panicle. For a fuller account of the differences between the two species, see appendix 1.

Fomin et al. (1938) also contains a comparative treatment of the Ukrainian members of the group, P. pannonica subsp. pannonica and P. versicolor. The former is referred to as P. podolica Błocki, a synonym of P. pannonica subsp. pannonica. Though I have only been able to examine limited material from the upper Dneistr valley, it appears to me that both taxa are present and that therefore those floras which treat P. podolica Błocki ex A. & Gr. and P. polonica Błocki as synonyms of the same species are incorrect. Flora RSS Ucrainica does not provide very detailed descriptions, with the result that it is unlikely whether plants could be matched to the correct species on the basis of these diagnoses alone (see table 7.3).

Recent work in Romania (Dihoru, 1966 and 1968; Şerbănescu, 1967a, 1967b) appears to have been carried out independently by the two authors, since Şerbănescu (1967a, b) cites duplicates of the specimens

from Dobrogea which were first referred to by Dihoru (1966). Şerbănescu (1967a) came to the conclusion, with which I concur, that P. romanica Prodan is not worthy of specific status and should be regarded as synonymous with P. sterilis (with which conclusion I do not concur). Şerbănescu (1967b) also pointed out Hayek's error in identifying the material from Epirus as P. pannonica, and re-identified it as P. sterilis. As Dihoru (1968) demonstrated, southern Balkan 'P. sterilis' is in fact P. versicolor.

The latest account of Romanian members of the P. sterilis group was provided by Ghişa & Beldie in Savulescu, Flora R.P.R. 12 (1973). Their treatment is in accord with the work of Dihoru in assigning the material from Dobrogea to P. versicolor, and in identifying the plants of the Siebenburgen (Transcarpathian) region as P. pannonica. The differences between Ghişa & Beldie's descriptions of P. pannonica and P. versicolor are included in table 7.4).

For comparative purposes, table 7.5 has been prepared by extracting the relevent information from the key and descriptions of P. pannonica and P. versicolor in the Flora Europaea account.

7.4 The infraspecific variation of P. pannonica.

Two collectors, Błocki and Nyárády, have contributed not only to the enrichment of herbaria with specimens from the upper Dneistr valley and from Romania respectively, but also to the nomenclatural confusion surrounding this group. Their failure to identify their own material satisfactorily has led to incorrect interpretations of the limits of variation of two taxa in particular: P. pannonica subsp. pannonica and P. pannonica subsp. scabra (Kit.) Soó (syn.: P. scabra Kit.).

TABLE 7.3 Comparison of descriptions of *P. pannonica* (sub *P. podolica* Blocki) and *P. versicolor* in Fl. RSS Ucrainica.

P. PANNONICA	P. VERSICOLOR
Plant 30 - 70 cm tall	Plant (30-) 40 - 75 cm tall
Leaves narrowly linear, to 2 mm broad	Leaves narrowly linear, 1.5 - 3 mm broad
Ligule to 2 mm long	Ligule to 4 mm long
Panicle 5 - 10 cm long	Panicle (6-) 10 - 14 (-18) cm long
Spikelets 5 - 6 mm long, cuneate-lanceolate, dirty green, eventually yellowish	Spikelets (5-)6(-8) mm long, lanceolate-acuminate, versicoloured
Glumes lanceolate-acuminate	Glumes narrowly lanceolate
Lemma pubescent on keel and nerves below.	Lemma densely and more or less long-pubescent on keel and nerves below.

TABLE 7.4 Comparison of characters in key and descriptions of *P. pannonica* and *P. versicolor* in Ghişa & Beldie, Flora R.P.Romania 12 (1973).

P. PANNONICA	P. VERSICOLOR
a) key, dichotomy 20, p. 366:	
Upper nodes of the stem not enclosed by a leaf sheath	Upper nodes of the stem enclosed by a leaf sheath
Distance from base of uppermost leaf to (base of) panicle 7.5 - 13 (-17) cm	Distance from base of uppermost leaf to (base of) panicle 2 - 6 cm
Glumes ovate, upper glume 3.5 - 3.7 mm long	Glumes lanceolate, upper glume 4.5 - 5 mm long
b) text, pp. 407 - 408:	
Plant with an elongate rhizome	(No reference to a rhizome)
Stem to 40 cm tall, more or less scabrous	Stem 25 - 70 cm tall, fistulose, very scabrous
Ligule elongate, somewhat lacerate	Ligule to 3 mm long, truncate, sometimes ± lacerate
Panicle branches erecto-patent, scabrous, 2 - 5 together below	Panicle branches to 8 cm long, rigid, ± scabrous, 3 - 5 together below
Spikelets with 3 - 4 florets	Spikelets with 3 - 5 florets
Glumes with a broad hyaline margin	Glumes with a narrow hyaline margin
Lemma lanceolate, acute, green, with a narrow membraneous margin	Lemma narrowly lanceolate, acute, lanate at base, green or violet-tinged, margin membraneous
Fl. June - August	Fl. April - August

An example of Nyárády's confusion over the application of names is provided by a lengthy comment appended to the herbarium label of one of his gatherings, no. 2630, which is given the name (on the label) "Poa scabra Kit. f.(orma) pannonica (Kern.) Nyár." and was collected from Crişana in north-west Romania, close to the type locality of P. pannonica Kern. For the translation which follows, I acknowledge the help of Marcella Vlad.

"Nyárády no. 2630.

"The plants from Coltişor, no. 2629 with the shorter panicle and with a more compact spike, can be matched with the type of P. scabra. This plant (no. 2630) was collected at Soimus-Milova; it has a bigger panicle, which is laxer and has longer, patent branches. It is similar to P. pannonica Kern.

"If the specimens 'Gramina Hungarica no. 29' and 'Flora Hungarica Exsiccata no. 700' are compared, we can see that they are not identical and represent, at least, different ecotypes. Likewise, 'Gramina Hungarica no. 83' and 'Flora Exsiccata Austro-Hungarica no. 1091', both labelled P. pannonica, are not identical. However, no. 700 (sub P. scabra)is very similar to no. 83(sub P. pannonica).

"The differences between these plants are more ecological than systematic; they are not geographically separate. For this reason, these plants are better staying together in the same species, and it is more correct to subordinate P. pannonica to P. scabra, described earlier".

To deal with the last sentence first, Nyárády overlooked the fact that P. scabra Kit. was predated by P. scabra Ehrh., and is thus nomenclaturally invalid. The legitimate name for the whole group thus becomes P. pannonica.

His comments are best explained with reference to my own

identifications of the plants discussed by Nyárády:

2629 Rm: Coltişor = P. pannonica subsp. scabra

2630 Rm, prov. Crişana: Soimus-Milova = P. pannonica subsp. pannonica.

By treating the exsiccata material uncritically, by regarding it as typical of the different taxa, Nyárády naturally found himself unable to come to the conclusion that two different species were involved. 'Gramina Hungarica 83' from Magyarad, leg. G. Perlaky (herb. BM) and 'Flora Hungarica Exsiccata 700' are in my opinion not referable to P. pannonica subsp. pannonica; though not at all typical material of subsp. scabra, they originate from the region of northern Hungary from where P. scabra Kit. was first described, and are best regarded as variants of P. pannonica subsp. scabra.

Now that the geographical distribution of the two subspecies is better known, a tentative map can be drawn up (map 7,1) based on specimens I have examined; neither literature records, nor specimen citations, can be relied upon.

By recognizing P. scabra as a subspecies of P. pannonica, a nomenclatural new combination and new rank is required. The necessary change was published by Soó (1959).

Błocki collected a number of specimens in the P. sterilis group from the upper Dneistr region. Many of the place-names used have become obsolete owing to boundary changes and consequent linguistic substitutions. All the material from western Galicia seems to me to be referable to P. pannonica subsp. pannonica; some of the specimens from Podolia are however referable to P. versicolor, e.g.:

"Bilcze prope Borszczow" (= Borshchëv, 55 km N of Chernovtsy), leg. Błocki, 1894 (before the region became part of the Ukraine), herb. BM. Other specimens sub P. podolica Błocki, which according

to Ghişa & Beldie (1973) is synonymous with P. versicolor (which it is to the extent of the specimen cited above) are clearly specifically distinct, and are identical with P. pannonica subsp. pannonica, e.g.:

Schultz, nov. ser. Cent. 23: 2292 (herb. BR);

Sinkow prope Mielnica, leg. Błocki, 1889 (herb. BR).

Material of the latter gathering is also found in the herbarium of the British Museum (Natural History), where it bears the name "P. pannonica an (towards) var. pannonica Błocki 1894", in the collector's own hand. The difficulty he, and later workers, had in identifying the material from the south-western Ukraine may be due to introgressive hybridization between originally pure populations of the two species. The group can be recommended as the subject of a biosystematic exercise.

7.5 In eastern Russia another species occurs which is referable to the P. sterilis group: P. relaxa Ovcz. Although more familiar under the name P. stepposa (Kryl.) Rozhev. (1934) this name is predated by the name P. relaxa Ovcz. (1933), which therefore has priority over the later name. Suspected of being a variety of P. attenuata by its original author, Krylov, it was elevated in rank by Rozhevits in 1934 during the publication of the second volume of Flora SSSR. Ovchinnikov published P. relaxa as a separate species, and the distinction between the two was maintained by Rozhevits, but the two were eventually united in synonymy by Tsvelev (1968). The latter author has since changed his mind, and in his latest works (Tsvelev, 1973 and 1974) treats it as a subspecies of P. versicolor, a view with which I do not concur. Clearly a revision of the whole group is needed. The relationship between P. relaxa and P. sterilis was investigated by Serbanescu (1968).

TABLE 7.5 Comparison of characters in key and descriptions of *P. pannonica* and *P. versicolor* in Flora Europaea account.

P. PANNONICA	P. VERSICOLOR
a) in key:	
Stem more or less densely scabrid below panicle	Stem smooth or slightly scabrid below panicle
Uppermost node usually not concealed by sheath of leaf below	Uppermost node concealed by sheath of leaf below
Glumes ovate-lanceolate, the upper (3-) 3.5 - 3.8 mm	Glumes rather narrow, the upper (3.5 -) 4 - 5 mm
Lemma usually not variegated	Lemma often violet- and gold-tinged
b) in text:	
Stem 25 - 45 cm; leaves 1.5 - 2.5 mm wide	Stem (20-) 25 - 40 (-65) cm; leaves 1 - 2 mm wide
Ligule up to 3 mm, oblong rounded or somewhat lacerate	Ligule up to 2.5 mm, oblong, obtuse to acute
Panicle 3 - 6 (-10) cm, branches rigid, very scabrid	Panicle 6 - 17 cm, branches sparsely to densely scabrid
2 - 4 panicle-branches together at each lower whorl	Up to 5 panicle-branches together at each lower whorl
Spikelets greenish, with 2 - 4 florets	Spikelets violet- and gold-tinged, with 2 - 4 (-5) florets.
Lemma densely long-hairy on marginal veins	Lemma sparsely long-hairy on keel and marginal veins

7.6 Evaluation of taxonomic 'macrocharacters' in the P. sterilis group.

The relative value of the morphological characters of the vegetative parts of the plant in delimiting the taxa of the P. sterilis group is rather small compared to the value of the so-called 'microcharcters', i.e. those characters of the parts of the spikelet which are only seen easily under a low-power binocular microscope. A selection of characters is presented here which (a) serve to define the group, and (b) serve to delimit the various taxa within the group.

(a) Characters in common through the P. sterilis group.

(A fuller account of the morphological characters of the members of sect. Stenopoa in general, can be found in chapter 5).

i. Growth-form.

In each species, the structure of the tussock is compact, without rhizomes, and the number of leaves imbricated near the base is few. The sheaths of the cauline leaves clothe the stem almost to the base of each shoot, in which region the stem is much branched and is enclosed by short primordial sheaths or scales (see Serebryakova 1965, fig. 4, p. 1549). The scales are termed 'cataphylls' by Vickery (1970, p. 152). The oldest stem at the centre of the clump frequently extends several centimetres below the surface of the soil; this observation, in pressed material in which the level of the soil has not left a distinct trace, may have led to Bor's interpretation of this structure as a "short, thick, almost horizontal rhizome" (Bor, 1948, p. 63), in P. araratica Trautv. which helps to distinguish this species from P. sterilis sensu lato. However, in order to be classed as a true rhizome it must be shown that growth is occurring in a

direction which is orientated away from the centre of the tussock. This does not appear to me to be so in P. araratica.

ii, Colour.

The tawny colour of the upper part of the stem in dried specimens contrasts with the darker brown of the region nearer the stem base. Fresh material shows a purplish-brown colour in the lowest sheaths; the stem is conspicuously purple-tinged at the nodes, when these are exserted. The high ratio of sclerenchyma to chlorenchyma in the stem (see chapter 6.4) masks its underlying green colour, while anthocyanin is deposited in the leaf-sheaths, particularly towards the base.

iii. Leaf blade.

The width and degree of folding of the leaf blade varies within the group to only a limited extent, although the range of variation of these features within the individual plants is quite large. Consequently, this organ cannot be used to provide characters of diagnostic value.

iv. Stem.

The stem is rather rigidly erect, with inconspicuously swollen nodes and faint longitudinal striations. Older dried specimens have a tendency to become more obviously striate; this presumably results from shrinkage of the less rigid bands of chlorenchyma. The leaf sheaths clothing the lower part of the stem are provided with both upward- and downward-pointing prickles on the ribs; the degree of scabridity varies.

v. Panicle branches.

The panicle varies greatly in length and shape, but the number of panicle branches at each pseudowhorl is seldom fewer than two or greater than four; five branches together are known only in

P. pannonica. The branches are very scabrid with upward-pointing aculeoli in all species.

b) Characters not in common throughout the P. sterilis group.

i) Ligule.

The ligule varies greatly in length and prominence. At one extreme is P. sterilis, upland variants of which (e.g. the type specimen) have scarcely any ligule. An examination of a wider range of material of P. sterilis showed that there is usually a small but distinct ligule which, with a truncate apex and a length not exceeding 1 mm, is very inconspicuous. At the other extreme, P. pannonica has an elongate ligule 1.5 - 2.5 (-3) mm in length. A consequence of the length of the ligule is a tendency for it to be lacerated. If entire, the apex is rounded. P. versicolor also has a ligule which is quite long - 1.5 - 2 (-2.5) mm - and the overlap of ranges prevents this character from being used to separate P. pannonica and P. versicolor.

ii) Glaucosity.

Both P. sterilis and P. relaxa are rather glaucous. This feature is characteristic of dried material; it has not been noted whether there is a marked glaucous appearance when fresh. Fresh material of P. sterilis grown from seed originating from Krym is most markedly glaucous on the leaf blades and sheaths, by contrast to the other noted glaucous species of sect. Stenopoa, P. glauca, which is most glaucous on the upper part of the stem. P. araratica and material of P. sterilis sensu lato from Anatolia are not glaucous; this is an additional feature to cast doubt on the view expressed by Bor (1948) that the Crimean-Caucasian and Anatolian-Iranian material are conspecific. One of the non-European species of the P. sterilis group, P. litwinowiana Ovcz., is described as being extremely glaucous.

The nature of the glaucous surface has been established only recently. It appears to be a waxy deposit on the surface of the cuticle; it is not however a layer that is impervious to water (Miroslavov & Zhigar 1973). These authors showed through electron microscopic studies that the cuticle has marked porosity, even in xerophytic grasses, above the veins and along the margins of the leaf blade, where the waxy deposit is least.

iii) Leaf width.

The broadest leaf blades (henceforth 'leaves') are found in some specimens of P. pannonica subsp. pannonica, which can attain a width of 4 mm in some cases. P. sterilis has the narrowest leaves, at least among the European species, seldom attaining 2 mm wide. In general, however, the width varies considerably between specimens of the same species and ranges observed in the different taxa overlap; this prevents the characters from being used to separate the various taxa. Since the leaf blade tapers gradually to the apex, measurements are taken near the base, and minimum widths are of little value.

iv) Extent of the sheath of the next-to-uppermost leaf.

In all grasses, the uppermost leaf arises from the uppermost node of the vegetative part of the stem. The leaf below normally encloses the uppermost stem node, by enveloping it in its sheath. P. pannonica and P. araratica are unusual in that the node is usually exserted. The selective value of this feature is not obvious. The widespread state, where the node is enclosed, can be considered more normal for the following reasons:

(a) Since the node forms an articulation of the stem, greater rigidity is obtained when it is enclosed by a leaf sheath.

(b) The length of the internode on which the panicle is borne must exceed the length of the sheath of the uppermost stem leaf, if the

panicle is to be exserted ; otherwise, the panicle would never emerge, which would be highly unsatisfactory. In order to have an adequate number of stem leaves, the remaining internodes must in general be much shorter.

v) Scabridity of the stem below the panicle.

This character is highly variable both within and between taxa, making it of little use in distinguishing the various taxa. The stem is generally quite densely scabrid with upward-pointing aculeoli borne on the raised portions of the stem, but P. versicolor is usually much less densely scabrid than P. pannonica at comparable levels of the stem, so that where difficulty is encountered in separating the two species this character may be helpful.

7.7 Evaluation of the 'microcharacters' from the floret.

Floras generally refer to characters such as the length of the spikelet, the number of its florets, and the shape of the glumes and/or lemma; characters, in fact, which are observable with the naked eye or at most with a hand-lens. The reason for this can only be a sense of obligation on the part of the Flora-writer to include in his description at least a passing reference to the floral parts, together with his disinclination to dissect the spikelet. The characters mentioned are of almost no diagnostic value, either because of the overlap of ranges of variation of the different taxa or because of the lack of suitable terminologies to describe shapes such as those of the glumes and lemma.

Fortunately, there are several other characters of the spikelet which provide useful diagnostic features; less fortunately, special preparative methods are required if these characters are to be seen satisfactorily. The procedure I have adopted is described in appendix 2. Though the characters to be described are sometimes difficult or impossible to observe in the 'dry' state, even with

a good binocular microscope, features such as the indumentum of the palea keels and the rhachilla can sometimes be seen clearly if the spikelet is manipulated with needles.

i) 'Wool' at the base of the lemma.

Long, flexuous or crimped hairs arising from the callus (the pad on which the lemma, palea, androecium and gynoecium are borne) appear to originate from the base of the lemma, since it is to this organ that the callus normally adheres. Numerous terms are used to describe this feature, such as 'wool', 'cottony hairs', 'callus hairs', 'wavy hairs' etc.; in Flora Europaea, the occurrence of this character is recorded in the form "lemma..... lanate at base".

In the P. sterilis group, the amount of wool varies from almost none to very abundant. It is never consistently absent in any of the taxa studied, but is particularly sparse, or lacking, in P. sterilis and P. versicolor, and in the non-European species P. araratica. P. versicolor sometimes has an abundant amount of wool, as does P. pannonica subsp. scabra (with a few exceptions). P. pannonica subsp. pannonica generally has a sparse amount; but taken overall this character is of little use in distinguishing the European taxa of Poa. Crimean material of P. sterilis has a more substantial quantity of wool, on average, than material of P. sterilis sensu lato (Bor, 1970) and P. araratica from Turkey, Iran and Afghanistan.

ii) Indumentum of the rhachilla.

The rhachilla, or spikelet axis, is a rather neglected organ in the systematics of Poa. Bor (1952), one of the first authors to pay special attention to this character, remarked that it is "smooth and glabrous in about half of the Indian species, while in the remainder it is shortly hairy, verrucose or covered with scabridities. It is not possible to use these features to any

extent in the separation of species". Though the last statement is broadly true for the P. sterilis group, the different taxa exhibit a variety of rhachilla indumentum types, as shown in table 7.6 and table 7.7.

The only taxa in Europe with teeth or hairs on the rhachilla are P. pannonica subsp. pannonica and P. sterilis. This is in partial contrast to P. pannonica subsp. scabra, which is consistent in the material examined in having a verrucose rhachilla, as do the hairless and teeth-less specimens of P. pannonica subsp. pannonica and P. sterilis. Where hairs are present in these two taxa, they are never copious. None of the taxa mentioned has a smooth and glabrous rhachilla.

At the other extreme of an apparently continuous range of variation, hairs were never observed in material of P. versicolor; unlike P. pannonica, the rhachilla in P. versicolor appears to be either verrucose or, more commonly, glabrous and smooth.

The tentative state of naming of material from south-west Asia may explain why there is such a lack of uniformity in their rhachilla indumentum. The results seem to indicate that the copiously hairy rhachilla is indicative of P. sterilis sensu lato, while this state is rare in P. araratica. Sparsely hairy rhachillae are occasionally found in both species, while only P. araratica has a range of specimens with verrucose but glabrous rhachillae. A more general discussion of the indumentum of the rhachilla is given in chapter 5.

iii) Type of apex of hairs borne on lateral veins of the lemma.

A general survey of this character has shown that its various states usually coincide with sectional divisions in the European members of Poa. Section Stenopoa forms the main exception to this

statement, and it was hoped that a study of this character in the P. sterilis group would reveal a greater degree of uniformity at the level of species. Quite the opposite of this result was obtained; the lack of consistency shown by this character was the greatest of any of the characters studied in this group. The only uniform feature was the absence of hairs with club-shaped apices from the specimens which were examined.

The three character states present are described as 'acute', 'ogival' and 'obtuse'. The term ogival is defined in chapter 5. The acute apex is found in both subspecies of P. pannonica and in P. versicolor, but is their least frequent character state. In P. sterilis and P. araratica it is the most frequent state.

The ogival apex occurs in all the taxa studied, but is relatively infrequent in P. sterilis, P. araratica and P. versicolor. It is the commonest state in P. pannonica subsp. pannonica, but is less frequent in subsp. scabra.

The obtuse apex is the commonest state in P. versicolor and P. pannonica subsp. scabra. It is relatively infrequent in subsp. pannonica and in P. araratica and P. sterilis.

The frequency of occurrence of the three states is given in table 7.8; these results should be treated with caution, since the number of specimens examined has been insufficient to permit a high level of statistical significance. This is at present inevitable, since all available specimens, excepting duplicates, from the herbaria listed in appendix 3 have been examined. There is clearly still a need to obtain further material from a wider range of localities.

iv) Palea indumentum.

The vestiture of the palea keels can often be used to provide useful characters for delimiting species. It is less

useful in providing sectional characters, and in view of its apparent heterogeneity the indumentum of the palea in sect. Stenopoa has generally been ignored. This is unfortunate, since it turns out to be one of the most valuable microcharacters.

Von Oettingen (1925) makes no reference to the presence of tangled hairs on the surface of the palea lying between the keels. I have encountered this character only in the P. sterilis group of species within sect. Stenopoa, and elsewhere only in sect. Bolbophorum. The presence of this characteristic feature, which though not easily apparent to the taxonomist who examines the palea under reflected light with a binocular microscope can clearly be seen with transmitted light in mounted preparations, is a good diagnostic character of P. pannonica and P. versicolor; with the exception of one specimen of P. araratica (from outside Europe), both it and P. sterilis sensu lato have consistently glabrous palea surfaces.

The keels of the palea are regularly aculeolate (i.e. aculeolate along their whole length) in nearly all specimens of P. pannonica subsp. scabra. In subsp. pannonica, the keels usually have short unicellular hairs in the lower half, becoming progressively shorter and then replaced by aculeoli towards the upper half of the palea keels. This difference is sufficiently well developed to provide a useful guide to distinguishing the two subspecies, taken in conjunction with other characters such as those listed in table 7.5.

7.8 Conclusions.

The main fact that emerges from this study of the macro- and micro-characters of the P. sterilis group is that there is a parallel between the variation shown by the cryptic characters and the variation of the features to which floristic accounts normally refer. There is no reason to suppose, given these results, that the impression of extremely large external variability masks an underlying clear-cut

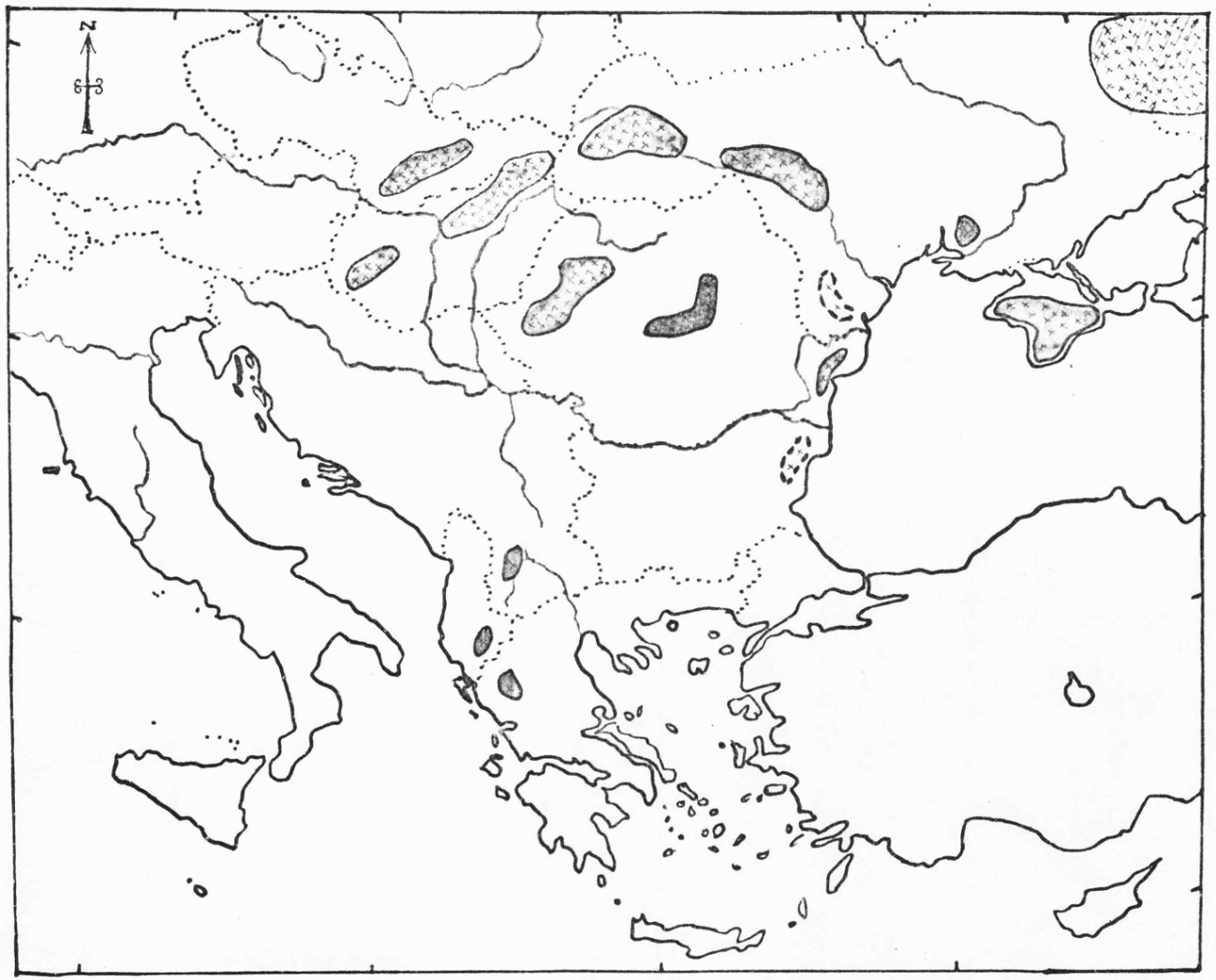
set of characters; if so, these characters have yet to be discovered.

In evolutionary terms, it is clear from the pattern of variation in this group that we are dealing with a rapidly-changing, recently-formed assemblage with little stability either of morphology or of geographical range. A study of the interfertility of the taxa in the region of south-eastern Europe where all three taxa occur, together with an account of their breeding systems and chromosome numbers, would be very desirable as it would throw light on the mechanism by which the high variability is retained. The information which is available at present is quite inadequate as an indication of the evolutionary history of the group. Nevertheless, it seems clear from the literature survey that a better knowledge of the Central Asian species must be obtained if the systematics of the group as a whole are to be more fully explored.

The historical features which underlie the present-day distribution of the group must also be taken into account. Şerbănescu (1968) found that the centre of origin of P. relaxa must lie in the eastern part of the present-day range of the species, and that some of the taxonomic features that the two taxa, P. relaxa and P. sterilis, have in common may be due to introgression between the two species in the zone of contact between them. This may have led, in Şerbănescu's view, to their acquiring an affinity for each other's ecological requirements. For example, while P. relaxa occupies non-calcareous habitats in the east of its range, it is found on calcareous substrata in extreme Eastern Europe, where it is presumed to have introgressed with P. sterilis. Similar processes may have operated in south-east Europe between P. pannonica and P. versicolor. While our knowledge of the distribution and ecological preferences of the taxa of the P. sterilis group in south-east Europe is as yet very incomplete, it can be said that they are often found

in zones of unstable soil or of vegetational boundaries, since these situations favour the survival of plants which are intolerant of competition. There are frequent references, on the herbarium labels of the members of the group, to "eroding river banks" and "scree slopes", usually in dry situations. The occupation of such habitats is favoured by an inbreeding or apomictic reproductive strategy, since such breeding systems maximise the production of plants which are fully adapted to unstable substrata, at the expense of the longer-term flexibility which an outbreeding sexual system confers.

The few available chromosome counts by no means rule out the apomictic breeding system as the likely type in this group. The present-day distribution of the members of the group is largely fragmented, lessening still further the opportunities for genetical exchange which may still exist in a mainly apomictic plant (see map 7.1).



MAP 7.1 Distribution of the Poa sterilis group in Europe.

TABLES 7.6 & 7.7 Key to microcharacters of the P. sterilis group.

Column A. Rhachilla:
(a) glabrous and smooth
(b) glabrous, with verrucose papillae
(c) verrucose, with a few teeth or hairs
(d) densely hairy

Column B. Callus wool:
(a) copious
(b) sparse
(c) absent

Column C. Palea keels:
(a) long-ciliate below, aculeolate above
(b) a few short hairs at base, then aculeolate
(c) regularly aculeolate, hairs absent

Column D. Surface of palea:
(a) with tangled hairs
(b) with sparse hairs
(c) glabrous

Column E. Age of floret:
(a) pre-anthesis, anthers undeveloped
(b) pre-anthesis, anthers mature
(c) at or just after anthesis, ovary undeveloped
(d) post-anthesis, ovary developed
(e) ripe caryopses present

Column F. Type of apex of hairs on lateral veins of lemma:
(a) acute
(b) ogival
(c) obtuse (rounded)

Column G. Number of florets in the spikelet dissected:
2, 3, 4 fertile florets
st.: sterile forets at apex of rhachilla.

Note: numbers of sample refer to a particular specimen, but have no further significance; they are simply running numbers allocated in the order in which the preparations were made.

TABLE 7.6 Microcharacters of European members of *P. sterilis* group.

P. pannonica subsp. *pannonica*	A	B	C	D	E	F	G
136	b	b	c	b	*	a	*
137	*	*	b	c	*	c	*
154	c	b	b	c	b	b	2
159	c	b	b	a	d	b	2
164	c	b	a	b	d	c	2
167	c	b	c	b	d	b	3
168	b	c	b	b	e	b	2
173	b	b	c	c	a	b	4
P. pannonica subsp. *scabra*							
139	*	*	a	a	*	c	*
140	*	*	c	c	*	c	*
156	b	c	c	c	*	a	2
160	b	c	c	b	a	c	*
161	b	a	c	c	b	b	2
165	b	b	c	c	b	b	2
172	b	b	c	b	a	c	2
174	b	b	c	c	b	b	3
176	b	c	c	c	d	c	3
P. sterilis							
166	b	b	b	c	b	c	2+
175	d	c	c	c	d	c	2
178	b	c	c	c	c	c	2
P. versicolor							
133	*	*	c	b	*	b	*
134	*	*	c	b	*	c	*
135	*	*	c	c	*	a	*
138	*	*	a	a	*	c	*
141	*	*	c	b	*	b	*
142	b	b-c	c	b	*	a	*
143	b	b	a	c	b	c	2
155	a	b	b	b	b	c	2
157	a	b	c	b	a	c	2
158	b	b	c	a	b	c	2
162	b	a	a	b	b	c	2
169	b	c	c	c	b	c	2

TABLE 7.7 Microcharacters of non-European members of the *P. sterilis* group.

P. araratica sensu Bor (1970)	A	B	C	D	E	F	G
181	d	b	c	c	b	b	3
183	b	c	c	c	a	c	2
184	b	c	c	c	d	a	2
185	b	c	c	c	c	a	3
(Note: col. G, *keel* hairs scored as a; lateral veins glabrous in 185)							
186	b	c	c	b	b	a	4
187	*	b	c	c	a	c	1 + 1 st.
188	c	b	c	c	*	c	4 + 1 st.
189	b	c	c	c	b	b	2 + 1 st.
192	b	c	c	c	d	a	3
193	d	c	c	c	*	a	2
194	b	c	c	c	c	a	2 + 1 st.
195	b	c	c	c	e	a	3
196	b	c	c	c	d	@a@	3
(@@: see note under 185 above)							
197	*	c	c	c	d	a	2
198	b	c	c	c	d	b	3
199	a	c	c	c	c	a	2 + 1 st
P. sterilis sensu Bor (1970)							
182	c	c	c	c	a	a	2
200	b	c	c	c	a	a	3
201	c	a	c	c	b	c	3
202	b	b	c	c	a	a	3
203	d	c	c	c	a	b	2
204	d	c	c	c	*	a	3
205	*	c	c	c	*	a	3
206	*	c	c	c	c	a	2
207	b	c	b	c	a	a	4
208	b	a	*	*	a	a	3
210	d	c	c	c	a	c	2

TABLE 7.8 Frequency of occurrence of types of apex of the hairs on the lateral veins of the lemma in the members of the *P. sterilis* group.

	Acute	Ogival	Obtuse	Total
P. araratica	9	2	3	14
P. sterilis	8	1	4	13
P. pannonica subsp. *pannonica*	1	5	2	8
P. pannonica subsp. *scabra*	1	3	5	9
P. versicolor	2	2	8	12
Total of each type:	21	13	22	

CHAPTER 8. Geographical distribution.

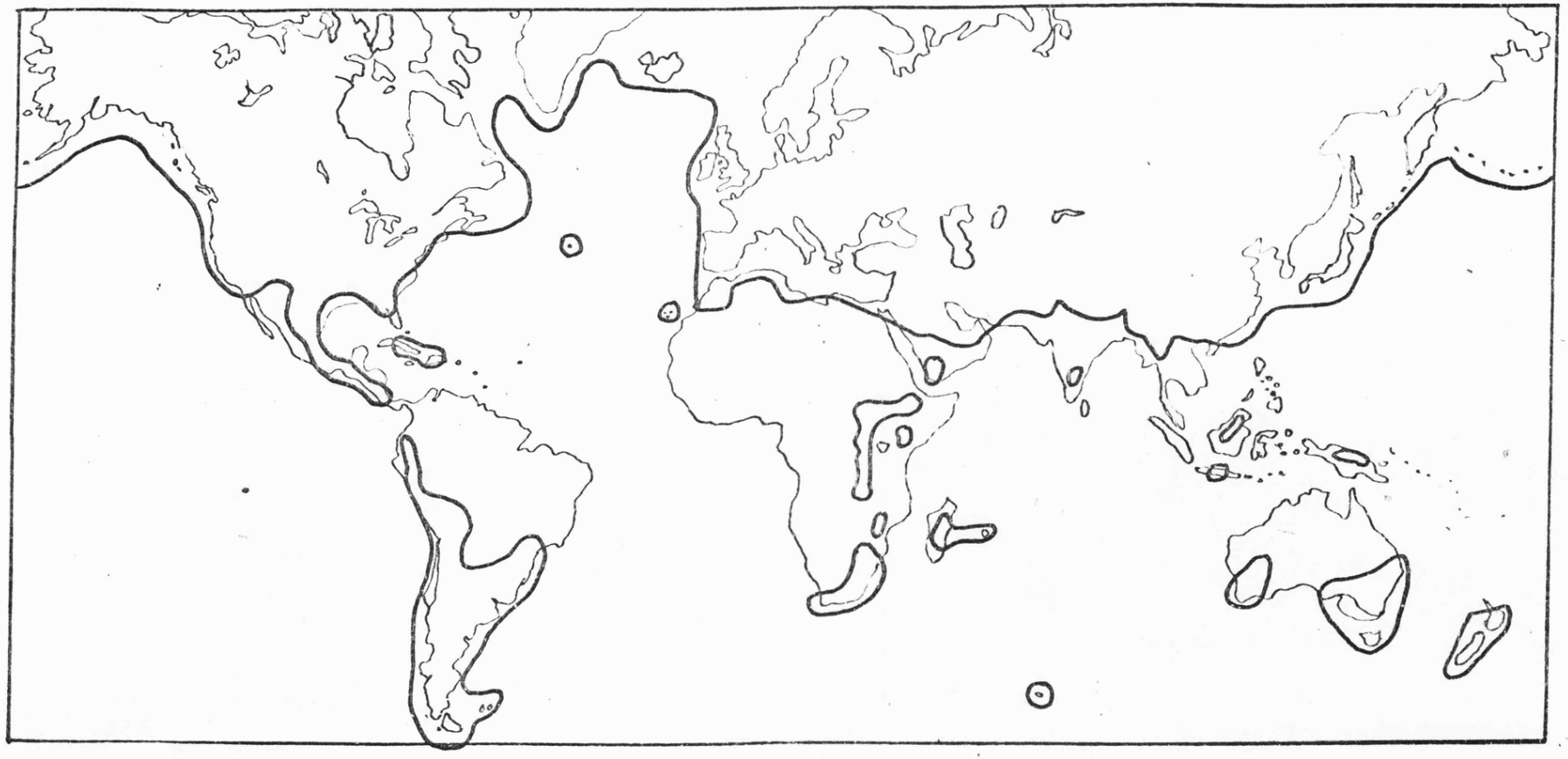
8.1 Introduction.

The names given to plant distributional areas should ideally express the topographic and climatic characteristics of the areas, as well as their geographical extent. Various attempts have been made to produce comprehensive systems of names for plant distribution areas, but as yet there is no standardized system which takes account of the major climatic variables which influence large-scale distribution patterns. A recent attempt to codify information on the distributions of Central European plants and of species closely allied to these plants, was made by Meusel, Jäger & Weinert (1965) accompanied by distribution maps of both categories of species. Current schemes for mapping the flora of Central Europe (Niklfeld, 1971) and of the whole of Europe as defined by Flora Europaea (Jalas, 1969) will soon render superfluous any attempt to make more accurate outline maps on the pattern of the maps in Meusel et al. Purely as a sample, a map has been prepared using the 50km UTM grid showing the known distribution of P. ligulata in Europe and Morocco, based on specimens in herbaria visited by me in the course of my studies (see appendix 3).

For the purpose of describing the distributions of the European species and sections of Poa, therefore, no attempt was made to provide more accurate distribution maps than are already available; for a bibliography of published data, see Index Holmensis part III (ed. H. Tralau, 1973). In the account which follows, a primarily geographical, and secondarily altitudinal, terminology has been employed to describe the broad distributions of the European species of Poa.

8.2 World distribution of the genus and its subgenera.

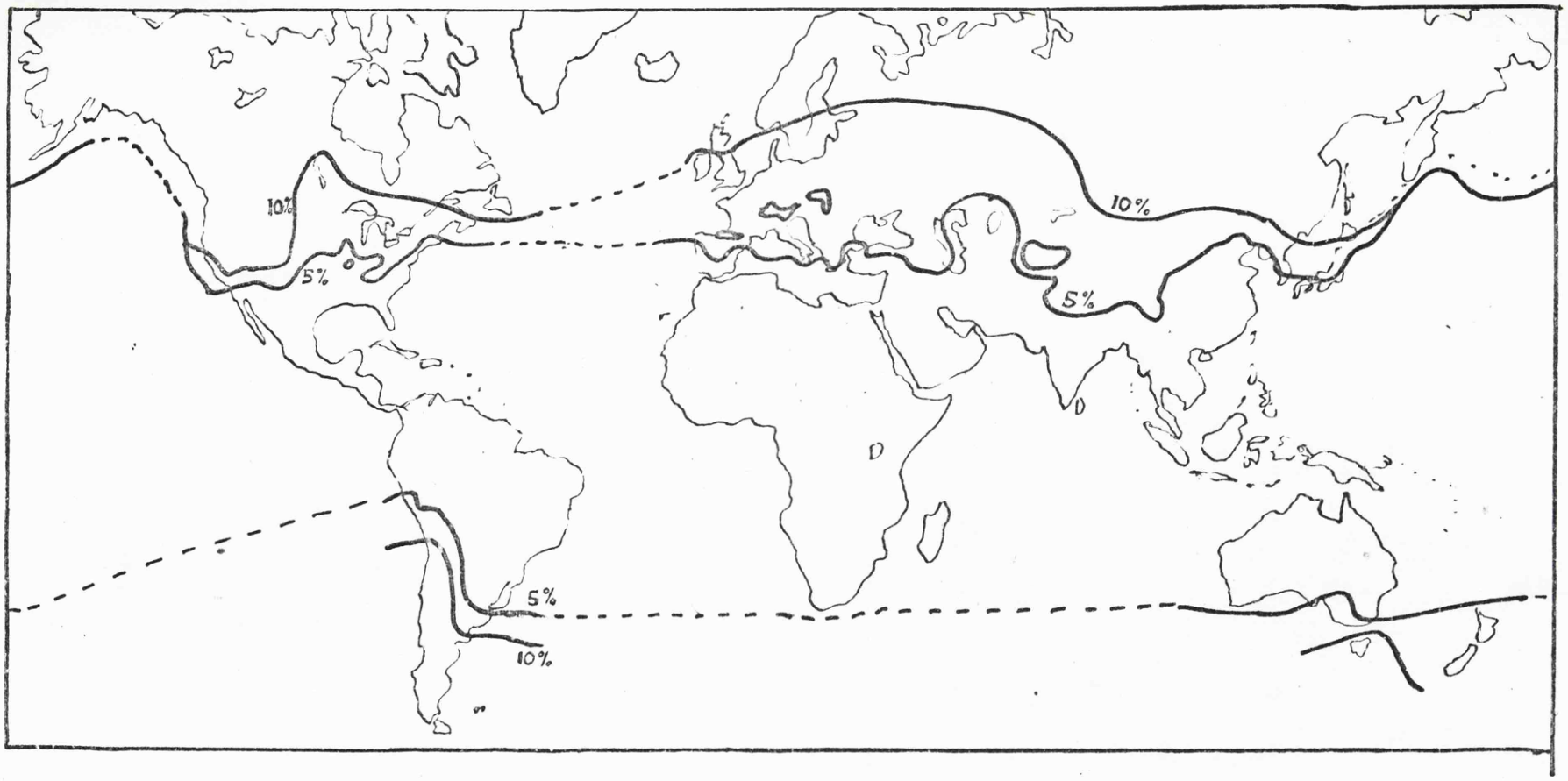
Species of the genus Poa are native to all the continents of the world, but are generally absent from the tropics and humid



MAP 8.1 World distribution of the genus Poa.

subtropics except in tropical high-mountain regions having an essentially temperate climate. Map 18.1 (adapted from Hartley, 1961) shows the overall distribution of the genus Poa in the world. With the exception of permanently glaciated areas, the northern limit of distribution corresponds to the limits of the available land surface. The genus just fails to qualify as one of the southernmost naturally-occurring grasses, but is present in the Antarctic as an adventive. The distribution of Poa in the southern hemisphere is very disjunct, owing to the fragmentation of land areas having more or less temperate climates. These areas are largely isolated from the broad distributional area in the northern hemisphere by the tropical lowlands, though the occurrence of species throughout the highly disjunct alpine areas of the tropics suggests that continuity may have been much greater during past epochs when the alpine vegetation extended to lower levels.

The southern limits of the distribution of the genus in the northern hemisphere coincide in lowland areas with the zones of transition from dry subtropical/mediterranean to humid subtropical, or tropical, climates. As Hartley demonstrates, there are few species of Poa (expressed as a percentage of the total grass flora) in areas with a July (N) or January (S) summer maximum which averages more than 24° C. (75° F.). In the Eurasian continent, the line which divides areas with more than 5% species of Poa from areas with fewer than 5% species of Poa in the total grass flora more or less coincides with the boundary of the zone having a temperate humid montane climate with cold winters, and the zone with a subtropical arid montane mediterranean or continental climate. In the south-east of Asia, the line coincides with a zone of transition between upland (temperate) and lowland (subtropical) climate; the limit here is primarily altitudinal. In terms of the natural vegetation, the 5% limit



MAP 8.2 Percentage of species of Poa in the total grass flora.

is broadly the same as the southern limit of broad-leaved deciduous woodland, although a few species of Poa can tolerate steppic conditions with a very cold winter and a hot dry summer. Further details of temperature adaptations are provided by Loginov & Akhmedov (1970).

Historical factors have played a part in influencing the relative abundance of Poa species as a percentage of the total number of species of the grass flora. It is particularly noticeable that southernmost Africa is relatively poor in species of Poa compared to the southern part of South America which occupies comparable latitudes. Migration of a temperate flora along the Andean chain is relatively easily accomplished, whereas migration of temperate grasses into southern Africa cannot have been accomplished before the temperate Afro-alpine connection was severed. The present-day native Poa flora in southern Africa probably owes its presence there to long-distance dispersal across the Atlantic ocean from other areas in the southern hemisphere having mediterranean climates, such as Australia and South America.

Hartley's map (on which map 8).2 is based) gives little information for the region extending from the Himalayas through China to Japan. It is evident from Bor's account (1948), however, that the Himalayan mountain chain is a centre of diversity of the genus, with a large number of endemic species. China, also, appears to be rich in endemic species (Keng, 1961), and the Kamchatka peninsula has long been recognized as having a particularly rich Poa flora, (Rozhevits, 1927).

The Pamir-Alai and Altai ranges form a secondary centre of endemic diversity (Ovchinnikov, 1933) though the number of endemic species may have been exaggerated on account of the rather narrow species concept adopted by the compilers of Flora SSSR. The historical reasons for the rich development of endemic species of Poa

in these regions has not yet been explained.

There are other subsidiary centres of diversity of endemic species in the mountain regions of western Eurasia; from east to west, these comprise the Caucasus, Carpathian, Balkan, Alpine and Pyrenean mts. Their importance has perhaps been given too great a stress in the past through the extreme fragmentation of floristic studies in Europe by political and linguistic boundaries, and the consequent multiplicity of taxonomic treatments of the genus in Floras produced for different regions. The opportunity to prepare an account of the genus throughout Europe for 'Flora Europaea' has allowed, probably for the first time, an assessment of the distributions of the various species occurring in Europe on the basis of a single taxonomic treatment.

The account of the overall distribution of the genus applies equally to its principal subgenus Poa, which contains the great majority of the species of Poa. Subgenus Dioicopoa E. Desf. in C. Gay is not well known taxonomically and is overdue for revision; its distribution is apparently centred upon the Andean chain of South America, though isolated dioecious species are recorded in western North America and from the Pacific seaboard of E. Asia. In the absence of a taxonomic revision, these are assumed to belong to subg. Dioicopoa.

8.3 Distribution of the European species of Poa.

Taxa mapped by Meusel, Jäger & Weinert (1965) are listed in table 8.1; table 8.2 gives a list of nomenclatural changes required to bring the nomenclature of their work into line with my account for Flora Europaea. Table 8.3 is a classified list of the geographical distribution of the European species. Certain expressions used in this list require clarification. The term 'alpine' is used in a purely geographical sense, and refers to the mountain chain centred on Switzerland and Austria. Where 'alpine' is traditionally used

TABLE 8.1 Taxa mapped by Meusel, Jäger & Weinert (1965).

Note: taxa not occurring in Europe are underlined.

P. alpina L.
P. altaica Trin.
P. arctica R.Br.
P. badensis Haenke ex Willd.
P. bulbosa L.
P. cenisia All.
P. chaixii Vill.
P. commutata Roem. & Sch.
P. dolosa Boiss. & Heldr.
P. glauca L.
P. grandis Hand,-Mazz.
P. hybrida Gaud.
P. interior Rydb.
P. laxa Haenke subsp. fernaldiana (Nannf.) Hyl.
P. laxa Haenke subsp. flaxuosa (Sm.) Hyl.
P. laxa Haenke subsp. laxa
P. macroclada Rydb.
P. masenderana Freyn & Sintenis
P. nemoralis L.
P. palustris L.
P. parnassica Boiss. & Heldr.
P. podolica Błocki
P. pumila Host
P. radula Franch. & Savat.
P. rehmannii (A. & Gr.) Wołoszcz.
P. remota Fors.
P. tolmatchewii Rozhev.
P. tristis Trim.
P. versicolor Bess.
P. viridula Palib.

TABLE 8.2 Nomenclatural changes needed to bring the maps of Meusel, Jager & Weinert into line with the Flora Europaea account.

P. commutata Roem. & Sch.	=	P. chaixii Vill.
P. dolosa Boiss. & Heldr.	=	P. cenisia All. subsp. contracta Nyár.
P. laxa Haenke subsp. fernaldiana (Nannf.) Hyl.	=	P. fernaldiana Nannf.*
subsp. flexuosa (Sm.)Hyl.	=	P. flexuosa Sm.
P. parnassica Boiss.& Heldr.	=	P. pumila Host
P. podolica Błocki	=	P. versicolor Bess.
P. tolmatchewii Rozhev.	=	P. arctica R.Br.

*Non-European species.

TABLE 8.3 Geographical distribution of the European species of *Poa*.

A. CIRCUMPOLAR ARCTIC SPECIES

- ☐ *P. abbreviata*
- *P. alpigena*
- *P. arctica*

B. SUBARCTIC SPECIES

(i) North European species

- ● *P. flexuosa*

(ii) Eurosiberian species

- ☐ *P. sibirica*

C. BOREAL SPECIES

(i) Eurosiberian species

P. angustifolia	*P. palustris*
P. compressa	*P. pratensis*
P. nemoralis	*P. trivialis*

(ii) European - West Asian species

- ▲ *P. remota*

(iii) Eastern Central European species

- ● *P. stiriaca*

D. ARCTIC - MONTANE SPECIES

- *P. alpina*
- *P. glauca*
- *P. subcaerulea*

E. MONTANE SPECIES

(i) Eurasian species

- *P. supina*

(ii) European - Western Asian species

- ▲ *P. chaixii* (also naturalized in the lowland boreal zone)
- ▲ *P. hybrida*

(iii) West European - Anatolian species

▲ P. cenisia

(iv) Crimean - South West Asian species

□ P. longifolia

(v) Balkan - Carpathian - Anatolian subspecies

▲ P. cenisia subsp. contracta

(vi) Balkan - Carpathian species

● P. media

(vii) Balkan species

● P. pirinica

● P. trichophylla

(viii) Carpathian species

● P. granitica

● P. rehmannii

(ix) Alpine - South East European species

● P. molineri

● P. pumila

(x) Alpine - North Balkan species

● P. perconcinna

(xi) Alpine subspecies

● P. cenisia subsp. cenisia

(xii) West - Central - East European species

● P. laxa

● P. minor

(xiii) Pyrenean - Tyrrhenian subspecies

● P. cenisia subsp. sardoa

(xiv) Pyrenean - Galician species

● P. feratiana

(xv) Iberian - Moroccan species

▲ P. flaccidula

▲ P. ligulata

F. SUBMEDITERRANEAN THERMOPHILOUS SPECIES

(i) Eurasian steppe species

P. bulbosa

(ii) Central Asian species (extending into Ural region)

□ P. relaxa

(iii) Crimean - Western Asian species

□ P. sterilis

(iv) Crimean subspecies

● P. longifolia subsp. fagetorum

(v) Balkan - Anatolian - South West Asian species

□ P. timeoleontis

(vi) South European - South West Asian subspecies

P. trivialis subsp. silvicola

(vii) South East European species

● P. pannonica

● P. versicolor

(viii) Central European - Balkan lowland species

● P. badensis

G. MEDITERRANEAN COASTAL SPECIES

P. infirma (also present on the Atlantic coast)

● P. jubata (endemic to the EastAdriatic coast)

H. COSMOPOLITAN SPECIES

P. annua

KEY TO SYMBOLS:

● endemic to Europe.

▲ largely confined to Europe.

□ distributed mainly outside Europe.

No symbol: widely distributed both within and outside Europe.

in a broader sense to indicate mountainous areas in general, the term 'montane' is used. Strict endemism is defined in terms of the boundaries of Flora Europaea; species confined to Europe in this sense are indicated with a solid circle. A rather larger number of species is mainly confined to Europe, but whose distribution extends into adjacent regions such as the Caucasus mts. and the Atlas mts.; such species are indicated with a solid triangle. At the other extreme, some species almost fail to extend into Europe; these are distinguished by an open square. Species lacking an accompanying symbol in table 8.3 are widely distributed both within and outside Europe.

In distinguishing these four categories of distribution, their relative proportions can be stated: of the 44 species of Poa native to Europe, 17 (39%) are endemic to Europe; 6 (14%) are largely confined to Europe; 6 (14%) are distributed mainly outside Europe; and 15 (34%) are widely distributed both inside and outside Europe.

The distribution of the species which are endemic to Europe is of particular interest, since different historical reasons may present themselves according to the taxonomic relationships of the endemic species with each other, and with widely distributed species. Two types of endemism can be distinguished; the first type is recognized principally by its lack of closely related species in the modern flora, and is known as palaeoendemism, and the second type - neoendemism - is conversely recognized by having closely related species which are likely to have had a recent common ancestry with the endemic taxon, (Contandriopoulos, 1962).

8.3.1 Palaeoendemism.

Of the seventeen species of Poa which are endemic to Europe, only two are true palaeoendemics in that each belongs to a monotypic section and hence has no close relatives: P. stiriaca (sect. Leptophyllae) and P. trichophylla (sect. Nanopoa). However, two

other sections contain species which are taxonomically isolated from the remaining species in the section: P. feratiana (sect. Coenopoa) and P. pirinica (sect. Oreinos). All four species have very limited distributional areas, and two of the four species are known to have diploid chromosome numbers; the other two species, P. feratiana and P. pirinica, have not yet been examined karyologically. As pointed out by Davis & Heywood (1963, p. 428) the close relatives of palaeoendemic taxa have presumably become extinct, leaving a surviving taxon which is presumably only adapted to living in specialized habitat conditions which are found only in limited areas corresponding to the limited distribution of the taxon, which is therefore a relict. This certainly appears to be the case with P. trichophylla, whose distribution is now confined to the upper zone of a single mountain in Greece (mt. Parnassos).

8.3.2 Neoendemism.

In contrast to the previous four species, the neoendemic species of Poa can be further subdivided according to the evolutionary history of the species in relation to their taxonomic relatives. Contandriopoulos (1962) proposed three subsidiary categories:

a) schizoendemics, where two vicarious species having the same chromosome number appear to have a common origin;

b) patroendemics, where an endemic species appears to have given rise by polyploidization to a more widespread species (either by autopolyploidy, or more commonly by allopolyploidy in conjunction with a second parent species);

c) apoendemics, where a widepread, usually diploid, species has given rise to a polyploid endemic.

These categories are more appropriate to the study of endemics which are distributed over relatively small areas, and of course they

are inapplicable to taxa above the level of species.

a) Schizoendemics.

Examples of this type of endemism can be found in sect. Bolbophorum, sect. Coenopoa, sect. Oreinos and possibly also in sect. Stenopoa. In section Oreinos, two pairs of apparently schizoendemic species can be recognized: P. flexuosa and P. fernaldiana Nannf., both hexaploids, occur on the eastern and western sides of the Atlantic Ocean respectively; and P. minor and P. laxa, both tetraploids, both occur in central Europe but have distinctly different ecological preferences (P. laxa having the larger geographical range and inhabiting base-poor habitats). In sect. Bolbophorum, the situation is rather more complex, since it contains five partly sympatric, partly allopatric species which are diploid, two of which are tetraploid (one only doubtfully so). It seems unlikely that any of these species have been directly implicated in recent times in the formation of polyploid species; they cannot therefore be classed as patroendemics. I prefer to regard P. badensis, P. media, P. molineri and P. pumila as schizoendemics of rather ancient origin; the status of P. perconcinna is rather ambiguous, since although there is some affinity between it and P. bulbosa it seems more probable that the latter species originated from central Asia. While it is possible that P. perconcinna is patroendemically related to P. bulbosa, it seems equally possible that it may have originated from the diploid group mentioned above, the similarities with P. bulbosa being due to convergent evolution. The tetraploid strain of P. badensis, which appears to be more limited in its distribution than the diploid strain and the species as a whole, can be regarded as a cryptic apoendemic, if it is assumed that it originated from the diploid through autopolyploidy.

Another pair of species in sect. Bolbophorum show clearer signs of being related schizoendemics: P. ligulata (SW Europe and Morocco)

and P. timoleontis (SW Asia and the Balkan peninsula), which are both diploids, share a number of taxonomic features and in my opinion form a vicarious species pair.

On distributional grounds, the three subspecies of P. cenisia would appear to have originated from a recent common ancestor, and hence to be schizoendemically related. Their karyology, however, suggests a more complex origin; whereas subsp. sardoa is known only at the octaploid level, subsp. cenisia has a wider variety of numbers. The eastern subspecies contracta has not been studied karyologically.

In sect. Stenopoa, the two largely allopatric species P. pannonica and P. versicolor are probably schizoendemics, though in the absence of reliable chromosome number determinations this can only be speculation.

In sect. Ochlopoa, taxonomic changes have been proposed (Fröhner, 1968) which have the effect of creating a species-pair with P. supina occupying the western part of the range of the species as previously understood, plants in the eastern part of its range being re-named as a separate species, P. ustulata Fröhner. The morphological differences mentioned in Fröhner's paper are only slight, and it is possible that the two taxa are conspecific but warrant recognition as subspecies.

b) Patroendemics.

The most noteworthy example of a relatively local endemic species hybridizing with a more widespread species to give rise to an allopolyploid with a world-wide distribution is the case of P. annua, the allotetraploid derivative of P. infirma and P. supina. The distributional ranges of the two parent species hardly overlap, and since they also occupy quite different habitats at the present day the opportunity for hybridization to occur may have been only a rare event. P. annua has been immensely more successful than

either of its parents, colonizing disturbed habitats in every continent.

P. rehmannii, the only known diploid member of sect. Stenopoa, may be a patroendemic in relation to other woodland species of the section, such as P. nemoralis. The possibility that other relict diploids may occur, and that they may have been overlooked by taxonomists or have been given a subordinate taxonomic rank, cannot be ruled out as the great range of variation encompassed by such species as P. nemoralis, P. palustris and P. glauca might well conceal other such diploid species.

c) Apoendemics.

The only clear-cut example of a high polyploid species of Poa in Europe having a restricted distribution is P. granitica (sect. Genisia). This plant has a very localized geographical distribution, which can perhaps be best explained if we suggest that it has originated only recently from a more widespread species of sect. Genisia. After the formation of a species, the two most probable courses of events are either that it becomes extinct or that it progressively enlarges its geographical range. The fact that P. granitica has done neither suggests that it is of recent origin.

Some of the stabilized hybrids between widespread species of Poa have relatively local distributions in relation to the distributions of their parents: for example, P. x hartzii Gandoger, which is known only from Svalbard and Greenland.

8.3.3 Distribution patterns of species largely restricted to Europe.

As in the case of species endemic to Europe, the six species which are largely (but not entirely) restricted to Europe show a number of interesting distribution patterns.

Sect. Homalopoa accounts for three of the six species. All three extend from western Europe to the Caucasus mts., but have

slightly different ranges. P. remota is classed as a boreal species, on account of its more northerly distribution which extends into central Sweden. P. chaixii and P. hybrida are placed in the montane group of species, in view of their habitat preferences for woodlands at intermediate altitudes. P. chaixii has been widely introduced in the lowlands of north-west Europe, having been included in seed mixtures supplied for agricultural purposes. The distribution of the three species in the south-eastern part of their range is not known with such precision as their European distribution; P. chaixii extends into the Transcaucasus and Pontus mountains, while P. hybrida and P. remota appear to be confined to the Ciscaucasus mts.

P. cenisia subsp. contracta has a distribution which is unusual among plants of the montane zone of the Balkan peninsula, in that it extends into the highlands of Anatolia. Though the western groups of mountains in Asiatic Turkey have no lack of suitable habitats for Balkan oreophytes, the climate becomes progressively more severe (especially in winter) as one travels east, and most species infiltrating from the Balkans reach only at most to about half-way through the peninsula. Another alpine plant which undergoes modification is P. alpina, which is represented in most of Anatolia by subsp. fallax F. Hermann. Only in the extreme north-east of Turkey, where the extremely humid climate allows Transcaucasian elements to achieve limited penetration, does typical P. alpina occur (along with other species of Poa such as P. chaixii and P. longifolia).

A third pattern of distribution which overlaps the frontier of Europe is shown by P. flaccidula and P. ligulata. Both species occur in the mountains of eastern and southern Spain, and have also been recorded from the Atlas mountains of northern Morocco. They are taxonomically unrelated; P. flaccidula belongs to sect. Stenopoa,

and P. ligulata is a member of sect. Bolbophorum. Their periods of initial expansion evidently antedate the formation of the straits of Gibraltar.

8.3.4 Distribution of species occurring mainly outside Europe.

The six species belonging to this group all occur mainly in Asia, their ranges extending into quite limited areas of eastern or south-eastern Europe, with the exception of arctic P. abbreviata.

P. timoleontis (sect. Bolbophorum), although it occurs in the southern Balkan peninsula from Greece and Turkish Thrace to Bulgaria and Yugoslavian Macedonia, is more widely distributed in south-west Asia than is generally realized; its extra-European distribution extends easwards through southern Anatolia and northern Syria and Iraq to Iran. Along with P. sinaica, a taxon doubtfully distinct from P. bulbosa, it reaches the southernmost limits of distribution of the genus Poa in south-west Asia by penetrating into Palestine.

P. abbreviata (sect. Abbreviatae), a high-Arctic species with a circumpolar distribution, occurs in Europe only in Svalbard.

P. relaxa (sect. Stenopoa) is widely distributed in Central Asia, extending from west Kazakhstan through Turkmenia and the smaller Central Asian republics to Dzhungaria, southern Siberia, and northern Mongolia. Until recently its only station in Europe was the western salient of Kazakhstan, but it is now recorded from five of the easternmost provinces of European Russia in the region of the Ural mts.

P. sterilis (sect. Stenopoa) cannot be given a definitive range of distribution, since it is taxonomically critical and has been confused with other taxa. It is fairly certain that it occurs in the northern foothills of the Caucasus mts., as well as in Krym. Some interpretations of this species suggest that it extends through Iran and Afghanistan to Kashmir; I believe this to be insufficiently well established, as the plants involved may well belong to a

separate species.

P. sibirica has a very extensive distribution in Asia, extending in the east to the Far-Eastern coastal belt of east Siberia, northern China and Mongolia. It is found further south in the mountains of Central Asia, and is common almost throughout Siberia with the exception of the high-Arctic areas. In the west, it just manages to cross the Urals.

The final species of this group, P. longifolia, is interesting in that it is represented in Krym by an endemic subspecies fagetorum, originally described as a separate species. The overall range of the species, which is centred on the Caucasus mts., extends into north-east Turkey (Pontus mts.), north-east Iraq (Algurd Dagh) and western Iran (Zagros mts.). The Caucasian material, which includes some which was originally described as P. iberica Fischer & Meyer, requires further study in order to establish whether additional subspecies may exist.

8.3.5 Distribution of species widely distributed both inside and outside Europe.

The fifteen species in this category include the majority of the species of sect. Stenopoa with the exclusion of the P. sterilis group, together with the whole of sect. Ochlopoa and sect. Poa, and members of sect. Bolbophorum, sect. Cenisia and sect. Coenopoa.

All three members of sect. Ochlopoa are of widespread distribution; P. annua as a cosmopolitan weed species, P. infirma in coastal habitats around the Mediterranean and elsewhere (having originally been described from South America, where it is undoubtedly introduced), both exploit their capacity for rapid growth and flowering and their annual or ephemeral habit to colonize disturbed ground with great rapidity; P. supina, the only consistently perennial member of the group in Europe, occurs in most of the montane regions of Europe as well as possibly in Central Asia and the Himalayas (but

see Fröhner, 1968, who proposes that Central Asian material named as P. supina belongs to a separate species, P. ustulata).

In sect. Stenopoa, two of the three species in this category are Eurosiberian species of the boreal zone. The third, P. glauca, has a disjunct distribution since it occurs in arctic/subarctic grassland, and also turns up in some (but not all) of the montane regions much further south. It occurs in the Alps, but not in the Pyrenees and in only the most northerly part of the Carpathians. In western Asia it is not recorded from the Caucasus mts., but apparently does occur in the Alborz mts. of northern Iran. It is also recorded from the mountains of Central Asia, where it seems to have a very scattered distribution.

P. nemoralis and P. palustris are very widespread in Europe and Asia; P. nemoralis also occurs in North America (possibly as an introduction), along with a closely related species P. interior Rydb. The distribution of P. palustris in western and north-west Europe is curiously incomplete; it appears to shun areas with a highly oceanic climate, as well as arctic regions.

P. trivialis (sect. Coenopoa) extends from Europe into North Africa and western Central Asia, as well as being recorded from the Himalayas, where it is very probably introduced. It is unusual in being widespread, and apparently native, in Macaronesia (the Atlantic islands). Its more thermophilous subspecies silvicola is more abundant in mediterranean parts of the range of the species, and is particularly widespread in Anatolia.

P. compressa (sect. Tichopoa) is known from Europe and south-west Asia and from the western part of Central Asia. It possibly also occurs in China. It is now widespread in North America, having probably been introduced there in seed used in agriculture.

In sect. Poa, P. pratensis and P. angustifolia are both very

widespread in Europe and Asia. P. pratensis sensu stricto is probably commonest in northern Europe and the central belt of Asia, while P. angustifolia is probably more abundant in somewhat drier areas such as southern Europe, south-west Asia and Central Asia. Both also occur in North America, where they are apparently native.

P. subcaerulea has a rather scattered distribution; in the northern parts of its range, it occupies damp habitats in subarctic regions, while in the southern parts of its range it inhabits marshy habitats and is often overlooked. It is introduced into Far-Eastern regions of Asia and into North America.

P. alpigena (sect. Poa) and P. arctica (sect. Cenisia) have a circumpolar arctic distribution. The former is common in northern Siberia, Scandinavia, Greenland and arctic Canada; the latter has a rather more northerly distribution, with disjunct outlying populations in central Scandinavia and the Rocky mts. of North America and perhaps elsewhere. It is taxonomically close to P. tibetica Stapf; the two species are perhaps even conspecific.

An even more strongly disjunct arctic-alpine species is P. alpina (sect. Bolbophorum). It occurs throughout the arctic regions, and (rather like P. glauca, but more abundantly) reappears in montane habitats throughout Europe, Asia and North America.

The only other widely distributed species of sect. Bolbophorum in Europe, P. bulbosa, is probably centred upon the Irano-Turanian region. It is evidently well-adapted to the arid summers and very cold winters which are characteristic of this region; most other species of Poa occurring in this region are more or less confined to montane habitats, where water stress is not so acute. The distribution of P. bulbosa extends from the Mauretanian steppes of north-west Africa, through the Syrian desert and the interior of

Anatolia and Iran to the Turanian desert, Mongolia and northern China. This is almost exactly the extent of the Irano-Turanian phytogeographical region. Besides being widespread and extremely common in these areas (where it often occupies secondary or overgrazed rangeland, of which there is an abundance) it occurs also in Mediterranean Europe, extending in the west as far as the southern coast of England. Its range in central Europe has been extended in recent times through the influence of Man (Sukopp & Scholz, 1968).

CHAPTER 9. Evolutionary trends.

The absence of fossil evidence as an aid to the interpretation of the history of the genus Poa requires that any comments to be made on its evolutionary origin and diversification must be derived from present-day relationships. Since my new classification of the genus differs in only relatively minor details from previous attempts, the interpretation of the evolution of the various groups can largely be based on earlier observations. These have been relatively few in number; I shall refer only to the accounts of Nannfeldt (1935), Achtarov (1939) and Serebryakova (1965).

Nannfeldt, while reserving his detailed remarks for the members of sect. Oreinos, gives a general account of the then state of classification of the genus. His observations on growth-form are of particular importance, since these not only provide good evidence for separating sect. Coenopoa and sect. Poa (= sect. Pandemos), but also reinforce other changes. This led to a relatively new idea; that changes in shoot-formation which lead to differences in growth-form can be related to stages in an evolutionary sequence (Poyarkova, 1963; Serebryakova, 1965).

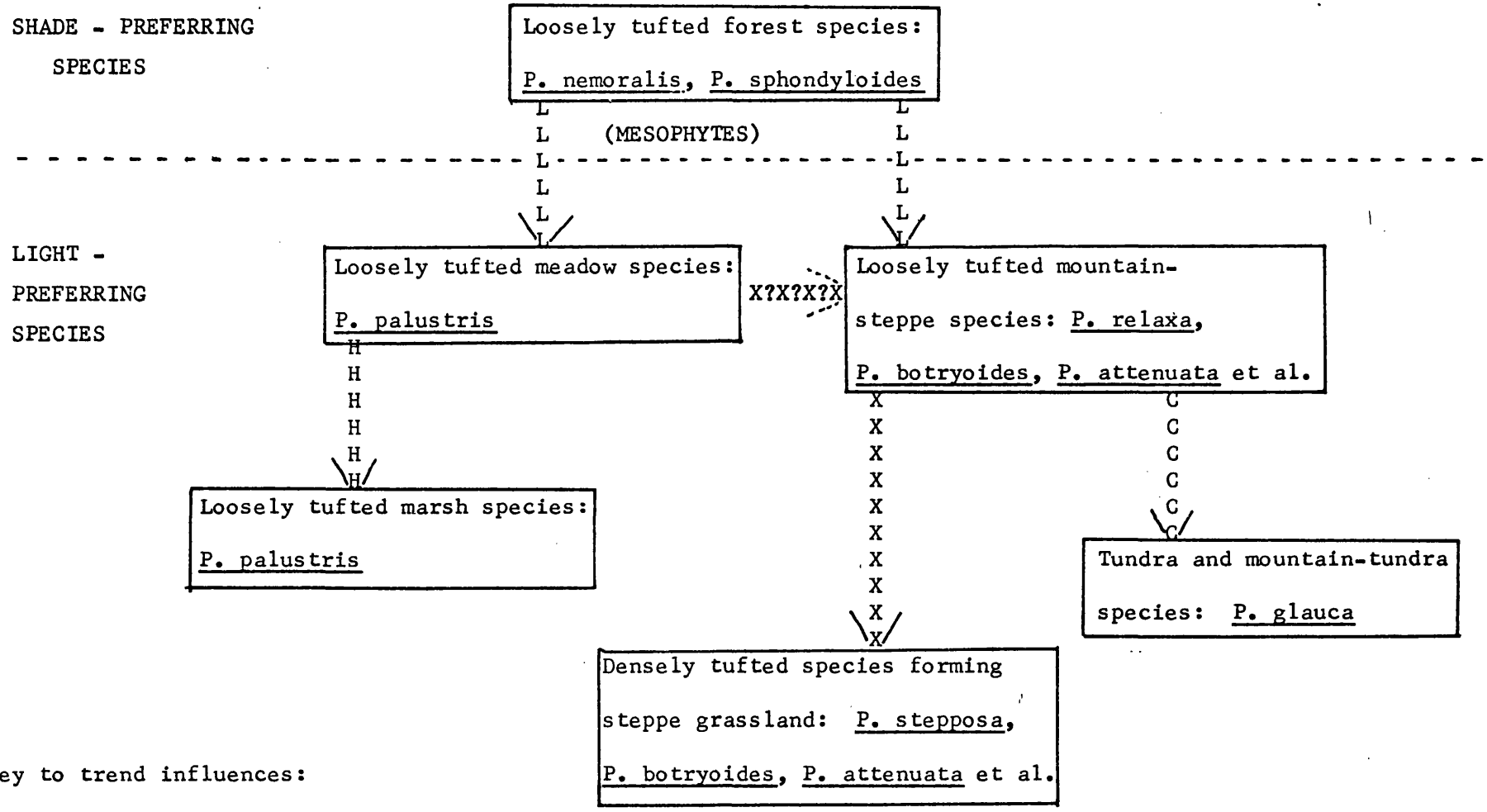
The evolutionary trends which Serebryakova puts forward in her diagram of the changes in life-forms of Poa (fig. 12) are:

a) a trend from shade conditions to conditions of high light intensity;

b) a trend from relatively mesophytic conditions towards an increasingly hydrophytic habitat, as in the change in P. palustris from meadowland to marsh-land;

c) a trend from relatively mesophytic conditions towards xerophytic conditions such as those in the montane species of central Asian steppes (e.g. P. attenuata);

d) a trend from relatively mesophytic conditions towards



Key to trend influences:

LLLLLL = adaptation to high light intensities

HHHHHH = adaptation to waterlogged conditions

XXXXXX = adaptation to shortage of water

CCCCCC = adaptation to low temperatures

Fig. 12. Trends in life-form changes within sect. Stenopoa (after Serebryakova, 1965, p. 1552).

adaptation to arctic conditions, leading to loosely tufted growth-forms characteristic of tundra and sub-tundra species such as P. arctica.

These trends are related to changes in the rates of shoot production which are of adaptive value. A different type of shoot is the type which originates intravaginally (a state not referred to by Serebryakova), leading to greater protection for the young shoot. This is found in sect. Abbreviatae (adapted to arctic conditions) as well as in sects. Nanopoa and Bolbophorum (adapted to xerophytic conditions).

Intravaginal shoots are also encountered in P. longifolia (sect. Macropoa), the more xerophytically adapted of the two species of this section. In this case, however, the intravaginal shoot type occurs together with extravaginal shoots; this is the only example known where both types of shoot occur together.

On morphological grounds, the intravaginal state is likely to be the more primitive type; the extravaginal habit involves the reduction of the lowest leaf sheaths into specialized units, "cataphylls" (sensu Vickery, 1970, p. 152). However, since the sections of Poa in Europe are not those evolutionarily primitive types which have intravaginal innovations (cf. however the often bizarre species of the Flora Malesia area's highlands; Jansen, 1953) we must assume that the intravaginal state is secondary.

Achtarov (1939) in his account of evolutionary trends in Bulgarian species of Poa, particularly the members of sect. Bolbophorum, considers that the principal trend operating in this section is progressive drought adaptation, the most highly evolved members of this section being those which occupy the most xerophytic habitats at the present day. Indeed, some of the species selected by Achtarov as representative of the extreme

or most highly modified taxa forming the end-points of different evolutionary lines are not to be regarded as members of sect. Bolbophorum; P. pirinica, for example, is now placed in sect. Oreinos. The stress placed by Achtarov on the role of increasing aridity as a stimulus to xeromorphic trends in sect. Bolbophorum is particularly valid in connection with the feature of the bulbous stem base (e.g. P. bulbosa); see chapter 5, section 5.2.2.

9.2 Chart of phenetic relationships.

The classification of the European members of Poa which is presented in this work is a purely phenetic one; it is intended only to convey the broad phenetic relationship between groups of different species which are assembled together on the basis of the overall resemblance between them. Only after the process of classification was completed was an attempt made to determine the probable direction of evolutionary changes. Some of the characters with which these changes have been particularly clearly associated are set out in the accompanying table 9.1; the inspiration for this method of presentation was the chart for Thea (Sealy, 1958) illustrated in Davis & Heywood (1963).

9.3 Examples of evolutionary trends.

A discussion of the evidence provided by the data on ploidy levels will be found in chapter 4. Some morphological trends are discussed below.

A. Tall plants become reduced in size.

This trend is associated with drought adaptation in most species, but is also encountered in the arctic as an adaptation to frost damage. The height at which the panicle is borne is determined by the height of the surrounding vegetation; too great an exposure, in adverse conditions, leads to damage of floral parts, while too short a stem will fail to expose the panicle to the breeze. Dry grassland is

shorter, as a rule, than moist grassland; there is thus a pressure towards the reduction in the height of grasses which is one of the forms of drought adaptation.

B. Reduction in number of cauline leaves.

The leaves are mostly basal in most arctic species of Poa, and the trend is also apparent in alpine and drought-adapted taxa. In the case of arctic species - P. abbreviata, P. alpigena, P. arctica and P. glauca - each belongs to a different section and the trend can therefore be said to be a case of convergent evolution. Grazing pressure may also tend to produce a reduction in the number of cauline leaves, since plants having mainly basal leaves will be better fitted for survival.

C. Adoption of an annual habit.

This is an uncommon trend in the genus Poa, but is far from uncommon in related genera of the Festuceae and in these it has proceeded much further; so much so, in Festuca, that annual species placed in such genera as Vulpia are regarded as generically distinct mainly on the basis of this character.

The overall characteristics of section Ochlopoa, the only European section with annual species (other than the unplaced species P. jubata), suggest that it has had a relatively long history of independence from the rest of the genus. The geographical distribution of the members of the section suggests a similar history; the members of the group are scattered over a wide area and have a very disjunct distribution in relation to the distributional centre of the section, which appears to lie in the Himalayas. The sectional diagnosis suggests that the section is highly evolved in other respects; some authors regard it as a distinct subgenus Ochlopoa (A. & Gr.) Hyl. (1953) and point out an affinity between the group and the Puccinellia - Phippsia group. In some respects, however, sect. Nanopoa lies closer

to these genera than does sect. Ochlopoa and it, like Puccinellia, has channelled glumes and lemmas and is perennial in habit.

Another section in which the species are distinguished by their annual habit is sect. Diversipoa V. Jirásek, described in a paper by Chrtek & Jirásek (1962) and including three north American species. The only other annual species of Poa known to me is P. fax WIllis & Court, occurring in Australia, whose taxonomic position, like that of P. jubata, is not known.

D. Reduction in leaf width.

This is accompanied by certain anatomical changes such as a change in the ratio of primary to subsidiary bundles (narrower leaves having fewer secondary bundles) as well as by changes in the bulliform cells and the shape of the keel. A separate trend has probably operated in the reverse direction in sect. Homalopoa and, to a lesser extent, in sect. Macropoa, leading to an increase in leaf width. Neither trend is linked to any very obvious adaptive feature of selective value.

E. Changes in ligule size and shape.

As with leaf width, two separate trends have probably operated in opposite directions. On the one hand, short acute hyaline ligules have become modified to form more elongate, often lacerate milky-white ligules; on the other hand, short acute to rounded ligules have become reduced in length, first to truncate ligules and ultimately to the ligule being obsolete or absent.

The first trend, involving an increase in the length and prominence of the ligules, is associated with drought-adapted species, and by increasing reflectivity at the base of the leaf-blades, it may confer protection against high radiation intensities at high altitudes and in Mediterranean climates. The prominent milky-white ligules of P. ligulata and P. timoleontis, for example,

show a parallelism with other high-mountain groups which achieve protection by a cushion-forming habit or by various types of reflective hairs, spines or cuticles. The importance of the position of the ligule in rendering such protection is that it shields the intercalary meristem from damage.

The second trend has no obvious functional significance. The extreme state, in which the ligule is very short or entirely absent, is found in only a few species of Poa; these are generally found in quite shady conditions in forests, e.g. P. nemoralis (sect. Stenopoa) and P. chaixii (sect. Homalopoa) though another member of sect. Stenopoa with a very short ligule - P. rehmannii - occurs in the montane zone of the Carpathian mts.

F. Compression of the stem.

There is little doubt that the flattening of the stem in some species of Poa is a secondary modification, and that the terete stem is the primitive condition. The functional significance of a flattened stem is obscure; it may facilitate the photosynthetic function of the stem by exposing a greater area of chlorenchyma to the light, in proportion to the volume.

In sect. Ochlopoa, where the whole of the stem is slightly compressed, and in sect. Tichopoa (P. compressa) and sect. Stenopoa (P. rehmannii) where the upper part of the stem is strongly compressed, the flattening is more likely to be seen as a modification in its own right, whereas in sect. Homalopoa and sect. Macropoa, where only the base of the stem is flattened, the stem is clearly compressed in order to accomodate the flattening of the strongly-folded leaf-sheaths.

G. Loss of scabridity of the stem and panicle-branches.

The occurrence of aculeoli on the upper part of the stem is relatively rare, and does not appear to be a primitive feature in

the genus Poa. Unless they have arisen de novo, however, it is apparent that the stem aculeoli are a primitive feature which has been retained by taxa which are now highly evolved in other respects. In the case of the panicle branches, the direction of the trend is relatively unambiguous; those sections in which the panicle branches are smooth are, in general, more highly specialized than those with aculeolate panicle branches, and the direction of the trend must therefore be towards the loss of aculeoli. The significance of such a change is obscure.

H. Reduction in number of panicle branches at each pseudowhorl.

This trend is associated with a reduction in the size, and particularly the width, of the panicle and with the shortening of the length of the panicle branches, (see section I below).

The number of branches appears to relate to the size and density of the panicle; the number is rather variable, however, and direct measurements of panicle length are of greater systematic value than accounts which refer to the number of branches at each pseudowhorl (e.g. Fiori, 1923).

I. Changes in length of panicle branches.

A trend towards a reduction in the length of the lowest panicle branches is the principal feature in the genus Poa. The more strongly xeromorphic members of sect. Bolbophorum, which have a narrowly elliptic to ovoid panicle, are clearly derived from taxa ancestral to P. alpina (a species which itself has probably a rather complex evolutionary history), in which the panicle is more or less pyramidal in shape. Similarly, the vicarious pair of species P. ligulata (Ibero-montane) and P. timo--leontis (Balkan - South-west Asian xerophyte) illustrate this difference; P. ligulata has a more or less pyramidal panicle, while P. timoleontis has a more or less ovoid panicle.

Another trend appears to have operated in the reverse direction in P. remota (sect. Homalopoa) which has developed extremely long, rather pendulous branches in which the spikelets are grouped towards the apex. P. flaccidula (sect. Stenopoa) is also characterized by its rather elongate lower panicle branches, and again the feature is accentuated by the tendency of the spikelets to be grouped towards the apex of the branches.

J. Trends within the spikelet.

These are almost totally obscure. The two characters showing most correlation with sectional divisions are illustrated in table 9.1; these are the indumentum of the lemma, and of the palea keels. A good deal of imagination is required to propose reasons for these differences. Even features with a functional significance, such as the presence of wool on the callus attached to the base of the lemma, show no obvious trend within the genus. Other characters, such as rhachilla indumentum features, have a similar significance as possible aids to dispersal, while others have no obvious significance at all; for example, the width of the glumes, and the indumentum of the palea surface between the keels.

The following list presents a number of possible factors which may have influenced the development of these characters:

a) prevention of water loss from tender sexual organs;

b) the effective exposure of stamens and stigmata at anthesis;

c) the aerodynamics of the spikelet at anthesis in relation to the dispersal and capture of pollen;

d) the prevention of insect attack;

e) drainage and/or retention of rain water.

As it would be impossible to quantify these characters, their influence on evolutionary trends in the characters of the spikelet remain obscure.

K. Changes in the type of apex of the hairs on the lemma.

Variation in the shape of the apex of the hairs which occur on the lateral veins of the lemma was first revealed by Chrtek & Jirasek (1965b), who also suggested that there might be an evolutionary trend from hairs with a shortly acute (ogival) apex, to those with long-pointed apices and further to those with club-shaped apices. They draw an analogy between these hairs and the hairs on the margins of the palea in P. alpina, which are blunt-tipped towards the base and which become progressively more pointed above before becoming shortened and eventually being replaced by aculeoli towards the apex. I am rather doubtful whether this analogy holds true, but I am prepared to agree that the evidence suggests that hairs with rounded or ogival apices are characteristic on the whole of the more primitive taxa, while taxa with long-acute or club-shaped apices of hairs on the lemma are mostly more highly evolved. For a fuller account of the distribution of hair types, see chapter 5.

9.4 Rates of evolution of characters and of taxa as a whole.

The discussion above has referred to changes in individual characters. These changes are not necessarily linked to the processes of speciation, and these two aspects of evolutionary change have often been confused. Speciation preserves modifications which have caused successful populations to diverge in different ways from their parental stock; it does not introduce new characters as such, except where the process of speciation involves hybridization where the interplay of dominant and recessive alleles of genes causes new combinations of features to occur.

In other words, the erection of a breeding barrier during speciation may not in itself bring about immediate taxonomic differences between

two halves of an 'incipient species assemblage', though it will tend to accentuate differences already existing between geographically separate populations. Likewise, the process of modification of particular organs in response to selection pressures does not lead invariably to the formation of a new species, since the modifications may be proceeding in concert throughout all the populations of the species.

At a supra-specific level in the taxonomic hierarchy, the character states which are used to define the taxonomic groups are derived from two sources: those which have undergone parallel modification in the separate members of the group in question, and those which were attributes of the ancestral species from which the present-day members of a group are originally derived. Since in the absence of any fossil evidence in the genus Poa it is impossible to distinguish between these two types of source of variation, there is no scientific basis for statements which designate certain sections as being derived from certain other sections as presently constituted.

A section which combines the maximum of characters which can reasonably be regarded as primitive, with a minimum of 'derived' or 'advanced' characters, can be regarded as having an ancient origin; sections with a maximum of highly-derived characters can be regarded as being of recent origin. Despite the fact that most sections of Poa combine primitive and advanced forms of different characters, some are clearly more primitive overall than others. The possibility therefore exists of allocating the sections of Poa to different positions on a phylogenetic tree (Sporne, 1948; Davis & Heywood, 1963). Such an exercise has little value unless it is performed on all the members of the genus, and not merely on those members which happen to occur in Europe. For this reason, I will merely suggest which are the more primitive, and which the more advanced,

sections of Poa with reference to a modified diagram of a phylogenetic tree (taken from Sporne's original) incorporating those features which can be recognized in the likely evolutionary history of the genus Poa (fig. 13).

P. pratensis is the type species of the genus, subgenus, and section Poa. While it is clearly primitive in certain respects - growth-form, for example - it is clearly an advanced group overall and its complex karyology indicates a long history of evolutionary changes. Sect. Ochlopoa, on the other hand, though annual in some species (a derived state) incorporates a number of primitive features and it, and sect. Nanopoa, come closest to my idea of a primitive or 'ancestral' taxon, corresponding to E in the diagram.

Two other main types can be distinguished; those corresponding to groups A to D and H, J & K in the diagram. In the latter group, evolutionary modifications have occurred at an early stage and the resultant taxa have survived relatively unaltered to the present day. Such groups as sect. Abbreviatae, Homalopoa and Oreinos correspond to this type. Such sections can be further identified by their stable, generally low, chromosome numbers, since groups with high and irregular chromosome numbers will be prone to continuing to be modified, to hybridize etc. The sections with low, stable chromosome numbers are also often characterized by relict distributions (if taxonomically isolated) or by disjunct distributions (if polytypic). Examples of the former sub-type include sect. Nanopoa and sect. Leptophyllae; the sections mentioned earlier comprise the latter subtype.

In contrast to these sections are such sections as sect. Poa and sect. Cenisia, which correspond to groups A to D in the diagram. The diagram has been modified to illustrate a probable occurrence in

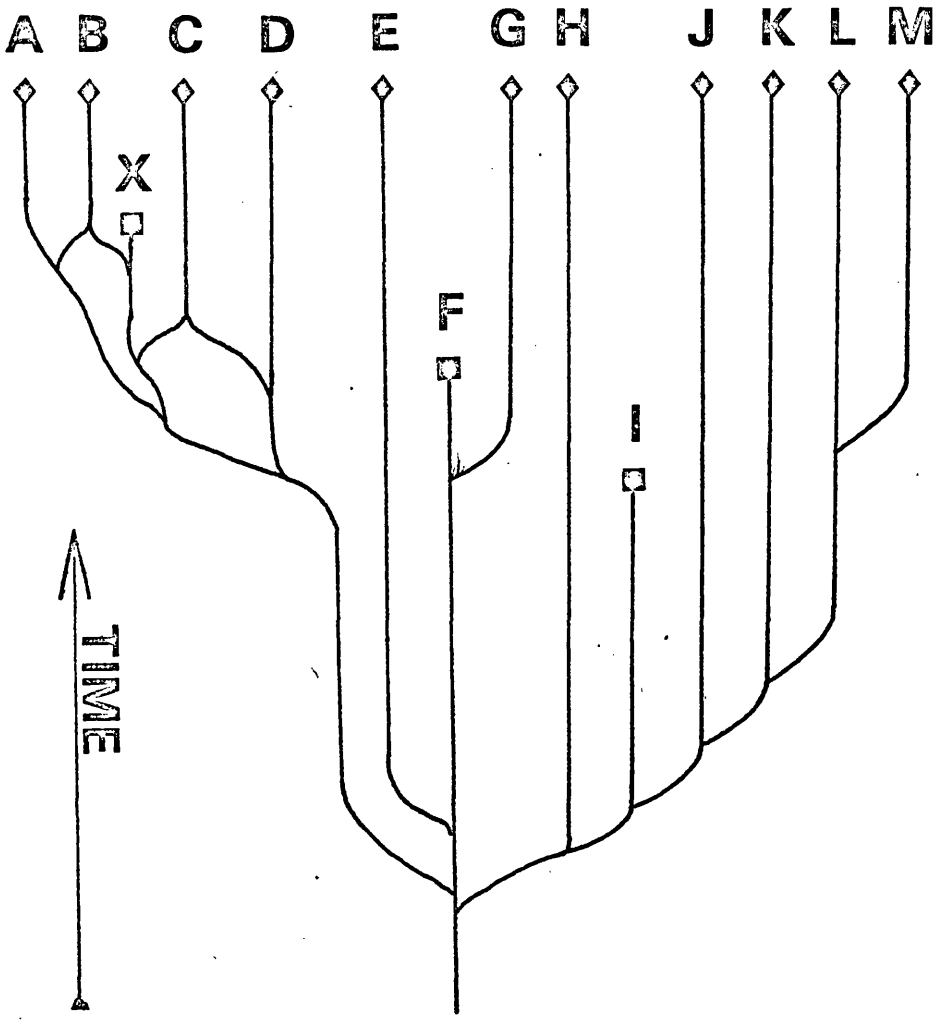


Fig. 13. Hypothetical phylogenetic tree.

(See text for explanation)

□ Extinct taxa

◇ Taxa at the present day

the ancestry of groups A to D (represented by sects. Cenisia, Poa and Stenopoa) in which intersectional hybridization between a now extinct ancestor X with groups A and D respectively.

In view of the very restricted present-day distribution of sect. Nanopoa, it is not difficult to imagine its occupying the position of group I (extinct).

Besides the overall phenetic resemblances shown in table 9.1, two other sources of information can give further clues to the degree of evolutionary advancement of the various sections of Poa. The first is biosystematic data. From detailed data on karyotype morphology, evolutionary sequences can be deduced with greater consequent accuracy. Such data is almost non-existent for Poa. The second source is distributional data; see also chapter 8. The correlation between the geographical areas occupied by the constituent members of a group, and its evolutionary history, was first explored by Bunge (1872) in his monograph of Acantholimon (Plumbaginaceae). He presented a phylogenetic tree in which the most important diagnostic morphological features are indicated by means of a colour-code. Combinations of characters are indicated in a similar way. By mapping the species with the same colour code, the geographical extent of the various 'phylogenetic lines' can be seen at a glance, and it is evident from the diagram (p. 74 of the monograph) that the various lines have characteristic areas of distribution.

Willis (1922) developed this line of investigation into a novel and rather controversial theory, the Theory of Age and Area. He proposed that the age of a taxon is indicated by the size of the area over which it is distributed, rather as the diameter of a patch of lichen indicates the age of the colony. While this

theory takes no account of extinction, and thus greatly over-simplifies the question, it can help in characterizing the different types of area of distribution of the members of the genus Poa. Its importance for evolutionary interpretation lies in the fact that it shows that a group which is widely and often disjunctly distributed (e.g. sect. Oreinos) cannot be evolutionarily young, even though its members may not have diverged greatly from one another or from the remaining members of the genus.

At the other extreme, the minimal areas occupied by the SE European endemic members of the P. sterilis group (see also chapter 7) are shown by this theory to be due to the extreme youth, in evolutionary terms, of the species such as P. versicolor and P. pannonica.

Taken in conjunction with one another, geographical, morphological, anatomical and karyosystematic evidence permits certain broad conclusions to be drawn on the evolutionary relationships between the different European sections of Poa. These are tabulated in table 9.2, and further illustrated in fig. 14. The disposition of the sections in the figure is the same as their arrangement in table 9.1; only the lines linking the different groups are intended to be significant. These suggested relationships may serve as a basis for future studies.

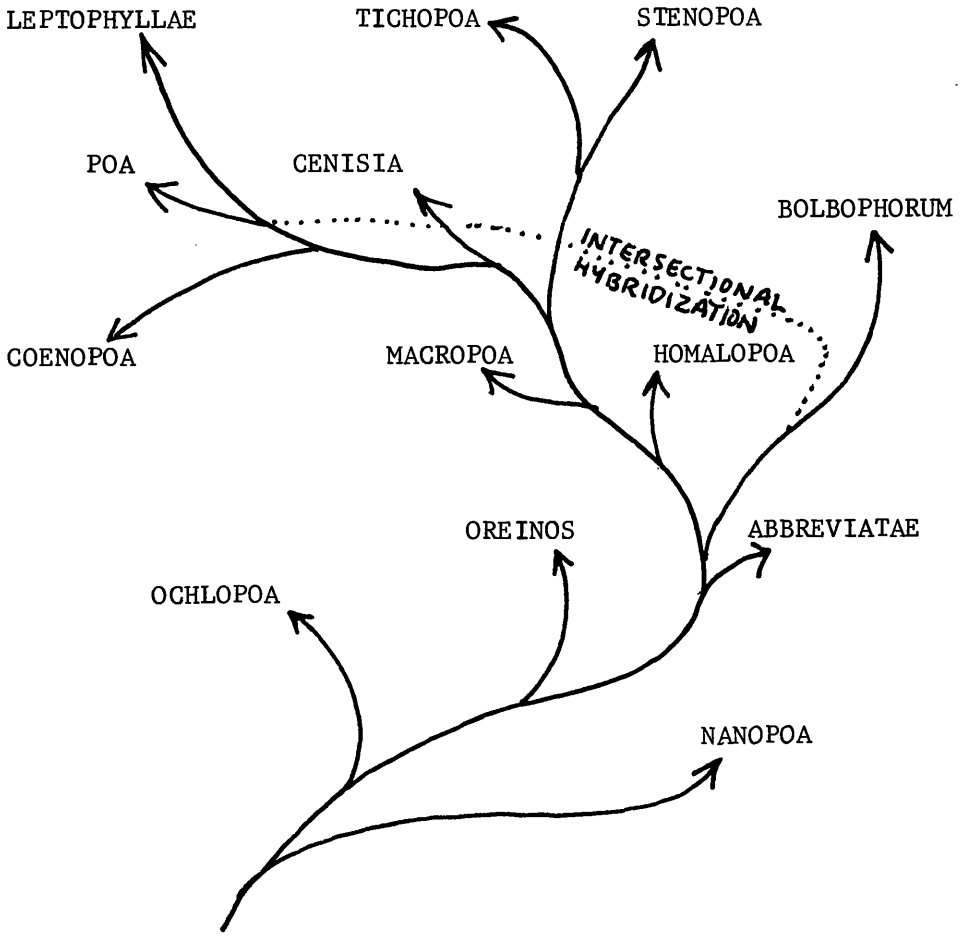


Fig. 14. Projected evolutionary relationships between the European sections of Poa.

B I B L I O G R A P H Y

The bibliography comprises references to works cited in the text. Floras etc. in which the names of supraspecific taxa (e.g. sections) have been published are also included; places of publication of names of sections accepted in the present classification are cited in chapter 1 (paragraph 1.7, pp. 31 - 35). Places of publication of the currently accepted European species and subspecies are cited in Appendix 1.

Russian and Bulgarian authors' names, and the titles of works originally published in Russian or in other languages using the Cyrillic script, have been transliterated according to the system of the British Standards Institute (B.S. 2979), except that the superscript bar over the letter ы (ȳ) has been omitted.

An asterisk (*) is used to indicate titles which have been transliterated. The following table gives the Russian and transliterated Roman equivalents:

А = A	М = M	Ч = CH
Б = B	Н = N	Ш = SH
В = V	О = O	Щ = SHCH
Д = D	П = P	ъ = " (hard sign)
Е = E	Р = R	ы = y
Ж = ZH	С = S	ь = ' (soft sign)
З = Z	Т = T	Э = É
И = I	У = U	Ю = YU
Й = Ĭ	Ф = F	Я = YA
К = K	Х = KH	
Л = L	Ц = TS	

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A P P E N D I C E S T O T H E T H E S I S

Appendix 1: Flora Europaea account of the European taxa of *Poa*.

Appendix 2: Preparative techniques employed.

Appendix 3: Loans received from other herbaria.

Appendix 4: Original chromosome determinations.

APPENDIX 1. Flora Europaea account of the European taxa of Poa.

Note: sectional diagnoses, literature references, and chromosome numbers are omitted; these can be found at appropriate places in the main body of the thesis.

Poa L.

Annuals or perennials. Inflorescence a panicle. Spikelets laterally compressed, with (1-)2-10 florets. Glumes keeled, membranous, usually 3-veined or the lower 1-veined; lemma 5-veined, keeled, membranous, awnless or rarely with a short terminal awn. Palea 2-keeled, the keels aculeolate or ciliate. Caryopsis ellipsoidal; hilum basal, punctiform. Rhachilla disarticulating at the base of each floret.

Measurements of ligules refer to those of the leaves of flowering stems unless otherwise stated. Measurements of the panicle refer to well-grown panicles from the middle of the flowering season. Anthers are measured when mature but undehisced.

A. Key to proliferous taxa of Poa.

1 Rhizomatous

2 Ligule not more than 1 mm

3 Base of stem enclosed by thickened leaf-sheaths

.. .. .. 6 x 43. x herjedalica

3 Base of stem not enclosed by thickened leaf-sheaths

.. .. 6. alpigena

2 Ligule 1 - 5 mm

4 Stem 25 - 40 cm; ligule 2 - 5 mm, subacute; spikelets with two florets, usually only the upper proliferous

.. .. .. 48. x nobilis

4. Stem 10-20 cm; ligule 1-3.5 mm, acute to rounded; spikelets with 2-4 florets

5 Leaves (1-)1.5-2.5 mm wide, flat, with a slightly cucullate apex .. .. 10. arctica

5 Leaves 1-2 mm wide, flat or folded, tapering gradually to the apex .. .. 19 x 43. x jemtlandica (47. in flora)

1 Caespitose

6 Base of stem bulbous

7 Stem 15-40 cm; ligule up to 3 mm, hyaline; propagules bulb-like .. .. 35. bulbosa

7 Stem 12-20 cm; ligule 3-6 mm, milky-white; propagules leaf-like .. .. 38. timoleontis

6 Base of stem not bulbous

8 Leaves 1-2 mm wide, flat to folded, tapering gradually to the apex; uppermost leaf-blade arising more than half way up the stem .. .. 47. x jemtlandica

8 Leaves 2-4.5 mm wide, flat, apex cucullate; uppermost leaf-blade arising less than half-way up the stem .. .. 43. alpina

B. Key to non-proliferous material of Poa.

1 Lemma with a short terminal awn .. .. 45. flabellata

1 Lemma awnless

2 Annual or perennial; palea keels ciliate along at least ⅔ of their length with flexuous,or crispate hairs

3 Stems solitary or few, purple-tinged at base; marginal veins of lemma densely tomentose with crispate hairs .. .. 44. jubata

3 Stems grouped together, greenish; marginal veins of lemma densely ciliate with short, straight hairs

4 Lower panicle-branches erecto-patent after anthesis; spikelets with rather distant florets; anthers 0.2-0.5 mm, scarcely longer than wide .. .. .. 2. infirma

4 Lower panicle-branches patent or deflexed after anthesis; spikelets with crowded florets; anthers 0.6-2 mm, at least twice as long as wide .. ..

5 Spikelets distributed along most of length of panicle-branches; anthers 0.6-0.8(-1) mm, 2-3 times as long as wide .. .. 1. annua

5 Spikelets crowded towards apex of panicle-branches; anthers 1.6-2 mm, 5-8 times as long as wide .. 3. supina

2 Perennial; keels of the palea aculeolate, or ciliate only in the lower half

6 Leaves 0.3-0.6 mm wide, tightly convolute to filiform

7 Base of stem bulbous .. .. 35. bulbosa

7 Base of stem not bulbous

8 Stem (30-)50-80(-100) cm; panicle 4-18 cm, branches densely scabrid .. .. 18. stiriaca

8 Stem 6-30 cm; panicle not more than 2.5(-4) cm, branches smooth

9 Stem 6-10 cm; ligule 1.5-2 mm, acute; glumes obtuse, scarcely keeled .. .. 34. trichophylla

9 Stem 5-30 cm; ligule c. 0.5 mm, truncate; glumes acute, distinctly keeled .. .. 21. pirinica

6 Leaves more than 0.6 mm wide, flat or folded

10 Stem stout, strongly compressed towards the base

11 Rhizomatous; leaves 1-2 mm wide .. 13. longifolia

11 Caespitose; leaves (4-)7-12(-15) mm wide

12 Leaves tapering gradually to the apex; ligule 3-5 mm, acute to rounded .. .. 16. hybrida

12 Leaves abruptly contracted to a cucullate apex; ligule 1-3 mm, rounded to truncate

13 Panicle-branches long, arcuate-pendent; glumes subequal; lemma sparsely hairy on the keel, lanate at base .. .. 17. remota

13 Panicle-branches short, erecto-patent; glumes unequal; lemma usually not lanate at base .. 15. chaixii

10 Stem ± slender, terete or compressed mainly above

14 Stem bulbous at base; glumes widest below the middle, with a strongly curved keel

15 Leaves (0.6-)1-2 mm wide; stem 15-40 cm; lemma lanate at base; spikelets with 2-6 florets .. .. 35. bulbosa

15 Leaves 0.6-1 mm wide; stem 5-20 cm; lemma not lanate at base; spikelets with 5-10 florets

16 Stem 12-20 cm; spikelets purple-tinged; ligule up to 6 mm, prominent, milky-white .. 38. timoleontis

16 Stem 5-10(-25) cm; spikelets greenish; ligule not more than 2 mm, inconspicuous, hyaline .. 36. perconcinna

14 Stem not bulbous at base; glumes usually widest at or near the middle, with a rather weakly curved keel

17 Base of stem enclosed by thickened leaf-sheaths; lateral shoots intravaginal; lower panicle-branches 1-3 together

18 Ligule c. 1mm, inconspicuous, rounded to truncate; anthers up to 0.7 mm .. .. 33. abbreviata

18 Ligule 1-7 mm, ± conspicuous, acute to tuuncate

19 Lemma hairy between the veins

20 Leaves 4-10 cm, green; lower cauline and basal leaves with a short, rounded to truncate ligule; panicle ± pyramidal .. .. 43. alpina

20 Leaves (1.5-)2.5-6 cm, glaucous; lower cauline and

basal leaves with an elongate, acute to rounded ligule

21 Leaves 1.5-2.5 mm wide, channelled to strongly folded; stem leaves with a 1-2 mm, ± rounded ligule .. .. 41. molineri

21 Leaves 2-4.5 mm wide, flat to weakly folded; stem leaves with a 2-6 mm, acute ligule .. .. 42. badensis

19 Lemma glabrous between the veins

22 Stem (15-)20-30(-40) cm; panicle 3.5-5 cm, ellipsoid-oblong .. .. 39. media

22 Stem 6-20(-30) cm; panicle 1-5 cm, ovoid to pyramidal

23 Ligule 1-2 mm, hyaline; glumes subequal .. .. 40. pumila

23 Ligule 2.5-6.5 mm, milky-white; glumes unequal

24 Leaves 1.2-1.8 mm wide, flat .. 37. ligulata

24 Leaves 0.5-1.0 mm wide, folded .. 38. timoleontis

17 Base of stem not enclosed by conspicuously thickened leaf-sheaths; lateral shoots extravaginal; lower panicle-branches 2-7 together

25 Panicle-branches smooth; plant ± densely caespitose

26 Panicle-branches terete; uppermost leaf without a distinct sheath .. .. 22. minor

26 Panicle branches sulcate; uppermost leaf with a distinct sheath

27 Panicle rather compact; marginal veins of lemma hairy for most of their length; hairs obtuse .. 20. laxa

27 Panicle lax; marginal veins of lemma for c. ¼ of their length; hairs acute .. .. 19. flexuosa

25 Panicle-branches ± scabrid

28 Long-creeping rhizomes absent

29 Ligule of uppermost leaf 3-10 mm, acute

30 Spikelets with 2 florets; lowest panicle-branches

in pairs .. .. 5. feratiana

30 Spikelets usually with 3 or more florets; lowest panicle-branches 3-5 together .. .. 4. trivialis

29 Ligule of uppermost leaf not more than 3.5 mm;

31 Ligule not more than 0.5 mm; stem smooth

32 Sheaths of cauline leaves compressed, with a distinct raised keel; stem compressed; leaves (3-)4-5 mm broad .. .. 28. rehmannii

32 Sheaths of cauline leaves terete, without a prominent keel; stem terete; leaves 1.5-2(-3) mm wide .. 27. nemoralis

31 Ligule 1-3.5 mm, acute to truncate; stem smooth to scabrid

33 Stem (10-)17-35(-55) cm, stiffly erect; stem usually very glaucous .. .. 26. glauca

33 Stem 30-80(-120) cm, geniculate-ascending to erect; stem not or slightly glaucous

34 Ligule 2.5-3.5 mm, acute; panicle branches in pairs at each lower node; lemma adpressed-hairy between the veins .. .. 24. flaccidula

34 Ligule up to 3 mm, acute to truncate; panicle branches up to 5 together at each lower node; lemma hairy on keel and marginal veins, glabrous between the veins

35 Plant ± laxly caespitose; stems (15-)40-80 cm, smooth; panicle (8-)12-20(-30) cm .. .. 25. palustris

35 Plant ± densely caespitose; stems 20-45(-65) cm, scabrid; panicle 3-12(-17) cm .. .. .. (29-32). sterilis group.

28 Long-creeping rhizomes present

36 Stem strongly compressed, especially above, often purple-tinged at the nodes; lemma glabrous or sparsely hairy .. .. 23. compressa

36 Stem terete, without purple-tinged nodes; lemma usually hairy on the veins

37 Stem leafy for about half its length; ligule 1.5-9 mm

38 Stem 10-15(-20) cm; panicle 3-5 cm, rather open, with few spikelets; glumes unequal, the upper wider and longer than the lower .. .. 10. arctica

38 Stem 24-50(-70)cm; panicle 5-10 cm, open or contracted, with ± numberous spikelets; glumes subequal

39 Ligule (3-)5-9 mm, acute; spikelets greenish; lemma shortly hairy on keel and marginal veins; anthers (1.2-)1.5-2 mm .. .. 12. cenisia

39 Ligule 2-5 mm, rounded to truncate; spikelets variegated in colour with brownish, golden or violet bands; lemma lemma ± long-hairy on keel and marginal veins; anthers 2-2.4 mm .. .. 11. granitica

37 Stem leafy for ¾ or more of its length; ligule usually less than 1 mm, truncate

40 Lemma glabrous, not lanate at base .. 14. sibirica

40 Lemma hairy on keel and marginal veins, lanate at base

41 Leaves 2-3.5(-4) mm wide, abruptly cucullate at apex; lower panicle-branches mostly in pairs 6. alpigena

41 Leaves 0.8-3 mm wide, gradually narrowed to apex; lower panicle-branches (2-)3-5 together .. (7-9). pratensis group

Sect. OCHLOPOA Ascherson & Graebner.

1. P. annua L., Sp.Pl. 68 (1753).

Usually annual, flowering throughout the year; erect to shortly creeping. Stems 5-30 cm, slightly compressed. Leaves (1-)2-3 mm wide, thin, flaccid, often transversely wrinkled. Panicle (1-)3-8 cm, ± pyramidal; lower branches in pairs, patent or deflexed after anthesis. Spikelets distributed along most of length of panicle-branches, with 3-5 florets. Glumes unequal. Lemma sparsely hairy on veins. Palea

ciliate along whole length of keels. Anthers 0.6-0.8(-1) mm, 2-3X as long as wide. Throughout Europe. All except Sb.

An allotetraploid formed after hybridization of 2 and 3; a successful, almost cosmopolitan weed which forms sterile hybrids with the following two species.

2. P. infirma Kunth in Humb., Bonpl. & Kunth, Nov. Gen. Sp. 1: 158 (1815) (P. annua subsp. exilis (Tomm.) Murb.).

Like 1 but flowering in spring; stems more strongly compressed; leaves 1-2 mm wide; panicle elongate-ovoid, the branches erecto-patent after flowering; spikelets with 5-6 relatively widely spaced florets; anthers 0.2-0.5 mm, scarcely longer than wide. S. & W. Europe northwards to S.W. England. Al Bl Br Co Cr Ga Gr Hs It Lu Sa Tu.

3. P. supina Schrader, Fl. Germ. 1: 289 (1806) (P. annua subsp. supina (Schrader) Link, P. foucaudii Hackel).

Like 1 but stouter, creeping and perennial, flowering in spring; panicle laxly pyramidal, the lower panicle-branches patent after flowering; spikelets crowded towards apex of panicle-branches; lemma glabrous on keel, hairy on marginal veins; anthers 1.5-2.5 mm, 5-8 times as long as wide. Mountains of C. Europe, S. to Pyrenees and Appennines; Fennoscandia; one station in Latvia. Au Co Cz Da Fe Ga Ge He Ha Hu It Ju No Po Rm Rs(N,B,C,E) Su.

Sect. COENOPOA Hylander.

4. P. trivialis L., Sp.Pl. 67 (1753).

Stems (30-)50-90 cm, smooth or weakly scabrid at apex. Leaves 2-4.5 mm wide, rather thin and soft; ligule 3.5-10 mm, acute. Panicle (9-)15-25 cm, ovoid-pyramidal, lower branches 3-5 together. Spikelets usually with 3 or more florets. Lemma shortly hairy on keel, lanate at base. Palea keels aculeolate. Throughout Europe. All except Sb.

(a) Subsp. trivialis: Stolons slender, terete. Leaves pale green; ligule 3.5-5(-6) mm. Panicle pyramidal, rather open. Throughout

most of the range of the species, but rare in the south.

(b) subsp. silvicola (Guss.) Lindb. fil., Finska Vet.-Soc. Förhandl. 38 (13): 9 (1906) (P. silvicola Guss.): stolons moniliform, fleshy. Leaves bright green; ligule 5-10 mm. Panicle narrowly ovoid, rather contracted. S. Europe.

5. P. feratiana Boissier & Reuter, Pugillus 128 (1852).

Like 4 but leaves 1-2 mm wide; ligule 3.5-6.5 mm; panicle-branches mostly in pairs; spikelets always with 2 florets; lemma not lanate at base. Endemic; W. Pyrenees and N.W. Spain. Ga Hs.

Sect. POA.

6. P. alpigena (Fries) Lindman, Svensk Fanerogamfl. 91 (1918) (P. pratensis subsp. alpigena (Fries) Hiitonen).

Plant 20-30(-50) cm, without long rhizomes, not forming compact tussocks; non-flowering shoots distichously leafy. Leaves 2-3(-4) mm wide, abruptly contracted into a cucullate apex. Panicle 6-8 cm, compact, ovoid to pyramidal, the lower branches usually in pairs. Spikelets with 3-5 florets, sometimes proliferating; palea keels ciliate below. N. Europe. Fe Is No Rs(N,C) Sb Su.

Plants from the Arctic with proliferating spikelets have been named P. pratensis subsp. colpodea (Th. Fries) Tsvelev, Nov. Syst. Pl. Vasc. (Leningrad) 9: 47 (1972); they are sometimes confused with 10 and with the following hybrid, which usually has a proliferous inflorescence.

6 x 43. P. x herjedalica H.Sm., Veg. Utvecklingshist. Centralsvensk. Högfjällsomr. (Norrl. Handbibl. 9) 159 (1920): appears to be an unstabilized hybrid, since it is rather variable and occurs only in areas where the parents, P. alpigena and P. alpina, grow together. Like 6 but with short rhizomes; stem base enclosed by conspicuously thickened leaf sheaths; ligule 1-2.5 mm, rounded; inflorescence usually proliferous. Fennoscandia; probably endemic. Fe No Rs(N) Su.

(7-9). P. pratensis group.

Moderately to densely caespitose, without distichously leafy non-flowering shoots. Leaves 0.8-3 mm wide, tapering gradually to the apex. Panicle more or less lax, ovoid to pyramidal, the lower branches 2-5 together. Spikelets with 3-5 florets, not proliferating. Anthers 1.4-2 mm.

The members of this group are highly variable and largely apomictic; specific limits are therefore difficult to define. The three taxa treated here as species may be considered ecotypic variants of Poa pratensis in its broadest sense. However, these taxa have probably arisen on more than one occasion, as a result of the hybridization of various ancestral species followed by an increase in the chromosome numbers of the offspring, and disruption of their breeding system. Intercrossing is probably now only a rare event; within the limits imposed by their predominantly agamospermous breeding systems, they can therefore be regarded as species.

1 Stems ± isolated, with few dead leaf-sheaths at base; ligule tomentose on the abaxial surface; glumes equal, usually both 3-veined .. .. 7. subcaerulea.

1 Stems clustered, forming distinct tussocks, with numerous remains of leaf-sheaths at the base; ligule glabrous or subglabrous; glumes unequal, the lower shorter than the upper and usually 1-veined

2 Plant laxly caespitose; basal leaves flat or channelled, much shorter than the stem; ligule decurrent on sheath-margins; panicle scarcely longer than wide .. 8. pratensis

2 Plant densely caespitose; basal leaves strongly folded, wiry, nearly as long as the stem; ligule not decurrent; panicle up to twice as long as wide .. .. .. 9. angustifolia

7. P. subcaerulea Sm., Engl. Bot. 1: 1004 (1801) (P. irrigata Fries, P. pratensis L. subsp. irrigata (Fries) Lindm., P. athroo-

-stachya Oett.).

Somewhat glaucous, with rather isolated stems (15-)20-30(-45) cm. Leaves 1.5-2.5 mm wide, fringed with hairs at the base. Ligule c. 1 mm. Panicle (3-)4-6.5 cm, the branches mostly in pairs. N. & C. Europe. Br Cz Da Fa Fe Ga Ge Hb Ho Hu Is No Rs(B,C,N,W) Su.

8. P. pratensis L., Sp.Pl. 67 (1753) (incl. P. pinegensis Rozhev., ?P. turfosa Litv.).

Bright green, rather laxly caespitose; stems (15-)20-50(-70)cm; leaves 2-3 mm wide, flat or channelled, shorter than the stem. Ligule c. 1 mm. Panicle 6-15 cm, the lower branches mostly 3-5 together. Throughout Europe. All except Az Bl. I casual record only from Az.

9. P. angustifolia L., Sp.Pl. 67 (1753) (P. pratensis subsp. angustifolia (L.) Gaudin).

Greyish green, densely caespitose; stems (30-)50-70 cm. Leaves up to 40 cm x 0.8-1.5(-2) mm, the basal wiry, strongly folded, the upper shorter, sometimes almost flat. Ligule 1-3 mm. Panicle 6-10 cm, the lower branches 3-5 together. Most of Europe. Au Az Be Br Bu Co Cz Da Fe Ga Ge Gr He Ho Hs Hu It Ju Lu No Po Rm Rs(all) Sa Su Tu. Introduced into Is.

Sect. CENISIA Ascherson & Graebner.

10. P. arctica R.Br. ex Parry, Jour. Voy. N.W. Pass. (Supp. App.) 11: 288 (1823) (incl. P. petschorica Rozhev.).

Laxly caespitose; stems 10-15(-20) cm. Leaves (1-)1.5-2.5 mm wide, dark green.. Ligule 1.5-2(-3.5) mm, rounded or sometimes acute. Panicle 3-5 cm, ± pyramidal, rather open, with few spikelets; spikelets with (2-)3-4 florets, tinged blackish-purple, sometimes proliferating. Glumes unequal. Lemma adpressed hairy on surface, lanate at base. Palea keels aculeolate or shortly ciliate below. Anthers 1.8-2 mm. Arctic and subarctic Europe, S. to 61° N. in

Norway. Fe Is No Rs(N,C) Sb Su.

A very variable species, numerous varieties of which have been described.

11. P. granitica Braun-Blanquet, Arch. Bot. 3: 46 (1929).

Laxly caespitose; stem 25-50(-70) cm, rather leafy. Leaves (2-)3-5 mm wide, bright green. Ligule 2-5 mm, rounded to truncate, often lacerate. Panicle 5-10 cm, ovoid, somewhat contracted. Spikelets with 2-5 florets. Glumes subequal. Lemma short- to long-hairy on keel and marginal veins, lanate at base. Palea keels ciliate in lower half. Anthers 2-2.4 mm. Endemic; Carpathian mts. Cz Po Rm Rs(W).

(a) subsp. granitica: stems 25-40 cm, robust. Leaves 3-4 mm wide, Panicle 7-10 cm; spikelets strongly violet-tinged. Lemma abundantly crispate-hairy on keel and marginal veins, densely lanate at base. N. & W. Carpathians.

(b) subsp. disparilis (Nyárády) Nyárády, Rev. Roum. Biol. 10: 355 (1965) (P. deylii Chrtek & Jirásek): stems 30-50(-70) cm, rather slender. Leaves 2-3 mm wide. Panicle 5-7(-9) cm; spikelets tinged bronze or golden-brown or occasionally violet. Lemma with short, straight hairs on keel and marginal veins, sparsely lanate at base. E. & S. Carpathians.

12. P. cenisia All., Auct. Fl. Pedemont. 40 (1789).

Laxly caespitose; stems 24-40 cm, with distichously leafy non-flowering shoots. Leaves 2-3 mm wide, slightly glaucous. Ligule of stem leaves 3-9 mm, acute; ligule of basal leaves very short and truncate or lacking. Panicle (2-)4.5-10 cm; spikelets with 3-5 florets, greenish or weakly violet-tinged. Glumes subequal. Lemma shortly hairy on keel and marginal veins, lanate at base. Mountains of C. & S. Europe. Al Au Bu Co Cr Ga Ge Gr He Hs It Ju Rm Sa.

1 Panicle open, with patent branches; marginal veins of lemma hairy in lower ⅓; keels of the palea aculeolate (b) subsp. cenisia

1 Panicle contracted, ± spicate; marginal veins of lemma hairy in lower ½; keels of the palea ciliate in lower half or rarely aculeolate

2 Lemma with long, adpressed hairs on marginal veins; panicle-branches sparsely scabrid for most of their length

.. .. (c) subsp. contracta

2 Lemma with short, patent hairs on marginal veins; panicle-branches sparsely scabrid towards the apex, smooth below

.. .. (a) subsp. sardoa

(a) subsp. sardoa Schmid, Viert. Naturf. Ges. Zürich 78: 239 (1933): (P. fontqueri Br.-Bl.): stem leafy to above the middle; panicle (2-)3-5(-9) cm, narrow, contracted, the branches sparsely scabrid in upper ½. Marginal veins of lemma hairy in lower ½. Keels of the palea ciliate in lower ½, or occasionally aculeolate. Anthers 1.8-2 mm. Endemic; Pyrenees, Corse, Sardegna.

(b) subsp. cenisia: stem usually leafy only in lower ½; panicle 5-10 cm, lax, rather open, the branches more or less patent, sparsely to densely scabrid. Marginal veins of lemma hairy in lower ⅓. Palea keels aculeolate. Anthers 1.5-1.7(-2) mm. Endemic; Alps.

(c) subsp. contracta (Nyár.) Nyár., Bull. Gard. Muz. Bot. Cluj 11: 8 (1931) (P. psychrophila Boiss. & Heldr.): stem leafy to about the middle; panicle 4-7 cm, narrow, somewhat contracted, the branches moderately scabrid for most of their length. Marginal veins of lemma hairy in lower ½; palea keels ciliate in lower half. Anthers 1.7 - 2 mm. S. Carpathians, mountains of Balkan peninsula, Kriti.

Sect. MACROPOA F. Hermann ex Tsvelev.

13. P. longifolia Trin., Mem. Acad. Sci. Petersb. ser. 6, 1: 69 (1836). Stem 30-50(-60) cm, stout, somewhat compressed and with the

greyish remains of leaf-sheaths at the base. Leaves 1-2 mm wide, tapering gradually to an abruptly mucronate apex. Ligule 0.7-1.4(-2) mm, truncate. Panicle 6-9 cm, narrow, spike-like; branches short, more or less erect, weakly scabrid. Spikelets with 2-4 florets. Glumes unequal. Lemma glabrous. Anthers 2.5-3.7 mm. Mountains of Krym. Rs(K). (Caucasus, Pontus and Zagros mts.).

Represented by the endemic subspecies fagetorum (Smirnov) Tsvelev in Europe; subsp. longifolia is confined to S.W. Asia.

14. P. sibirica Rozhev., Bull. Jard. Bot. Petersb. 12: 121 (1912).

Stem (20-)50-120 cm, slender, somewhat compressed at base. Leaves 2-5 mm wide, tapering gradually to the apex. Ligule c. 1 mm, obtuse. Panicle 6-18 cm, pyramidal; branches elongate, more or less patent, weakly aculeolate. Spikelets with (2-)3-4(-5) florets. Glumes unequal. Lemma glabrous. Anthers 1.5-2.5 mm. NE. & E. Russia. Rs(N,C,E). (N. & N.C. Asia).

Sect. HOMALOPOA Dumortier.

15. P. chaixii Vill., Hist. Pl. Dauph. 1: 7 (1786) (P. haemi Hermann).

Stems 50-120(-150) cm, stout. Leaves 6-10(-15) mm wide, abruptly contracted to the cucullate apex. Ligule 1-2 mm, truncate. Panicle 10-15 cm, ovoid, compact; branches short, erect or patent, densely scabrid. Spikelets with 4-5 florets. Glumes unequal; keel scabrid at the apex. Lemma glabrous, with a scabrid keel, usually not lanate at base. C. & S. Europe; introduced elsewhere with grass seed and naturalised in lawns and pastures. Au Be Bu Cz Ga Ge He Hs Hu It Ju Po Rm Rs(B,C,W). Introduced into Br Da Fe Ho No Su.

16. P. hybrida Gaudin, Alpina 3: 46 (1808).

Sometimes shortly creeping; stems 50-150 cm, stout. Leaves (4-)5-8 mm wide, flat, tapering gradually to the apex. Ligule 3-5 mm, acute to rounded. Panicle 15-20 cm, conical; branches somewhat elongate, patent, sparsely scabrid. Glumes unequal; keel smooth

or scabrid at the apex. Lemma hairy on the keel, sparsely lanate at base. Alps, Jura, E. & S. Carpathians, mountains of Jugoslavia. Au Ga Ge Gr He It Ju Rm Rs(W).

17. P. remota Fors., Linn. Inst. Skr. 1: 6 (1807).

Like 16 but often with short epigeal stolons; lower leaves abruptly contracted to the cucullate apex; ligule 2-3 mm; panicle-branches very long, arcuate-patent; glumes subequal, scabrid on keel and marginal veins. Scandinavia, C. & E. Europe. Au Cz Da Fe Ge He Hu No Po Rm Rs(N,B,C,W,E) Su.

Sect. LEPTOPHYLLAE mihi.

18. P. stiriaca Fritsch & Hayek ex Dörfler, Wien. Bot. Tauschanstalt Jahreskat. 226 (1904).

Slightly glaucous; stems (30-)50-80(-100) cm. Leaves (10-)30-40 cm x 0.2-0.3 mm, mostly arising from near the base of the stem, strongly folded, shortly hairy between the veins on the adaxial surface. Ligule 1-2 mm, rounded. Panicle (4-)7-11(-18) cm, pyramidal, rather lax; branches densely scabrid, sulcate. Spikelets with (2-)4-6 florets. Endemic; E. C. Europe to Montenegro. Au Cz Ju Po Rm.

Sect. OREINOS Ascherson & Graebner emend. Nannfeldt.

19. P. flexuosa Sm., Fl. Brit. 1: 101 (1800). (P. laxa subsp. flexuosa (Sm.) Hyl.).

Laxly caespitose; stems 10-20(-30) cm, mostly leafy at the base only. Leaves 1-2 mm wide; ligule up to 3.5 mm, rounded-lacerate. Cauline leaves with a distinct sheath. Panicle 2.5-5.5 cm, ovoid; branches sulcate. Spikelets with 2-3 florets. Lemma hairy on keel and for c. ⅓ of the length of the marginal veins; hairs acute. Palea keels aculeolate. Endemic; mountains of NW Europe. Br Is No Su.

20. P. laxa Haenke, Beob. Reis. Riesengeb. 118 (1791).

Laxly to densely caespitose; stems (10-)13-20 cm, mostly leafy at the base only. Leaves 0.8-1.5(-2.5) mm; ligule up to 3 mm, acute, rounded-lacerate or truncate. Cauline leaves with a distinct sheath. Panicle (2-)2.8-3.5(-7) cm, ovoid; branches sulcate. Spikelets with 3-4 florets. Lemma hairy on keel and for c. ⅔ of length of marginal veins; hairs obtuse. Palea keels aculeolate. Anthers 1-1.3 mm. Endemic; mountains of C. & E.C. Europe, extending into Sierra Nevada and SW. Bulgaria. Au Bu Co Cz Ga Ge He Hs It Ju Po Rm Rs(W).

P. nyaradyana Nannf., Symbol. Bot. Upsal. 5: 35 (1935) is a glaucous variant of 20. occurring near the upper altitudinal limit of the species in the Carpathian mts. It has longer, acute ligules and rather longer anthers (up to 1.7 mm).

21. P. pirinica Stoj. & Acht., Bull. Inst. Roy. Hist. Nat. (Sofia) 12: 181 (1939).

Densely caespitose; stems 5-30 cm. Leaves 0.2-0.4 mm wide, filiform, rather rigid, mostly basal; ligule c. 0.4-0.6 mm, truncate. Cauline leaves with a distinct sheath. Panicle (1.8-)3-5.5(-6.5) cm, elongate-ellipsoid, branches ± erect, with relatively few spikelets, terete. Spikelets with 3-6 florets, strongly violet-tinged. Lemma hairy on keel and for c. ½ length of marginal veins; hairs acute. Palea keels sparsely long-ciliate for most of their length. Endemic; SW. Bulgaria, N. Greece. Bu Gr.

22. P. minor Gaudin, Alpina 3: 44 (1808).

Densely caespitose; stems 5-30 cm, leafy for most of their length. Leaves 1-1.5(-2) mm wide; ligule 2-2.5 mm, subacute. Uppermost leaf without a distinct sheath. Panicle 2.5-3 cm, ovoid; branches terete. Spikelets with 4-6 florets. Lemma hairy for c. ½

length of keel and marginal veins; hairs obtuse. Palea keels aculeolate. Endemic; Pyrenees, Alps, mountains of Jugoslavia. Au Ga Ge He It Ju.

Sect. TICHOPOA Ascherson & Graebner.

23. P. compressa L., Sp.Pl. 69 (1753).

Stems 20-40 cm, geniculate-ascending, smooth, strongly compressed in upper half. Leaves 2-4(-5) mm wide, smooth, flat. Panicle 2-7(-10) cm, rather narrow to pyramidal; branches moderately scabrid. Spikelets with (2-)4-8 florets, often rather open. Lemma glabrous, or shortly adpressed-hairy below on keel and marginal veins. Anthers 1-1.2 mm. Most of Europe except the extreme N. and W. and some Mediterranean islands. All except Az Bl Cr Fa Is Lu Sb; not native in Hb.

Sect. STENOPOA Dumortier.

24. P. flaccidula Boiss. & Reuter, Pugillus 128 (1852).

Laxly caespitose. Stems 30-60 cm, smooth. Leaves 1-2 mm wide, flaccid; margins smooth or weakly scabrid. Ligule 2.5-3.5 mm, acute. Panicle 8-12 cm, lax, pyramidal; branches in pairs at each lower node, patent, spikelets borne towards the ends of each branch. Spikelets 3.5-4 mm, mostly with 3 florets. Glumes subequal. Lemma adpressed-hairy between the veins, sparsely lanate at base. Mountains of S. & E. Spain. Hs. (N.W. Africa).

25. P. palustris L., Syst. Nat. ed. 10, 874 (1759) (incl. P. tanfiljewii Rozhev.).

Rather laxly caespitose. Stems (15-)40-80 cm, smooth. Leaves 1-2(-3) mm wide; margins smooth. Ligule 1-2.5 mm, rounded. Panicle (8-)12-20(-30) cm, narrowly pyramidal; branches up to 5 at each lower node, erecto-patent. Spikelets 3-5 mm, with 2-5 florets;

glumes subequal. Lemma hairy on keel and marginal veins, sparsely lanate at base. Much of Europe, but absent from most of the west and parts of the south. Au Be Br Bu Cr Cz Da Fe Ga Ge Gr He Ho Hu It Ju No Po Rs(all) Su.

26. P. glauca Vahl, Fl. Dan. 17: 3 (1790) (P. caesia Sm., incl. P. ganeschinii Rozhev.).

Densely caespitose; stem (10-)17-35(-55) cm, stiffly erect, usually very glaucous, smooth to somewhat scabrid at apex. Leaves rather short and tapering, 2.5-3 mm wide. Ligule 1.2-2 mm, truncate. Panicle 3.5-7(-10) cm, ovoid, compact; branches 2-3(-4) together at the lowest nodes. Spikelets 4-6 mm, with 2-4(-5) florets; glumes subequal. Lemma hairy on keel and marginal veins, lanate at base. N. Europe; mountains of Europe southwards to the Pyrenees, Alps and N. Greece. Au Br Cz Fa Fe Ga Gr He Is It Ju No Po ?Rm Rs(N,C,W) Sb Su.

Some records of (26) from the Carpathian mts. may be referable to (28).

27. P. nemoralis L., Sp.Pl. 69 (1753). Laxly caespitose; stem 30-70 cm, smooth, rather leafy. Leaves 1.5-2(-3) mm wide; margins smooth, sheaths terete. Ligule up to 0.5 mm. Panicle 5-8(-10) cm, lax, elongate-ovoid; branches 2-5 together at lower nodes. Spikelets up to 4 mm, numerous, with 2-4 florets. Glumes unequal, the lower glume narrow, more or less subulate. Lemma hairy on keel and lower part of marginal veins, lanate at base. Throughout Europe. All except Az Bl Cr Sb.

P. balbisii Parl., Fl. Ital. 1: 360 (1850) (P. capitata Balbis), a poorly understood variant described from Sardegna and occurring also in Corse, probably does not warrant separation from (27).

28. P. rehmannii (Ascherson & Graebner) Wołoszczak, Fl. Polon. Exs. 10-11; 1020 (1904) (P. anceps Rehmann, non Forster).

Moderately densely caespitose; stem 30-40 cm tall, compressed, smooth. Leaves (3-)4-5 mm broad, slightly glaucous, margins scabrid; sheaths of cauline leaves compressed, with a distinct raised keel. Ligule 0.3-0.5 mm, truncate. Panicle 10-12 cm, linear-triangular in outline, often drooping at the apex; branches 3-5 together at lower nodes. Spikelets 4-5 mm, with 3-5 florets; glumes subequal. Lemma hairy on keel and lower part of marginal veins, not lanate at base. Anthers 1.6-1.9 mm. Endemic; S. & E. Carpathians. Rm Rs(W).

(29-32) P. sterilis group.

Densely caespitose. Leaves flat or slightly folded or channelled, especially when dry, more or less scabrid on margins. Stem usually rather leafy. Spikelets narrow. Glumes subequal to equal.

1 Panicle narrow, subspicate, with short, erect, ± sparsely scabrid branches; palea glabrous between the keels; plants often somewhat glaucous

2 Stem not leafy; leaves 0.5-1.3 mm wide; rhachilla scabrid, not hirsute .. .. 32. relaxa

2 Stem leafy; leaves (0.8-)1.2-2 mm wide; rhachilla finely papillose to hirsute .. .. 31. sterilis

1 Panicle narrow to wide, ovoid to pyramidal; branches patent to erect, sparsely to densely scabrid; palea glabrous or hairy on surface between the keels; plant not or scarcely glaucous

3 Stem smooth or slightly scabrid below the panicle; uppermost node concealed by sheath of the leaf below; glumes rather narrow, the upper (3.5-)4-5 mm; lemma often violet- and gold-tinged .. .. 30. versicolor

3 Stem ± densely scabrid below the panicle; uppermost node usually not concealed by sheath of the leaf below; glumes ovate-lanceolate,

the upper (3-)3.5-3.8 mm; lemma usually not variegated

.. .. 29. pannonica

29. P. pannonica A. Kerner, Österr. Bot. Zeitschr. 14: 84 (1864).

Stems 25-45 cm. Leaves 1.5-2.5 mm wide. Ligule up to 3 mm, oblong, rounded or somewhat lacerate. Panicle 3-6(-10) cm, the branches rigid, very scabrid, 2-4 together at lower nodes. Spikelets greenish, with 2-4 florets; rhachilla usually finely papillose. Lemma densely long-hairy on marginal veins, densely lanate at base. Endemic; E.C. & S.E. Europe. Cz Hu Ju Rm Rs(W).

(a) subsp. pannonica (P. podolica Błocki): stems 35-45 cm. Panicle rather wide, ± pyramidal, with elongate, somewhat patent branches. Palea keels ± ciliate in lower half. Endemic; S.W. Ukraine, Hungary, Romania.

(b) subsp. scabra (Kit.) Soó, Acta Bot. Acad. Sci. Hung. 5: 479 (1959) (P. scabra Kit. ex Steudel, non Ehrh.): stems 25-30(-35) cm. Panicle narrow, spicate to ovoid, with short, more or less erect, branches. Palea keels usually aculeolate. Endemic; E.C. Europe.

30. P. versicolor Besser, Enum. Pl. Volhyn. 41 (1821) (P. romanica Prodan).

Stems (20-)25-40(-65) cm. Leaves 1-2 mm wide. Ligule up to 2.5 mm, oblong, obtuse to acute. Panicle 6-12(-17) cm; branches sparsely to densely scabrid, up to 5 together at lower nodes. Spikelets violet- and gold-tinged, with 2-4(-5) florets. Lemma c. 3.3 mm, sparsely long-hairy on keel and marginal veins, densely lanate at base. Rhachilla finely papillose. Endemic; SE. Europe, N. part of Balkan peninsula. Al Gr Ju Rm Rs(W).

31. P. sterilis Bieb., Fl. Taur.-Cauc. 1: 62 (1808).

Stems 25-35 cm, smooth or sparsely to densely scabrid above. Leaves (0.8-)1.2-2 mm wide. Ligule up to 1 mm, truncate. Panicle 8-12 cm, narrow, subspicate. Spikelets greenish, with (2-)3-4 florets.

Lemma c. 2.5 mm, usually not lanate at base. Rhachilla with a line of hairs or finely papillose. S. Ukraine; Krym. Rs(W,K). (Caucasus, S.W. Asia).

32. P. relaxa Ovch., Izv. Tadjik.bazy Akad. Nauk SSSR 1: 20 (1933). (P. stepposa (Krylov) Rozhevits).

Like (31) but stems (15-)25-30 cm, smooth, often leafless above; leaves 0.5-1.3 mm wide; rhachilla scabrid, not hirsute. S.C. & S.E. Russia. Rs(C,E). (Siberia).

Sect. ABBREVIATAE Nannfeldt ex Tsvelev.

33. P. abbreviata R.Br., Chlor. Melv. 29 (1823).

Densely caespitose; stems 5-15 cm, smooth. Leaves mostly basal, numerous, tending to curve upwards especially when dry. Ligule 0.5-1 mm, rounded. Uppermost cauline leaf more or less adpressed to the stem, without a distinct sheath. Panicle up to 1.5 x 0.8 cm, compact, ellipsoid. Spikelets rather few, purple-tinged. Lemma shortly adpressed-hairy to sericeous on the abaxial surface. Anthers 0.6-0.8 mm. Svalbard. Sb. (Circumpolar Arctic).

Sect. NANOPOA mihi.

34. P. trichophylla Heldr. & Sart. ex Boiss., Diagn. Pl. Or. Nov. 3(4):136 (1859).

Stems 6-10 cm, smooth, almost leafless. Leaves 1-2 cm x 0.3-0.5 mm, setaceous, convolute. Ligule 1.5-2 mm, prominent, milky-white, finely tapering, acute. Panicle-branches terete, smooth, 1-2 at each node. Panicle 1.5-2.5 x 0.8-1 cm, narrowly ellipsoid. Spikelets c. 2.5 mm, strongly tinged with purple. Glumes unequal, obtuse, with a distinct hyaline margin. Lemma not strongly keeled, glabrous, obtuse; lateral veins indistinct. Endemic; C. Greece (Mt. Parnassos). Gr.

Records from Pindus and Kiona (Hermann, 1939) must be considered doubtful.

Sect. BOLBOPHORUM Ascherson & Graebner.

35. P. bulbosa L., Sp.Pl. 70 (1753).

Usually moderately densely caespitose; stems 15-40 cm. Leaves somewhat glaucous, mostly basal, the basal leaves 2-10 cm x (0.5-)1-2 mm, folded or flat; margins not cartilaginous. Ligule up to 3 mm, acute. Panicle 2-6 cm, compact, ovoid; branches in pairs at each lower node, scabrid. Spikelets more or less purple-tinged, in certain areas often proliferating, with 2-6 florets. Glumes broadly ovate, subequal; lemma densely lanate at base. Most of Europe except the extreme west and north; adventive in parts of C. & N.C. Europe. All except Az Fa Hb Is Sb. Introduced in Rs(N) and possibly elsewhere.

36. P. perconcinna mihi, nomen novum. (P. concinna Gaudin, non R.Br.)

Like (35) but stems 5-10(-25) cm; leaves 1-6 cm x 0.5-1.5 mm; ligule 0.8-2.2 mm; panicle narrowly elliptical; spikelets greenish, with 6-10 florets, never proliferating; lemma not lanate at base. Endemic; from S.E. France to the Balkan peninsula. Ga He It Ju.

37. P. ligulata Boiss., Voy. Bot. Midi Esp. 2: 659 (1841).

Densely caespitose; stems (8-)12-20 cm. Leaves 1.2-5 cm x 1.2-1.8 mm, glaucous, flat; margins not cartilaginous. Ligule 2.5-6 mm, prominent, milky-white, acute, lacerate. Panicle (1-)1.8-3 cm, compact, ovoid to pyramidal; branches 1-2 at each lower node. Spikelets ± purple-tinged, never proliferating, with 5-10 florets. Glumes unequal. Lemma shortly hairy on keel and marginal veins, not lanate at base. Palea keels aculeolate. Anthers 1.4-1.6 mm. S. & E. Spain. Hs.

38. P. timoleontis Heldr. ex Boiss., Fl. Or. 5: 607 (1884) (P. bulbosa subsp. timoleontis (Boiss.) Hayek).

Like (37) but leaves 0.5-1 mm wide, folded; ligule 3-6.5 mm; panicle ovoid; spikelets sometimes proliferating; anthers 1-1.2 mm. S. & E. parts of the Balkan peninsula, Aegean region. ?Al Bu Cr Ju Tu.

39. P. media Schur, Verh. Siebenb. Ver. Naturw. 4: 87 (1853) (incl. P. ursina Vel.).

Laxly caespitose, glaucous; stems (15-)20-30(-40) cm. Leaves 4-9 cm x 1-1.5(-2) mm, flat or folded, mostly basal; margins not cartilaginous. Ligule 1-2.5 mm, rounded, ± lacerate. Panicle 3.5-5 cm, compact, ellipsoid-oblong; branches (1-)2 at each lower node. Spikelets violet-tinged, never proliferating, with 3-5 florets. Glumes unequal. Lemma moderately hairy on keel and marginal veins, not or sparsely lanate at base. Palea keels ciliate in lower half. Anthers c. 1.6 mm. Endemic; S. & E. Carpathians, Balkan peninsula. Al Bu Gr Ju Rm Rs(W).

40. P. pumila Host, Fl. Austr. 1: 146 (1827) (P. thessala Boiss. & Orph.).

Densely caespitose; stems 6-18(-30) cm. Leaves 2-5 cm x (0.2-) 0.5-1.5 mm, mostly basal, folded or flat; margin not cartilaginous. Ligule 1-2 mm, that of the basal leaves truncate, longer and acute in the cauline leaves. Panicle 2.5-5 cm, rather open, ellipsoid to ovoid, with 2-3 slender branches at each lower node, occasionally narrower with short, patent branches. Spikelets greenish to violet-tinged, with 4-6 florets; glumes subequal. Lemma shortly hairy on keel and marginal veins, sparsely lanate at base. Palea keels finely aculeolate or with a few short hairs below. Anthers 1.4-1.8(-2) mm. Endemic; E. Alps and mountains of the Balkan peninsula. Al Au Gr It Ju Rm.

41. P. molineri Balbis, Elenco 85 (1801) (P. badensis var. xerophila (Br.-Bl.) Suess.).

Densely caespitose; stems (8-)12-18 cm. Leaves 2-6 cm x 1-2.5 mm, glaucous, mostly basal, usually tightly folded but sometimes flat to channelled; margin often more or less cartilaginous. Ligule of basal leaves up to 1 mm , obtuse, often lacerate, of cauline leaves

1-2 mm. Panicle 1.5-4 cm, compact, narrowly ellipsoid to ovoid, branches rather rigid, mostly in pairs at each lower node. Spikelets ± violet-tinged, with (2-)3-5 florets; glumes subequal. Lemma ± long-hairy on keel and marginal veins, sparsely hairy between the veins, lanate at base. Keels of palea either ciliate below or aculeolate throughout. Anthers (1.3-)1.5-2 mm. Endemic; mountains of S. & S.C. Europe. Al Au Bu Cz Ga Gr He Hs It Ju Rm.

Closely related to 40 and 42; transitional forms are occasionally encountered, and further work is needed to clarify their relationships.

Plants from It: Abruges, Mte. Amaro, agreeing with 41 in other respects but with elongate, acute, milky-white ligules to 7 mm, have been named P. magellensis Rigo in sched. They suggest a link between 41 and 37.

42. P. badensis Haenke ex Willd., Sp.Pl. 1: 392 (1797) (P. alpina subsp. badensis (Hänke ex Willd.) G. Beck).

Densely caespitose; stems (15-)20-35 cm. Leaves mostly basal, glaucous, margins cartilaginous; basal leaves (1.5-)2.5-6 cm x 2-3 (-4.5) mm, flat to canaliculate; ligule to 2 mm, rounded, often lacerate. Stem leaves folded, short; ligule 2-6 mm, acute. Panicle 4-7 cm, compact, ovoid; spikelets greenish or occasionally purple-tinged, densely clustered, with 5-9 florets. Glumes unequal. Lemma moderately hairy on keel and marginal veins, sparsely hairy between the veins, usually sparsely lanate at base. Palea keels aculeolate. Endemic; C. Europe and N. part of Balkan peninsula. Al Au Bu Cz Ga Ge He Hu ?It Ju Rm.

43. P. alpina L., Sp.Pl. 67 (1753) (P. borisii Stef.).

Laxly caespitose; stems 15-30(-40) cm. Leaves 4-10 cm x 2-4.5 mm, flat; margins not cartilaginous. Ligule of basal leaves 1-2(-3) mm, truncate; stem leaves with a 3-5 mm, acute, often lacerate ligule. Panicle 4-9 cm, compact to diffuse, more or less pyramidal;

lowest panicle branches in pairs. Spikelets purple-tinged, with 4-6(-9) florets, in certain areas often proliferating. Glumes unequal. Lemma densely hairy on keel and marginal veins, sparsely hairy between the veins, usually sparsely lanate at base. Palea keels ciliate below. Mountains of Europe, except the extreme S.; widespread N. of the Arctic Circle. Al Au Br Bu Co Cz Fa Fe Ga Ge Gr Hb He Hs Is It Ju No Po Rm Rs (N,B,C,W) Sb Su.

Subsp. insularis (Parl.) Hayek, Prodr. 3: 264 (1933) (P. bivonae Parl. ex Guss.) is recorded from Si and Pindus mts., Greece. A seldom collected and rather poorly understood variant of 43, it differs in its 4-7 mm wide, elongate leaves; panicle shortly branched with 2-5 branches at each lower node; spikelets not proliferating; lemma glabrous, or hairy on keel and marginal veins; palea keels dentate.

INCERTAE SEDIS.

44. P. jubata A. Kerner, Österr. Bot. Zeitschr. 23: 6 (1873) (P. grimburgii Hackel).

Annual. Stems 12-27 cm, usually solitary, slender, smooth, purple-tinged at the base. Leaves up to 3 cm x 0.3-0.6 mm, folded. Ligule up to 2.5 mm, acute. Panicle up to 5cm, lax, ellipsoid, with few spikelets; branches weakly scabrid, arising singly. Spikelets with 4-11 florets, tinged with purple. Glumes unequal, the upper broadly ovate, subacute, wider than the lower. Lemma very densely long-hairy on keel and marginal veins, ciliate on intermediate veins, sparsely lanate at base. Palea keels ciliate for c. ⅔ their length. Rhachilla smooth, glabrous. Anthers 0.6-0.7 mm. Endemic; W. coast of Balkan peninsula.

A seldom-collected species with no obvious relatives. It occurs in sandy ground by the sea; a far from usual habitat for a species of Poa. Possibly an extreme environmental modification of a member of sect. Bolbophorum; further work is required.

45. P. flabellata (Lam.) Hooker fil., Phil. Trans. Roy. Soc. London 168: 22 (1877).

Densely caespitose perennial; stems stout, 45-55(-150) cm. Leaves 30-40(-70) cm x 4-12(-15) mm, flat to channelled; ligule 8-12 mm, acute or obtuse, often lacerate. Panicle 8-21 x 1-4 cm, narrow, spicate, dense. Spikelets with 1-4 florets. Glumes subequal, the lower 1-veined, the upper 3-veined. Lemma scabrid on the veins, with a short (to 2 mm) scabrid terminal awn. Palea keels aculeolate. Naturalized in the Shetland Is. Br. (Native to the Falkland Is., South Georgia and the N. side of the Straits of Magellan).

HYBRIDS.

46. P. x hartzii Gandoger, Bull. Soc. Bot. Fr. 66: 302 (1919).
Putative parents: 26. glauca and 33. abbreviata.

Densely caespitose; shoots extravaginal. Stem (10-) 15-25(-30) cm; leaves mostly basal, folded, c. 2.5 mm broad. Uppermost leaf with a distinct, elongate sheath. Ligule 2-3(-4) mm, acute. Panicle 3-5 cm, narrow, contracted; branches scabrid. Spikelets with 3-5 florets; lemma hairy on keel and marginal veins and between the veins. Svalbard. Sb. (Greenland, Canadian Arctic).

47. P. x jemtlandica (Almq.) K. Richter, Pl. Eur. 1: 84 (1890).
Putative parents: 19. flexuosa and 43. alpina.

Densely caespitose; shoots intra- and extra-vaginal. Stem 10-20 cm, clothed with the remains of leaf-sheaths at the base. Leaves 1-2 mm wide, flat or folded, tapering gradually to the apex; ligule 1-2.5 mm, acute; panicle 2-5 cm, lax, ± ovoid; spikelets rather few in number, occurring towards the apex of the panicle-branches. Spikelets with 2-4 florets; lemma hairy on keel and marginal veins. W. Fennoscandia, Scotland (mts.). Br ?Is No Rs(N) Su. Not recorded from Fe, but likely to be recorded there.

48. P. x nobilis Skalińska, Acta Soc. Bot. Polon. 24: 751 (1955).

Putative parents: 11. granitica and 43. alpina.

Rhizomatous, with intra- and extra-vaginal shoots. Stem 30-40 cm, with few leaves. Leaves 2-3 mm wide; ligule c. 3 mm, subacute, sometimes lacerate. Panicle 4.5-8.5 cm, nodding at apex. Spikelets with 2 florets, the upper proliferating. Glumes unequal. Lemma densely crispate-hairy on keel and marginal veins. Palea keels ciliate in lower half. Endemic; Tatra mts. Po.

49. P. x taurica Poyarkova, Not. Syst. Pl. Vasc. (Leningrad) 1965: 51 (1965).

Putative parents: 23. compressa and 29. sterilis.

Perennial, rhizomatous, laxly caespitose. Stem 25-40(-80) cm, geniculate-ascending, scabrid, distinctly compressed in upper part. Leaves 1-2.5 mm wide, scabrid, flat to folded; ligule c. 1 mm, truncate. Panicle 3-7(-12) cm, with few spikelets; branches very scabrid. Spikelets with 2-4 florets. Lemma shortly hairy below on keel and marginal veins, not lanate at base. Palea keels aculeolate. Anthers 1.4-1.5 mm. Endemic; Krym. Rs(K).

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Note: taxa here treated as synonyms, or mentioned only in observations, are underlined.

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APPENDIX 2. Preparative techniques employed.

i. Procedure for preparing microscopic mounts of spikelet parts.

The spikelet selected for dissection is normally one of those paired on one of the longer panicle branches (in order to minimise changes in the overall appearance of the panicle, single apical spikelets are not normally used). There is no evidence to suggest, however, that characters of the spikelet differ quantitatively or qualitatively according to the position they occupy in the panicle, although spikelets near the apex of the panicle are the first to reach anthesis.

After removal from the specimen on a herbarium sheet, the spikelet is soaked for 24 hrs in cold water to which a drop of Teepol or other wetting agent has been added. This stage can be omitted when fresh material is being dealt with. The operation is usually carried out in a solid glass staining-pot. At the end of the period of soaking, the spikelet is transferred for a few seconds only (under 15 secs.) to a small beaker of boiling water. This softens the tissues. The spikelet is then transferred to a fresh staining pot containing lactic acid, and left to soak for a further 4-8 (-24) hrs. The spikelet is then ready for dissection. It is placed in a drop of lactic acid on a glass slide under a binocular dissecting microscope, and the parts are separated with tweezers (the upper part of the spikelet being held with a needle). The parts are then placed on a fresh slide in a conventional order: lower glume, upper glume, lemma of first floret, palea of first floret, anthers and ovary (if present) of the first floret, segment of rhachilla linking first and second florets, lemma of second floret, etc. The segment of the rhachilla which links the first floret to the base of the spikelet is short

and does not handle easily; the second, longer, segment of the rhachilla (which normally remains attached to the base of the palea of the first floret) is therefore employed.

The first lemma is conventionally placed on its side in a folded position; it is sometimes helpful, when observing the features of the nervature of the lemma, if the second lemma is placed flat (having been opened out by being slit near the base). A further variation is to mount the second palea with the adaxial side uppermost; the first palea is usually mounted with the abaxial side uppermost, as any hairs which may be present are more easily seen.

A drop of lactophenol is added before the slide is covered by a thin glass slip, and the mount can be rendered semi-permanent if the edges of the cover-slip are sealed with a mixture of gum mastic and beeswax, applied with a hot wire.

An alternative mountant is gum chloral, following clearing in chloral hydrate. While this gives a more permanent form of preparation, and its optical qualities are satisfactory, I dislike the fumes of chloral hydrate as they cause headaches.

ii. Chromosome counting procedures.

The conventional procedure is described below. Variations in the techniques employed in the various stages were experimented with; much depends on the state of the material used for counting, and the root tips of *Poa* are not easy to handle.

a) Collection of rapidly-growing root tips.

Plants chosen to provide material were kept in the roof-top greenhouse above the Adrian Building. They were either grown from seed and potted on in the greenhouse, or were brought into pots from Leicester University Botanic Garden. John Innes' no. 2 mixture was preferred, and plastic plant pots were used. Root-tip specimens were

collected in the mornings, preferably at around 10 am. Up to 5 cm of root was taken and placed in a saturated solution of paradichlorobenzene in water (10° C.) and kept thus for 2 hrs.

In the preparation of anther material, recently-emerged panicles were placed directly into fixative; no pre-treatment was used.

b) Fixation.

Freshly-prepared ethanol - acetic acid 3:1 was found to give satisfactory results. More complex mixtures were tried without noticeable advantage, and were more messy to prepare (e.g. the mixture containing chloroform and mercuric chloride described by Ostergren & Heneen (1963)).

After 24 - 48 hrs.' fixation at 20° C. (room temperature), material not to be used immediately was first washed in distilled water and then placed in $70^{\circ}/_{o}$ ethanol in water for storage.

c) Staining.

Feulgen's reagent was used. It has the advantage that although hydrolysis of the material prior to staining is absolutely essential, it leads to better separation of the cells of the root tip during squashing.

Hydrolysis is carried out by first soaking the root tips in cold N HCl and then transferring them to N HCl at 60° C. for 12 mins. in a temperature-controlled cabinet. The length of hydrolysis is critical if staining is to be successful; too short a period of treatment renders the chromosomes insufficiently receptive to the stain, while too long a duration of hydrolysis causes the cytoplasm to take up the stain.

Staining is achieved by placing the hydrolysed root tips in Feulgen's reagent at room temperature (20° C.) for from 2 - 4 hrs. Surplus material may be re-stained at a later date with such stains as proprionic orcein.

d) Preparation of chromosome squashes.

The root tip is cut transversely, after first trying to remove unstained root-cap material from the apex, and discs a few cells thick are placed on a glass slide under a cover slip and squashed between layers of filter paper.

Root tips of Poa are notoriously difficult to squash; even after hydrolysis, which tends to dissolve the middle lamellae of the cells and to allow them to separate, the individual cells are very difficult to compress. Enzymic digestion was attempted as a means of further softening of the tissue, but without noticeable improvement.

iii. Procedure for studying leaf anatomy.

Transverse sections of the leaf blade can be cut by hand when ample supplies of fresh material are available; herbarium specimens can be sectioned by first softening the tissues and then using a freezing microtome, but the procedure is lengthy and gives poor results.

Several leaf blades are placed together between the halves of a piece of elder pith sectioned longitudinally; a single-edged razor blade, or cut-throat razor, is used to produce a large number of sections which are then floated on water in a watch-glass and then transferred, a few at a time, to a drop of lactic acid on a glass slide which is then gently warmed over a gas flame for a few seconds.

Sections which are sufficiently thin will clear immediately, and can then be separated easily from the much larger number of over-thick sections which remain green. Thin sections are lifted onto a second slide which has a drop of water on it, and are warmed gently so that the lactic acid remaining in the tissues is removed.

Preparations can be rendered permanent by staining with any of a number of stains and by mounting in Euparal.

APPENDIX 3. Loans received from other herbaria.

Herbarium abbreviations conform to the 6th edition of "Index Herbariorum", ed. P.K. Holmgren & W. Keuken (1974).

BM: *Poa* sect. Stenopoa.

Total number of sheets: 33.

BR: *Poa* sect. Stenopoa.

Total number of sheets: 18.

CGE: *Poa* sect. Bolbophorum
sect. Macropoa
sect. Nanopoa
sect. Stenopoa.

Total number of sheets: 12.

E: *Poa* sect. *Bolbophorum*
sect. Macropoa
sect. Stenopoa

Total number of sheets: 32.

G: *Poa feratiana* (sect. Coenopoa)

Total number of sheets: 1 (type).

KW: *Poa versicolor* (sect. Stenopoa)

Total number of sheets: 2.

LIVU: all available European species except sect. Ochlopoa;

Total number of sheets: 253.

MANCH: *P. masenderana*;
Poa sect. Bolbophorum

Total number of sheets: 13.

M: *Poa* sect. Bolbophorum

Total number of sheets: 43.

MA: material examined, not sent on loan.

Poa ligulata (sect. Bolbophorum), c. 20 sheets seen.

P: *Poa* sect. Bolbophorum
sect. Macropoa
sect. Nanopoa
sect. Stenopoa.

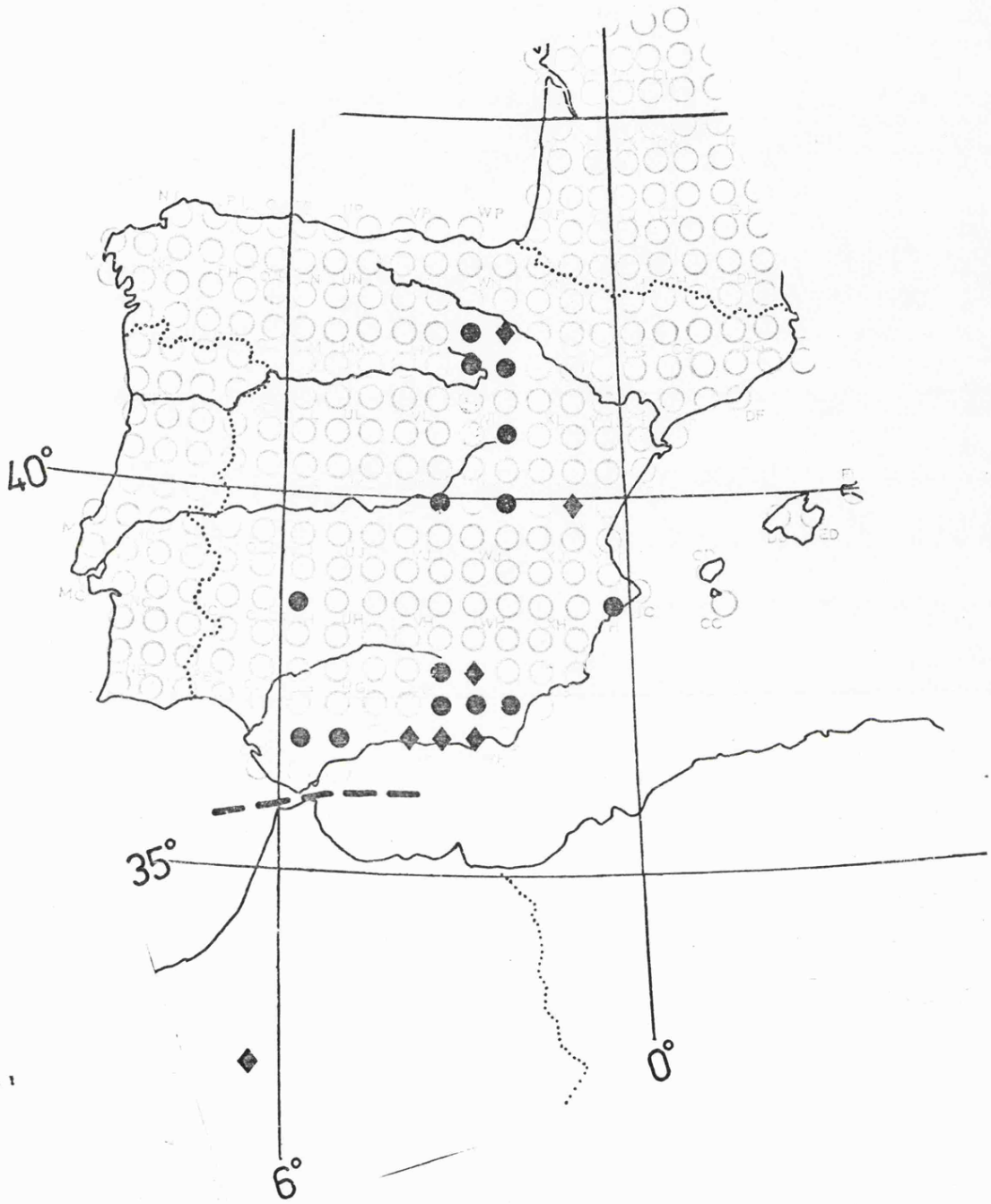
Total number of sheets: 23.

SOM: *Poa pirinica* (sect. Oreinos)

Total number of sheets: 3 (incl. 1 type).

W: *Poa* sect. Bolbophorum
sect. Leptophyllae
sect. Macropoa
sect. Oreinos
sect. Stenopoa.

Total number of sheets: 22.



Map A1. World distribution of

Poa ligulata Boiss.

● Herb. MA.

♦ Herb. LIVU.& LTR.

APPENDIX 4. Original chromosome determinations.

Sect. Homalopoa.

P. remota Fors. (Bot. Garden Accession no.) 27-71C. 2n = 14.

Plants grown in Leicester University Botanic Garden from seed supplied by Uppsala Botanic Garden. The seed came from plants grown at Uppsala from seed collected in nature. The packet in which the seed was supplied gave only the following indication of the locality of origin: "Sweden: Jemtland".

Voucher plant: in Leicester Botanic Garden order bed.

Type of preparation: root tip squash.

Sect. Leptophyllae.

P. stiriaca Fritsch & Hayek ex Dörfler. 26-71C. 2n = 14. (First count of this species).

Plants grown in Leicester University Botanic Garden from seed supplied by Uppsala Botanic Garden. The seed came from plants grown at Uppsala from seed collected in nature. The packet in which the seed was supplied gave only the following indication of the locality of origin: "Czechoslovakia: Slovakia".

Voucher plant: in Leicester Botanic Garden order bed.

Type of preparation: root tip squash.

sect. Macropoa.

P. longifolia Trin. 421-71C. 2n = 14.

Plants grown in Leicester University Botanic Garden from seed supplied by Copenhagen Botanic Garden. The seed originated from Copenhagen under the name P. iberica Fisch. & Mey.; I have treated this name as synonymous with P. longifolia Trin., but further work is needed on the whole group. Information supplied with the seed indicated that the plants from which it was taken were grown from seed of wild origin, but no details were supplied of the locality

from which the seed was originally obtained.

Voucher plant: in Leicester Botanic Garden.

Type of preparation: root tip squash.

Sect. Nanopoa.

P. trichophylla Heldr. & Sart. ex Boiss. 779-71N. 2n = 14.

Plant grown in Leicester University Botany Department from seed taken from a herbarium specimen collected by Mr. Oleg Polunin.

Locality of origin: Greece, prov. Ellas: Mt. Parnassos, leg. O. Polunin no. 11221. First count of this species.

Voucher specimen (original specimen from which seed was obtained): herb. LTR. The voucher plant from which the chromosome count was obtained died after the summer (1972) in which the count was made.

Type of preparation: second pollen mitosis.

Karyotype: see accompanying figure (p. xli).

Sect. Bolbophorum.

P. media Schur. (No accession number). 2n = 14.

(First count of this species).

Plant grown in Leicester University Botany Department from seed taken from a herbarium specimen collected by P.W. Ball & A.O. Chater.

Locality of origin: Jugoslavia; Serbia: Novi Pazar. N. of Banja, 3.5 km NE of Novi Pazar, Ball & Chater no. 560B.

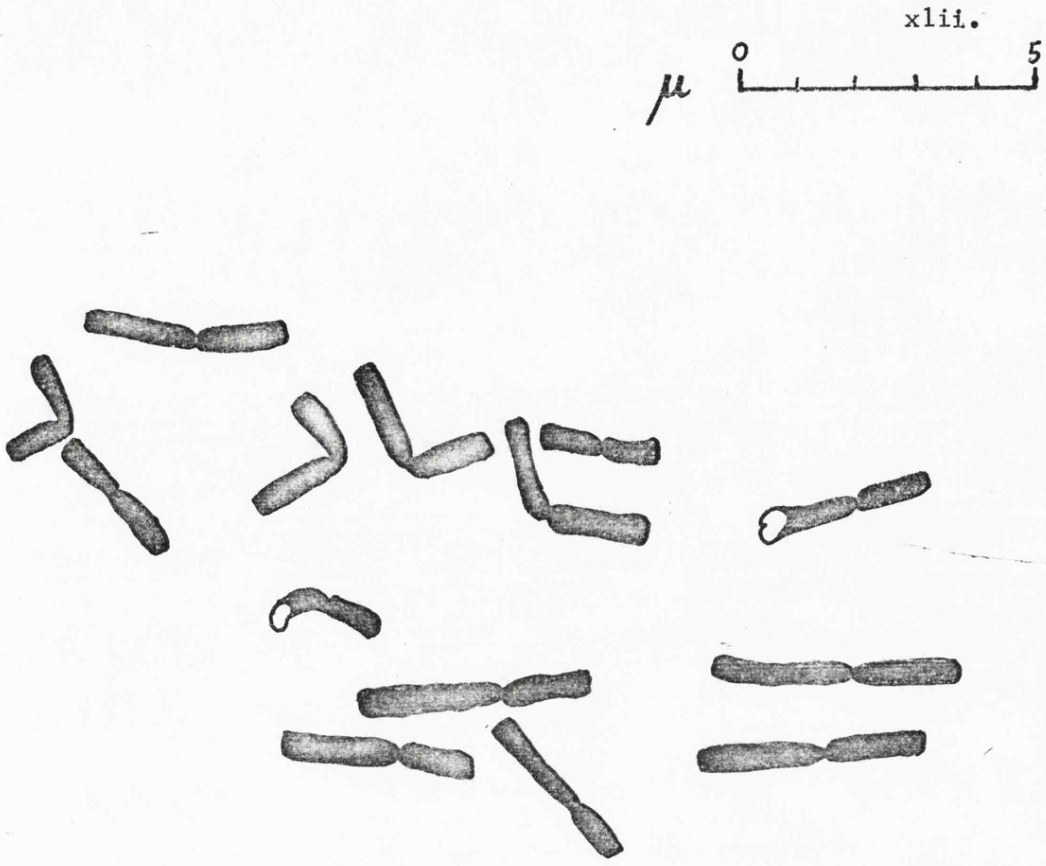
Voucher specimen (original specimen from which seed was obtained): herb. LIVU.

Type of preparation: root tip squash.

P. media Schur. B454N. 2n = 14 + 2B.

(Second count of this species).

Plant grown in Leicester from seed obtained in nature by Mr. Philip Brown. The plant from which the count was obtained had been



POA TRICHOPHYLLA HELDR. & SART.

O. Polunin 11221.

Somatic metaphase; anther wall. 2 n = 14.

growing for several years in the order bed of Leicester University Botanic Garden.

Type of preparation: anther squash (mitosis of wall tissue).

Locality of origin: Jugoslavia; Slovenija: Crna Prst, W. of Ljubljana, leg. P.D. Brown no. 68017.

Poa ligulata Boiss. (no accession number). 2n = 14. (Second count of this species).

Plant grown in Leicester University Botany Department from seed taken from a herbarium specimen collected by Mr. Chris Fraser-Jenkins.

Locality oforigin: Spain, prov. Granada: N.W. Sierra Nevada, upper Monachil valley, Borreguiles, 2400 m, leg. C.R. Fraser-Jenkins no. 3790.

Voucher specimen (original specimen from which seed was taken): herb. LTR.

Type of preparation: root tip squash.

P. pumila Host. 17-71N. 2n = 14.

Plant grown in Leicester University Botanic Garden from seed obtained in nature by O. Polunin.

Locality of origin: Jugoslavia; Makedonija: Šar Planina, above Popova Šapka, W. of Tetovo, leg. O. Polunin no. 11356.

Voucher specimen (collected with the seed): herb. LTR.

Voucher plant: Leicester Botanic Garden rockery.

Type of preparation: root tip squash.

P. alpina L. 781-71NT. 2n = 42.

Plant collected in nature by members of the Welsh Regional Office of the Nature Conservancy and cultivated at Bangor.

Locality of origin: Great Britain; Wales: Mt. Snowdon,

leg. Prof. Elfyn Hughes et al.

Voucher plant: Leicester Botanic Garden.

Type of preparation: root tip squash.

Addendum.

The following chromosome count came to my notice too late for inclusion in the body of my thesis:

"*Poa ursina* Vel. 2n = 16. Bulgaria: Znepole region, Golo bardo Mt., between Studena and Dolna dicanja. SK 19800." In: Kozuharov, S.I. & A.V. Petrova, IOPB Chromosome Number Reports XL (ed. A. Love). Taxon 22: 287 (1973).

P. ursina Vel. = *P. media* Schur (see index to appendix 1). A curious aneuploid count under an obsolete name. Together with the report above (B454N), where the count of 2n=14 + 2B also gives a total of 16 chromosomes, this suggests that further work on the karyology of *P. media* might prove particularly rewarding.

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J.R.EDMUNDSON . THESIS Ph.D. 1975.

Taxonomic Studies in the Genus Poa L. (Gramineae)

J.R. Edmondson.

Submitted for the degree of Ph.D., University of Leicester, 1975.

S U M M A R Y

The study embraced the sections of Poa L. (Gramineae) occurring in Europe: European species and subspecies received more detailed taxonomic treatment, partly because of the greater availability of material, but the work extended to cover non-European species which could be placed in European sections. The aim of the research was to produce a revised sectional classification of the genus.

In the course of the work, anatomical features of the leaf and stem were studied. A list of chromosome numbers was compiled, and nine original determinations were added in an appendix. Two of these were for species not previously counted, and two confirmed a single previous published count. Morphological characters were investigated, and a close study was made of variation in the Poa sterilis group. The geographical distribution and taxonomic limits of the European taxa were established, and an account was provided for Flora Europaea (appendix 1).

Diagnoses of the sections adopted in the revised classification of the genus were compiled, and the names of new taxa proposed will be validated in a forthcoming paper in the series "Notulae Systematicae ad Floram Europaeam Spectantes". Two new sections were proposed: sect. Leptophyllae mihi (type: P. stiriaca Fritsch et Hayek ex Dörfler) and sect. Nanopoa mihi (type: P. trichophylla Heldr. & Sart. ex Boiss.). A new name was shown to be required for Poa concinna Gaudin (1811) non R.Br. (1810); it is proposed to re-name the species P. perconcinna mihi. Several species and subspecies were reduced to synonymy, and the status of putative hybrid taxa was investigated.