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Autor: Horn af Rantzien, Henning
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**Some taxonomical and phytogeographical problems
in *Pleurospermum austriacum* (L.) Hoffm. em. Turcz.**

by

HENNING HORN AF RANTZIEN

INTRODUCTION

In a previous paper (HORN AF RANTZIEN, 1946) the author has dealt with the ecology of *Pleurospermum austriacum* with certain reference to the Swedish plant. In this connection, a brief account was given of the taxonomy and distribution. The purpose of this paper is to deal in more detail with these problems. Another reason for the publication of this paper is the increase in the material at my disposal regarding localities of *Pleurospermum*.

I am deeply indebted to Professor Dr. Ch. Baehni of the Geneva University, Professor Dr. A. U. Däniker of the Zürich University, Professor Dr. Tr. Savulescu of the Institute of Agricultural Research in Bucarest and Professor Dr. Al. Borza of the Cluj University, Roumania, for their kind assistance in informing me of localities. To Professor Dr. E. Hultén, the Riksmuseum, Stockholm, I should like to express my warm appreciation for some references to the literature. I have obtained localities or specimens from the following public herbaria: Riksmuseum, Bot. Dept., Stockholm (S); University of Stockholm, Bot. Inst., Stockholm (SH); University of Uppsala, Bot. Museum (U); Inst. of Plant Ecology, Uppsala (UV), all in Sweden; Conservatoire et Jardin Botaniques de la Ville, Geneva [the herb. E. Boissier (B), Barbey-Boissier (BB), Burnat (Bt), Delessert (D) and Palézieux (P)]; University of Zürich, Bot. Museum (Z), both in Switzerland; Inst. of Agricultural Research, Bucarest (Buc) and University of Cluj, Bot. Museum (Cl), both in Roumania. I am also very much indebted to the Directors of these Institutions.

To Professor Dr. Ch. Baehni I owe a profound debt of gratitude, for he has enabled me to have these studies printed in *Candollea*.

The investigation is based upon about 300 specimens and further over 1500 records as to localities from herbaria and published data.

I. HISTORICAL NOTES

The taxonomical foundation of further research in the subgenus *Eu-Pleurospermum* Drude was laid by HOFFMANN (1814: pp. VII-XI), who described 3 species, viz. *P. austriacum* (L.) Hoffm., *P. uralense* Hoffm. and *P. camtschaticum* Hoffm. The most important characteristics mentioned by HOFFMANN, regarding the morphology and anatomy of the mericarps, were subsequently summed up by LEDEBOUR (1844-46: 360) in the following way:

P. austriacum Hoffm.: valleculis univittatis, iugis obtusiusculis;
P. uralense Hoffm.: valleculis univittatis, iugis acutissimis;
P. camtschaticum Hoffm.: valleculis bivittatis, iugis subdenticulatis.

As far back as the middle of the 19th century, however, objections were raised to the opinion held by HOFFMANN. LEDEBOUR himself (1829: 368) seems to have considered *P. austriacum* Hoffm. and *P. uralense* Hoffm. as almost identical, and in his later great work (LEDEBOUR, 1844-46: 360) he questioned in precise terms the possibility of distinguishing the 3 species mentioned above. TURCZANINOW (1844: 753) emphasized that there were no constant characteristics by which to distinguish them. A great number of Russian taxonomists and phytogeographers agreed with the above-mentioned authors in this respect (cf. HORN AF RANTZIEN, 1946: 181), among whom especially KOMAROV (1905: 137) and GANESCHIN (1915: 155) discussed the problem in detail.

However, there has been some reaction to this tendency to group under one name the forms in question. Thus, some recent students in Eastern Asiatic Botany wish to maintain the name *P. camtschaticum* and the specific range of the plant of Eastern Asia (e.g. KOMAROV and KLOBUKOVA-ALISOVA, 1932: 799; SCHISCHKIN, 1930: 131; and TATEWAKI, 1933: 205).

Many authors have considered the European and the Asiatic population to belong to two separate species (e.g. HULTÉN, 1929: 156-157; KITAGAWA, 1939: 342; KORSHINSKY, 1898: 186; KRYLOV, 1935: 2059; KRYLOV and STEINBERG, 1918: 107; and SCHEUTZ, 1888: 118). SCHEUTZ emphasized that the plant which he had studied in Jeniseisk. was evidently a separate species, which differed from *P. austriacum* in that it has more bluegreen leaves, etc. Later investigations have shown that these characteristics are of minor importance and not always found together. HULTÉN (l.c.) made a thorough investigation into the taxonomy of these forms. He found

no important difference between the plant from Eastern Asia and that from Western Siberia, the characteristics in the oil-tubes described by HOFFMANN (l.c.) and LEDEBOUR (1844-46 : 360) being subject to variations. On the other hand, he found that the Asiatic populations differed from the European plant to some extent and that it was necessary to maintain their specific range. Consequently the Asiatic plant should be named *P. uralense* Hoffm. emend. Hultén. With regard to the most pronounced distinguishing characteristics, see HULTÉN (l.c.) and the following.

Yet another way was pointed out by SOMMIER (1896 : 73). He named the plant of Western Siberia "*P. Austriacum* β *Uralense* (Hoffm. sub specie)". However, the reasons for this change were not given, nor was it stated whether *P. camtschaticum* Hoffm. was to be included in " β *Uralense*".

2. TAXONOMY

My examination of the material has given the following results with regard to the characteristics stated by different authors as distinguishing the Asiatic and the European plant.

There is on the average a distinctive difference between the stalk length of the Asiatic and the European plants, the former being generally 50-100 cm. in height but the latter 75-150 cm. However, there are so many exceptions to this rule that its value as a characteristic is somewhat dubious. A fact worth mentioning is that the lower height in the Asiatic population seems to be more constant than the greater height in the European population.

It has been stated that there are differences between the plants discussed in the lobation and hairiness of the leaves, the Asiatic plant showing strongly dissected leaves with elongately acuminate sections and hairy margins and veins on the underside of the leaves. *P. austriacum* on the other hand, has its leaves less dissected, with broadly acuminate or blunt sections and the margins and veins less hairy. The same can in general be said about these characteristics as about the preceding one. The difference in the leaf form is rather evident in many cases, but its value is diminished by the great number of exceptions and the variation. Generally, the leaf of the Asiatic plant is smaller, more strongly dissected and has more elongately acuminate sections. But sometimes we meet with plants with large, less dissected and shortly acuminate or blunt sections (e.g. JAPONIA : Nippon media, 1866, *Tschonoski* [*Maximowicz*, Iter sec.] in hb. S). The variations in *P. austriacum* s. str. seem to be greater. Here we find many different forms of leaves in the same specimen. However, according to GANESCHIN (l.c.), such variations in the same specimen

may also be found in the Asiatic plant. The variations in the hairiness of the margins and veins seem to be even greater than those in the leaf form. Certain individuals of *P. uralense* are sometimes almost naked.

The involucre of the Asiatic plant is said to be composed of strongly dissected leaves, while that of the European form consists of simple or sometimes slightly dissected leaves. This difference cannot be supported, as the involucral leaves of *P. austriacum* s. str. can have entire margins or be slightly or strongly dissected in about the same frequency. A strongly dissected involucre in the European plant is by no means rare.

There is also another difference between the plants discussed in the involucral leaves, those of *P. austriacum* often being rather broad, while those of *P. uralense* are mostly narrow. This characteristic, however, varies a great deal.

The umbel-rays of *P. uralense* are often more scabrous and more sharply angulated than they are in *P. austriacum* s. str.

In the Asiatic form, the ribs of the carpel are said to be winged with a distinctly toothed edge. However, according to statements in published data this characteristic also occurs, though not so distinctively, in the European plant. The material examined shows all transitions from winged and toothed ribs to almost rounded or blunt-edged, smooth ribs. The Asiatic plant has oil-tubes with small rounded lumina, while in the European form the corresponding parts are broader and flatter. In general, this latter difference appears to be rather pronounced, but it must be emphasized that in this case also there are irregularities and transitions.

An examination of the available material has indicated that there are no constant differences, either between the West Siberian plant and the form of the Far East, or between the entire Asiatic and the European population. No differences between the East European plant and specimens from other parts of Europe are to be found (cf. DOWNAR, 1861 : 180), and as TRAUTVETTER (1882-84 : 405) and LEHMANN (1895 : 389) have indicated, the name *P. lithuanicum* Down. must be regarded as a synonym. GANDOGGER (1910 : 223) has considered the Swedish plant to be a separate species. However, there seem to be no reasons for such an arrangement, as the Swedish population does not deviate in any characteristics at all from other European specimens.

The two populations under discussion seem to be rather indistinct stages in a series of continuous morphological variations. The characters of the different plants given by HOFFMANN (l.c.), LEDEBOUR (1844-46), SCHEUTZ (l.c.) and others show mostly evident transitions. On this account, it seems impossible to maintain the Asiatic and European forms as separate species.

TURCZANINOW (1838: 93 and 1844: 753), KOMAROV (1905: 135-136) and GANESCHIN (1915: 155) are of the opinion that the plants of Siberia and the Far East are *identical* with the European plant. However, this does not seem to be entirely correct, the reason being that it is possible to distinguish one Asiatic from one European type of habit on account of some of the characteristics discussed above. The same could be said with regard to the fact that there are great variations and that many exceptions occur; the bulk of the European population for example is distinguished from the other by greater length of stalk, larger and less dissected leaves with shortly acuminate or blunt sections and broader, often entire, involucre leaves.

The areas where these habitus types are found are separated from each other by a gap in Central Russia. As no material has been examined from the most advanced outposts of this gap, it is not clear whether the populations form a transitional zone. In the material examined, the transitions do not show any geographic localisation.

Crossing tests with plants from Asia and Europe would be highly desirable in order to obtain an adequate idea of the genetic relations between them. However, it has been impossible for me to procure germinative seeds of the Asiatic form.

In view of the facts presented, the impossibility of finding constant distinctive characteristics, and the presence of two different habitus types which are geographically isolated from each other, the author (HORN AF RANTZIEN, l.c.: 182) has proposed *placing the populations as subspecies (=geographic races) of P. austriacum s. lat.*

3. SYNONYMY

Pleurospermum austriacum (L.) Hoffmann emend. Turczaninow in *Bull. Soc. Nat. Mosc.* 11: 93 (1838); 17: 753 (1844) = *Ligusticum austriacum* Linné *Sp. Pl.*: 250 (1753) = *P. austriacum* Hoffmann *Gen. Plant. Umb. (Praemonenda)*: p. X (1814) et auct. cet. = *P. uralense* Hoffmann l.c., p. IX et auct. cet. = *P. camtschaticum* Hoffmann l.c., p. X et auct. cet. = *P. lithuanicum* Downar in *Bull. Soc. Nat. Mosc.* 34: 180 (1861) = *P. boreale* Gandoger *Nov. Conspect. Fl. Eur.*: 223 (1910).

ssp. **eu-austriacum** Horn af Rantzien in *Svensk Bot. Tidskr.* 40: 182 (1946) = *Ligusticum austriacum* Linné *Sp. Pl.*: 250 (1753) = *P. austriacum* Hoffmann l.c., p. X et auct. eur. = *P. austriacum* Turczaninow l.c.: 93 (1838) et 753 (1844) et auct. ross., jap. et sin. pro parte.

ssp. **uralense** (Hoffmann) Sommer *Fl. dell'Ob inf.*: 73 (1896) sub: *Pl. Austriacum* β *Uralense*; Horn af Rantzien l.c.: 182 =

P. uralense Hoffmann l.c., p. IX et auct. cet. = *P. camtschaticum* Hoffmann l.c., p. X et auct. cet. = *P. uralense* Hultén *Fl. of Kamtch.* III: 155 (1929) = *P. austriacum* Turczaninow l.c.: 93 et auct. ross., jap. et sin. pro parte.

4. GEOGRAPHY

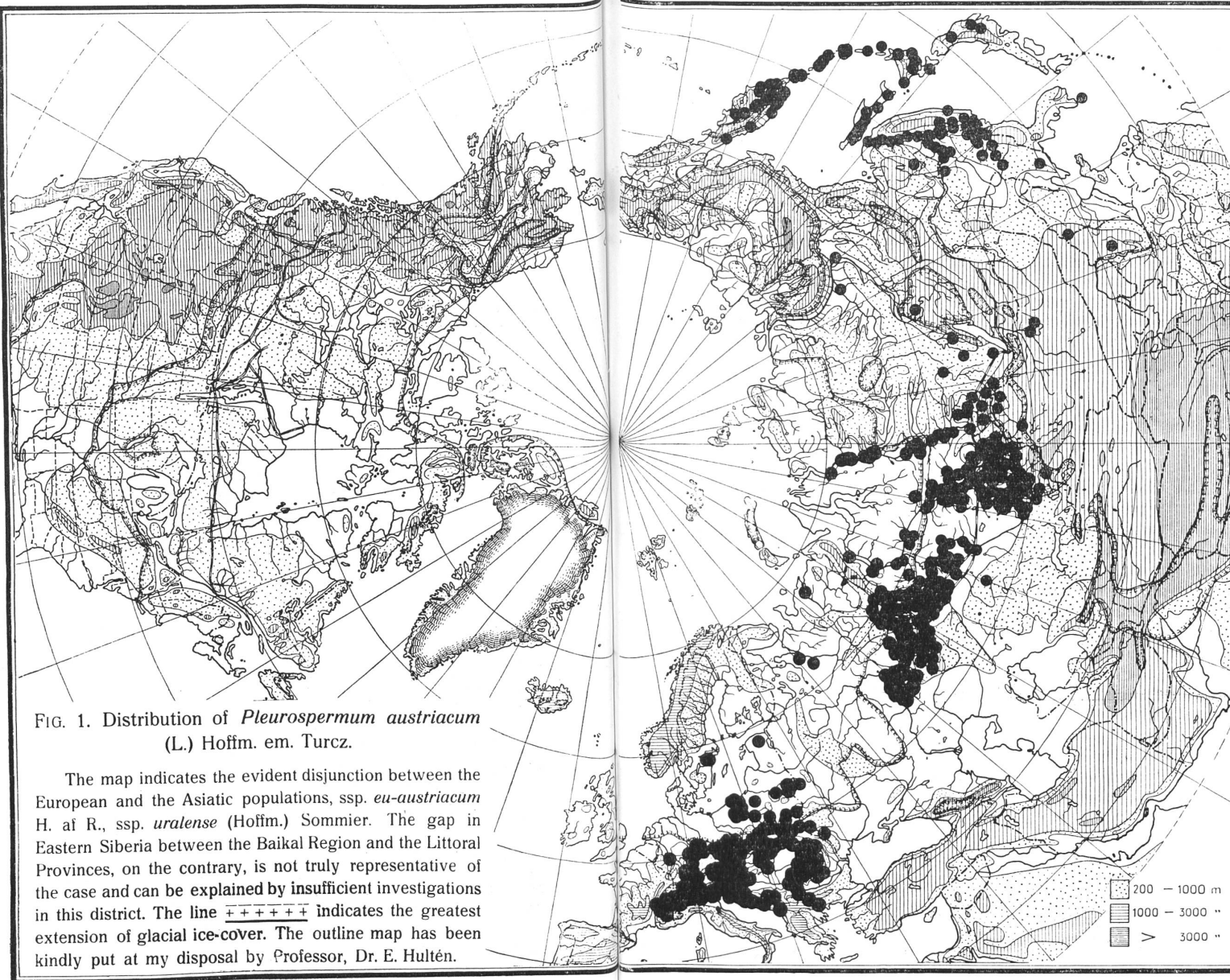
The present distribution map is a rearrangement of my earlier maps (1946) with later additions. For various reasons, above all the great distribution area and the insufficient investigations made of some parts of it, it is very difficult to map down the distribution of this plant. It seems to be almost impossible to give a detailed and completely correct view of the distribution in all parts of the great area.

Ssp. *eu-austriacum* is completely restricted to Europe. In the West it reaches the Rhone valley (LAMARCK and DE CANDOLLE, 1815: 307; VERLOT, 1872: 153) at about long. 5° E and extends beyond the Rhine (THELLUNG in HEGI, 1926: 1089) at long. 7° E. From here the area stretches over the continent to the outmost loc. in South East European U.S.S.R. (Podolia and Minsk.; SCHMALHAUSEN, 1886) at about long. 27° E. In a N-S direction it inhabits ca 16 degrees of latitude, the northernmost loc. (Central Sweden: SYLVÉN, 1912; HORN AF RANTZIEN, 1946; Esthonia: LIPMAA, 1936) being situated at about lat. 59° N, and the southernmost (Bulgaria, Vitosch: STOÏANOFF and STEFANOFF, 1925: 812) at lat. 43° N. One of the most characteristic features, clearly shown in the map, is the splitting up of the area into isolated populations. The distribution centre lies in Central Europe (the Alps, the West Carpathians and the mountain district of Southern Germany). However, the areas are not confluent there, but show some evident gaps, e.g. parts of Switzerland and Austria proper (see THELLUNG in HEGI, 1926: 1089; VIERHAPPER, 1911; SCHINZ and KELLER, 1923: 485, HALÁCSY, 1896: 238; BRITTINGER, 1862: 1080; HINTERHUBER and PICHLMAYR, 1879: 93; DALLA TORRE and SARNTHEIN, 1909: 911; SAGORSKI and SCHNEIDER, 1891: 198). In other districts within this centre our plant is more common, e.g. Southern Bavaria (ERDNER, 1911: 368; WOERLEIN, 1893: 67), Western Czechoslovakia (ČELÁKOVSKÝ, 1874: 590; SCHUBE, 1903: 236; SAGORSKI and SCHNEIDER, l.c.) and, above all, in Lower Austria (HALÁCSY, l.c.; BECK VON MANNAGETTA, 1892: 633). This distribution centre is surrounded by a border zone, generally characterized by a low frequency; mostly, the species is expressly stated as rare being there (cf. for instance SCHMALHAUSEN, l.c., ROSTAFÍNSKI, 1872: 193). In some districts, e.g. Transylvania (SIMONKAI, 1886: 273 and later records from there), it seems to be scattered—common. To this border zone may be referred South West France (BURNAT, 1906: 101; LAMARCK and DE CAN-

DOLLE, l.c. ; VERLOT, l.c.), the transitional districts of the great Eastern European Plain (DEGEN, 1914 : 210 ; SIMONKAI, l.c. ; SCHMALHAUSEN, l.c. ; JÁVORKA, 1924 : 770 ; ROSTAFÍNSKI, l.c. ; PAX, 1918 : 32 ; KLINGGRÄFF, 1848, 1854 and 1866 ; ABROMEIT 1898 : 344) from the Vistula area in the North to Roumania in the South and, further, parts of the Balkan Peninsula (HEUFFEL, 1858 : 120 ; BECK VON MANNAGETTA, 1895 : 209 ; HAYEK, 1927 : 1067 ; HIRC, 1886 : 380 ; ROSSI, 1913 : 82 ; DEGEN, 1937 : 470 ; SCHLOSSER and FARCAŠ-VUKOTINOVÍČ, 1869 : 505 ; STOĀANOFF and STEFANOFF, l.c. ; VELENOVSKÝ, 1898 : 138 ; PANČIĆ, 1856 : 523). Furthermore, there are some localities at the northern limit of the subspecies area which are completely isolated.

Ssp. *uralense* occupies a much greater distribution area which extends from Japan proper (e.g. MATSUMURA, 1912 : 442), the Kuriles (MIYABE, 1890 : 236 ; KUDO, 1922 : 137 ; TATEWAKI, 1933 : 205-299) and Kamtchatsk. (HULTÉN, 1929 : 156 ; KOMAROV, 1927-30 : 336) in the east (Kamtchatsk. from long. 160° E) to European U.S.S.R. in the west [to Wiatsk., Kazansk. and Samarsk. at long. 50° E (KORSHINSKY, 1898 : 186 ; FEDTSCHENKO, 1931 : 775) and to Archangelsk. at long. 40° E (KUZNEKOW, 1888 : 118)].

Though the map indicates a somewhat uneven distribution, the ssp. *uralense* is probably rather homogeneously distributed through the whole of Siberia between lat. 50° N and 65° N. North, and south of this belt there are isolated localities or isolated groups of localities but probably no coherent distribution. In the north there are some interesting records from northern Archangelsk. (Schenkursk. and Cholmogorsk. : KUZNEKOW, l.c.) and Jeniseisk. (the northernmost known loc., Dudino at lat. 69° 30' N : SCHEUTZ, 1888). In Semipaladinsk. it reaches the southernmost loc. at lat. 48° 45' N (Marka Kul : KRYLOV, 1935). Towards the south the distribution is limited by a line from Orenburgsk. and Turgai (KORSHINSKY, l.c. ; FEDTSCHENKO, l.c. ; BUNGE, 1851 : 316) passing over northern Akmolinsk., Semipaladinsk., Altaisk. and the mountain districts of northern Mongolia to Urga (KRYLOV, l.c. ; PRINTZ, 1921 : 336 ; FEDTSCHENKO, 1915). Within the area mentioned (incl. the Baikal region) ssp. *uralense* is said to occur in a rather high frequency in most districts. In Tomsk. and Tobolsk. it seems to be common (KRYLOV, l.c. ; SOMMIER, 1896 : 73), the gaps in the Jenisei region are probably due to lack of information (cf. KRYLOV and STEINBERG, 1918 ; SCHEUTZ, 1888 ; BRENNER, 1910), in great parts of Irkutsk., it is stated as common (GANESCHIN, 1915) and from Olekminsk. (GLEHN, 1876) and Transbaikalsk. (TURCZANINOW, 1844) there are also records which indicate a high frequency. However, the statements are few and scattered from the districts east of the Baikal region. There are only some localities known from Wiliuisk. and Jakutsk. (MEINSHAUSEN, 1871 ; CAJANDER, 1903 and



1904: 19; KOMAROV, 1926: 149). But it is very evident *that the frequency is rather understated here* and is due to lack of floristic investigations (cf. the map!).

The distribution in Eastern Siberia is better known. From the Littoral Provinces (the Amur region, Priamur and Primorsk.) and from Manchuria there are many records (for instance KOMAROV, 1905: 137 and 1923: 93; KITAGAWA, 1939; SCHISCHKIN, 1930; MAXIMOWICZ, 1859: 130; SCHMIDT, 1868: 47). The statements from China proper and Korea are very few (MORI, 1929: 273; HSIEN-WU and TSO-PIN, 1934: 354; FORBES and HEMSLEY, 1887: 893) but it has probably a wider distribution here than the map indicates. The collections of *H. Smith* from Northern China contain a specimen (SHANSI, 1924, *H. Smith*, Pl. Sin., 7077, *P. austriacum* Hoffm., det. Wolff, in hb. S) which is a typical ssp. *uralense*. Another specimen from Southern China (SIKANG, about lat. 30° N, 1934 *H. Smith*, Pl. Sin., 10533, undetermined, in hb. S) is very like ssp. *uralense* in most characteristics, but differs in the very large involucre leaves. It is probably a hitherto undescribed species, which may perhaps represent a transition between the subgenera *Eu-Pleurospermum* and *Hymenolaena*. The distribution of ssp. *uralense* on the Pacific isle-bridges is rather well known. From Kamtschatka (KOMAROV, 1927-30: 336-337; HULTÉN, 1929: 156), the Kuriles (TATEWAKI, 1933: 205-299; MIYABE, 1890: 236; KUDO, 1922: 137), Sakhalin (SCHMIDT, 1868: 140; KUDO, 1923: 48) and Japan proper (cf. among many others espec. MATSUMURA, 1912: 442) there are many records. In these districts the ssp. seems to be scattered to common.

Ssp. *uralense* has advanced considerably farther to the north and south than ssp. *eu-austriacum*. The area of the latter comprises about 16 degrees of latitude in a N-S direction, while that of the former 21° in Western Siberia and about 30° in Eastern Siberia.

During the investigation, there have proved to be comparatively few papers which contain information about our plant. This is somewhat strange in view of the high frequency which is often stated and of the striking appearance of the species. This can probably be explained by the periodicity in the number of fertile specimens during different years, by the mode of vegetative development which lasts several years and by the fact that fertile individuals die after fructification (HORN AF RANTZIEN, l.c.).

While the distribution centre of ssp. *eu-austriacum* is located to the mountain districts of Central Europe, ssp. *uralense* does not seem to have any partiality for mountain areas (see for instance CAJANDER, 1903: 63). On the contrary, the map shows a concentration of localities to the alluvial districts. It is impossible to decide at present if this reflects the true nature of the case or is due simply to the fact that the river areas have been more intensively investigated.

The disjunction between the distribution areas of ssp. *eu-austriacum* and ssp. *uralense* varies in width, at the narrowest part about 1000 km. Some uncertainty, however, is attached to the taxonomy of the plants inhabiting the border-zones of this gap, as no material from the most advanced outposts of the two populations has been examined. The following specimens have been seen from these zones:

Ssp. *uralense*: U.S.S.R., Archangelsk., Petschora ad ostium flum., 1912, *Enander* in hb. S; Ufinsk., Ufa Gluminsko 1911 *Noskov* in hb. S; Permsk., Iljalskoje, 1898, *Teplouchhov* in hb. S; Tepleskoje, 1898, *idem* in hb. S; Kotume, 1898, *Ekstam* in hb. S; Iljinskyi, 1898, *Teplouchhov* in hb. U.

Ssp. *eu-austriacum*: ROUMANIA, "In Transsilvanicae alpibus Rädrensibus", 1858, *Czetz* in hb. S; POLAND, Lublin, 1911, *Jan óz* in hb. S; without loc. *Raciborski* in hb. S; CZECHOSLOVAKIA, Brno, 1929, *Svestka*, in hb. S and U.

It would have been most interesting to examine the plant from Esthonia and, above all, those from eastern Archangelsk. However, they are expressly said to belong to "*P. austriacum*" (LIPMAA, 1936) and to "*P. uralense*" (KUZNEKOW, 1888 : 118) respectively. No marked increase in transitional forms in this border-zone is to be seen.

5. DISCUSSION

The facts presented in the foregoing form the basis for the following discussion of the taxonomical and phytogeographical position of *Pleurospermum austriacum*.

The genus *Pleurospermum* comprises more than 30 species, distributed over a great part of northern Eurasia. The distribution centre lies in Central Asia, above all in Thibet and Himalaya. About 20 species only are found here. Outside this centre the genus occurs, with a certain partiality for the mountain regions, from the Far East through Siberia, Afghanistan and Caucasus to Central Europe.

The limitation of the species is somewhat uncertain and a great number of them have been described in the last decennia. *Pleurospermum* is in general divided into four subgenera which have often been dealt with as separate genera. However, their position as subgenera seems more appropriate, as the characteristics already mentioned as separating them from each other are only differences of degree. The taxonomy and distribution of these subgenera show many interesting features.

From a morphologic point of view the subgenus *Hymenolaena* (incl. *Aulacospermum*) is probably the most primitive one. It forms also the group richest in species, it contains a great number of endemisms inhabiting very small areas and, further, is confined in general

to the distribution centre of *Pleurospermum*. Single members of *Hymenolaena* have a greater distribution, thus for instance *P. multifidum* Schmalh. stretches its distribution area into SE European U.S.S.R. The morphologically more typical *Hymenolaena* species, such small delicate species as *P. Candollei* (DC.) C. B. Clarke and *P. densiflorum* Benth. are limited to Central Asia.

The subgenus *Eu-Pleurospermum* has the greatest distribution area among the groups in question, forming an irradiation from the centre to the N, NE, and NW.

Another diverted branch, *Eleutherospermum*, containing only a few species, is distributed West of the centre (Caucasus, Armenia).

The fourth subgenus, *Hymenidium*, comprising some Himalayan species, appears to be rather strongly separated from the other groups.

In this connection, *Eu-Pleurospermum* is of particular interest. To this subgenus four species have been attributed, viz. *P. austriacum* (L.) Hoffm., *P. uralense* Hoffm., *P. camtschaticum* Hoffm., and *P. Archangelica* Ledeb. The last species can be left out of account as it is completely unknown. It was described by LEDEBOUR (1829: 369) from Altai and was said to resemble *Archangelica*. However, according to LEDEBOUR (l.c.) the original material was destroyed. I am not aware of any other references to this species. As has been shown above (see also HORN AF RANTZIEN, l.c.), the other three species are in reality only one species, which in two subspecies is distributed over the Boreal Belt from China, Japan and Kamtschatsk. to Central Europe.

The development of the recent geographical areas of *Eu-Pleurospermum* seems to have been caused by different, and, in particular, by historical factors. The morphology and geography of *Hymenolaena* make it very evident that this is a somewhat old group among the *Apioideae*, probably going back to Tertiary times. Towards the end of this period the *Eu-Pleurospermum* forms seem to have been spread out from the centre in Central Asia in a N, NE, and NW direction, so that there finally existed a coherent area in the whole of Central and Boreal Asia and probably also in the corresponding parts of Europe. This great area was inhabited by the plant from which ssp. *uralense* and ssp. *eu-austriacum* later developed. The glaciations of the Quarternary Period, however, split up the distribution into several sections of various sizes. On the contrary, during the interglacial period, there was a tendency to form a confluent area again. The influence of the two earlier glaciations on the distribution of boreal plants is almost unknown, as most deposits from this time were disturbed by later glaciations. The long D interglacial (as to the terminology see BECK, 1933) following the second glacial period has probably enabled our plant to form a confluent area. As the maximum of this interglacial period seems to have been characterized by a dry and hot climate forming steppes and deserts in the central parts of

the continents, it possibly had a restrictive influence on the distribution of *Pleurospermum* (see the species' ecology below), forcing the plant towards the more suitable regions in the N, NE, and NW. The maximum glaciation ("Riss") was responsible for a sudden change. The ice-cover forced the plant to the south again and the hard climatic conditions enabled it to survive only in specially favoured localities. Concerning the localisation of such "refugia", see for instance HULTÉN (1937), OBRUTSCHEW (1930), and NORDHAGEN (1935). There is every probability that *Pleurospermum* only survived South of the ice-cover. The E interglacial probably enabled the plant to spread out from its refugia. It is impossible to decide whether its rapidity in spreading involved the formation of a completely confluent area. In general the same events were repeated during the last glaciation and the postglacial period. During this period the Asiatic areas formed a \pm confluent distribution, whereas, on the contrary, the gap between the European and the Asiatic populations was not bridged over.

Concurrent with a splitting up into separate primary areas, there gradually appeared a taxonomic differentiation, which seems to be the causal basis of the present conditions of two different subspecies. Further, it is an established fact that populations forced aside to less favoured ice-free refugia can lose their capability of spreading (see e.g. FERNALD, 1925). Perhaps this is the case within some parts of the European area, where the species has a very split distribution and where no recent spreading seems to occur. The plant has in such localities been stated as a relict from various times; see for instance BLOCKI (1908: 283), SCHULZ (1899: 282-285 and 1902: 52), VIERHAPPER (1911: 39-41).

The postglacial history of the European *Pleurospermum* has been dealt with by many authors. In general it is regarded as a relict, but views on its origin are very different. BLOCKI (l.c.) considers our plant to be a relict from the last glaciation. SCHULZ has emphasized in some papers (1899, 1902, and 1910: 214) that the species is an eastern immigrant, which could only have immigrated into Europe "während des kältesten Abschnittes der letzten grossen Vergletscherungsperiode". VIERHAPPER (1911) is more or less of the same opinion. On the other hand, GRADMANN (1900 and 1904) and OLTMANNS (1922), speaking of "the pontic origin" of *P. austriacum*, were of the opinion that the species is a xerothermic plant which could only have immigrated into Central Europe during a very warm and dry period, "a climate of steppes". With reference to the statements above and to the brief survey of the species' ecology below, none of these interpretations seems to be correct. With respect to the last theory, see also THELLUNG in HEGI (1926: 1089).

The historical factors do not appear to explain the distribution completely. As to the edaphic and climatic requirements *P. austria-*

cum is as yet rather unknown. The very diverging statements can perhaps be attributed to regionally different requirements. At present it is possible to distinguish three different ecological types, inhabiting Sweden, Central Europe and Asia, which will be treated separately below.

The Central European plant has a rather narrow ecological amplitude. As to the altitude, there are a great number of statements given in the published data and on the herbarium labels, generally referring to the belt between 500 and 2000 m. above sea-level. Mostly they lie above 1000 m. Consequently, the species occurs in Central Europe as a pronounced mountain plant. Among the many edaphic records of Central European *P. austriacum*, the most detailed and comprehensive are to be found in THELLUNG in HEGI (1926), VIERHAPPER (1911) and SYLVÉN (1912) (see also the extensive citations in the two latter papers). *P. austriacum* is here in general restricted to the calcareous districts. In primary rock districts it is only very scattered and shows great gaps. The gypsophilia of the species will explain very much of the strange distribution, for instance, in Switzerland and in the Austrian mountain districts. The most typical localities are stated to be wet, rocky and scrubby slopes along the mountain rivers, often in the "Voralpenwald". It is said to be very exacting as to soil humidity and shade. On account of the fruit morphology (HOFFMANN, 1814 p. IX; DRUDE, 1898:171; THELLUNG in HEGI, l.c.) and experiments with the buoyancy of the mericarpia (THELLUNG in HEGI, l.c.), it is stated that the most important factor for dispersal is the agency of running water. The germination percentage is low (2% : THELLUNG in HEGI, l.c.). THELLUNG explains in this way the fortuitous occurrence of the plant.

The few ecologic statements from the Eastern European border-zone of ssp. *eu-austriacum* give a somewhat divergent picture. Our plant occurs here at a much lower altitude, 50-600 m. above sea-level, in drier and more exposed biotopes. As typical localities may be mentioned the argillaceous humus soil of the ravines (Vistula district), light xerophilous *Quercus* forests and dry woody meadows (Moravia). From South West Russia only "forests" is in general stated, e.g. by SCHMALHAUSEN (1886:248). The statements from Eastern Europe seem to indicate that from an ecological point of view these *Pleurospermum* populations may have a transitive position between the plants inhabiting Central Europe and the Swedish and Asiatic populations, on the other hand.

The Swedish population is analysed ecologically in HORN AF RANTZIEN (1946), to which paper the reader is referred for details. The ecology of the Swedish *Pleurospermum* differs from that of the Central European plant in having a wider ecological amplitude. The localities are situated between 10 and 75 m. above sea level. Generally

the plant occurs in deciduous forests of various types. The biotopes show a great change regarding soil humidity and exposure to the sun and to the wind. The Ca standard is low, regionally and locally, and the soil samples examined show pH values which are dispersed in the area 4.6-6.8 with a concentration about 5.0-5.2. The humus standard of the soil varies very much (3-27%). The plant is in general restricted to rivulets and stream gullies and to slopes facing north. The production of mericarpia is high, about 6600 per year per individual, but several experiments with seeds show a very low percentage of germinations (0-2%). In the latter case, the cause is unknown. The striking confinement of *Pleurospermum* to the vicinity of streams and rivulets can be explained through the buoyancy of the mericarpia and the elasticity of the stalk which are the most important factors in the dispersal capability of the species. On account of the elasticity already mentioned the wind throws some of the buoyant diaspores into the water, where they can be carried away long distances. During autumn inundation they are transported up on to the slopes of the gullies, where they become deposited at low water in the winter. The species is a hapaxanthic, pleiocyclic plant. On account of this, and the fact that the individuals die after fructification, there is a very great change in the number of fertile specimens in different years. In this connection, it should be emphasized that there is every probability that originally the species was introduced into Sweden by human agency.

The ecology of ssp. *uralense* is rather unknown. From the few statements collected it appears, however, that the Asiatic plant, from an ecological point of view, shows a greater resemblance to the Swedish population than to the Central European one. In South East European U.S.S.R. it is stated to inhabit light *Betula* and *Quercus* forests in "regio substepposa" and also *Pinus* and *Picea* forests (BUNGE, 1851; KORSHINSKY, 1898). KRYLOV (1935) mentions as most typical localities in Western Siberia *Betula*, *Populus* and coniferous forests (with scattered deciduous trees), forest meadows and steppes. PRINTZ (1921) states "shady meadows and open Bushwood" (Sayansk.), GANESCHIN (1915) meadows; *Picea* forests of various types and burned woodlands (Irkutsk.), and KOMAROV (1927-30) dry meadows and light *Betula* forests (Kamtchatsk.). Detailed statements are to be found in HULTÉN (1929) and CAJANDER (1903). HULTÉN gives analyses of the vegetation at 15 localities of ssp. *uralense* from Kamtchatsk. They are all meadow communities occurring in alluvial lowland districts (see also HULTÉN, 1927). *Pleurospermum* occurs always singly or sparsely in the communities mentioned. CAJANDER (l.c.) gives a report of the vegetation in a "*Salix vagans*-Gebüsch" in the lower Lena valley and mentions from here *Pleurospermum* as occurring in a low frequency. He attributes this plant community to the associa-

tions of "hainartigen Waldungen" (see CAJANDER, 1903: 63). Our plant is also mentioned as a common and typical representative of the vegetation in the "taiga" of the lowlands (CAJANDER, 1904: 19). From the statements quoted and other records not mentioned here, it appears that ssp. *uralense* is rather less exacting as to altitude, shade, humidity and humus-content of the soil and probably also of the Ca standard than is the Central European plant.

P. austriacum lives under very varying climatic conditions, both macroclimatic and microclimatic in its great distribution area. However, it probably has a partiality for a continental type of climate. In its relation to human agency, it must be regarded as indifferent or hemerophobic, though this possibly varies in some degree in different regions.

Finally, with reference to the facts presented in this paper, the author will endeavour to give a short outline of the causal connection behind the phenomena analysed.

From *Hymenolaena*, the oldest group within the genus *Pleurospermum*, a branch was differentiated out during late Tertiary or early Quaternary times which was adapted to a colder climate and perhaps also to different edaphic conditions (lowlands). This northern group, *Eu-Pleurospermum*, was from the beginning probably a homogeneous one. It suffered considerably from the great climatic changes during Quaternary times, being forced back and partly exterminated by the ice-cover and by cold during the glaciations. Possibly also the interglacial climate, sometimes characterized by dryness and heat, had an unfavourable influence. The glacial periods split up the confluent distribution area into several isolated populations in favoured localities south of the ice, whereas the interglacials involved a tendency to form a confluent area again. There was also a taxonomic differentiation in connection with the splitting up of the area. The post-glacial period enabled *Eu-Pleurospermum* to spread out again from its "refugia"; however, it has not yet been able to recover the whole of its Eurasiatic area. There is a gap in Central Russia separating a European population, ssp. *eu-austriacum* from an Asiatic one, ssp. *uralense*. The localisation of this gap seems to be dependent on two important factors. On the one hand, there was a greater gap between the European and the Asiatic "refugia" than between the Asiatic ones themselves, where the disjunctions were more quickly bridged over, and on the other hand, the European population probably suffered more than the Asiatic from the great climatic changes. This was the fate of the whole European Tertiary biota which, for topographic reasons, was in a very unfortunate state as compared with the North American and Eastern Asiatic biotas. To a certain degree, therefore, the European *P. austriacum* lost its capability of spreading.

It formed a "rigid" area in the mountains of Central Europe and could not bridge the Central Russian gap from its own side. But this loss in dispersal capability had an important result : As is often the case with plants of "rigid" areas it was strongly specialized within a narrow ecologic range. This fact, combined with the low spreading ability, resulted in the maintenance of the restricted area and also explains the apparent contrast between the narrow ecological range of the European plant and the broad one of ssp. *uralense*. As to the Swedish population, other conditions prevail. The species does not seem to be an old member of the flora of Sweden, and probably was introduced by man during recent centuries. There, the plant of Central Europe found a more suitable climate and it thrived. Consequently, it regained its spreading capability and widened its ecological range. Now, it is able to grow again on low levels in dry and open biotopes and on soil poor in lime content.

Botanical Department of the Riksmuseum, Stockholm 50.
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