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Some Remarks on the Genesis of the Flora of Southern Slovakia.

By *Karel Domin* (Praha).

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In 1923 I published a new regional division of Slovakia and Subcarpathian Russia; later on, in 1928, I gave a regional division of Czechoslovakia, and supplemented it in 1930. Two years later I published a coloured map of Czechoslovakia on which 86 chief geobotanical districts are defined and on a smaller map I showed the expansion of our main vegetational regions. Of these regions there are in Slovakia only two of wide distributions, i. e. the Westcarpathian, and the Pannonian region.

The Pannonian region is fully developed in the most southern part of Slovakia, its plant-communities, however, as well as numerous Pannonian species, extend into Central Slovakia, and locally even into the northern part of our Western Carpathians; along the river Poprad they approach the Polish frontier.

The characteristic species of this region are thermophilous and nearly all of them xerothermic, though there are among them — especially in the lowlands of Southern Slovakia — also some hygrophilous types. Of trees the most characteristic are *oaks*, then *Carpinus* and of shrubs *Cornus mas* and *Prunus nana*; a speciality of this region is *Fraxinus ornus*. The Pannonian region is accompanied by a very rich ruderal flora; there are also sand-plains and sandy hills (especially in the so-called Moravské pole) and very interesting rock-steppes, as well as a few salt-marshes. The xerothermic oak-forests (a special type of a European xerodrymum), interspersed with more or less extensive steppe-openings, are sometimes regarded as a type of the so-called « Waldsteppe ». The species of this region are of various origin (especially Pontic, meridional and oriental) and may be called Pannonian only with regard to their more or less regular distribution along the Pannonian danubial basin; only a smaller part of these species is to be found in the Alföld. I am giving an enumeration of these species in alphabetical order :

Abutilon Theophrasti
Acer tataricum
Achillea crithmifolia
— *ochroleuca*
— *pannonica*
— *setacea*

Aconitum anthora
Acorellus pannonicus
Adonis vernalis
Aegilops cylindrica
Agropyrum cristatum
— *intermedium*

Dianthus collinus
— *Lumnitzeri*
— *Pontederæ*
— *serotinus*

Dictamnus albus

Echium italicum
— *rubrum*

Echinops commutatus
— *ruthenicus*

Eragrostis cilianensis

Erodium Neilreichii

Eryngium planum

Erysimum canescens
— *erysimoides*

Euclidium syriacum

Euphorbia pannonica

— *polychroma*

— *verrucosa*

— *villosa*

Eurotia ceratoides

Evonymus verrucosa

Festuca Dominii

— *pseudodalatica*

— *vallesiaca*

Ficaria calthifolia

Fraxinus ornus

Fritillaria meleagris

Fumana vulgaris

Galega officinalis

Galium parisiense

— *pedemontanum*

— *pseudoaristatum*

— *rubroides*

Genista ovata

Geranium lucidum

Gypsophila arenaria

— *paniculata*

— *stepposa*

Helianthemum canum

— *nummularium*

Helichrysum arenarium

Heliotropium europæum

Herniaria Besseri

Hesperis tristis

Hibiscus trionum

Holoschoenus vulgaris

Hordeum Gussoneanum

Hornungia petraea

Hypericum elegans

Hyssopus borealis

Inula germanica

— *ensifolia*

— *oculus christi*

Iris aphylla

— *graminea*

— *pumila*

— *variegata*

Isatis præcox

Jurinea mollis

Kickxia elatine

— *spuria*

Kochia laniflora

— *prostrata*

Koeleria gracilis

Lactuca Chaixii

— *perennis*

— *quercina*

Laser trilobum

Lathyrus latifolius

— *nissolia*

— *pannonicus*

Leonurus marrubiastrum

Lepidium perfoliatum

Lepturus pannonicus

Leucocjum aestivum

Lilium bulbiferum

Limodorum abortivum

Limonium Gmelinii

Linaria genistifolia

— *italica*

Linum austriacum

— *flavum*

— *hirsutum*

— *pannonicum*

— *tenuifolium*

Lithospermum purpureo-coeruleum

Loroglossum hircinum

Lotus siliquosus

— *tenuifolius*

Lychnis coronaria

Marrubium creticum

Medicago minima

— *prostrata*

— *rigidula*

Melampyrum cristatum

Melica picta

Melittis melissophyllum

Mentha pulegium

Micropus erectus

Minuartia fasciculata

- Minuartia frutescens*
— *glomerata*
Muscari botryoides
— *neglectum*
Myosotis suaveolens
- Nigella arvensis*
Nepeta pannonica
Nymphoides peltata
- Oenanthe fistulosa*
— *peucedanifolia* sbsp. *stenoloba*
— *silaiifolia*
Onobrychis arenaria
Onosma arenarium
— *tornense*
— *Visianii*
Ophrys aranifera
— *fuciflora*
Orchis militaris
— *pallens*
— *purpurea*
— *tridentata*
Orlaya grandiflora
Ornithogalum comosum
Orobanche arenaria
Oryzopsis virescens
Oxytropis pilosa
- Papaver dubium* var. *albiflorum*
— *hybridum*
Peucedanum alsaticum
— *arenarium*
— *carvifolia*
— *cervaria*
Phlomis tuberosa
Plantago altissima
— *indica*
— *laciniosa*
— *maritima*
— *tenuiflora*
Poa badensis
— *scabra*
Polygala major
Polygonatum latifolium
Polygonum arenarium
Potentilla arenaria
— *patula*
— *pedata*
— *recta*
— *thuringiaca*
Primula veris var. *canescens*
Prunus fruticosa
— *mahaleb*
— *nana*
- Pulicaria dysenterica*
Pulmonaria mollissima
Pulsatilla grandis
— *slavica*
- Quercus cerris*
— *lanuginosa*
- Ranunculus illyricus*
— *lateriflorus*
— *millefoliatus*
— *pedatus*
— *polyphyllus*
Rapistrum perenne
Reseda phyteuma
Rhamnus saxatilis
Rhaphis gryllus
Rosa spinosissima
Ruscus hypoglossum
- Salsola kali*
Salvia aethiopsis
— *austriaca*
— *nemorosa*
Saxifraga bulbifera
Scabiosa canescens
Scandix pecten-veneris
Scorzonera austriaca
— *hispanica*
— *purpurea*
Scrophularia vernalis
Scutellaria altissima
Sedum Krajiniae
Selaginella helvetica
Sempervivum Schlehanii
Serratula lycopifolia
Sesleria Sadleriana
Setaria ambigua
Sideritis montana
Silene conica
— *longiflora*
— *viridiflora*
Sisymbrium altissimum
— *irio*
— *orientale*
— *strictissimum*
Smyrniium perfoliatum
Sorbus dacica
Spiranthes aestivalis
Stachys annua
— *germanica*
Staphylea pinnata
Stipa capillata
— *pulcherima*

Stipa stenophylla
Syrenia cana

Taraxacum serotinum
Thalictrum flavum
— *foetidum*

Thesium Dollineri

Thymelaea passerina

Thymus glabrescens sbsp. *variae*

— *Marschallianus*

— *pannonicus*

Tragus racemosus

Tribulus terrestris

Trifolium angulatum

— *rubens*

Trigonella monspeliaca

Trinia glauca

Tunica saxifraga

Turgenia latifolia

Valerianella coronata

Ventenata dubia

Verbascum blattaria

— *phoeniceum*

Veronica incana

— *dentata*

— *orchidea*

Vicia pannonica

— *sparsiflora*

Vinca herbacea

Viola alba

— *ambigua*

— *austriaca*

— *Kitaibeliana*

Vitis silvestris

Waldsteinia geoides

— *ternata*

Xeranthemum annuum

— *foetidum*

The genesis of the Slovakian vegetation can be only understood when taking into consideration the whole Carpathian flora as well as that of the Hungarian Central hills (Pramatra, Ös-Matra) and the Hungarian basin (Alföld). It is hardly possible to determinate with any accuracy the age of individual species, as we know but little about the vegetation at the end of the tertiary period. Some types point already by their often very disjunct areas, to a great age. This is for instance the case with *Juniperus sabina* and *Chrysanthemum Zawadskii* in the Pieniny Mts., with *Ruscus hypoglossum* in the Little Carpathians, *Cotinus coggyria* (Slatina and V. Lodina), *Waldsteinia ternata* (Tisovec, Košické Hamry), *Ligularia sibirica* (Central Slovakia), *Dracocephalum austriacum* (Drevenik, Slovenský Kras), *Fumana vulgaris*, *Hyssopus borealis* (an endemic form in the district Slovenský Kras), etc. These are surely relic types of the tertiary period but there are many others the age of which it is difficult to define. The contradictory opinions on the origin of the vegetation of Alföld and Pramatra as well as the study of B. P a w ł o w s k i on the origin and the elements of the vegetation of the subnival zone of the High Tatras show how difficult these problems are. When the areas of all Slovakian species will be better known, then the discussion of these questions shall be based on a safer basis. The fact that the bulk of the Westcarpathian mountain flora belongs to the centraleuropean-alpine element and a part of these species is arctic-alpine, is often overlooked. This does not mean, however, that the bulk of the Carpathian mountain flora migrated from the Alps into the Carpathians; the origin of those species may be looked for either in this or that region, and their migration is possible in both directions. A polytopic origin seems to be a rare exception and could

be perhaps admitted for some oreomorphoses (*Solidago alpestris* — *S. virgaurea*, *Cerastium fontanum* — *C. vulgatum*, etc.). Some Carpathian types penetrated also into the Sudetic region, and vice versa, some species migrated via the Transsilvanian Carpathians into the Balcan peninsula (f. i. *Saxifraga carpatica*) or from the Carpathians into the Eastern Alps (f. i. *Gentiana frigida*). Of arctic origin is for instance *Salix herbacea*, a circumpolar-alpine species, a noteworthy relic species is *Astragalus oroboides* (the Tatras of Biela) growing — except its localities in the Southern Alps — in the most northern part of Europe and as far as Arctic Russia. Some trees, as *Pinus silvestris*, *P. cembra*, *Larix carpatica*, are in our Carpathians relic types which were probably much wider spread in the forest of the subarctic Pine epoch. *Pinus silvestris* grows in our region on relic rocky localities. Its wide distribution on the sandy soils of the Moravské pole is surely of more recent origin and cannot be compared with the occurrence of Pine in the Carpathians proper.

The various opinions on the genesis of the Westcarpathian flora and the more or less thorough knowledge thereof find their expression in the regional division of Slovakia, very differing in the view of various authors. In 1908 F e r d. P a x divided the Western Carpathians as follows :

- a) Districts with older relics : 1) the Pieniny Mts., 2) the southern Central Carpathians;
- b) Districts without older relics : 3) the Beskydy Mts., 4) the northern Central Carpathians;
- c) Peripheric westcarpathian districts : 5) the Malé Karpaty Mts., 6) the Větrné hole Mts., 7) the marginal hills and mountains along the river Nitra, 8) the Hungarian Ore-mountains and the Vjepor Mts., 9) the Gelnica-Bránisko Mts., 10) the Prešov-Tokaj trachytic mountains.

The division is, however, not satisfactory. A regional geobotanical division of the former Hungary (including Slovakia and Subcarpathian Russia) was published already by A. K e r n e r (1887), the author of the classic work « Das Pflanzenleben der Donauländer » (1863) and in more recent times by August von H a y e k (1907, 1926), and of the Hungarian botanists especially by V. B o r b á s (1896, 1904), L. S i m o n k a i (1891, 1901, the map was published by T u z s o n in 1910), J. T u z s o n (1911, with a coloured map), R. v. R a p a i c s (1910, 1918), S. J á v o r k a (1925), R. v o n S o ó (1929—1931).

R. von S o ó distinguishes in 1930 the following districts of his Carpathian province (C a r p a t i c u m) :

I. The section Northern Carpathians (E u c a r p a t i c u m) with the following districts :

1. P o s o n i c u m (Malé Karpaty).
2. P r a e m o r a v i c u m (Bilé Karpaty).
3. B e s c h i d i c u m (the Western Beskydy Mts. - Babia Góra).
4. S a n i c u m (the Eastern Beskydy Mts.).
5. N i t r i c u m (Inovec-Tribeč, the Nitra Mts.).
6. S u b f a t r i c u m (Větrné hole Mts.).
7. F a t r i c u m (The Kriváň et Velká Fatra Mts., Choč).
8. S u b t a t r i c u m (Nízké Tatry Mts.).
9. P r a e f a t r i c u m (Slovenské Krušnohoří Mts.).
10. S c e p u s i c u m (Gemersko-spišské Rudohoří Mts. including Bránisko or the so-called Gelnica-Bránisko Mts.).
11. T a t r i c u m (the High Tatras = Vysoké Tatry) with the following subdistricts : *a*) l i p t o v i e n s e (Liptovské hole), *b*) p o l o n i c u m (Polské Tatry), *c*) s c e p u s i e n s e (the High Tatras proper), *d*) b e l a i c u m (Bielské Tatry).
12. P i e n i n i c u m (the Pieniny Mts.).
13. C a s s o v i c u m (the Prešov-Tokaj Mts. or the Slánské hory Mts.).
14. V i h o r l a t i c u m (Poloniny); a transition to the Eastern Carpathians.

Of the Eastern Carpathian or Transsilvanian Subprovince (T r a n s s i l v a n i c u m) the district P o c u t i c u m (Eastern Carpathians between Latorca and Tisa) and a part of the district M a r m a r o s s i c u m (the group of the Mount Čorná hora) belong to the Czechoslovak Republic. The most southern part of Slovakia, approximately in a line from Želiezovce to Košice, forms in S o ó ' s classification already a part of the Province of Pramatra (M a t r i c u m).

Our Pannonian region is represented by the spurs of the Danubian lowlands, extending into southern Slovakia and southern Moravia as well as by the Carpathian foothills covered with oak-woods and thermophilous vegetation. The Pannonion region, however, is only a section of the great Pontic province, the origin of which is to be looked for in Central Asia wherefrom this vegetation, chiefly of a steppe character, penetrated into the steppe region along the Black Sea though many species have their proper home in the Orient (the oriental-pontic element). It is hardly possible to discuss here the extensive literature on the so-called p o n t i c v e g e t a t i o n which was looked upon in various manner since 1882 when A. E n g l e r designated as the pontic zone the eastern Mediterranean provinces, and 1887 when A. K e r n e r defined as pontic the vegetation extending from the shores of the Black Sea (Pontus) westwards to the plains of eastern Galicia and to the margin of the Alps and the Carpathians and nearly to the shores of the Adriatic Sea. K e r n e r distinguished in the region of the Pontic vegetation four divisions, the Illyrian, Pannonian, Dacian and Podolian. These questions were discussed in various publications by J o s. P o d -

p ě r a (V ý v o j, 1906), who accepted the Danubial way as means for the penetration of the steppe vegetation into southern Moravia. Aug. H a y e k deals with the problem of the Pontic and Pannonian flora in Oesterr. Bot. Zeitschr. **77**, 231 (1923). H a y e k points out that it is necessary to distinguish sharply the Pannonian vegetation as the relic of the tertiary vegetation of deciduous forest in the southern part of Central Europe and the northern part of South Europe from the true Pontic steppe vegetation which immigrated from the East, i. e. southern Russia and Asia. Rik. S t e r n e r (1922) introduced a new name (continental element of the European flora) for species widely distributed in Eastern Europe and extending more or less westwards, and divided this continental element into six groups according to the areas of the species. In 1931 Jos. P o d p ě r a discussed in detail the problems of the European steppe species with regard to S t e r n e r ' s point of view. The terms « Pontic » and « Pannonian », however, are so generally used that it seems hardly advisable to drop them. I accept the Pontic element in its broadest sense and propose the following division of Slovakia :

The Pontic province.

The Pannonian (Western Pannonian) region :

1. The Alföld subregion with the following principal districts: *a*) P r a e m a t r i c u m (the sandy territory between the rivers Danube [Dunaj] and Tisa); *b*) T i t e l i c u m (the Loess territory hence southwards); *c*) D e l i b l a t i c u m (the sandy territory of the Deliblat); *d*) C r i s i c u m (the Loess and swamp territory); *e*) S a m i c u m (Nyir-ség, a sandy territory) (cf. R a p a i c s, S o ó and others).

2. The proper Pannonian subregion.

a) P r a m a t r a (the Hungarian Central Mountains).

b) The Subcarpathian Pannonian district.

The two subregions have many characters in common though they differ not only in the composition of the vegetation and its physiognomy but especially epiontologically as the first subregion was colonised by a vegetation of lesser age, immigrated after the drying up of the Pannonian sea, whereas the vegetation of the second subregion is much older and (though of a somewhat different character) can be traced to the end of the Tertiary period when Alföld (the Pannonian basin) was covered by the sea.

Since K e r n e r Alföld was regarded as an arid steppe without natural forests and this picture of the so-called Hungarian puszta was accepted even by such distinguished geobotanists as E n g l e r, D r u d e, H a y e k. We know now that this conception of Alföld was quite wrong (cf. S o ó and R a p a i c s who gave us a detailed description of this territory) and that Alföld is a secondary steppe region and

had at the end of the prehistorical times extensive forests. There were hygrophilous gallery-forests along the rivers and on wet soil hygrophilous oak-woods, Saliceta, mixed deciduous forests, swamps and bogs, Phragmiteta and Cariceta whereas on drier soil there were oak-woods (chiefly *Quercetum roburis*) with openings with steppe vegetation or, on sandy soil, with *Festucetum vaginatae*; there were of course also shrubby communities as well as open halophilous plant associations and various other communities.

The vegetation of Alföld is of lesser importance for southern Slovakia as one might suppose with regard to its proximity. This vegetation originated and stabilised itself at a time, when the warm spurs and foothills of the Carpathians had its old vegetation. In the lowlands of southern Slovakia are of course analogical gallery woods and « Auwälder » but already much poorer and the true puszta penetrates into our region only in fragments. Some species reminding Alföld are recorded from Komárno and Parkán but are to be found also near Král. Chlumeč (here grow on sand *Plantago tenuiflora* and *Polygonum arena-rium*). Therefore it is not the Danubial but the Subcarpathian way which is determinative for the migration of our Pannonian flora. Species of which it may be said that they penetrated from the basin of Danube into Slovakia, are characterised ecologically as well as by their geographic area. Such species for instance are *Tribulus terrestris*, *Hordeum Gussoneanum*, *Cynoglossum montanum*, *Alkanna tinctoria*, *Gypsophila fastigiata*, *Cynodon dactylon* and perhaps even *Rhaphis gryllus*, *Ranunculus lateriflorus*, *R. polyphyllus*, *Corispermum canescens*, *C. nitidum*, *Chlorocyperus glomeratus*, *Acorellus pannonicus*, *Syrenia cana*.

The vegetation of Pramatra or the Hungarian Central Mts. differs essentially from that of Alföld and is of much greater importance for our Pannonian region. It is an autochton flora of great age developing itself gradually since the tertiary period. In the Postpliocen there were still coniferous forests (*Abies alba*, *Picea abies*, *Pinus silvestris*) but at present it is a region of deciduous woods, oak-woods and beech only in places dominating; the steppe vegetation is richly developed. There is no doubt that many species immigrated into Alföld from Pramatra and also from the Carpathian foothills. The spurs of Pramatra penetrate also into the most southern part of Slovakia. A branch of this district are especially the hills of Kováčov and those of Šahy and a chain of warm hills further eastwards (towards Lučenec). The Slovakian Karst district, however, is already a part of the Subcarpathian Pannonian region. We know a series of species in the Slovakian outspurs of Pramatra not known in the Pannonian Subcarpathian region.

The Subcarpathian Pannonian region is in Slovakia fully developed and may be — in a more or less broad stripe — followed from Kobyla (near Bratislava) to the most eastern part of Slovakia. In the warmest

part it has the character of a Xerodrymum or a « Waldsteppe » and its most characteristic trees are *Quercus lanuginosa* and *Q. cerris* but often even *Q. sessilis* is strongly represented. This oak is more xerophytic than *Quercus robur* which species grows on a moist or inundated soil gregariously also in the lowlands in a very warm and dry climate whereas on hills it becomes dominating only in more northern parts.

The oak woods have their openings with steppe vegetation; on places inaccessible to the forest, especially so on steep rocky slopes, the rocky steppes occupy not seldom rather wide areas; more extensive grassy steppes are, however, missing, but develop sometimes on deforested ground. The Slovakian rocky steppes, in best evolution on southern or southeastern slopes, are dependent chiefly on the configuration of the terrain. They are favoured by the microclimatic conditions but are not caused by the climate itself. This cannot be surprising when we know, that also the puszta and the steppes of Alföld are a cultural (anthropogen) and not a climatic steppe. The significance, difference and unequal age of the vegetation of Pramatra and Alföld was pointed out for the first time by Borbás (1886) and his « Pramatra theory » was acknowledged by Rapaiics, Sóó and others. The district of Pramatra has its own characteristic types but besides its flora was enriched by types which immigrated either by the old Transsilvanian (Subcarpathian) or the Illyrian way. Both streams of this vegetation, penetrating in big curves to the north approach or meet in Pramatra and the Subcarpathian Pannonian district. This vegetation of the Pramatra type is very well developed in the andesitic hills of Kováčov (on the Slovakian side of the Danube) with *Quercetum lanuginosae*, *Fraxinetum ornii*, the rocky steppes and with *Festucetum pseudodalmaticae*. Pramatra, though in possession of good many characteristic species is not sharply defined against the Subcarpathian Pannonian district. This district is of a special interest by the various grades of intermixture of the Pannonian and Carpathian vegetation which later is gradually getting the superiority northwards. The flora of the true Pannonian subregion (both districts) is of tertiary origin but was undoubtedly enriched by a new stream in the xerothermic interglacial and postglacial periods. Types are *Ruscus hypoglossum* (Malé Karpaty), *Cotinus coggyria* (Slatina, V. Lodina), *Fraxinus ornus* (from the hills of Kováčov eastwards to the Černohorská hegyalja), *Hyssopus borealis* (Slovakian Karst district) are surely relics of the oldest period, whereas the steppe grasses and herbs represent a mixture of species immigrated of old and more recently.

Of great importance for their expansion from the east were the northern spurs of the Gutin Mts. as well as the warm foothills of the Polonines, and also the most southern part of the Prešov Mts. (the

Tokaj hegyalja). Some characteristic species (for instance *Ferulago silvatica*, *Anchusa Barrelieri*, *Althaea hirsuta*, *Crocus banaticus*, *Tilia tomentosa* and others) do not reach any more eastern Slovakia, others (f. i. *Coronilla elegans*, *Veronica incana*) extend to eastern Slovakia but do not penetrate farther than the Prešov Mts., whereas many others spread to the southern part of Central Slovakia and others reach even western Slovakia. Analogical etappes may be distinguished in the western or Illyrian stream; in some cases the expansion may have taken place in both directions.

It is of great interest to follow the penetration of these Pannonian types northwards into the region of the Carpathian vegetation. It would take us too far to follow these questions in detail yet some examples may be given. A stream of Pannonian vegetation spreads from the Slovakian Karst district along Torysa northwards towards Prešov and branches off above Košice along the river Hornad westwards into the northern part of the so-called Slovensky ráj. Towards the north this stream continues in more or less isolated colonies along the river Poprad towards the Polish frontier.

Of great importance is the Váh stream. The thermophilous Pannonian vegetation penetrates in this direction along the river Váh not only as far as Trenčín and the hills called Sulovské skály but further westwards as far as the western part of the Nízke Tatry Mts. Both streams, that of the river Váh and that of the river Poprad, are closely approaching but do not exactly meet.

Of the especially interesting Pannonian plant communities, penetrating northwards along the river Váh, are to be named *Quercetum lanuginosae* which, however, does not proceed as far as *Caricetum humilis* and *Festucetum duriusculae*.

The study of the expansion of the Pannonian vegetation into the territory of the West Carpathian region has been carried out since 1919 by myself and my collaborators (especially P. Sillinger) and we hope to be able to draw in the near future a clear picture of the migration of single species as well as of whole associations.
