

Jindřich Chrtek and Václav Jirásek:

Contribution to the systematics of species of the *Poa* L. genus, section *Ochlopoa* (A. et GR.) V. JIRÁŠ.

The number of species of the studied section, quoted in literature most frequently as *Ochlopoa* A. et GR., emend. NANNF. has since its discovery (ASCHERSON et GRAEBNER 1900) increased about threefold if we consider *P. supina* and *P. infirma* independent species. NANNFELDT (1938) and TUTIN (1957) for instance include in the *Ochlopoa* section two diploid species ($2n = 14$), annual species *P. infirma* H. B. et K. [*P. exilis* (TOMM.) MURB.] and perennial species *P. supina* SCHRAD. and four tetraploid species ($2n = 28$). These are the annual species *P. dimorphantha* MURB. and *P. maroccana* NANNF., annual to perennial species *P. annua* L. and the perennial species *P. rivulorum* MAIRE et TRABUT. Of the hybrids originating spontaneously in nature only *P. annua* \times *supina* NANNFELDT (1935) and *P. annua* \times *infirma* NANNFELDT (1938) both triploid ($2n = 21$) are known so far.

Notes on the distribution

Except for *P. annua*, which has become secondary an almost cosmopolite plant and a weed ubiquitous (except for humid tropical regions, where it occurs only exceptionally and probably only transitorily), the other species spread to a much lesser extent. Among the other species of the section it is *P. infirma* which spreads to a more considerable extent, its area extends from the Canary Islands, the Mediterranean and the Orient to north-western India (compare with HUBBARD 1954). It also grows in England, in western Cornwall, on the Channel and Scilly Islands, on the Lizard Peninsula and on Jersey Island in the Normand Islands (compare with HUBBARD 1954 and CLAPHAM, TUTIN et WARBURG 1958). OVCHINNIKOV (1957) mentions *P. infirma* from south Tadzhikistan; but states at the same time: "Our plants differ from the typical form, it is possible that they represent a special race. It is necessary to collect further material". *P. infirma* also has habitats in South America (Bolivia, Peru) introduced there most likely by the Spanish colonisators, probably soon after the discovery of America. It is interesting that South American plants were described and properly discovered as an independent species (*P. infirma*) more than 60 years before (1815) the plants from the original area of the species in the Mediterranean (*P. annua* var. *exilis* TOMMASINI in FREYN Zool. Bot. Ges. Wien 27 : 469, 1877. Comp. e.g. NANNFELDT 1938). Introduced also near Amsterdam (comp. JANSEN in Flora Neerlandica 1,2 : 78, 1951).

P. dimorphantha is endemic of Morocco (sandy pastures, more humid clearings in forests of cork oak and coastal plains along the Atlantic Ocean), *P. rivulorum* endemic of the Large and Medium Atlas and the Anti-atlas zone where it grows on the banks of torrents at altitudes of 2200 to 3530 m. a. s. *P. maroccana* grows in humid places, in ditches, near creeks and pools in Morocco and Algeria, where it also grows in the Sahara region (e.g. Oasis d'Ouargla).

For *P. supina* the large area mountain regions of Eurasia are most frequently motivated: from the Pyrenees, Alps, Apenines, Swiss Yura, the Black Forest and the Voges, the Bohemian Forest and the Ore Mountains to the Sudeten and Carpathian mountains and further north to southern and central Scandinavia, east to Siberia. In addition *P. supina* from the Caucasus is cited (ROZHEVITS 1934; GROSSGEYM 1949), furthermore from the mountains of Central Asia (OVCHINNIKOV 1957) and of Himalaya (BOR 1952, 1960).

In the herbarium of the Department of Botany of the Faculty of Natural Sciences of the Charles University in Prague (PRC) we have found specimen of plants collected by Thècle

SYMONOWICZ (16. 5. 1899) in the vicinity of Vilnius, which he determined as *P. annua* L. An analysis of the various characteristics, particularly the length of anthers showed that these are plants belonging to the typical *P. supina*. The discovery of this species on the soil of the Lithuanian SSR is certainly remarkable; in the European part of the USSR *P. supina* was, for the time being, recorded only in the Caucasus. The habitat near Vilnius most expressively relates to the widespread distribution of this species in central and southern Sweden.

From the alpine and subalpine zones of the Corsican mountains *P. foucaudii* HACK. is quoted (*P. exigua* FOUQ. non DUMORT.). Views on the taxonomic evaluation of this bluegrass vary. Some authors classify it in relationship of the species of *P. annua* (e.g. ROUY 1913 who classified it as *P. annua* race *P. foucaudii* HACK.) while FOUCAUD (1900) states that it is a transitory type between *P. alpina* and *P. laxa*. We have not yet seen any herbarium specimen. It seems, that *P. jubata* KERN. (Dalmatia, Crete) can also to a certain extent be related to *P. annua* which ACHTAROV for instance (1939) considers to be the link of the line of evolution of *P. alpina* — *P. jubata* — *P. annua* row.

According to our preliminary studies we believe for the time being, that the focus of the area of the *P. supina* species lies most probably in the alpine-western central European-Scandinavian zone. A study of herbarium specimens from the Carpathians showed for instance that various mountain and high altitude forms of typical *P. annua* grow in this region but not the *P. supina* species. On the contrary though in the region from the Alps across the Czech-German highlands (e.g. Oberdorf in the Thüringer Forest, comp. HERMANN 1941) to central Sweden *P. supina* is much more abundant than indicated until now. It certainly can also be found in a number of places in the hilly regions, often together with *P. annua*. This opinion is also supported by MELZER's data (1960) who registered original *P. supina* (not introduced) in lower altitudes e.g. in Kärnten (400 m.a.s.) the Upper Steiermark (700 m.a.s., often together with *P. annua*), in Lower Austria and the Burgenland (400—650 m.a.s.) and who also cited the findings of BECHERER from Voralberg (400 m.a.s., in a number of places). This occurrence of both species in the same places in regions ranging from low hills to alpine grade and the stressing of distinguishing features at a later stage (NANNFELDT 1937) for a clear differentiation between the two taxa (primarily the length of anthers!) are in our opinion the main reason why the area of *P. supina* is not yet known in Europe in greater detail. Another reason is the almost universal distribution of the various forms of *P. annua* and the lack of interest of botanists in this annual, biennial and perennial grass with a varied period of flowering throughout the year.

A revision of accessible herbarium collections, e.g. the herbarium of the Department of Botany of the Charles University in Prague (PRC), the Department of General and Systematic Botany of the Jan Ev. Purkyně University of Brno (BRNU), the Botany Section of the National Museum in Prague (PR) and the Moravian Museum in Brno (BRNM) gave proof of the presence of *P. supina* in the ČSSR, e.g. Bohemian Forest, the Jizera mountains, Giant mountains, Ash mountains and a few collections from lower regions in Bohemia (e.g. Čkyně near Strakonice, Hostinné, Česká Třebová and Božejov NW of Pelhřimov). This year Z. POUZAR found *P. supina* near Jevany in central Bohemia.

On the other hand data on habitat of *P. supina* in the Carpathian mountains are problematic. In our herbarium collections we have found no proof of the *P. supina* species from the Carpathians. Plants collected in high altitudes in the Czechoslovak Carpathians all belong to the various forms of *P. annua*! PAWLOWSKI (1939) also says this about *P. supina*: "Species a botanicis plurimis hucusque neglecta et incorrecte interpretata et delimitata; omnes igitur indicationes a Carpatis de novo examinandae sunt. In herbariis eracoviensibus nullum specimen *P. supinae* e toto Carpatorum occidentalium nec non boreali-orientalium tractu obvium mihi fuit." PAWLOWSKI (l.c.) records *P. supina* only in the south-eastern Carpathians in the group Butea-Custura (2230 m.a.s.). The author's indication is supported primarily by the given length of the anthers (1,6—1,8 mm). According to NYÁRÁDY (1931) the plants from the Transylvanian Alps (today the Southern Carpathians) described by F. SCHUR as *P. supina* belong to *P. laxa* HAENKE or *P. pruinosa* NYÁR., BAUMGARTEN's collections from the Fogarasz mountains to *P. pruinosa* NYÁR. (= *P. nyárádyana* NANNF.); comp. also NYÁRÁDY 1933. SZAFER, KULCZYŃSKI et PAWLOWSKI (1953) indicate *P. supina* only from the Sudeten, but not from the Carpathians. At the present time though *P. supina* from the Southern Carpathians and the Bihar mountains has been indicated e.g. by Rumanian botanists (cf. BORZA 1947). On the Balkan Peninsula *P. supina* is not known (cf. e.g. HAYEK 1933, ACHTAROV 1939, STOJANOV et STEFANOV 1948).

It seems that further studies will only confirm the viewpoints of some authors (NANNFELDT, MELZER) that the distribution of *P. supina* and *P. annua* particularly in places where these species grow together, does not take place separately. In higher altitudes the density of *P. supina* habitats will \pm increase in some regions and *P. annua* will probably indicate a similar phenomena in the direction of lower altitudes up to the plains.

We were able to confirm this supposition while working in the terrain (June 1961) when we investigated the distribution of *P. supina* and *P. annua* in the Giant mountains and in the region below the mountains. The distribution of *P. annua* in these regions indicates that it is a penalpine species, naturally of a secondary nature, similarly as *Chenopodium bonus-henricus* or *Taraxacum officinale*. From the main distribution in regions under the forest zone it occurs in higher regions influenced by human activity up to the highest places (e.g. the peak of Sněžka). On the contrary *P. supina* manifests itself in the examined area as a dealpine, of the sydealpine type again of a secondary nature, because it grows in some places in surprisingly abundant quantities only, along old roads, paths, near buildings, fences, bridges, foot-bridges, etc. We shall publish a study on the distribution of *P. supina* in the territory of the ČSSR particularly in Bohemia, separately.

The rich variability and the widespread distribution of *P. annua* in the horizontal as well as vertical direction, and its habitation in the most versatile habitats have influenced botanists, particularly those of the older era, to such an extent, that they have described some types as individual species. In 1938 for instance NANNFELDT pointed out that the bluegrass described by J. Sv. PRESL as *P. aestivalis* PRESL (Relikv. Haenk. 1: 272, 1830; Peru) is a typical *P. annua* (comp. also HITCHCOCK et CHASE 1950). An analysis of the specimen of THAD. HAENKE's original collection which is in the herbarium of the Department of Botany of the Charles University only confirmed this conception. Similarly an analysis of the collection by M. GANDOGGER (in the same herbarium) showed that *P. ovalis* TINEO for instance (Pl. rar. Sic. p. 21, 1817) and *P. com-panoi* described by GANDOGGER (in sched.) are typical *P. annua*.

Taxonomic evaluation of diacritical features

We have used material from the herbarium of the above mentioned institutions for this task. For the species, where the herbarium specimens were lacking we took over the respective characters from literature.

The taxonomic characters for diacritical differences of the studied species are listed in the following survey in the order of the degree of their systematic importance.

We consider the most important diacritical characters to be the length of the anther and the ration of their length to the width, the ratio of the length of the rhachilla of the terminal flower in the spikelet to the length of its lemma, the distance between the flowers in the spikelet and the karyogram. The length of the filaments of stamens, the features of the leaf blades (finish, edges) the different shape of the terminal flowers in the spikelet and the overall character of the panicle (the branches all-round, the cluster of twigs of 4 [—2]) are characteristics distinguishing *P. dimorphantha* from the other species of the section, the panicles of which are two or one sided. The degree of vesture or glabrousness of the center nerve on the side of the lemma is a suitable characteristic for distinguishing *P. supina*, although as we have ascertained from studies of the herbarium material, the degree of vesture of lemma nerves increases in *P. annua* forms towards the south from the temperate zone to the subtropics (Mediterranean), and decreases when studying this species from the Mediterranean to the North and in the higher mountain regions. The character of dentation of the panicle branches and the spikelet rhachilla, or the colouring of plants and spikelet or the length of the lemma cannot be used as an expressive and typical distinguishing feature. Similarly the character of the anatomic structure of the cross cut of the root, cannot be used in distinguishing the studied species, although VUKOLOV (1928) e.g. considers the shape of the endodermis cells a taxonomic and diacritical characteristic for determining the species of *Poa*, growing in the ČSSR. The results of our studies in this respect show for the time being that the character of the anatomic structure of a cross cut of the roots can offer diacritical features only of taxa higher than species. It is obvious that in a majority

of cases, the significant effects of the habitat, particularly the degree of moisture will reflect in the structure of the roots.

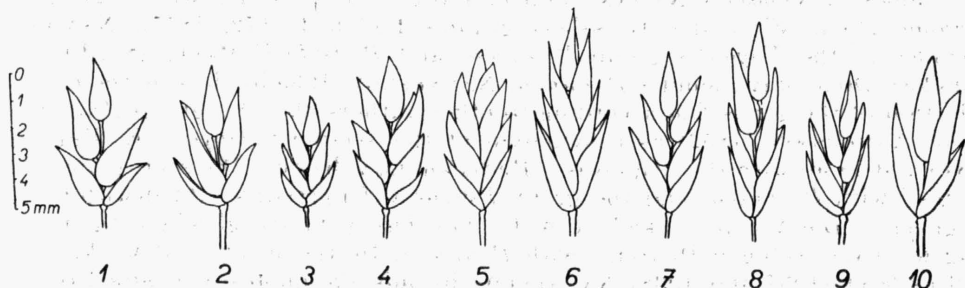
We have finally analysed in detail the shape and length of the ligule, primarily in species which are widespread on the territory of the ČSSR (*P. annua*, *P. supina*). We have found that particularly the length of the ligule is a diacritical characteristic in distinguishing the two species. In *P. annua* the length of the ligule of the highest (or the following) culm leave varies from 2 to 4,5 mm., in *P. supina* only 0,8—2 mm. This characteristic was not cited in literature until now.

Problem of a name for the *Ochlopoa* section

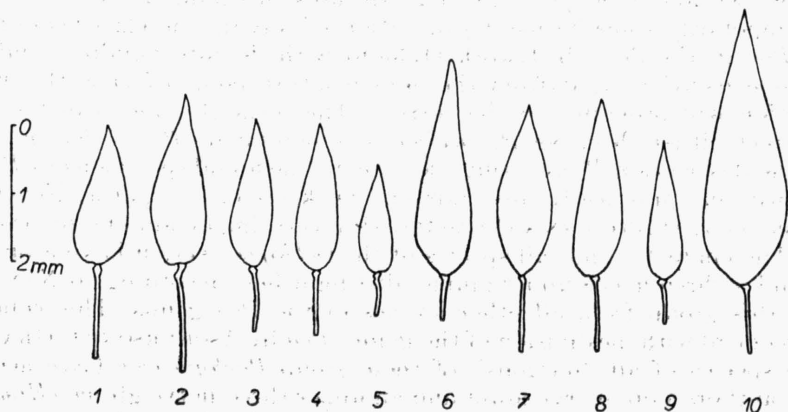
The group *Ochlopoa* quoted by the majority of systematic botanists as a section, was described and published by ASCHERSON et GRAEBNER in 1900 with the following diagnosis: "Untere Hüllspelze 1-, obere 3 nervig. Deckspelze mit Ausnahme der verbindenden Zotten kahl. Meist ein- bis zweijährige Art". And MAIRE (1955) supplements this: "... ou de petite taille". ASCHERSON et GRAEBNER classified into their group *P. dimorphantha*, *P. annua*, with the race *P. supina*, and *P. exilis*. As a synonym of the section they quote the names of *Vagantes* NYMAN (Consp. Florae Europaeae 1 : 837, 1882) and *Annuae* DÖLL (Flora des Grossherzogthums Baden 1 : 172, 1857). NYMAN includes in the *Vagantes* group *P. annua* and *P. balbisii* PARL. (Sardinia, Corsika), DÖLL only includes *P. annua*. NANNFELDT (1935 b) cites in the classification of the genus *Poa* according to other authors also the group *Annuae* N. J. ANDERSSON (1852) as a synonym of the section *Ochlopoa*, E. FRIES (1845 and 1846) with the diagnosis: "Radix annua v. biennis. Flosculi glabrescentes" with *P. annua*, and the group *Pilosae* v. OETTINGEN (1925) with the diagnosis: "Die Vorspelzenkiele vom Grunde bis zu Spitze gleichmässig mit langen, etwas wolligen Haaren" with *P. annua*. In the mentioned work, as well as later (1937 and 1938) NANNFELDT by mistake quotes *Vagantes* DÖLL instead of *Vagantes* NYMAN. In all the works which we had an opportunity of referring to, NANNFELDT classifies the species of bluegrass *P. dimorphantha*, *P. infirma*, *P. maroccana*, *P. annua*, *P. supina* and *P. rivulorum* exclusively into the "section" *Ochlopoa* A. et Gr. He uses this name as he states himself only temporarily since he has no intention of solving the classification of the genus *Poa* in the described work (1935 b) with definite validity; and at the same time mentions that from the nomenclature point of view this name of the section will probably not be correct. The term *Annuae* is in his opinion not correct either, because *P. supina* is a perennial (*P. rivulorum* as well) nor is the description *Pilosae* suitable, because he found specimens of *P. annua* plants without practically any hair on the keels of the palea. Nevertheless he considers v. OETTINGEN's characteristic a very important one for the entire group. The character that all species of the *Ochlopoa* section have a one-nerve lower and a three-nerve upper glume, distinguishes (according to NANNFELDT 1935 b) this group from all other species of the *Poa* genus. This conception is in agreement with the division of the genus *Poa* by ASCHERSON et GRAEBNER, but the species of all "sections" of their group *Pachyneuræ* have according to these authors a one-nerve lower and an upper three-nerve glume (*Homalopoa* and *Pandemos*, resp. *Homalopoa*, *Triviales* and *Stoloniferae*). ACHTAROV (1939) however classifies the species of the "sections" *Homalopoa*, *Stoloniferae*, *Triviales*, *Oreinos*, *Stenopoa* and *Tichopoa* into the group which has both glumes

with 3 nerves. NANNFELDT (1935 b) further indicates in agreement with PRAT (1932) that the leaves of *P. annua* have when viewed from the surface a simple but outstanding structure of the epidermis (only long cells) that the species of the *Ochlopoa* section have only intravaginal runners, the ligule quite long and above all wide, the nerves of the lemmas fine, but well discernable and finally that all species have a flower dimorphism, e.g. the upper flower (or the following ones below) only female. In view of these characters the *Ochlopoa* group holds an isolated position in the genus without any closer relationship to other groups. This viewpoint is in our opinion basically justified, and is also confirmed by some of the results of our studies of the morphology and anatomy of the palea of the species of this section and some related, e.g. East Asiatic species, *P. acroleuca* and *P. tuberifera*, or North American representatives of the group *Annuae* ANDERSS. 1852, emend. HITCHC. et CHASE 1950.

The oldest and at the same time valid name for the group, the section of the genus *Poa* L. where *P. annua* was originally classified but where today, in addition to these species belong all the formerly mentioned taxonomically related and phylogenetically similar species is in our opinion *Ochlopoa* (A. et GR.) V. JIRÁS. 1935.



Spikelets: 1. *Poa infirma*; 2. *P. maroccana*; 3. *P. annua*; 4. *P. supina*; 5. *P. chapmaniana*; 6. *P. bigelovii*; 7. *P. howellii*; 8. *P. bolanderi*; 9. *P. acroleuca*; 10. *P. tuberifera*



Terminal-flowers in the spikelets: 1. *Poa infirma*; 2. *P. maroccana*; 3. *P. annua*; 4. *P. supina*; 5. *P. chapmaniana*; 6. *P. bigelovii*; 7. *P. howellii*; 8. *P. bolanderi*; 9. *P. acroleuca*; 10. *P. tuberifera*

The morphology and anatomy of the paleas

A special task of our study work was an evaluation of the morphological shape and anatomic structure of the palea, which was not studied before in species of the *Ochlopa* section as a whole.

PILGER, who carried out a collective comparison of the morphology of the palea of some representatives primarily from the phylogenetic basic tribus of the family *Poaceae* (1949) primarily evaluates the general shape, but does not stress the characteristic vesture of the palea keels and the anatomic structure of its surface between the keels as a taxonomic characteristic. Both these characteristics though offer, in a number of cases, suitable diacritical characteristics, probably though for taxa higher than species.

The taxonomic significance of the character of the vesture of the palea keels particularly of *P. annua*, were mentioned already by MERTENS et KOCH (1823) later also e.g. by BRAUN (1834) who observed it in some species of the *Lolium* genus (his observations were elaborated by LAKON, 1919) numerous and very valuable data were compiled by KRAUSE (1909) who also took notice of the anatomy of the palea. The taxonomic significance of the character of vesture of the palea keels in representatives of some sections of the *Poa* genus were studied by v. OETTINGEN (1925) the results of his work were later applied for the taxonomic classification of other species of the same genus by some graminologists, e.g. NANNFELDT (1934), HERMANN (1939), MECENOVIĆ (1939), BUSCHMANN (1942), BOR (1952, 1960) and LEBAILLY (1960); ROSSBERG (1935) applied it even ascertaining the relationships between the basic tribus of the family *Poaceae*, FASSEAUX (1949) when classifying the tribus *Festuceae* into subtribes and genera. As far as the anatomic structure of the palea is concerned we had less sources at our disposal. The most valuable and practically basic data were furnished by the work of KRAUSE (1909) although of the species studied by us he only quotes *P. annua*, similarly as RADELOFF (1929) did at a later date.

OETTINGEN (1925) classifies *P. annua* according to the character of the vesture of the palea keel into the *Pilosae* group. HERMANN (1939) also considers the character of vesture of the palea keels in representatives of the *Poa* genus as partly diacritical characteristic for distinguishing the section of the genus. He says (l.c.p. 453): "So ist *P. annua*, das wohl sicher zu einer besonderen Rotte gestellt werden muss, in allen seinen Formen einschliesslich *P. exilis* TOMM. leicht kenntlich durch die langen Haare, die die Vorspelzenkiel vom Grunde bis zum Ende tragen. Genau dieselbe Bekleidung zeigen *P. balearica* PORTA und die nordamerikanische *P. autumnalis* MÜHLENB." This latter species though belongs according to HITCHCOCK and CHASE (1950) into the *Alpinae* group (*Bolbophorum* A. et Gr. 1900, *Subbulbosae* NANNFELDT 1935b, *Oreinos* HERMANN 1939), *P. balearica* according to ASCHERSON and GRAEBNER (1906) into the *Bolbophorum* group. Some outstanding characteristics indicate that not a single one of the mentioned species should belong into the *Ochlopa* section. E.g. the lemmas of *P. balearica* have bunch of wool on the lower part of the keel, the absence of which is one of the basic characteristics of the *Ochlopa* section, *P. autumnalis* belongs to the wide range of relationship of *P. alpina*, similarly the North American *P. stenantha* TRIN., which HERMANN (l.c.) says that it constitutes, by the character of its palea keel vesture, a transition between *P. alpina* and *P. annua*.

Even if we did not for the time being have any herbarium material for any of the quoted species, it can be assumed that *P. balearica*, *P. autumnalis* and *P. stenantha* most likely belong according to the character of their palea keel vesture to OETTINGEN's group of *Semipilosae* ("Die Vorspelzenkiel in der unteren Hälfte gleichfalls langhaarig, aber ziemlich unvermittelt gehen diese Haare in eine etwa 3-fache Reihe kurzer, hackenförmig gekrümmter Zähnchen über"). Either HERMANN had plants at his disposal where the soft paleas hairs in the flowers reached almost to the top of their keels and the teeth were \pm hidden under them (comp. similar in some North American species of the group *Annuae* ANDERSS., emend. HITCHC. et CHASE) or the described character is subject to a certain variability as was already mentioned by NANNFELDT (1935 b): "Such are under the microscope very unlike the illustration given by v. OETTINGEN, but still they are not totally glabrous and their few trichomes are of the characteristic shape. From all I have seen up to the present there exists no unrelated species with the same pilosity nor any obviously related species with dissimilar hairiness of the keels. Thus, the character pointed out by v. OETTINGEN seems to be very good for his group". This conception was also one of the motives why we tried to study the morphology and anatomy of the palea as fully as possible at least in those species of the *Ochlopa* section, which we had at our disposal in the herbarium collections.

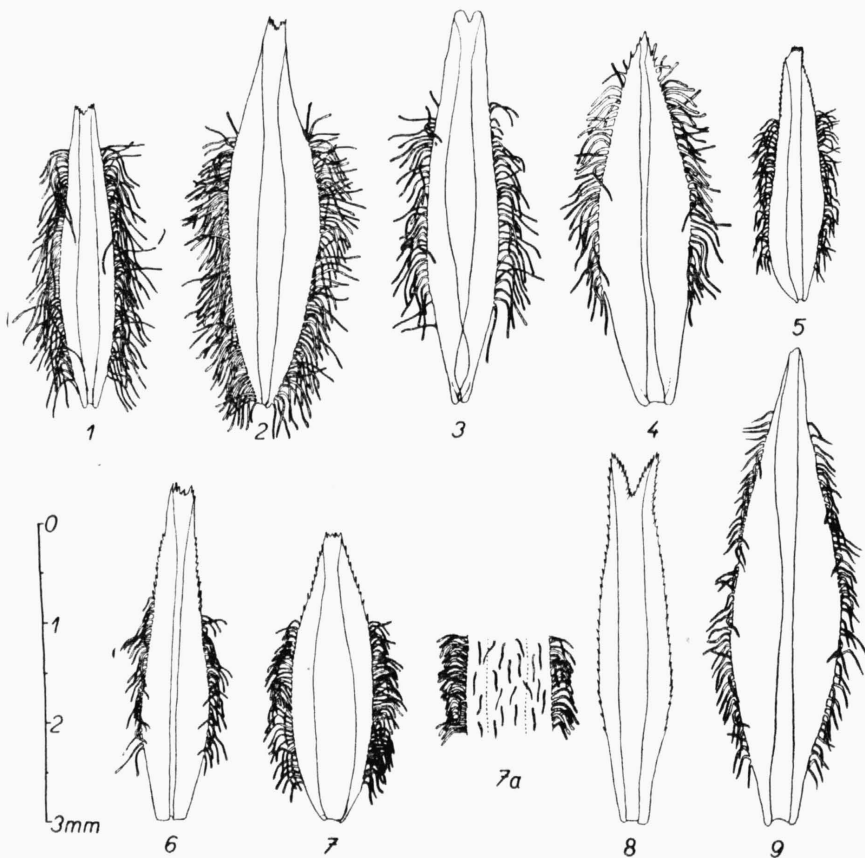
Methods

From the panicles of taxonomically reviewed plant specimens of the examined species we have first separated the entire spikelets and then under a magnifying lens (10 fold magnified) we have isolated the lowest flower of the spikelet. We softened the flower by boiling it briefly

in 1% KOH. We then separated the paleas and anthers from the flowers and washed the material in distilled water to remove the hydroxide and then transferred it into glycerol (or glycerol-gelatine) and made the preparations. A gentle boiling in 1% KOH proved to be more suitable than in 90% phenol as is recommended in some previous works. After a softening in phenol, the fine web of the palea especially in the center surface between the keels was frequently torn. The preparations were studied under a microscope of Czechoslovak make "Meopta A 25 V" in different enlargements. Schematic pen and ink drawings were made with the Abbé drawing apparatus.

Taxonomic evaluation of the palea characters

The paleas of all the examined species of the *Ochlopoa* section belong, according to PILGER's study (1949), to the "*Festuca*" type which is the most customary and also most typical among the representatives of the subfamily *Pooideae*. Its general description is: "The keels are strongly convex; narrower or broader side parts, i.e. surfaces outside of keels, on the keels sharply out into the center of the flowers, i.e. towards the inner surface of the lemma against the opposite palea sharply turned in; the center surface usually thinner

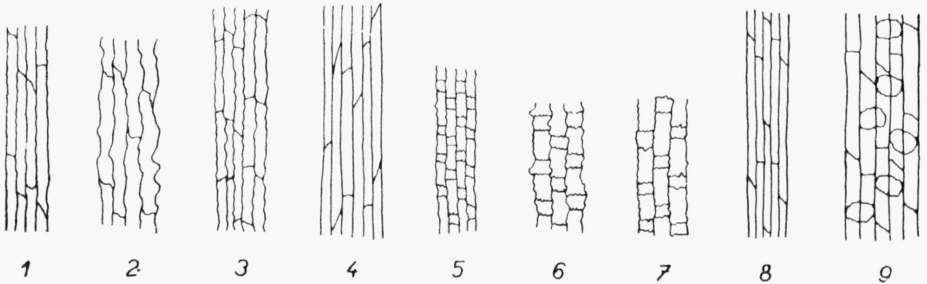


Paleas (adaxial side): 1. *Poa infirma*; 2. *P. maroccana*; 3. *P. annua*; 4. *P. supina*; 5. *P. chapmaniana*; 6. *P. bigelovii*; 7. *P. howellii*; 8. *P. bolanderi*; 9. *P. tuberifera*; 7a. *P. howellii*; hairs on the surface between keels (abaxial side)

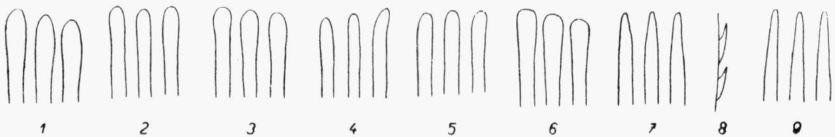
than the side surfaces, \pm concave, in the place where it incurves the palea keels brought closer together”.

In all the studied species, i.e. *P. annua*, *P. supina*, *P. infirma* and *P. maroccana* we found that the “composed” paleas, i.e. in a position where the keels form the margin and the palea lies on the outer margin of the center surface (on the back) are in *P. annua* lanceolate in *P. supina*, *P. maroccana* and *P. infirma* oblong. The keels in the center $2/4-4/6$, sometimes already at the base, have long thin, cylindrical hairs (not teeth!) which in *P. annua* and *P. supina* are in 2—3 rows (sparse), in *P. infirma* and *P. maroccana* in 3—6 rows (dense). In *P. infirma* and *P. maroccana* they are 1,5—2,5 times more dense than in *P. annua* and *P. supina*. In *P. annua* they are \pm as long as $2/3-3/4$ of the greatest width of the center surface of the palea, in *P. supina* and *P. maroccana* \pm equal to $1/2-2/3$, in *P. infirma* \pm equal to $2/3$ up to the entire width of the center surface. In the paleas of *P. annua* and *P. supina* the long hairs continue to the top of the palea, usually continuing in a few minute forward projecting teeth, while in the palea of *P. infirma* and *P. maroccana* the upper parts of the keels are glabrous and smooth. The long soft hairs are in some of the studied species unicellular and towards the end long and gradually clavate broadening. According to the degree of density of the long soft hairs on the palea keels we can in the *Ochlopoa* section distinguish the group *P. infirma* — *P. maroccana* (for the time being including the *P. dimorphantha*) from the *P. annua* — *P. supina* group (probably together with *P. rivulorum*).

A common feature of the paleas of all studied species is the outstanding vesture of the keels and the absence of short cells in the center surface between the keels which is composed exclusively of long cells, the walls of which are undulated to a certain degree. The thickness of the palea keels vesture is greater in the *P. annua* forms from southern regions than in the forms from the



Scheme of structure of palea between keels (abaxial side): 1. *Poa infirma*; 2. *P. maroccana*; 3. *P. annua*; 4. *P. supina*; 5. *P. chapmaniana*; 6. *P. bigelovii*; 7. *P. howellii*; 8. *P. bolanderi*; 9. *P. tuberifera*



Ending of hairs from keels of paleas: 1. *Poa infirma*; 2. *P. maroccana*; 3. *P. annua*; 4. *P. supina*; 5. *P. chapmaniana*; 6. *P. bigelovii*; 7. *P. howellii*; 8. *P. bolanderi*; 9. *P. tuberifera*

temperate zone and northern regions, but the hairs are never as dense (and in more rows) as in *P. infirma* and *P. maroccana*, the areas of which lie in the northern subtropical zone.

The structure of the leave epidermis when viewed from the surface

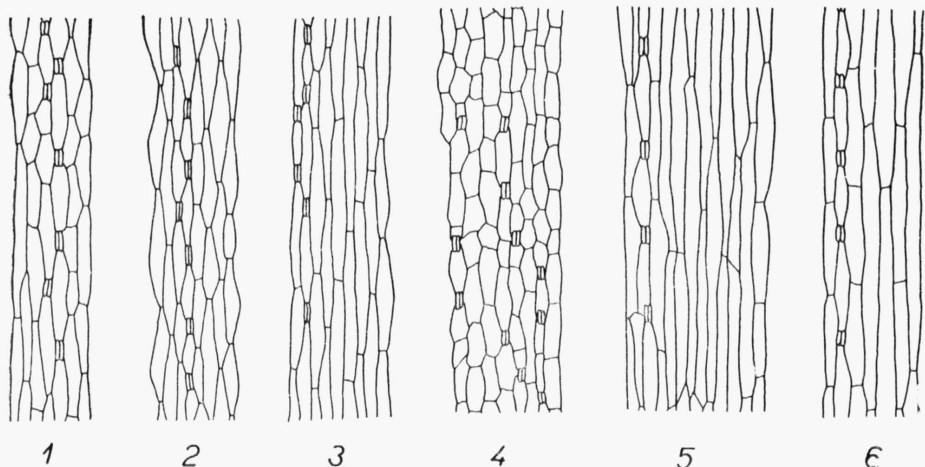
In the epidermis of grass leaves we can essentially distinguish (comp. e.g. GROB 1896, LOHAUS 1905, PRAT 1932) long and short cells, which sometimes project in differently shaped hairs. It is furthermore possible to ascertain whether the cell walls are straight or undulated to a certain degree and whether these are parallel or approach each other at certain points, in other words whether the shape of the cells resemble a square, rectangle, trapezium or double trapezium (widest in the center). The structure of the epidermis, of *P. annua* for instance is very simple. PRAT (l.c.p. 275) described it as follows: "Chez certaines espèces de *Poa*, tel *P. annua* L., la simplification des épidermes est poussée à l'extrême. Les nervures seules de la feuille terminale portent quelques cellules siliceuses dans leur partie moyenne; le reste de la face externe est recouvert d'un épiderme homogène à parois lisses. Les feuilles plus basses ont un épiderme totalement indifférencié. Cette espèce présente donc une très faible gradation et entre dans la catégorie des formes fructifiant à l'état infantile".

We have applied a very simple method to ascertain the character of the leave epidermis structure. We immersed the leave blades into warm water for a few minutes. Then we took a scalpel and cut off \pm 1 cm long particle from the center part of the blade and by applying slight pressure we pressed it onto the slide. With a razor blade we then carefully removed all the leave substance except for the layer of epidermis cells, which adhered directly to the slide. The preparations were then wiped off a few times, rinsed with distilled water, to remove the remnants of leave tissue and covered by glycerol-gelatine.

In order to be able to ascertain a possible variability in the shape or size of epidermis cells of the leave blades, the cells of the upper and lower epidermis of the leaves were observed both from flowering culms and from sterile shoots. In all cases, the same structure of epidermis cells was observed.

Taxonomic evaluation of anatomic features of the structure of the leave epidermis when viewed from the surface

In all the studied species (*P. annua*, *P. supina*, *P. infirma*, *P. maroccana*) the structure of the epidermis was very uniform. The epidermis is mostly composed of long cells and only rarely we also found short cells mixed in, which were particularly striking in *P. infirma*. The cell walls are usually straight, only exceptionally lightly undulated. The fact that the walls of cells are usually straight in other species of the *Ochlopoa* section was also ascertained by NANNFELDT (1935 b) who quotes PRAT and says (p. 13): "I have found the other species of *Ochlopoa* to show the same structure of the epidermis. Almost identical are also the species of *Triviales* (*P. trivialis*, *P. silvicola*), but in the rest of the genus the epidermis is of the common grass type with cell differentiation and the long cells with undulated walls". The cells are usually widest in the center part and narrow down towards both ends (equals \pm the double trapezium or barrel shape). The shape of the epidermis cells cannot be applied as a diacritical character in determining the various species of the section but it characterizes the species of the entire *Ochlopoa* section similarly as the feature of the paleas keels vesture and the structure of the center surface between the keels. But it increases the number of important characters for determining the *Ochlopoa* section which until now was identified in literature by a one-nerve lower glume and the absence of a bunch of wool on the bottom of the lemmas.



Scheme of structure of leaf epidermis (adaxial side): 1. *P. infirma*; 2. *P. maroccana*; 3. *P. annua*;
4. *P. supina*; 5. *P. chapmaniana*; 6. *P. bigelovii*

Some species of the *Poa* genus, closely related to the species of the *Ochlopoa* section

This concerns primarily the species of which we were able to revise in the herbarium material. According to some of the already mentioned characters, the Japanese *P. tuberifera* FAURIE ex HACKEL (1902) endemite of the Shikoku island belong into the relationship of species of the *Ochlopoa* section. The lower glume has one nerve, the palea on the keels to the end with long cylindrical hairs which are shorter than 1/2 of the center surface, of the widely oblong palea between the keels, which narrow down gradually, ending in a blunt point and are not clavate. The center surface of the palea consists of long and short cells. The bunch of wool on the bottom of the lemma is lacking.

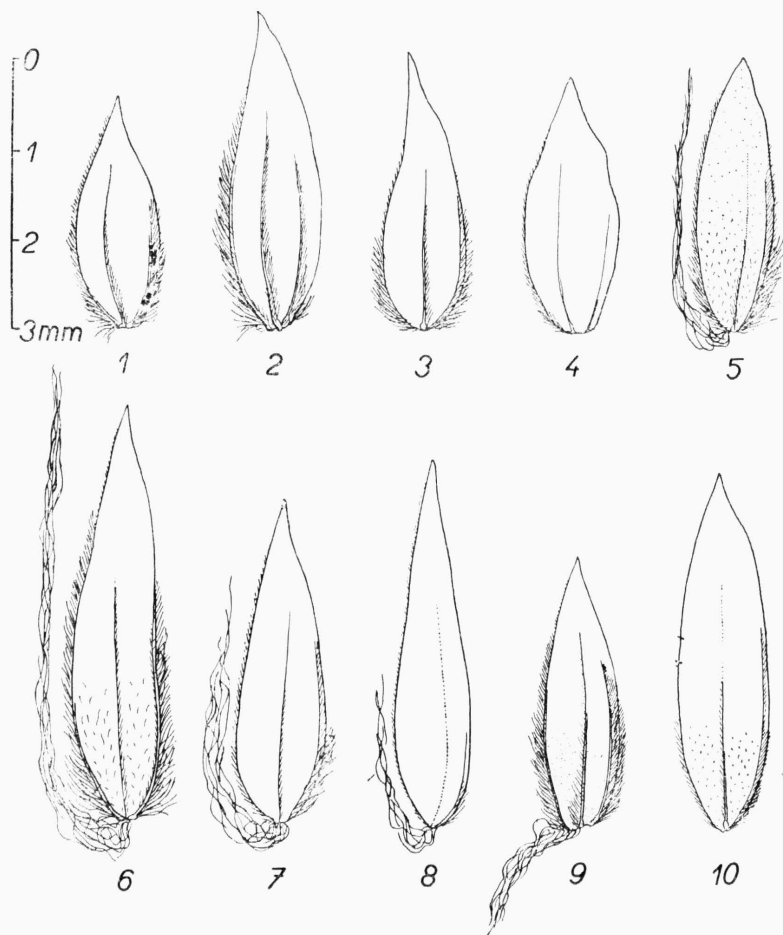
According to E. HACKEL (1902) *P. tuberifera* belongs into the relationship of *P. acroleuca* STEUD., which is distributed in Japan and Korea (introduced into Mandzuria). An analysis of the herbarium material showed us some diacritical characters different from the species of the *Ochlopoa* section as well as from *P. tuberifera*. It is first of all the presence of a bunch of wool on the bottom of the lemmas and teeth in the uppermost part of the palea keels. A common feature of both species, *P. tuberifera* and *P. acroleuca*, is the alternating long and short cells on the center surface of the palea between the keels. In the species of the *Ochlopoa* section this surface is composed of long cells exclusively.

BOR (1952, 1960) includes in the *Ochlopoa* section in addition to *P. infirma*, *P. supina* and *P. annua* another five species (*P. tibeticola* BOR — Sikkim, Tibet, *P. nepalensis* WALL. — Western Himalaya, *P. nephelophila* BOR — Burma, *P. sikkimensis* BOR — Sikkim and *P. stapfiana* BOR — Western Himalaya).

P. nephelophila most closely resembles the basic characters of species of the *Ochlopoa* section naturally in the event that the bunch of wool on the bottom of the lemma is missing. The author cites this character in the description of species but in the dichotomic key *P. nephelophila* belongs into the group of species the common characteristic of which is among other also "wool present on the callus".

Other species classified by BOR into the *Ochlopoa* section are according to the characters indicated by the author only remotely related to the species of section. The most remotely related species is *P. tibeticola* with palea keels only toothed. *P. sikkimensis* and *P. stapfiana* species have long soft hairs on the palea keels only in the lower half, towards the top of the palea they have teeth. *P. stapfiana* has on the callus also quite a considerable bunch of wool. And finally *P. nepalensis* has a similar palea keels vesture as the species of the *Ochlopoa* section, but the wool on the basis of the lemmas is richly developed.

According to BOR (1952) the group most closely related to the *Ochlopoa* section is the *Himalayenses* section with *P. himalayana* NESS, *P. stewartiana* BOR, *P. khasiana* STAPF and *P. wardiana* BOR species, the majority of which can according to BOR be distinguished only with great difficulty from the species of the *Ochlopoa* section. None of the species of the *Himalayenses* section can be classified in the *Ochlopoa* section.



Lemmas of the bottom flower in the spikelets: 1. *Poa infirma*; 2. *P. maroccana*; 3. *P. annua*; 4. *P. supina*; 5. *P. chapmaniana*; 6. *P. bigelovii*; 7. *P. howellii*; 8. *P. bolanderi*; 9. *P. acroleuca*; 10. *P. tuberifera*

HITCHCOCK and CHASE (1950) include in their *Annuae* ANDERSS. group the North American species *P. bolanderi* VASEY, *P. howellii* VASEY et SCRIBN. and *P. chapmaniana* SCRIBN., which have a one-nerve lower glume. *P. bigelovii* VASEY et SCRIBN., also belongs in this section although it has a marked three-nerve lower glume. All the mentioned species are annuals and their lemmas have the typical bunch of wool on the bottom part.

We were able to study the herbarium material of all these species and analyse their characters. *P. bolanderi* grows in open places in the thin forests (1500—3000 m. a. s.) in the West of the U.S.A. (Washington, Idaho, Oregon, Nevada and California states). According to the palea keel vesture they belong most likely into the v. OETTINGEN's group *Dentatae* ("Nur kurze, allerdings häufig verschieden lange Zähnechen, die in der Aufsicht sich vielfach decken"). The teeth are short and sparse, \pm in double rows and usually only in the upper half of the keels. The center surface of the palea is mostly composed of long cells, which sometimes terminate in a short spine, only exceptionally are there also short cells present. Only the character of a one-nerved lower glume would correspond to the character of the *Annuae* section but this feature is very significant, as we have already mentioned for other sections of the *Poa* genus as well. According to the palea keel vesture and the structure of its center surface *P. bolanderi* ($2n = 28$) would belong into the relationship of *P. trivialis* ($2n = 14$). Mature anthers are 1.0—1.2 mm. long, the lemmas has obscure, and practically hairless nerves, the surface between the nerves only sparsely and tubercularly hairy. According to NANNFELDT (1935 b) the leave blades of the species of the *Triviales* group also have a simple anatomic structure the same as the representatives of the *Ochlopoa* section. For the time being we classify *P. bolanderi* into the *Triviales* section where this annual species is a similar case as the annual species in the *Ochlopoa* section, where perennial species are also represented.

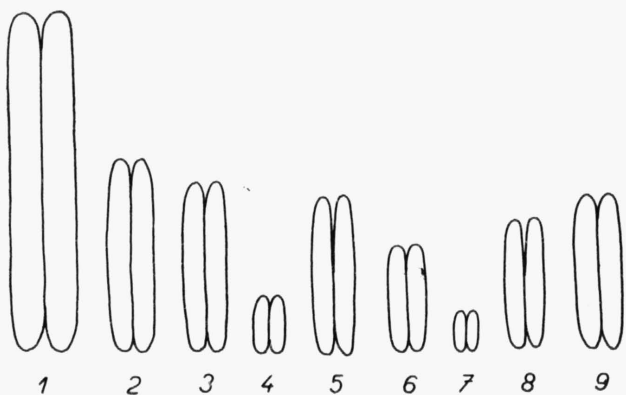
The other North American species which we have studied, i.e. *P. chapmaniana*, *P. howellii* and *P. bigelovii* constitute \pm uniform group by the vesture of the keels of oblong to widely lanceolate paleas. The keels have in the lower $2/3$ — $3/4$ long cylindrical hairs while towards the top the keels are dentate. The borderline between the two forms of vesture of the keels is a sharp one without a transitory form. These species thus belong most likely into the v. OETTINGEN's *Semipilosae* group ("Die Vorpelzenkiele in der unteren Hälfte gleichfalls langhaarig, aber ziemlich unvermittelt gehen diese Haare in eine etwa 3-fache Reihe kurzer, hackenförmig gekrümmter Zänchen über") where the representatives of NANNFELDT's group (1935 b) *Subbullosae* belong. The center surface of the palea between the keels is composed of long and short cells with undulated membranes.

In *P. howellii* which has a widely lanceolate palea, the ratio of long and short cells is approximately 1 : 1, the short cells usually terminate in small spines or in long and soft cylindrical hairs. The cylindrical hairs gradually narrow down into a blunt point. The anthers are 0.5—0.8 mm. long. In *P. chapmaniana* which has an oblong palea, the short and long cells are also in a \pm 1 : 1 ratio, but the anthers are only 0.1—0.3 mm. long (comp. e.g. *P. infirma*). The cylindrical hairs are not gradually elongated into a blunt point, nor do they broaden out clavate at the point, but are equally wide to the end and rounded at the top. In *P. bigelovii* where the palea is oblong, short and long cells are in the center part between the keels, the "long" cells are frequently

± of the same size as the short cells and are in a ratio of about 1 : 1. The anthers are 0.5—0.8 mm. long. The cylindrical hairs of the same width throughout or are to the end ± clavate.

P. howellii grows on rocky slopes and shady hillsides, usually under 1000 m. a.s. and only in the western-most regions of North America, from the Vancouver Island in south-west Canada to southern California, particularly in the coastal zone (Coast Rangers). *P. bigelovii* grows in open spaces of medium altitudes, in the southern part of the U.S.A. (southern California, Nevada, Utah, Arizona, Colorado, New Mexico, western Texas and Oklahoma) up to northern Mexico. *P. chapmaniana* grows in open places and cultivated fields of almost all states of the eastern part of the U.S.A. (from Nebraska, Kansas, Oklahoma and Texas to the Atlantic).

All of the four North American species are annuals, and were therefore joined together with *P. annua* into the group *Annuae* in the work of HITCHCOCK and CHASE (1950). This though is their only common characteristic (biological), in the case of *P. annua* only if it concerns the ephemeral or biennial forms. The striking bunch of wool at the base of the lemmas distinguishes them clearly from *P. annua*, they usually differ also in the length of their anthers and in the palea keel vesture and the structure of their center surfaces between the keels. The structure of the leaf epidermis basically corresponds with the species of the *Ochlopoa* section, but frequently short cells are mixed in. The character of a three nerve lower glume would exclude *P. bigelovii* from the *Annuae* group, resp. the *Ochlopoa* section, but we have already mentioned that representatives of other sections of the *Poa* L. genus have a one-nerve lower glume in addition to the species of the *Ochlopoa* section. On the other hand the palea keel vesture of this species corresponds with *P. howellii* and *P. chapmaniana*. In view of the presence of long soft cylindrical hairs both in representatives of the *Ochlopoa* section, as well as in the North American species — *P. howellii*, *P. bigelovii* and *P. chapmaniana* — we can infer at least a remote relationship of these two geographically separated groups, although this finding makes us presume that v. OETTINGEN'S *Semipilosae* group is not a synonym for NANNFELDT'S *Subbulbosae* section, but only an identification of a certain character which can occur in various taxa.



Anthers: 1. *Poa supina*; 2. *P. maroccana*; 3. *P. annua*; 4. *P. infirma*; 5. *P. howellii*; 6. *P. bigelovii*; 7. *P. chapmaniana*; 8. *P. tuberifera*; 9. *P. bolanderi*

There is no doubt that these three species have their independent evolutionary center in North America and that *P. chapmaniana* takes the very similar habitats in North America as *P. annua* in the Old World and finally also in the New World and that it recently began to spread secondarily in western Europe (found e.g. in 1932 in the vicinity of Amsterdam, comp. JANSEN et WACHTER 1933), similarly as *P. annua*, long before that, in North America and an other continents.

WEATHERWAX (1929) e.g. mentions the relationship and phylogenetic origin of *P. annua* and *P. chapmaniana*. He states (sec. JANSEN et WACHTER, 1933) that both species are very similar in appearance which in his opinion should be a sign of their close relationship. WEATHERWAX found *P. chapmaniana* to be definitely cleistogamous while *P. annua* on the contrary has chasmogamic flowers.

According to E. HACKEL (1904) in *P. annua* terminal flower in the spikelet opens up first and is usually female (or two of the top flowers are female if the spikelet has at least five flowers). Hermaphroditic flowers at the base of the spikelet flower in *P. annua* only after the top female flower withers, the pollination is prevalingly autogamic, because the ripe anthers, or their broken pollen sacks are erect and overtop the lemma of the flower only slightly so that the ripe pollen pours down onto the pistils in the flower especially when the atmosphere is calm. But an allogamy (xenogamy or geitonogamy) is not impossible because the emptying of the pollen from the anthers proceeds very quickly, the pistils rise above the flower, the flower remains open longer, and the ripe pollen from adjoining panicle spikelets or other plants can easily reach the pistils, particularly if the atmosphere is in motion.

WEATHERWAX believes that the method of pollination, the flowering, was in the two species — *P. annua* and *P. chapmaniana* the fundamental motive power of their development, i.e. that cleistogamy was in *P. chapmaniana* the primary mechanism evolution and that it was and is the most effective barrier preventing hybridization with related types, in this case (according to the author) with *P. annua*. He quotes: "In thinking of the formation of a new species from a pre-existing stock by any kind of mutative or selective process, we recognise the importance of barriers which prevent the blending of the two strains by hybridization. These barriers may be environmental, or they may take the form of anatomical or physical peculiarities of the organism itself. If we regard *P. chapmaniana* as having arisen as an offshoot from *P. annua* we have in cleistogamy a barrier more effective than a mountain range or a sea in keeping the new species from hybridizing with its parents". I am going to return to the question of the parental relationship between *P. annua* and *P. chapmaniana* and their origin, in the discussion of this work.

Relationships and opinions on the origin of some species

Species of the *Ochlopoa* section are diploid ($2n = 14$: *P. infirma*, *P. supina*) or tetraploid ($2n = 28$: *P. dimorphantha*, *P. maroccana*, *P. annua*, *P. rivulorum*). In isolated cases a type with $2n = 14$ (HOVIN 1958) was found in *P. annua*. The number of the chromosomes was determined by various authors (e.g. NANNFELDT 1937, and TUTIN 1957). Comp. also DARLINGTON et WYLIE 1955 and LÖVE et LÖVE 1959.

A comparison especially of morphological features of the species and the number of chromosomes constitute the basis for opinions on the degree of relationship and on the origin of tetraploid species, particularly *P. annua* which today grows in practically all climatic zones and altitude grades throughout the world, preferably in places influenced by man's activities.

There can be no doubt about the isolated position of *P. dimorphantha* in the species of this section. Particularly the length of filaments which are \pm twice as long as the lemmas, then the strikingly different shape of the top female flower in the spikelet, or its lemma, the form and braching out of the panicle and the leaf blades gradually narrowed down at the end and smooth on the edges, support this opinion which is for the time being generally accepted. A detailed analysis of the characteristics for the comparison of *P. infirma* and *P. annua* species on one side and *P. dimorphantha* on the other was e.g. given by ASCHERSON et GRAEBNER (1900). The other species of the section constitute a \pm closely related group whereby *P. annua* forms the center link between *P. infirma* and *P. supina*, *P. maroccana* is closely related to *P. infirma*, similarly as *P. rivulorum* to *P. supina*.

An enumeration of the intermediate characters of *P. annua* in *P. infirma* and *P. supina*, e.g. the duration of the plant, the shape of the panicle, the structure and colouring of the spikelets, the nervature of the lemmas and the length of anthers (comp. NANNFELDT, 1937) were later developed (1938) by the author and also by TUTIN (1957) who pointed out the colouring

of plants, the position of the panicle branches, the degree of fractures between the flowers (lemmas) in the spikelet, the time of flowering and the size of pollen grains. NANNFELDT (1937) already mentioned that a measuring of pollen grains even on relatively poor material showed that pollen grains of *P. annua* are considerably larger than those of both diploid species (*P. infirma* and *P. supina*), the pollen of which is almost of the same size.

It would therefore seem justified to accept the opinion that *P. annua* has its origin in some form or rather in forms (in view of its rich variability) which originated by hybridizing *P. infirma* and *P. supina*. NANNFELDT (1937) already correctly notes that we cannot be sure of the hybridogenic origin of the tetraploid *P. annua* as long as we do not succeed in creating it artificially by hybridizing the assumed parents. NANNFELDT's (1937) experiments were not successful, but on the basis of his ascertainment, that there are only few are quantitative characteristics in which *P. annua* does not manifest itself as the center link between the diploids, *P. infirma* and *P. supina*, and that the mentioned tetraploid apparently shows the basic influence of polyploidity, particularly by growing stronger and increasing the endurance of plants, in increasing its ecologic extent and in the presence of larger cells, particularly the pollen grains, the author (i.e.) expressed the opinion, that *P. annua* is a hybridogenic allotetraploid of diploid parents *P. infirma* and *P. supina*. Such tetraploids naturally developed by natural polyploidization from sterile diploid hybrids, which originated through the hybridization of two diploids.

NANNFELDT (i.e.) further states, that both species grow together in the mountains of the Mediterranean, e.g. in Spain and in Morocco and that possibly the original hybrid between them was formed there as the basis for the present multiformity (many forms) ecomorphosis and ecotypes of *P. annua* tetraploid. Another quality, significant for polyploid forms has to be taken into consideration, namely the delayed growth in the development of plants, their duration. If we leave out the isolated *P. dimorphantha*, which is always an annual, usually only an ephemeral plant (vegetation period only a few months, usually in spring), then *P. infirma* one of the presumed parental species of the *P. annua*, has the same character as *P. dimorphantha*, while *P. supina* is always a perennial, naturally with a short period of flowering at different periods of the year depending on the altitude where it grows. *P. annua* is an ephemeral to perennial plant with the time of bloom extending almost throughout the year (in favourable climatic conditions it flowers also in winter). The development of the plants though is highly irregular (depending on the nature of the habitat) and the vegetation cycle is completed within a few weeks or months, thus in favourable situations *P. annua* can gradually create even a number of short-duration generations within one year. In higher up to highest altitudes*) this species which in lowlands is an ephemeral weed, usually becomes a perennial plant. The rate of growth of the tetraploid is considerably slower than of the diploid *P. infirma*. NANNFELDT (1937) found in an experiment, that when seeds of the *P. annua*, *P. supina* and *P. infirma* species were sown at the same time, and the plants that sprung up were kept under the same conditions, *P. infirma* was the first to flower.

The genetic relationship between *P. annua* and *P. supina* was confirmed by the spontaneously grown hybrid of the two species, which NANNFELDT already cited in his work of 1935 (1935a) and later (1937) and which was also ascertained in a revision of herbarium material from Sweden (province of Småland, Uppland, Dalarna, Gästrikland; a total of 5 localities). It is a sterile triploid ($2n = 21$). M. DE LITARDIÈRE 1938 (see. MAGROU 1947) thought that "le type le plus primitif de *P. annua*, celui qui s'est conservé dans la région méditerranéenne, est représenté par le subsp. *exilis*. Par mutation, cette plante a produit une race tétraploïde, notre *P. annua* vulgaire." And furthermore (1939, see. TUTIN 1957) that "*P. annua* dérive d'une mutation du subsp. *exilis* (*P. infirma*) occasionnée par une duplication chromosomique". This conception though is according to TUTIN (i.e.) improbable, "since an autotetraploid would probably show quadrivalents at meiosis. The chromosome pairing in the hybrid *P. annua* \times *supina* and the intermediate morphology and increased variability of *P. annua* all favour an allotetraploid origin". Supporting the autotetraploid origin of *P. annua*, LITARDIÈRE also quotes that both of the presumed parental diploid species whose present day areas do not coincide (but compare. NANNFELDT 1937) differ considerably in the choice of habitat, in other words *P. annua* cannot be of allotetraploid origin. According to TUTIN (1957) it is however not difficult also today to figure out the conditions, under which both species could have once met. Presuming that *P. supina* had and still has a more northerly origin than the typically mediterranean *P. infirma*, this perennial diploid bluegrass receded in the quaternary glacial epochs in Europe,

*) Highest in Carpathians in Slovakia, e.g. Montes Liptovské hole; in valle Koprová dolina alt. cca 1500 m a.s., solo granitico, leg. 11. 7. 1933 J. DOSTÁL; *Myrtilletum* sub summo montis Osobitá, alt. cca 1680 m a.s., leg. 27. 7. 1933 J. DOSTÁL; ad lacum Horní Roháčské pleso, in locis graminosis-lapidosisque, alt. cca 1750 m a.s., leg. 15. 7. 1931 J. DOSTÁL (herbarium PRC).

similarly as other plant species moved before the glaciers towards the south. They could have thus reached southern Europe, the northern regions of the Mediterranean, even the mountains close to the coast. On the contrary, *P. infirma* again could have spread during the warmer interglacials or at least towards the end of the glacial epoch to new suitable habitats, possibly as far as the southern border of the rapidly melting glaciers. There it could have most likely met *P. supina*, which as a perennial could successfully vegetate over a longer period in glacial refugia. Lower and therefore warmer zones are namely not an insurmountable obstacle for the successful growth of the more persistent character of plants.

Today we know already that *P. supina* is not exclusively a mountainous up to high-mountainous species but on the contrary also a plant of lowlands (and on the hills). On the other hand *P. infirma* grows in an altitude of 1500 m.a.s. in Morocco for instance. In the place of contact of both species a hybrid could easily have originated (but more likely hybrids) at suitable periods also in more places as the bases of today's tetraploid *P. annua*. If we want to adhere to this theory, we can furthermore agree with TUTIN's conception that *P. annua* is a species of recent origin, which probably came into being in the regions of the northern Mediterranean.

P. annua could, in our opinion also have its origin in the mountains of Central Asia, where the occurrence of both assumed parental species according to data in literature cannot be eliminated by their distribution. According to BOR (1952, 1960) and ОУЧЕННИКОВ (1957) *P. infirma* also grows in the north-west of India (Proper) where it occurs up to 3500 m.a.s. and in somewhat untypical forms also in the southern regions of Tadzhikistan. In those regions *P. supina* if considered identical to the European populations grows much more abundantly. However we have not seen *P. supina* specimen from Asia in herbariums for the present. The polytopic origin of *P. annua* species is not impossible because the assumed parental species met in more places of the Old World. In places of primary contact of parents and the origin of hybrids certain types originated which then continued to spread. Their areas could after a certain time coincide and new types could originate in those places. Thus the variability kept increasing and covering up the character of the original forms of *P. annua*. Only in some places the original types persisted to a greater extent. An example is *P. annua* var. *criostyla* HACKEL ex NAKAI, distributed from the Kuril and Sachaline across Japan to Korea, Tchai-wan and Bonin Islands.

The relatively recent origin of *P. annua* (in one or more warmer eras of the quaternary glacial epoch) is according to TUTIN (i.e.) also supported by the perfect pairing of seven bivalents in two sterile triploid hybrids (*P. annua* × *P. supina* and *P. annua* × *P. infirma*) which also points to the close genetic relationship between the diploid and tetraploid. The second of the triploids originated spontaneously not only in NANNFELDT's bluegrass cultures in Uppsala, in 1936, but was also found on the territory of Morocco (comp. MAIRE 1955).

TUTIN (i.e.) hybridized in experimental cultures not only *P. annua* × *infirma* but also *P. infirma* (♂) with *P. supina* (♀), thus the reserve procedure from the one taken by NANNFELDT. Of the three (vital caryopsis one typical specimen of *P. supina* originated, while the two others produced tetraploid plants very similar to *P. annua*. In the course of three generations the degree of germination of the caryopsis produced by these two plants increased from the original less than 50 % to 95 % and 100 %, which is for *P. annua* quite a customary phenomena. On the basis of the finding that the morphological and biological features of *P. annua* are intermediate between those of *P. infirma* and *P. supina* and depending on the course of meiosis in the cited triploid hybrids and from the results of his experiments in which he obtained tetraploid plants very similar to the *P. annua* by hybridizing diploids by a consecutive natural polyploidization, TUTIN deduces that the *P. annua* is originally an allotetraploid derived from hybrids of two diploids.

The relatively recent age of *P. annua* is also confirmed by the high morphological variability of species, the different duration and the unusually flexible ecologic adaptability, which enables it to grow on the most versatile substrata, resp. in different habitats (comp. also CAMUS 1958 : 367). It therefore seems more acceptable to assume that the origin of *P. annua* does not derive from a single but on the contrary from more hybrids, genetically of the same origin. The increased possibility of hybridization of the presumed diploids is supported by the circumstance that the terminal flowers of *P. supina* (but also of *P. infirma*) is mostly female and breaking up day earlier than the hermaphroditic lower flowers, so that these can easily be pollinated by the pollen from the older hermaphroditic flowers of other panicles in a bush or other individuals.

The conception that the basis of the present forms of tetraploid *P. annua* originally came into being through the hybridization of two evolutionary older diploid species, was in the past years supported by the results of some cytotaxonomic studies of the *Poaceae* family. A very suitable example from this point of view is the contents of species of the *Dactylis* L. genus (comp. e.g. STEBBINS et ZOHARY 1959). A number of graminologists are as far as the origin of the most widespread species *D. glomerata* L. is concerned of a similar opinion as in the case of *P. annua*.

The forms and varieties of *D. glomerata* tetraploid ($2n = 28$) of which there is an immense number (comp. e.g. DOMIN 1943) take up a very large area in Eurasia, which is comparison with the area of other species of the genus which are diploid ($2n = 14$) is by far the largest. In the internal morphological features and their ecological adaptation the tetraploid forms are mostly transitory types between diploid species, of which e.g. *D. polygama* HORVAT. (= *D. aschersoniana* GRAEBN.) selects in its area in broader central Europe forest habitats (predominantly groves and meadows forests) *D. woronowii* OVCHIN. is distributed mostly in the steppes of the Crimea, Caucasus and the Turkmen SSR, to north-western Iran, *D. smithii* LINK only on the Canary Islands, other diploid species (comp. STEBBINS et ZOHARY 1959) in the Himalaya as far as the central China, Palestine, northern Italy, the Balear Islands, in Algeria and on the Pyrenean Peninsula. Except for *D. polygama*, the area of which is limited and forms an enclave in the area of *D. glomerata* (DOMIN l.c., p. 125—129 quotes 12 different forms of *D. glomerata* \times *polygama* = *D.* \times *intercedens* DOM. hybrid) the other diploid species are distributed in lesser and small areas mostly on the southern border of the largely distributed tetraploid forms belonging for the major part of the territory to the area of *D. glomerata*, in the Mediterranean also to *D. "hispanica"* ROTH, which e.g. STEBBINS and ZOHARY (1959) after discovery of some individual subspecies of *D. glomerata* particularly from the Western Mediterranean, no longer consider it an independent type. Tetraploid forms of *D. glomerata* s.l. can thus be distinguished from diploids only by the number of chromosomes, but not morphologically. They constitute a consistent and infiltrated network of mutually closely related types which also are related to the majority of diploid species (subspecies) so closely that the border line between tetraploids and diploids cannot be indicated.

A similar phenomena, even if not in the same extent (and contents) can be observed as literature shows, also between the forms of *P. annua* and the related forms of diploid species in the broader Mediterranean area, particularly in its western zones. In studying the distribution and the density of *P. supina* and *P. annua* in the Giant mountains and in the Sub-Giant mountains this year, we found particularly in the lower elevations, namely in the border zone where the *P. supina* distribution is receding and ceasing altogether stations of *P. annua*, a row of "*supinoid annuoids*" which did not differ from the forms of *P. annua* in appearance nor in duration, but had considerably longer anthers (medium length of anthers between *P. supina* and *P. annua*) and resembled *P. supina* considerably. The chromosome character of these remarkable forms will in the future have to be ascertained; for the time being we can only guess the possible forms of hybrids of both species (most likely "*super-annua*" \times *supina* types) but also of other "ploids" (not tetraploids) from the *P. annua* sphere.

Similarly as in the case of *P. annua* the origin of *Dactylis glomerata* supposedly stems from the hybridization of two diploid types; this was also confirmed in experimental cultures where after hybridization of *D. polygama* with other diploid, later some fertile forms resembling *D. glomerata* particularly from the northern regions of the area, originated. Present forms of *D. glomerata* manifest themselves morphologically and ecologically as the center link between *D. polygama* and *D. woronowii*, their origin can thus be derived from forms which originally came into being by a hybridization of these two diploids. In nature the areas of these diploids naturally do not meet, and a further hybridization is therefore impossible. An analysis of the areas, primarily the Mediterranean diploids and tetraploids showed that some tetraploid forms of *D. glomerata*, repps. *D. "hispanica"*, e.g. var. *maritima* [= *D. hispanica* ROTH B. *maritima* HACK. = = *D. glomerata* L. subsp. *hispanica* (ROTH) NYM. var. *hackelii* (A. et GR.) DOM.], are even today distributed in the regions of the Atlantic coast of the Pyrenean Peninsula, which are morphologically and ecologically very close, sometimes indistinguishably resemble forms of diploid types, namely *D. smithii* LINK from the Canary Islands or *D. juncinella* BORY from the subalpine gradus of the Sierra Nevada mountain chain (2200—2900 m.a.s.) in southern Spain. This is one of the proofs indicating that the areas of diploid species of the *Dactylis* genus occupied much larger areas in the past than at the present time and that on their border lines hybridization could have taken place. Reflecting on the possible origin of the var. *hackelii* (var. *maritima*) STEBBINS and ZOHARY (1959) consider the possibility of a hybridization of the forms *D. glomerata* subsp. *smithii* (LINK) STEBB. et ZOH. and *D. g.* subsp. *juncinella* (BORY) BOISS. Further tetraploid forms growing on the Atlantic coast of France and England and belonging to *D. glomerata* L.

subsp. *euglomerata* HAYEK var. *abbreviata* (BERNH.) JANSEN et WACHTER, resp. var. *collina* (SCHLECHT.) DOM. can according to these authors be taken for forms derived from hybrids of "typical" *D. glomerata* and var. *hackelii* forms, or according to the classification of K. DOMIN (1943) from a hybridization of *D. glomerata* subsp. *euglomerata* × subsp. *hispanica*.

It is thus obvious that the genus *Dactylis* and the *Ochlopoa* section of the *Poa* genus are very similar both as to the contents of polyploid forms as well as to the history of their origin and development. In both taxa the basic diploids could have already developed in the tertiary epoch and begun to stabilize. Glacials though caused a shift in the flora and their elements during which the diploid species could have met particularly in "the shade" of the southern walls of glaciers on common ground and protected areas where they grew together over a longer period of time, their hybridization could easily have taken place and given rise to new forms. Some of the products of hybridization could certainly later, when the glaciers receded, have distributed into conditions which were more suitable for their further development. They stabilized and distributed most successfully after a multiplication of the chromosome number by natural polyploidization, although it is still not certain what the actual causes of the introduction of the original hybrid forms among the tetraploids was. The final phase of development of diploids but primarily tetraploid forms in the *Dactylis* genus as well as in representatives of the *Ochlopoa* section, takes place in the historic era when the evolutionary younger tetraploids are in full degree of their variability and in places of their contact with older diploids create new triploid hybrids which were found in nature (*P. annua* × *supina* and *P. annua* × *infirmata*, resp. *Dactylis glomerata* subsp. *euglomerata* × subsp. *polygama*).

The present day distribution of *P. annua* all over the globe and an evaluation of the character of its habitats shows that it was primarily the activity of man, and in the past century mainly the population of Europe who contributed to the present day almost worldwide area of this all-round remarkable species. Wherever *P. annua* has distributed (still spreading) it has always taken up secondary habitats in the vicinity of human settlements and activities and near cultivated plants brought by man to new regions and cultivated there. Its "value" as a weed of soils influenced by human activity is of primary importance. In lower altitudes it flowers richly and is fertile with short intervals almost throughout the year, germinates rapidly, has a long vitality and an almost boundless adaptability. It is the most variable species of this section, the other types are mostly only forms conditioned by the character of the various habitats. Habitats and their plant associations where *P. annua* occurs as a perennial plant and where for the time being, it was not possible to prove the basic influence of man as far as influencing the place by his activity is concerned, deserve the particular attention of botanists.

Some of the new conceptions in the origin of species of the *Ochlopoa* section were also elaborated by NANNFELDT in his later work (1938). The tetraploid *P. dimorphantha* has, in comparison with the other species of the section, an isolated position; it is not yet known whether hybrids of *P. dimorphantha* and any other species of the selection exist. The tetraploid *P. rivulorum* is very close to *P. supina*, and includes plants indicated from Morocco (JAHANDIEZ et MAIRE 1931, sec. NANNFELDT 1938) such as *P. annua* L. subsp. *varia* GAUD. var. *supina* (SCHRAD.) REICHENB. f. *macranthera* LIT. et MAIRE. LINDBERG (1922, sec. NANNFELDT 1938) shows that the tetraploid *P. rivulorum* does not differ from the diploid *P. supina* in any way. The germinating seeds of this remarkable perennial bluegrass permitted NANNFELDT to make a thorough comparison with *P. supina* and ascertain a number of diacritical characters (e. g. the type of clusters of the spikelets on the end of the branches, the length of the lemmas, the degree of vestiture of nerves on its keel and margins and the length of anthers) in which *P. rivulorum* clearly shows the basic influence of an increased number of chromosomes (the increasing strength of the characteristics' degree). In addition to this *P. rivulorum* as far as we know is endemic in the mountains of the Atlas (2200—2530 m.a.s.).

The tetraploid *P. maroccana*, described by NANNFELDT (1938) on the basis of his collections from Morocco and Algeria, is the closest relative of *P. infirmata* and has many of the same characters. Particularly a more powerful growth, larger spikelets and the size of anthers as well as the slower development (when both species were sown in experimental cultures at the same

time, it flowered at least 1 week later than *P. infirma*) show the influence of polyploidy. An important and outstanding diacritical characteristic of *P. infirma* is the length of anthers. *P. maroccana* is a tetraploid the same as *P. annua*, and resembles it e.g. in the size and shape of anthers, as well as in the size of pollen grains. We could thus also consider it an extreme form of *P. annua*, which in appearance resembles *P. infirma*, if it were not ascertained that it constitutes a very uniform population, that it maintains all its biological qualities and taxonomic features also in cultures, that its area is limited to Morocco and Algeria and that together with *P. annua*, it forms a sterile hybrid (in 1936 in NANNFELDT's cultures of bluegrass in Uppsala from sowings of *P. maroccana* caryopses from Morocco). In the rich variability of *P. annua* we can naturally also find forms, particularly from shady places, which have the flowers in spikelets equally separated as *P. maroccana*, resp. *P. infirma* or the forms particularly from the broader Mediterranean where the nerves on the lemma are remarkably prominent and richly hairy similarly as *P. maroccana* (or *P. infirma*). *P. maroccana* thus seems to be most closely related to *P. infirma* but the difference in the length of anthers is a characteristic so striking and taxonomically significant that another influence than the effect of polyploidy must also be considered. It seems most likely (NANNFELDT 1938) that the large anthers could directly (or indirectly) come from *P. supina* although other characteristics of this perennial species are not apparent in the annual *P. maroccana*. We know that by hybrids the "central" features of both parents do not always have to appear.

MAIRE (1955) already quoted that "les sous-espèces du *P. annua*" — i.e. subsp. *exilis* (TOMM.) A. et GR. var. *exilis* TOMM. and var. *maroccana* (NANF.) LIT., subsp. *typica* (BECK) BR.-BL., subsp. *varia* GAUD. and subsp. *varia* GAUD. var. *rivulorum* (MAIRE et TRABUT) LIT. et MAIRE — "s'hybrident assez facilement, mais donnent des hybrides stériles". Spontaneously or artificially resulting hybrids *P. annua* × *infirma* ($2n = 21$), *P. annua* × *maroccana* ($2n = 28$), *P. annua* × *supina* ($2n = 21$) are given by NANNFELDT (1938) in a survey indicating their origin; these are supplemented by the artificial hybrid of *P. infirma* × *supina* ($2n = 28$) obtained by TUTIN (1957) to support the above mentioned theory on the origin of *P. annua*. According to NANNFELDT (i.e.) these four species and their mutual genetic relationships already proven by experiments, or for the time being assumed on the basis of the degree of their taxonomic affinity can be used as an example for the behaviour of polyploids (in our case the tetraploids) towards their "basic" diploids. The author applies a comparison with the genetic and chromosome conditions in the *Galopsis* genus and recalls the hybridization experiments of MÜNTZING (1932).

P. annua and *P. maroccana* are tetraploids; we have mentioned above their relationship to the assumed diploid parents. It is necessary to mention that the artificially obtained hybrid of *P. annua* × *maroccana* ($2n = 28$) is sterile, despite the fact that both parents have an equal number of chromosomes ($2n = 28$). The third tetraploid, *P. rivulorum* is similarly related to the same two diploids. In appearance it resembles most closely *P. supina*, but it is very difficult to find some obvious relation to *P. infirma* (NANNFELDT 1938), possibly only the form of the panicle and the somewhat separated flowers in the spikelets remind us of this assumed parental species. The powerfulness of all vegetative parts of the plants, the spikelets, lemmas and anthers though point to the influence of polyploidy.

A somewhat isolated conception of the origin of species in this case of *P. supina* is mentioned by J. MAGROU (1947). By the origin he considers it a lowland form of *P. annua*, which has changed in the mountains through the effects of mycorrhiza into *P. supina*. His hypothesis is documented by the results of experiments in which the roots of *P. annua* plants cultivated in soil from the mountains "se sont montrées largement envahies par un endophyte à arbuscules et à vésicules. Ces plantes symbiotique sont présenté, dès leur première année de végétation, des caractères les rapprochant des *P. annua* croissant en montagne. En particulier, elles n'ont fleuri que très discrètement, à la différence des témoins asymbiotiques cultivés, toutes choses égales d'ailleurs, en terre de plaine". He concludes (i.e.), that "partant de ces données, nous proposons l'hypothèse d'après laquelle le *P. annua* vivace des montagnes (*P. annua* subsp. *varia*) dériverait du *P. annua* vulgaire (*P. annua* subsp. *typica*) par adaption à la symbiose mycorrhizienne". This conception is certainly remarkable, even if it is doubtful that a diploid plant could originate from a tetraploid only by the effect of mycorrhiza "par adaption à la symbiose mycorrhizienne qui est de règle aux hautes altitude".

Discussion

P. dimorphantha holds a special position in the *Ochlopoa* section because until now no hybrids with other species of the section are known. But we were until now not able to carry out a detailed analysis of the taxonomic

and diacritical characteristics on material, but we would like to dedicate a separate study to this remarkable species and carry out an analysis of the anatomic structure of the leaf blades, the roots and palea, possibly the morphology of the lodicules and compare these with other species of the section. For the time being we have, on the basis of the strikingly long filaments of the stamena which are twice as long as the lemmas, discovered for the *P. dimorphantha* species in the *Ochlopoa* section an independent subsection called *Staminatae*, subsectio nova (staminum filamenta bis quam lemmata longiora). The other species of the section should, due to their close mutual relationship proven also genetically, belong into a typical subsection *Ochlopoa*, subsectio nova (staminum filamenta solum parum quam lemmata longiora). The different characteristics which are primarily in the sexual organs, can rightly be taken into consideration for taxonomic classification as well as for determining the degree of relationship as basic and most substantial.

It can be assumed that the majority of known species of the *Ochlopoa* section have their evolutionary center in the Mediterranean, most probably in the mountains of its western part. The present knowledge of species however does not entitle us to give in this respect preference to the south-western European region or on the contrary to north-western Africa. The primary areas of *P. infirma* and *P. supina* diploids which are much more extensive than the areas of the tetraploid species of the section (except for the secondarily formed *P. annua* area) and which thus increase the possibility of a meeting of both diploids (in the past) or their joint growth (at the present time) can support the conception that these species are indeed the basis of today's contents of the section, particularly the typical subsection *Ochlopoa* and that all the presently known tetraploids can have their original, primary beginning in some hybrid forms of these diploids. The central morphological and biological position of *P. annua* between the *P. infirma* and *P. supina* can also be expressed by a nomenclature formula of *P. infirma* × *supina* hybrid, the close relationship and similarity in appearance of *P. maroccana* and *P. infirma* by the formula *P. superinfirma* × *supina* (thus a "infirmoid" type) the very close relationship of *P. rivulorum* and *P. supina* (particularly as far as the habitat is concerned) by the formula *P. infirma* × *super-supina* ("supinoid" type). The probability of the mentioned origin of *P. annua* is supported by the incidence of hybrids (hybridization possibilities) in the *Ochlopoa* subsection, namely *P. annua* × *infirma*, *P. annua* × *supina*, but particularly *P. infirma* × *supina*. Neither hybrids of *P. infirma* × *maroccana* and *P. maroccana* × *supina*, nor hybrids *P. infirma* × *rivulorum* and *P. rivulorum* × *supina* are known for the time being (not even in experiments). The above mentioned view on the nature of the origin of *P. maroccana* and *P. rivulorum* tetraploids by hybridization of various parental forms and by hybridization in different places at different times is not for the time being supported only by the identification of a close taxonomic relationship between *P. maroccana* and *P. infirma*, resp. *P. rivulorum* and *P. supina*. Before TUTIN (1957) was successful in obtaining of *P. infirma* × *supina* followed by a natural polyploidization from hybridization plants resembling in appearance and producing in later generations *P. annua* plants from caryopsis, the conception of the origin of this species was supported, solely by the degree of relationship, resp. the central taxonomic (morphological, and biological) position of *P. annua* between the *P. infirma* and *P. supina*.

The vesture of the palea keels, the anatomic structure of their center surfaces between the keels and the structure of the leaf blade epidermis when viewed from the surface are further and new features which substantiate the unity of the *Ochlopoa* section purport, which has a completely independent taxonomic and phylogenetic position in the *Poa* L. genus. Another very important characteristic of the section is the absence of bunch wool on the basis of the lemma. In all the North American annual species classified until now into the group *Annuae* ANDERSS., emend. HITCHC. et CHASE on the contrary, the wool is most typically developed. The absence of wool, in *P. chaixii*, of the *Homalopoa* section, or its presence, can in a detailed taxonomic analysis of related species indicate that this character can have a similar degree of taxonomic and diacritical value as the characteristic feature that

in some bluegrass groups the lower glume is one- and the upper three nerved or that the *Annuae* group contains annual to biennial (ANDERSSON 1852) or only annual species (HITCHCOCK et CHASE 1950), in other words these characteristics are not significant for taxa higher than species. The characteristic of an annual is in our opinion not a characteristic (quality) which would always be valid for a higher taxon than the species, it seems more likely that in the *Poa* L. genus, annual plants can be in various sections. Similarly the number of nerves on the glumes, particularly the lower glume (comp. above). It depends on other phylogenetic and taxonomic characteristics, primarily on those which we describe as basic for the discovering and classifying of the species and which are in the representatives of the *Poaceae* family chiefly in the sexual organs or in formations placed in the spikelet in their proximity (lemma, palea, lodicules).

Special attention was dedicated to the character of the anatomic structure or the roots on a transversal cut. In all the examined species (*P. annua*, *P. supina*, *P. infirma*, *P. maroccana*) a uniform type of thickened cells of the protective sheath of the center root cylinder was observed (endodermis). Differences occurred only in the thick of the walls of the cells even within the limits of one species. The thickness of the cell walls certainly depends on the ecological conditions. In drier habitats (also physiologically drier, e.g. in the mountains) the walls of the endodermis cells are thicker than in roots of plants from more moist habitats. From the comparison of the examined material we reached the conclusion, that the character of the endodermis cell structure cannot be used as a diacritical phenomenon for distinguishing the various species, but on the contrary it can be used very well for the characteristics of the entire section.

Phenomena offered by the anatomic structure of the leaf epidermis when viewed from the surface are not investigated as yet and therefore used only very rarely for a phylogenetic-taxonomic evaluation of grass species. In our opinion, these phenomena are very important because they show new aspects of the degree of related affinities between the taxa, particularly higher ones than species. It is not surprising that the character of the anatomic structure, particularly the center part of the surface between the keels (nerves) of the palea is identical, or differs only slightly from the structure of the leaf blade epidermis when viewed from the surface. In any case the palea is of phyllomic origin regardless of whether it is considered a uniform bracteole (prophyllum) opposite to the lemma or two perigone leaves (tepala) grown together, the outer circle of the basic five, circles flower as the prototype of flower in monocotyledon plants.

Also the type of vesture of the palea keels offers an important permanent characteristic of considerable phylogenetic and taxonomic value, but which belongs as can be assumed from the present research in the *Poaceae* family rather to the tribus character, genera and its section, than for distinguishing the various species. It seems that a detailed study of the morphological and anatomic structure of the paleas will also show the need for discovering some other types, in addition to those indicated e.g. by v. OETTINGEN (1925). In any event, the morphological and anatomic characters of the palea cannot be overlooked and underestimated, on the contrary, it is necessary to follow them much more closely than was the case until now. The characteristic offered by the palea belongs according to our opinion among the basic taxo-

monic and diacritical, sometimes also phylogenetic features of taxa of the *Poaceae* family because the palea is an organ which by its location in the flower of grass has very close relations to the sexual organs and plays an important role in their biology.

North American species classified until now with *P. annua* in the group *Annuae* ANDERSS., emend. HITCHC. et CHASE, must necessarily be separated from *P. annua* and other species of the *Ochlopoa* section. Its character of an annual as the only feature (quality) in common with the species *P. bolanderi*, *P. chapmaniana*, *P. howellii* and *P. bigelovii* for the time being correspond with only some species of the *Ochlopoa* section (*P. dimorphantha*, *P. infirma*, *P. maroccana* and with annual to biennial forms of *P. annua*). All the mentioned North American species though have, bunch of wool on the base of the lemma which is missing in the species of the *Ochlopoa* section. Both groups have the same number of nerves on the glumes with the exception of *P. bigelovii* where the lower glume is also clearly three-nerved. Different are the characteristics of the palea keels vesture and the anatomic structure of the center part of the surface between the palea keels. The character of the palea keels vesture and the bunch of wool on the base of the lemmas in *P. bolanderi* though shows that this annual species is different from the other three and it seems to be most closely related to the *P. trivialis* group. The remaining North American annual species are however joined into a uniform group by some essential features, e.g. the morphological and anatomic structure of the palea the presence of wool on the base of the lemmas and finally also the time of their duration (in this case annual). The representation of long and short cells, observed in the center surface between the palea keels differs according to the species, and so does the ending of the cylindrical hairs, which are in the lower 2/3 to 3/4 of the palea keels and finally the length of anthers. In the toothed type of the keels in the upper 1/3 to 1/4 no differences were ascertained. All of the three studied species are distributed exclusively in North America. *P. chapmaniana* area covers the eastern half and *P. bigelovii* roughly the south-west of the U.S.A. (up to northern Mexico) and *P. howellii* extends along the coastal zone from south-west Canada to southern California. According to the division of the areas it seems justified to place the evolutionary center of these species solely on the territory of North America, also from the phyto-geographic point of view these species are completely independent. It therefore seems justified to classify *P. chapmaniana*, *P. bigelovii* and *P. howellii* on the basis of the ascertained taxonomic-morphological and chorological characteristics which distinguished them clearly from the other species of the *Ochlopoa* section into a special section *Diversipoa*, sectio nova [plantae solum annuae; palea inferior ad basin fasciculo lanae distincto obsita; area media inter paleae superioris (glumellae) carina cellis longis brevibusque \pm alternis occupata; species origine solum boreo-americanae, rarissime (*P. chapmaniana* exempli causa) in continentibus aliis adventivae].

If we want to stress the high phylogenetic and taxonomic value of the anatomic structure of the center surface between the palea keels, than we again point out other bluegrass species, where the morphology and anatomy of the palea e.g. form a transition between the paleas structure of the *Ochlopoa* and *Diversipoa* sections. There are *P. tuberifera* and *P. acroleuca* ($2n = 28$) which resemble in some characteristics such as the presence of long soft hairs on the palea keels, the contents of species of the *Ochlopoa* section but by the

alternation of long and short cells in the leaf epidermis (when viewed from the surface) and in the surface between the palea keels resemble the species of the *Diversipoa* section. The *P. acroleuca* resembles this section closely, by the presence of a bunch of wool on the lemma base which is however absent in *P. tuberifera*. For insufficient quantities of material we were not able to classify these bluegrass species into higher taxa (section).

In the other Asiatic species, mentioned before *P. nephelophila*, described from northern Burma (Myitkhina: Chimli Pass; BOR 1949) very closely related to *P. annua* species, as indicated by BOR (l.c.) himself, probably belongs into the *Ochlopoa* section. The paleas have on the keels only hairs.

If we consider the type of vesture of the palea keels one of the fundamental taxonomic and phylogenetic characteristics, then it may for the time being, be assumed that in working out the contents of species of the *Poa* L. genus, groups of forms were created independently in various geographical regions, which differ strikingly from other sections of the genus particularly by the long and soft cylindrical hairs on the palea keels (e.g. section *Ochlopoa*, *Diversipoa* and subsection *Caespitosae*, resp. *Alpinae* section *Bolbophorum*) which according to the results of studies by v. OETTINGEN (1925) belong either to the *Dentatae* or *Pectinatae* types but not to the *Pilosae* or *Semipilosae* types. Already this comparison, made only for orientation purposes in the course of studies of herbarium material, indicates how important it is to evaluate in an analysis of taxonomic features also or even primarily the morphologic and anatomic structure of the palea.

Key for determining the studies species

1a) Bunch of wool on the basis of the lemma missing; the palea keels in the center 2/4—4/6, sometimes already from the base, with long soft cylindrical one-cell hairs; center part of the surface between the palea keels only of long cells; lower glume one, the upper three nerved; annual or perennial plants 2

b) Bunch of wool on the base of the lemma distinctly developed; the palea keels in the lower 2/3—3/4 with long soft cylindrical one-cell hairs; towards the top of the palea the keels distinctly and \pm densely dentate (teeth forward pointed towards the top of the palea); the front part of the surface between the palea keels of long and short cells in a ratio of $\pm 1 : 1$; lower glume one, the upper three nerved or both three nerved; annual plants 7

2a) Stamens twice as long as the lemmas; anthers 1,8—2,0 mm. long; the lemma of the top female flower ovoid to broadly ovoid, its shape strikingly different from the lanceolate lemmas of the lower hermaphroditic flowers of the spikelet; the rachilla of the terminal flower as long or only slightly longer than the length of the flower; the panicle oblong in outline, oblong-lanceolate or lanceolate, narrow 2,5—5 times as long as it is wide, its branches pointing directly obliquely upward, upright, rarely the lowest ones \pm horizontal; the leaf blades glabrous on the margins smooth, towards the end gradually narrowing down into a soft point; annual; tetraploid ($2n = 28$); Morocco: *P. dimorphantha* MURB.

b) Stamens as long or slightly longer than the lemmas; anthers 0,2—3 mm. long; the lemma of the top female flower (or two female flowers, if the spikelet has at least five flowers) elliptically oblong, distinguished from the lemmas of the lower hermaphroditic flowers in the spikelet by its smaller size; rachilla of the terminal flower at least by 1/4 but often several times shorter than the lemma; the panicle in outline of various forms, usually \pm three times as long as it is wide; its branches freely projected, slightly ascending or horizontal, the lower ones frequently bent; the leaf blades along the margins particularly in the upper 1/2, scabrous with the teeth directed upwards, towards the end \pm subito contracted; diploids ($2n = 44$) or tetraploids ($2n = 28$) 3

3a) Rachilla of the terminal flower shorter only by $\frac{1}{4}$ — $\frac{1}{2}$ that of the lemma; cylindrical hairs on the palea keels very dense, in 3—6 rows; the flowers in the spikelet distinctly spaced,

not covered by the rhachilla; center nerve on the side of the lemma particularly in the lower $\frac{1}{2}$ densely adherensively hairy; anthers 0.2—1.0 (1.2) mm. long; annuals 4

b) Rhachilla of the terminal flower at least twice as short as the lemma; cylindrical hairs on the palea keels dense, in 1—3 rows; flowers in the spikelet dense, usually \pm covering the rhachilla; center nerve on the side of the lemma sparsely to densely hairy or on the contrary glabrous; anthers 0.6—3 mm. long; annuals or perennials 5

4a) Anthers 0.2—0.4 (0.5) mm. long, at the most twice as long as they are wide; the lemma of the lowest flowers in the spikelet 2—2.5 mm. long; the palea narrow and oblong, 2.2—2.5 mm. long; cylindrical hairs on the palea keels \pm as long as $\frac{2}{3}$ of the largest width of the center part of the surface between the keels of the palea; diploid ($2n = 14$); Mediterranean and north-western Europe, introduced into South America (Bolivia, Peru): *P. infirma* H. B. et K.

b) Anthers 0.7—1.0 (1.2) mm. long, 3—5 times as long as they are wide; the lemma of the lowest flower in the spikelet 3.2—3.5 mm. long; the palea oblong, 3.2—3.4 mm. long; cylindrical hairs on the palea keels \pm long as $\frac{1}{2}$ of the largest width of the center part of the surface between the keels of the palea; tetraploid ($2n = 28$); Morocco, Algeria: . . . *P. maroccana* NANNE.

5a) Anthers 0.6—0.8 (1.0) mm. long, 4—5 times longer than wide, palea lanceolate, 3—3.2 mm. long; cylindrical hairs on the palea keels \pm as long as $\frac{2}{3}$ — $\frac{3}{4}$ of the largest width of the center part of the surface between the keels of the palea; the rhachilla of the terminal flower 2—3 times shorter than its lemma; the panicle ovoid to triangularly oblong in outline, 1.2—1.6 times as long as it is wide; spikelets at the end of the branches not in clusters (distributed over the larger part of the branches); center nerve on the side of the lemma sparsely or more densely hairy; annual to perennial; tetraploid ($2n = 28$); almost secondary a cosmopolite weed: *P. annua* L.

b) Anthers 1.6—3.0 mm. long, 5—8 times as long as is wide; the palea oblong, 3.2—3.6 mm. long; cylindrical hairs on the palea keels \pm as long as $\frac{1}{2}$ of the largest width of the center part of the surface between the keels of the palea; the rhachilla of the terminal flower 4—6 times shorter than its lemma; panicle in outline equilateral or isosceles triangular, same in length and width or as much as three times longer than wide; the spikelets at the end of the branches clustered; the center nerve on the side of the lemma hairless, only very rarely in the lower $\frac{1}{2}$ slightly hairy; perennial 6

6a) Lemma of the lowest flower in the spikelet 2.3—3 mm. long; anthers (1.2) 1.6—2.0 (2.5) mm long; the panicle in outline almost equilaterally triangular, \pm as long as it is wide; branches particularly the bottom ones horizontal to overlapping; spikelets at the end of the branches considerably clustered; perennial; diploid ($2n = 14$); hilly to alpine gradus western and central Europe (probably also the Caucasus and Central Asia): *P. supina* SCHRAD.

b) Lemma of the bottom flowers of the spikelet 3.0—4.0 mm. long; anthers (1.6) 1.9—2.5 (3.0) mm. long; panicle in outline equilaterally triangular, 2.5—3 times as long as wide; branches freely projecting, frequently slightly ascending; spikelets at the end of the branches \pm clustered; perennial; tetraploid ($2n = 28$); Atlas mountains: *P. rivulorum* MATRE et TRABUT

7a) Both glumes three nerved; anthers 0.5—0.8 mm. long; the palea oblong, 2.5—2.8 mm. long; cylindrical hairs on the palea keels \pm as long as $\frac{2}{3}$ of the greatest width of the center part of the surface between the keels of the palea, same length as width or towards the end \pm clavate; panicle narrow by contracted, \pm interrupted; the sheath scabrous; southern part of the USA and northern Mexico: *P. bigelovii* VASEY et SCRIBN.

b) Lower glume one, upper three nerves; cylindrical hairs on the palea keels \pm as long as $\frac{1}{2}$ — $\frac{2}{3}$ as the greatest width of the center part of the surface between the keels of the palea 8

8a) Anthers 0.1—0.3 mm. long; palea oblong, 2—2.3 mm. long; cylindrical hairs on the palea keels longitudinally of equal width, at the end rounded, length $\frac{1}{2}$ — $\frac{2}{3}$ of the largest width of the center part of the surface between the keels of the palea; glumes \pm 2 and 2.5 mm. long; center nerve on the edge of lemma prominent, densely covered by long and projecting hairs; eastern part of the U.S.A.: *P. chapmaniana* SCRIBN.

b) Anthers 0.5—0.8 mm. long; palea widely lanceolate 2.3—2.6 mm. long; cylindrical hairs on the palea keels gradually narrowing down into a blunt point, length equals as much as $\frac{1}{2}$ of the largest width of the center part of the surface between the keels of the palea; glumes \pm 1,5

and 2 mm. long; center nerve on the edge of lemma indistinct, covered by thin, short and closely adhering hairs; short cells in center part of the surface between the palea keels usually jut out into a small thorn or hair; westernmost region of North America:
. *P. howellii* VASEY et SCRIBN.

Results of study

1. We have carried out a detailed analysis of the systematic characteristics of species of the *Ochlopoa* section (A. et GR.) V. JIRÁS. and of the *Annuae* ANDERSS., emend. HITCHC. et CHASE group and some related Asiatic species on accessible herbarium material;

2. we have evaluated the significance of the morphological and anatomic structure of the paleas, the anatomic structure of leaf blades when viewed from the surface, the length of anthers and for orientation purposes also the anatomic structure of roots in transversal cut in order to ascertain the degree of phylogenetic relationship, taxonomic value and diacritical differentiation of the studied species; in *P. annua* and *P. supina* also the length and shape of the ligule of the upper culm leaves;

3. we have determined the authors of the name of the section, i.e. *Ochlopoa* (A. et GR.) V. JIRÁS., divided the contents of its species into two new subsections (*Staminatae* and *Ochlopoa*). and have excluded the North American annual species classified until now by mistake together with *P. annua* in the group *Annuae* ANDERSS., emend. HITCHC. et CHASE, identical with the *Ochlopoa* section and united them in a new section *Diversipoa*;

4. a taxonomic study showed that *P. bolanderi* does not belong into the *Ochlopoa* section nor into the *Diversipoa* section;

5. an analysis of existing conceptions on the origin of some species of the *Ochlopoa* section lead us to the conclusion that in this polyploid group the present tetraploids (*P. annua*, *P. maroccana* and *P. rivulorum*) came into being most probably from the descendants of original sterile diploid hybrids between parental diploids (*P. infirma*, *P. supina*) and their consequential natural polyploidization; a comparative analysis of the group of characteristics showed that *P. annua* constitutes the \pm center link between diploid parents, *P. maroccana* is close to *P. infirma*, and *P. rivulorum* on the contrary to *P. supina*; the tetraploid *P. dimorphantha* has in the *Ochlopoa* section an isolated position (subsection *Staminatae*), nothing is known of its origin for the time being;

6. in examining the "annuoid" or "supinoid" types in the herbarium material, we have for comparison also carried out an analysis and evaluation of the systematic characteristics of the Japanese endemic *P. tuberifera* and the East Asiatic species *P. acroleuca*;

7. the rich variability of *P. annua* confirms the relatively recent origin of this tetraploid, the forms of which have spread mainly in the regions of the broader Mediterranean and are by the vesture of the lemma very similar to *P. infirma* forms;

8. it can be assumed that the contents of the species of the *Ochlopoa* and *Diversipoa* sections originated in independent and very remote evolutionary centers: the first in the Mediterranean, most likely in the higher altitudes of its western part, the second somewhere in the territory from the southern regions of the temperate zone to the northern regions of subtropical North America;

9. using all suitable and once more verified material or newly by study

Characters	<i>P. dimorphantha</i>	<i>P. infirma</i>	<i>P. maroccana</i>	<i>P. annua</i>	<i>P. supina</i>	<i>P. rivulorum</i>
Anthers (length)	1.8—2.0 mm.	0.2—0.4 (0.5) mm.	0.7—1.0 (1.2) mm.	0.6—0.8 (1.0) mm.	1.6—2.0 (2.5) mm.	(1.6) 1.9—2.5 (3.0) mm.
Anthers (width : length)		not more than twice as long as wide	3—5 times as long as wide	4—5 times longer than wide	5—8 times longer than wide	5—8 times longer than wide
Filaments of stamens	when flowering \pm twice as long as the lemma	when flowering only slightly longer than the lemma	when flowering only slightly longer than the lemma	when flowering only slightly longer than the lemma	when flowering only slightly longer than the lemma	when flowering only slightly longer than the lemma
Length of terminal flower rhachilla in spikelet	length as flower or slightly longer	shorter than flower by $\frac{1}{4}$ — $\frac{1}{2}$ (lemma)	shorter than flower by $\frac{1}{4}$ — $\frac{1}{2}$ (lemma)	2—3 (4) times shorter than flower (lemma)	2—3 (4) times shorter than flower (lemma)	2—3 (4) times shorter than flower (lemma)
Lemma of terminal flower	ovoid to broadly ovoid, strikingly different from lanceolate lemmas of lower flowers in spikelet	elliptical-oblong resembling other lemmas in spikelet but much smaller	elliptical-oblong resembling other lemmas in spikelet but much smaller	elliptic-oblong resembling other lemmas in spikelet but much smaller	elliptic-oblong resembling other lemmas in spikelet but much smaller	elliptic-oblong resembling other lemmas in spikelet but much smaller
Flowers (intervals between them, e.g. between the places where the lemmas adhere)	\pm spaced	distinctly spaced not covering the rhachilla	spaced not at all or only slightly covering the rhachilla	\pm dense, mostly covering the rhachilla	dense, strongly contracted covering the rhachilla	\pm dense, contracted, mostly covering the rhachilla
Center nerve in middle of lemma	densely silky wool, particularly in lower $\frac{1}{2}$	densely adherensivly hairy particularly in lower $\frac{1}{2}$	densely adherensivly hairy particularly in lower $\frac{1}{2}$	hairy (to various degrees) particularly in lower $\frac{1}{2}$	glabrous	glabrous only rarely sparingly hairy particularly in lower $\frac{1}{2}$
Panicle (in outline)	narrowly oblong, oblong-lanceolate to lanceolate, 2.5 to 5 times longer than wide; branches erect, directly intendent	elliptic to oblong- elliptic, 1.5 to 3 times longer than wide; branches loosely spreading, ascending upwards	triangular-elliptic to elliptic oblong (lozenge), 2—3 times as long as wide; branches loosely spreading, ascending upwards	ovoid to triangular, 1.2—1.6 times longer than wide; branches usually loose, only the lower ones after flowering deflected	equilaterally triangular to broadly triangular, \pm as it is wide; branches horizontal or deflected	oblong-ovoid to oblong, 2.5—3 times longer than wide; branches loosely spreading, often ascending upwards
Distribution of spikelets on the panicle branches		on the larger part of the branches	on the larger part of the branches	on the larger part of the branches	conspicuously clustered at the end of the branches	on the larger part of the branches sometimes slightly clustered at the end of branches
Length of lemma of bottom flower		2—2.5 mm.	3.2—3.5 mm.	2.5—4.0 mm.	2.3—3 mm.	3—4 mm.
Termination and margin of leaf- blades	towards point \pm gradually narrowed down into soft point; smooth on margins	towards point suddenly tapered down; on the margins particularly in upper $\frac{1}{2}$ tending upwards little teeth scabrous	towards point suddenly tapered down; on the margins particularly in upper $\frac{1}{2}$ tending upwards little teeth scabrous	towards point suddenly tapered down; on the margins particularly in upper $\frac{1}{2}$ tending upwards little teeth scabrous	towards point suddenly tapered down; on the margins particularly in upper $\frac{1}{2}$ tending upwards little teeth scabrous	towards point suddenly tapered down; on the margins particularly in upper $\frac{1}{2}$ tending upwards little teeth scabrous
Colouring of spikelets	green and purple or purple tinged	yellowish green to light green, generally purple tinged	yellowish green to light green, purplish streak sometimes	green to yellowish green red to purple (all colours in various shades)	usually deep purplish red	generally purple tinged
Colouring of plants	green	yellowish green to light green	yellowish green to light green	green (various shades)	yellowish green, brownish green to \pm purplish	
Duration of plants	annual	annual	annual	annual (produces even a number of generations during the year), biennial or perennial	perennial	perennial
Flowering period	February-May	March-May	April-May	January-December (a number of generations during the year)	in lower altitudes April-May, in higher zones June-August	February (March)— May (June)
Chromosome number	2n = 28 tetraploid	2n = 14 diploid	2n = 28 tetraploid	2n = 28 tetraploid (HOVIN 1958, 2n = 14)	2n = 14 diploid	2n = 28 tetraploid

determined diacritical characteristics we have compiled a dichotomic key for the easy identification of the studied bluegrass species of the *Ochlopoa* and *Diversipoa* sections;

10. the conception that in a systematic study of the representatives of the *Poaceae* family it is necessary to stress the characteristics which the sexual organs and the vegetative organs offer and which are brought their biological functions closely related to them (the palea, lemma, possibly also the lodicules) seems justified.

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Systematic survey of the studied taxa

Sectio *Ochlopoa* (A. et Gr.) V. JIRÁS. Plantae annuae aut perennes; palea inferior ad basin fasciculo lanæ non obsita; area media inter paleae superioris (glumellae) carinas cellis solum longis occupata; species origine gerontogæe, *P. annua* exempli causa in orbe terrarum fere toto secundarie distributa. Typus: *Poa annua* L.

Subsectio *Ochlopoa*, subsect. nova. Staminum filamenta solum parum quam lemmata longiora. Typus: *P. annua* L.

P. infirma H. B. et K. Syn.: *P. annua* L. β *exilis* TOMM.; *P. exilis* (TOMM.) MURB.; *P. annua* L. subsp. *exilis* (TOMM.) A. et Gr. var. *exilis* MAIRE; *P. annua* L. f. *remotiflora* HACK.; *P. remotiflora* (HACK.) MURB.

P. supina SCHRAD. Syn.: *P. annua* L. var. *supina* (SCHRAD.) LINK; *P. annua* L. subsp. *varia* GAUD.; *P. annua* L. subsp. *supina* (SCHRAD.) A. et Gr.; *P. annua* subsp. *varia* GAUD. var. *supina* (SCHRAD.) REICHENB.

P. maroccana NANNF. Syn.: *P. annua* L. subsp. *exilis* (TOMM.) A. et Gr. var. *maroccana* (NANNF.) LIT.

P. rivulorum MAIRE et TRAB. Syn.: *P. annua* L. subsp. *varia* GAUD. var. *supina* (SCHRAD.) REICHENB. f. *macranthera* LIT. et MAIRE; *P. annua* L. subsp. *varia* GAUD. var. *rivulorum* (MAIRE et TRAB.) LIT. et MAIRE

P. annua L. Syn.: *P. triangularis* GILIB.; *P. ovalis* TINEO; *P. aestivalis* PRESL; *P. compagnoi* GANDOGER (in sched.); *P. annua* L. subsp. *typica* (BECK) MAIRE; *P. annua* L. subsp. *eu-annua* V. JIRÁS.

P. nephelophila BOR

Hybrids of spontaneous origin: *P. annua* \times *infirma* NANNF.; *P. annua* \times *maroccana* NANNF.; *P. annua* \times *supina* NANNF.

Subsectio *Staminatae*, subsect. nova. Staminum filamenta bis quam lemmata longiora. Typus et species unica: *P. dimorphantha* MURB.

Sectio *Diversipoa*, sect. nova. Plantae solum annuae; palea inferior ad basin fasciculo lanæ distincto obsita; area media inter paleae superioris (glumellae) carinas cellis longis brevibusque \pm alternis occupata; species origine solum boreo-americanæ, rarissime (*P. chapmaniana* exempli causa) in continentibus aliis adventivæ. Typus: *Poa chapmaniana* SCRIBN.

P. chapmaniana SCRIBN.

P. bigelovii VASEY et SCRIBN. Syn.: *P. annua* L. var. *stricta* VASEY

P. howellii VASEY et SCRIBN. Syn.: *P. bolanderi* VASEY var. *howellii* (VASEY et SCRIBN.)

JONES

I view of the present lack of documentary herbarium material, particularly specimens of types and due to the inaccessibility of important basic literature, we do not intend at this time to include *P. acroleuca* STEUD. and *P. tuberifera* FAURIE ex HACK., nor any further species indicated for instance by BOR (1952, 1960) from Pakistan and India, in the discovered sections. All the mentioned species have exclusively Asiatic areas.

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