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Bohdan Křísa:

Relations of the ecologico-phenological observations to the taxonomy of the species *Juncus effusus* L. s. l.

In the following I am presenting the preliminary results of several years' study of two interesting species of Czechoslovak rushes of the section *Juncus* (L.) JANCHEN 1959 [syn.: sect. *Genuini* (BUCHENAU 1875 pro subgen.) VIERHAPPER 1930]. They are the two Linnaean species *Juncus effusus* L. and *Juncus conglomeratus* L., which, although forming a homogeneously and sharply defined group as compared with the other species of the genus, represent a very plastic whole with a considerable interspecific variability. On the basis of the study of the populations of both species in their habitats, and especially of the ecological and phenological conditions, I have formed certain opinions regarding their taxonomy, more suitably expressing the morphogenetic plasticity of both species, which, with regard to their specific ecological environment, form a much more complex specific variability, than was revealed by means of the descriptive systematic methods. Although my observations are based on measurings carried out in only a small part of their geographical area (south-Bohemian district), I am of the opinion that a thorough study of the populations under the given ecological conditions with respect to the whole biotype and to their associations, will contribute considerably to the forming of a rounded picture of the variability of the species. I have compared and thoroughly examined the facts learned in the field by means of morphologico-anatomical analyses of the herbarium material.

The following contains the nomenclative and geographical evaluation of both species accepted in the Linnaean sense, and after an analysis of their ecology and phenology I have arrived at a new taxonomical evaluation of the whole hybrid complex between both species. The purpose of this study can never be an exhausting and final conclusion as regards the evaluation of the taxonomy of the species, but it is only a component part of a whole series of views regarding their specific variability.

The phylogenetic picture of the genus shows simultaneously also the morphogenesis of the individual groups, which have probably developed from the cenoman with a parallel developmental tendency. On the basis of their genetic and ecomorphical plasticity the individual sectors of the genus attained a certain developmental stage. The section *Juncus* (L.) JANCHEN 1959 belongs to the highest branches of the phylogenetic development of the genus with a great adaptability in the whole breadth of the geographical area, so that frequent hybridogeneous possibilities may form fixed hybrid populations in some biotypes of the area.

This problem still remains unsolved as regards the population of the species *Juncus effusus* in the neo-arctic region, where in most localities almost in the whole region of the Cordilleras from Chile to the Canadian Pacific the species grows by itself without the presence of *Juncus conglomeratus*. I have had no opportunity of seeing to a larger extent the herbarium material of American collections, the study of which would illuminate the problem of the hybridity of both taxa.

Nomenclature

1. *Juncus effusus* LINNÉ Spec. pl., ed. 1., 326, 1753.

The following synonyma refer to this species:

?*Juncus bogotensis* HUMB. et KTH. Nov. Gen. 1., 235, 1815. — *Juncus communis β effusus* E. MEY., Junci gen. monogr. sp., 20, 1819 et Synops. Juncor., 12, 1822. — *Juncus laevis β effusus* WALLR. Sched. crit. I., 142, 1822. — ? *Juncus Pylai* (*J. Pylaei*) LAHARPE Monogr. Junc., 119, 1825. — ? *Juncus mauritianus* BOJER, Hort. Maurit., 360, 1837.

2. *Juncus conglomeratus* LINNÉ Spec. pl., ed. 1., 326, 1753.

The following synonyma refer to this species:
Juncus bogotensis HUMB. et KTH. Nov. Gen. 1., 235, 1815. — *Juncus communis a conglomeratus* E. MEY., Junci gen. monogr. sp., 20, 1819. — *Juncus laevis a conglomeratus* WALLR. Sched. crit. I., 142, 1822. — *Juncus Pylai* (*J. Pylaei*) LAHARPE Monogr. Junc., 119, 1825. — *Juncus Leersii* MARSSON Fl. Neu-Vorpomm. Rügen, 451, 1869. — *Juncus Matthioli* BUBANI, Fl. pyren. IV., 177, 1901.

Notes

In the work KUNTH Enumer. pl. 320, 1841 the name *J. bogotensis* HUMB. et KTH. is cited below *J. laevis* WALLR. *conglomerata* (*J. conglomeratus* L.). According to E. MEYER's opinion it ought to have been cited together with *J. effusus* L. BUCHENAU (1906) who accepted MEYER's unfounded opinion and cites this name as a synonym of the species *J. effusus* L. GRAEBNER in HEGI, 151, 1909 even puts a sign of equality between *J. bogotensis* and *J. Pylai* (*J. Pylaei*) LAHARPE. Together with this name there is a clear diagnosis by KUNTH (KUNTH 1841): "... panicula glomerulata, vix composita; capsulam subglobosam triquetram aequantibus." This, as well as the preceding name, is a synonym for *J. conglomeratus* L. GRAEBNER's placing might be valid only if the marks correspond to the type *J. effusus* L. var. *compacta* HOPPE, which, however KUNTH's description does not appear to be the case. MEYER (1819) as the first after LINNÉ introduced the collective species *J. communis* and separated two subspecies, *a conglomeratus* and *β effusus*, with the possibility of mutual transition.

WALLROTH (1822) points out LINNÉ's erroneous separation and reintroduces the collective species *J. laevis* with two subspecies. MARSSON (1869) forms further new combinations. He points out that LINNÉ's dividing criterion for both species based on the form of the inflorescence is not critical, and considers the Linnaean *J. conglomeratus* to be *J. communis* MEY. *a conglomeratus*, but he considers the taxon differing from *J. effusus* L. not only by its inflorescence but also by the structure of the flower and of the stem, as a new species with the name *J. Leersii* MARS. He bases his opinion on the work of LEERSE, Fl. Herborn, 87, 1789. According to him *J. Leersii* is therefore a fixed species, not changing into *J. effusus* as is the case with the Linnaean *J. conglomeratus*. Very likely the author had before him several transitional individuals half-way between the two species, which he overevaluated taxonomically. The name given by MARSSON is used by a number of authors: BUCHENAU (1906), KREČETOVIČ et GONČAROV (1935). WIEGAND et FERNALD (1910) consider *J. conglomeratus* in N. America to be a variety of *J. effusus*.

STRELKOVA (1928) adheres to MEYER's conception, but does not distinguish both subspecies geographically but, according to ALPATOV (1924), ecologically. Her evaluation comes closest to the expression of the exceptional variability between the two species. In the latest systematic works division is carried out exclusively according to LINNÉ: DOSTÁL et al. (1948—1950), CIFERRI et GIACOMINI (1950), SOÓ et JÁVORKA (1951), CLAPHAM, TUTIN et WARBURG (1952), HYLANDER (1953), SZAFER, KULCZYŃSKI et PAWLOWSKI (1953), FENAROLI (1955), ROTHMALER (1955), JALAS (1958), JANCHEN (1959).

In no case is it possible to deny the value of the Linnaean taxa, which, as regards their diagnostic value, are, of course, of a definitely lower taxonomic standard than had originally been thought. In the following conclusions I shall therefore adhere to the original dividing criteria with the following new adjustments:

With regard to the tremendous ecological and geographical breadth of both species I exclude any stability of forms and varieties as systematic categories, if no study of the population in the terrain has been taken into consideration.

I therefore consider both species as an inseparable whole in which both taxa represent definitely formed types in the system of the hybrid complex.

Juncus effusus L. s. s.

Description: Perennial plant (15) 30—80 (120) cm tall, dark green, very dense tussocks, with slender horizontal roots and thicker vertical roots; rhizome short, lateral, with shorter internodes. The stem is leafless, erect, glossy and smooth or faintly ridged without conspicuous longitudinal ribs, at cross-section from 2 to 5 mm strong, ovoid; pith of stem continuous, formed of starlike actinenchyma without interruptions. The leaves are erect, ovoid, from light to dark green, and mostly do not exceed length of stem. At lower part of stem the leaves are changed into sheaths, from 1 to 12 cm long, most frequently from yellowish brown to dark reddish brown, upper leaves long and lower shortly acute, at point with conspicuous bristle-like, rudimentary blades. Inflorescence with spreading, slightly overhanging branches, mostly (2—4) up to 10 cm long, anthelas seemingly lateral as bract continues in the direction of the stem and, as regards length, reaches only about one third of its height and is not curved. Bractlets under flowers are scarious, from broadly ovoid to elliptical and mostly long acute. Perianth segments 2,2 to 2,8 mm long, narrowly lanceolate and acute with scarious margin, from straw coloured to brownish, outer segments only somewhat longer than inner. Stamens three, rarely from four to six. Anthers erect and of approximately equal length as filaments. Style short with three erect stigmata. Capsule obovate along perianth segments, from yellowish brown to dark reddish brown, on top blunt or slightly impressed without point of style, top edges of segments of capsule tend to break in, especially after disconnection of capsule. Seeds brown (0,38) 0,52 (0,58) mm long and on the average 0,25 mm broad, ovoid oblong, rarely asymetric and conspicuous; on glossy surface longitudinal ribs resembling dark, narrow stripes.

Juncus conglomeratus L. s. s.

Description: Perennial plant 30—75, rarely 150 cm high, light green, densely tufted with fine, densely branching root system; rhizome with short internodes, and sometimes forming laterals. Stem erect, oval, leafless, with outstanding longitudinal ridges; pith continuous only in lower part of stem. Leaves erect, oval, and ridges lengthwise. At base of stem there are from 2 to 10 cm long sheaths, from rusty brown to purple-red. Inflorescences are contracted, headlike, with flower branches not more than 2 cm long; they are seemingly lateral, as bract continues in direction of stem, and curved after flowering. Bractlets under flowers inconspicuous and mostly pressed close to perianth segments. Perianth segments 2,5—3 mm long, linearly lanceolate with scarious margins, rusty brown, and with a central, green keel, outer segments somewhat longer than inner. Stamens three, rarely from four to six. Anthers linear, only somewhat shorter than filaments. Style very short with three reddish, erect stigmas. Capsule obovate, frequently exceeding perianth, from light to dark brown and on top changing into distinct point. Top edges of segments of capsule fluently ascensive from side and do not break in at top. Seeds ovoid, 0,4—0,5 mm long, approximately 0,25 mm broad, short acute, rust brown and transversely netted.

Total distribution

In the sense of the conspecies mentioned in the following both species intermix with larger or smaller disjunctions on the territory of the whole area, and only in some parts of the geographical area is their spreading of a vicarious character.

Juncus effusus L. s. s.

According to the total area this is an amphiboreomeridionally (sub) montane species with a considerably disjunctive area (MEUSEL 1943).

It is most coherent in Eurasia from the British Isles via the Mediterranean region up to the upper Irtysh. The eastern Mediterranean region is probably the developmental centre of this species. In the whole area the species breaks up into a great number of varieties, which are sometimes considered subspecies. It is the E. Asian population of *ssp. decipiens* BUCHENAU. The E. African populations are conspicuous by their free inflorescence and by their very thin branches in the anthela (WEIMARCK 1946).

It grows in Europe, including the whole Mediterranean region, with the exception of the islands of the Aegean Sea and Crete (RECHINGER fil. 1943). It extends also to the countries of the African Atlas. In Scandinavia it grows northernmost in Norway, where it reaches latitude 66° N. In the European part of the USSR it follows approximately the basin of the Dvina and Pechora rivers up to the Urals, which it crosses in the vicinity of Sverdlovsk, and in western Siberia it ranges from the basin of the upper Irtysh to the upper Ob and continues via Djungaria (Sinkiank province of W. China) through eastern Turkestan, Cashmere, to western Afghanistan, and through N. Iran and Iraq to the Sinai peninsula. The western part of the Tarim basin is probably the easternmost point of its coherent geographical area in Eurasia.

The Far East is represented by Sakhalin and N. E. China, where it ranges from the Little Chingan through the whole of Manchukuo, Korea, and the whole of Japan. On the Filipines it grows only on Luzon. In N. America it follows the Atlantic coast from Newfoundland down to Florida, and upstream along the Mississippi through Mississippi, Arkansas, Oklahoma, Missouri, Iowa, Minnesota, the Great Lakes, and Quebec up to southern Labrador. On the Pacific coast it extends from the border of Alaska to California. It skirts the region of the Cordilleras (White and Rocky Mountains). In the countries of Central America it is found sporadically in Mexico, Guatemala, and Haiti.

In South America it follows the Cordilleras from Venezuela (the Miranda mountain range) across the Peruvian and Bolivian Andes to the region of Conception in Chile. On the Atlantic coast of South America it grows only in Brasil in the provinces Rio Grande, Paraná, and Sao Paulo.

In Africa it occurs in the vicinity of the Kilimanjaro on the borders of Kenya and Tanganyika, further in the eastern and western Cape provinces (WEIMARCK 1946). In the Atlantic it also grows in Iceland, the Azores, the Canary Islands, Madeira, and on St. Helena. In the Indian Ocean it occurs on Madagascar and on the islands Mauritius and Reunion.

Juncus conglomeratus L. s. s.

According to WIINSTEDT (1937) this species is a semicosmopolitan with an area including America, Europe, and Asia. On the American continent the species extends only to the SE coast of the U.S.A., to Nova Scotia, Brunswick, and Newfoundland. In Eurasia it has a coherent geographical area ranging from the British Isles to the Tarim basin with small disjunctions in Syria and in northern Kurdistan (Iraq). The developmental centre of this species is probably the eastern Mediterraneanpontic region, and from there it gradually spreads to the sub-Atlantic and Atlantic zone. In Scandinavia it is found in greater heights than *J. effusus*, in Norway it is found up to a longitude of 68° N (HULTÉN 1950). In the Mediterranean it avoids the Peloponnese, the Cyclades, the Sporades, and Crete (RECHINGER fil. 1943), and from the Balkans it spreads through northern Turkey (Lazistan) to link up with the Caucasian populations.

In the countries of the Near East it is found in isolated localities in Syria, Libanon (BOULOUMOY 1930), in northern Kurdistan in Iraq (HAUSSKNECHT in BUCHENAU 1906). In N. Africa it extends from Marocco to Tunis. The easternmost localities in the whole of Eurasia are in Djungaria (Sinkiank province of W. China) and in the neighbourhood of Lake Balchash.

Geographical distribution in the Czechoslovak Socialist Republic:

Both species are almost common on the territory of this country. Their increased ecological amplitude and ecomorphical plasticity results in a considerable adaptability in the various biotopes of the geographical area. I therefore desist from enumerating their localities and from giving a map of distribution, as the occurrence of both species covers the whole territory of this country, with the exception of high-mountain regions.

Phytocoenology

In the whole of their area both species have a similar ecological and phytocoenological character.

Juncus effusus L. — on the territory of this country it forms physiognomically outstanding associations, which are parts of *Magnocariceta*. These are mostly sublittoral stands of *Carex rostrata*, *C. inflata*, and *C. vesicaria*, or often typical Sphagno-cariceta with *Lysimachia vulgaris*, *Galium palustre*, and with *Calamagrostis canescens*. On short grass pastures the species appears as a dominant of the reduced association *Agrostidetum vulgaris* (e.g. the peatified drained pastures in the Soběslav-Veselí district, submontane pastures in the region of the Muráň highland near Tisovec, etc.).

Juncus conglomeratus L. — is also a component of *Carex* associations, especially on shallow peat-bogs it grows in the association *Caricetum lasiocarpe* Koch 1926. On peat soil it forms typical eutrophic formations and occurs also abundantly in moist meadow cavities, where it is accompanied by some mesophilic species.

Ecology

I have carried out analyses of ecotypes in the populations of both species parallelly on two related localities.

a) on peaty, partly already drained meadows with an advanced saprofication.

b) on swampy meadows in the littoral and limose belt of fish-pond basins and in the cavities of the river Lužnice, where a great number of associations and subassociations alternated from the moistest to the driest localities.

I have investigated the floristic composition of phytocoenoses, the flower aspect of outstanding species, the ecological conditions of stands, and above all, the influence of atmospheric and soil moisture.

a) A considerable part of the rush aspect on these localities consisted of species of the section *Juncus* (L.) Janchen 1959. These considerably eutrophic species required soils of rather medium acidity or slightly acid soils. On all of these soils there was an advanced degree of saprofication and a considerable anaerobe decomposition of organogenic substances, causing, together with anorganic substances, the forming of humolith. The thickness of the peat layer usually ranged between 60 and 100 cm or more, and the peat rested on a loamy base. Where meadows changed into uncovered peat the ground water level was high. The other rush species (*J. articulatus*, *J. bulbosus* and *J. bufonius*) occurred here already only sporadically and pointed towards a quite different ecological amplitude from that of the preceding species. I am of the opinion that on these meadows the ecological stages or ecophases are not so outstanding, even if the species *J. effusus* and *J. conglomeratus* are of a dominant character and sometimes form pure stands. This has been caused by the gradual invasion of meadow species (*Alopecurus pratensis*, *Phleum pratense*, and also *Molinia coerulea*) from the neighbouring cultivated stands. With a gradual lowering of the water level these species find optimum conditions in the soil. Here also devastating factors make themselves felt which, on the one hand, push out undesirable rushes from moss-grown, acid meadows and, on the other hand, in cases where the forming of peat has been too strong, they support the forming of extensive monotonous pastures with the following species:

J. conglomeratus L.
J. effusus L.
Carex fusca ALL.
Carex panicea L.
Polygonum hydropiper L.
Agrostis tenuis SIBTH.
Hydrocotyle vulgaris L.
Hieracium pilosella L.
J. bufonius L.
J. bulbosus L.
Carex serotina MÉRAT
Prunella vulgaris L.

The analysis of the aspect segment on the locality of the type a): height 410 m. M.S.L., exposition 0, substratum — peat layer of a thickness of about 80 cm on fine, loamy substratum.

Juncus conglomeratus formed strong tufts (height of tufts 65—80 cm.), in which the stem sheaths were raised above the water level filling the spaces between the patches of sod. With the gradual falling of the water column the soddy patches changed into a mossy pad with the species *J. effusus*, where the frequency of the preceding species weakened markedly. However, it strengthened the share of the *Carex* aspect (*C. fusca*, *C. panicea*, *C. polygama ssp. hartmanii* and *C. stellulata*) together with the species *Molinia coerulea*, *Potentilla erecta* and *Baldingera arundinacea*. The sphagnous sod was made firmer by the root system of the *Magnocariceta*, especially of *C. gracilis*, *C. canescens* and *C. rostrata*. In the water pools *J. bulbosus*, *Lysimachia nummularia*, and *Galium palustre* are found at places. Where the water level was without any sod pads also *Glyceria fluitans*. *J. articulatus*, and *J. bufonius* appeared sporadically only in the zone of small *Cariceta - Parvocariceta*, where *J. effusus* had optimum conditions. The frequency of these two rushes was by far more distinct only in a loosened stand, which had already a considerable terrestrial character. From the above mentioned analysis it can be seen that in the ecology of rushes one factor is outstanding — moisture simultaneously in soil and air.

Evaluation of analysis: The localities were in the zone of intensive peatification, where the high level of ground water and the advanced saprofication caused optimum conditions for the growth of rushes of the section *Juncus* (L.) JANCHEN 1959 — *J. conglomeratus*, *J. effusus*, and *J. filiformis*. The reaction of the substratum was slightly acid and in many cases it approached the neutral line. I am of the opinion that this factor is not influential to such an extent as is sometimes thought. The high degree of moisture of these soils, which do not dry up even in summer, results in their comparatively small air capacity. All these properties are suitable for the vegetative propagation of rushes and for pollination. The patches of sphagnous sod are a suitable factor for this propagation and the water in the small pools provide the desirable moisture in the ground air layers. Where the ground water level sinks a loosening of the rush stands sets in and the grass aspect including *Molinia* gains ground; this means that the density and the number of the various species of rushes in the stands decreases.

According to my opinion any predominant ecophase in the vegetation of a certain species is always a manifestation of the common affect of the specific properties of the species and of the climatic and ecological factors of the environment. By specific properties of the species I understand the ecomorphical and genetic plasticity of the species, i.e. the capability of reacting to certain factors within certain limits. The genetic plasticity is given by the inner potency of each individual and leads to the forming of more or less constant types, whereas the ecomorphical plasticity of a plant species within the range of its life possibilities gives rise to inconstant ecomorphoses. To this must be added also the biological properties of the species as, e.g., the specific capacity of reproduction, the ecological amplitude, etc.

b) On localities of this type considerable influence is exerted by neighbouring cultivated meadow stands, which, according to the degree of moisture, more or less disturbed the vegetation cover of extremely moist localities. The whole of this vegetative formation was characterized by eutrophic associations and passed from medium moist meadows via an alternatively flooded zone to reed-grass stands with a constantly waterlogged root system. Of interest, as regards the occurrence of rushes, was especially the intermediate zone lying between the two extremes of moisture. Of the rushes predominated *J. filiformis*, the frequency of which on the preceding type was very low or did not appear at all. *J. filiformis* formed tuft groups of from 10 to 25 specimens with a coherent sod pad, which was made firm by the root system of *Cariceta* (*C. vesicaria*, *C. canescens*, *C. panicea*, *C. fusca*). The sod pads formed elevations above the mossy cavities, which, in this zone, were not filled with water. Also the following associated species grew here: *Galium uliginosum*, *Ranunculus acer*, *Filipendula ulmaria ssp. pentapetala*, *Heleocharis palustris ssp. eupalustris*. This characteristic rush belt was not constantly waterlogged even in rain. The sod pads gradually passed into coherent soil with an increase of the frequency of species of a grass aspect from the neighbouring mesophilic meadows (*Alopecurus pratensis*, *Phleum pratense*, *Ranunculus auricomus*.) It is interesting to note that in this zone no other species of the section *Juncus* (L.) JANCHEN 1959 appeared. According to observations carried out on a whole series of localities the species *J. effusus* and *J. conglomeratus* find optimum conditions for vegetative propagation on such localities where there are great differences as regards the fluctuation of water. However, under the conditions of a constant high water level these species are able to form sod pads, as their vegetative propagation (the forming of shoots) is considerable. A quite similar situation exists as regards associations and on the margins of fish-ponds, where even more characteristic transitions between the various grades of associations according to the water level can be seen.

Evaluation of analysis: similarly as in localities of the first type also here an important part is played by soil moisture, which is most acceptable in the form of capillary water in the sphagnous or mossy sod pads. Therefore a seemingly great quantity of water in an coherent area in most cases affects the development of vegetation adversely. The soil moisture on these areas causes an expressive limitation of the various vegetative stages with regard to their ecological properties.

Phenology

I carried out the phenological observations in the course of two vegetation periods (1957, 1958) from May till September, and in the years 1960 and 1961 I checked the single pictures obtained from the extended area. The aim of the work was the determination of the beginning and of the extent of the flowering phase of the species *J. effusus* and *J. conglomeratus*. The phenological periodicity differed considerably in both species.

Methods of work: I carried out the phenological examinations on approximately 35 localities the ecological conditions of which were almost identical (drained peat meadows). Similar localities were selected intestionally so as to obtain as many data as possible regarding the extent of the variability under certain ecological conditions which are natural and almost primary for rush associations, and the specificity of which has not been rubbed off through the influence of other associated formations. So as to eliminate the influence of the relief and of exposure on the course of phenological phases I carried out measurings on localities with zero exposure and with an approximately identical mean sea level (420—450 m. M.S.L.) The localities were in the region of the Soběslav — Veselí marshes and in the northern part of the Třeboň basin. The greatest distance between the marginal localities of the whole examined district was about 30 km. A number of localities belonged to the type of transitional peat bogs with a peat layer of considerable strength resting on tertiary kaolin clays or sands. Of the climatic factors of great importance was the air moisture, the value of which depended on the degree of insulation which was proportional to the state of the conditions of exposure on the examined localities. On each locality I marked off a square which was, as regards the quantitative representation of both species, most typical for the locality in question. The square measured 5 × 5 m., and on this square I evaluated the per cent relationship between non-flowering and flowering individuals of both species growing together on more than a half of the locality. I carried out the evaluation of the numerical relationship on the basis of measurings performed four times a month on each locality during the whole vegetation period of the species. In cases where both species did not occur in a conclusive quantity on a certain area (less than 100 fertile individuals), I marked off two squares, one for each species on the same locality. I arranged the values obtained in a graph. I based the grading of the flower phase for the determination of the flowering optimum of the various species on the quantitative representation of flowering individuals on the given examined area. As soon as this number exceeded 50 per cent of the total number of individuals in the square I denoted this state as the characteristic flower phase or the flowering optimum of the species. In carrying out the measuring I compared the phenological properties of rushes with the phenological properties of other companion species, especially with those of *Cariceta* (*C. fusca*, *C. panicea*, *C. gracilis*, *C. stellulata*, *C. rostrata*, *C. vesicaria*, *C. pallescens*, and *C. canescens*.)

The following differences appeared:

1. the flower aspect of *Cariceta* was homogenous, thus it was very expressive but considerably short.

2. the vegetation periods of *Cariceta* began at the beginning of May, reached their optimum in June, and ended at the beginning of July. The longest vegetation period was that of *C. fusca* and *C. gracilis*, the shortest that of *C. canescens.*

3. as compared with the inexpressive flower aspect the vegetation period of rushes is much longer and lasts on the average from the beginning of May till the end of September.

The course of the phenological phases in both species:

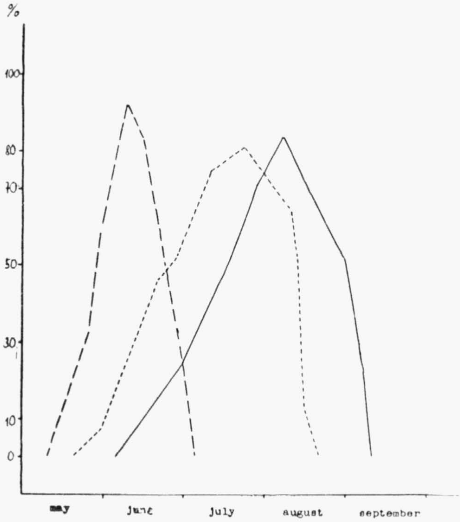
Juncus effusus L. (s. s.)

The vegetative growth before flowering is somewhat longer and the first flowers do not appear until the first third of June and its progress up to the optimum, even if equal, is much slower, so that the flower phenophase begins in the middle of July and extends to the end of August. The fruit phase lasts up to the middle of September, and therefore the whole vegetative growth after the falling off of the fruits is prolonged until the beginning of November. The culminating values of the flowering optimum are approximately the same as in the following species (this is connected with the succedaneous character of the flowering). Also the spread of the flower phenophase is almost the same as in the following species.

Juncus conglomeratus L. (s. s.)

The vegetative growth before the flowering begins at the end of April or at the beginning of May within a range of from two to three weeks according to the S.M.L. (also according to the length of time and the thickness of the snow cover, even if the vegetative shoots remain green during the whole winter season.) The first flowers appeared in the second half of May, and together with the rising of night and day temperatures also the share of flowering individuals up to the last week in June increased equally. Approximately beginning in the third week of June, during the whole of July, and up to the first quarter of August the species passes through its optimum flowering phase, which, on some localities, reaches up to 80 per cent of the value of all flowering individuals. According to my own observations the whole flowering phase has a succedaneous character as compared with the characteristic simultaneous phenophase in *Cariceta*, where the natural per cent values of flowering individuals may reach up to 100 per cent. Beginning in the first quarter of August the first phase sets in and the percentage of flowering individuals markedly decreases until the middle of August when it reaches zero value. This phenophase is not precisely outlined and ends at the end of August or at the beginning of September. Sometimes the setting in of the first phase is accelerated, which is caused by parasitizing Coleophores. I have observed inflorescences that had been attacked by cocoons of Coleophores and which were overripe already in the second half of August (of course, the capsules were without any seeds, or the seeds had a disturbed endosperm and did not germinate). After the falling off of the fruits vegetative growth continued until the end of October.

RICHARDS et CLAPHAM (1941) write about the phenological properties of both mentioned above species from the territory of Great Britain and point out that flowering is dependent exclusively on the geographical latitude and on the vertical formation of the terrain. According to these authors the flowering optimum of the species *J. conglomeratus* on localities in Great Britain occurs up to one month earlier than that of the species *J. effusus*. The differences between the setting in of the flower phase seem to be more or less constant in various geographical latitudes, of course the extent or intermingling of the phenophases of both species is greater or smaller according to the geographical position and the sea mean level.



Graphic illustration of phenophases in the course of the vegetation period of the species according to the percentage of flowering individuals. Above the 50 per cent line an expressive flowering phase or the flowering optimum of the species takes place. (Measured on 35 localities).

— — — — — *Carex rostrata* STOKES
- - - - - - - - - - *J. conglomeratus* L.
————— *J. effusus* L.

Conclusion

On the basis of phenological observations I have found that the setting in of the flowering optimum and the connected setting in of the fruit phase differ considerably in the species *J. conglomeratus* and *J. effusus*. In the species

J. conglomeratus the optimum begins at the end of June and continues until the first third of August, so that the range of the optimum phenophase is approximately 45 days. In the species *J. effusus* the optimum begins in the middle of July and lasts almost up to the end of August, i.e. approximately 40 days. The difference in the setting in of the optimum amounts to approximately three weeks (see graph).

If we consider the succedaneous character of the flowering of these species, this difference may, under certain ecological and climatic conditions, still increase or decrease; this means that the differential value obtained is the average of extreme cases. On the localities an interesting relationship between moisture and flowering appeared. On localities with visibly extensive moisture the species always flowered somewhat earlier than on drier localities. As the flowering is of a succedaneous character the phenophases of both species overlap considerably. Differences in the setting in of the flowering optimum, may be of great influence on the limitation of hybrid individuals, and that especially where there is a greater number of one species (i.e. either earlier *J. conglomeratus* or later *J. effusus*). On the localities that I examined both species were never equally represented, and therefore newly arising hybrid individuals always converged towards one of the parents predominating quantitatively in the locality. I consider this fact to be the explanation of the absolute absence of intermediary types, which I missed on these localities.

I am of the opinion that both species form a hybrid complex, the existence of which is confirmed by the gradual scale of morphologically transitional types between both parents. The forming of hybridogenous transitions is also conditioned by the very closely related genetic properties (the somatic number of both species is 40, Darlington 1955) and by the almost identical ecological requirements on the territory of the whole geographic area.

For the expression of the hybrid complex I have decided to use the taxonomical unit conspecies with the following nomenclature: conspecies *J. effusus* s.l. with two good species *J. effusus* L. and *J. conglomeratus* L., between which there is a whole system of morphologically and anatomically transional types, which I denote as effusoid and congloméroid vergents. (cf. Křísa 1959 : 96—100).

In these vergents I combine some forms and varieties mentioned in the literature (Ascherson et Graebner 1904, Buchenau 1906), which, according to the mentioned marks, are not defined individuals and are only components of a variable line between both parents. Of the morphological marks, which are important for the evaluation of both groups of vergents, I mention the following: length and breadth of inflorescence, length of flower anthela, size of terminal beak of the capsule, and the ratio of the length of the perigone to the capsule. In correlation with these marks are the following anatomical marks: height of the subepidermal sclerenchymatic blocks in the chlorenchyma, the character of the sclerenchymatic sheath round the primary and secondary vascular bundles — both refer to the stem.

These morphological and anatomical marks are, of course, only auxiliary values for the definition of transitional types between both species, and their placing in the key would lead again to a descriptive classification of forms and varieties of both species. For the evaluation of the various transitional types their ecomorphical and generic character is an inseparable part.

A. Group of effusoid vergents: (types approaching the species *J. effusus*)

a) vergent proliferoides Křísa

Syn.: *J. effusus* L. *var. prolifer* Sonder Fl. Hamb., 191, 1851.

Main marks: inflorescence overhanging with branches of flower anthelas from 5—7 to 10 cm long. Perianth segments of equal length or only about 0,2 mm exceeding capsule, which is from 2,5 to 2,7 mm long, apex of capsule strongly pressed inside. Subepidermal sclerenchymatic blocks in stem reach phloem only in those secondary vascular bundles that are nearest to the epidermis. Sclerenchymatic sheath of equal strength, epidermis only insignificantly corrugated.

b) vergent compactoides Křísa

Syn.: *J. effusus* L. *var. compactus* Lej. et Court. Comp. Fl. Belg. II., 23, 1831. — *J. effusus* L. *var. conglomeratus* Beck, Fl. Nieder-österr., 1890.

Main marks: inflorescence contracted or slightly overhanging, branches of flower anthelas from 3—4 to 6 cm long. Perianth segments of equal length as capsule. Capsule blunt, 2.6—2.8 mm long, so that top edge of segment of capsule is slightly pressed inside from side. Subepidermal sclerenchymatic blocks in stem reach phloem in some secondary vascular bundles, but are not connected with the sclerenchymatic sheath of the xylem. Sclerenchymatic sheath in primary vascular bundles of equal strength. Epidermis slightly bent. As regards growth and character of inflorescence the limits of this type spread to the other group of vergents.

B. Group of conglomeroid vergents: (types approaching the species *J. conglomeratus*)

c) vergent laxoides Křísa

Syn.: *J. conglomeratus* L. *var. laxus* Beck, Fl. Nieder-österr., 135, 1890.

Main marks: inflorescence sparse, from prolonged to slightly overhanging with branches of the flower anthelas from 2—4 to 6 cm long. Perigone mostly does not reach length of capsule, or only reaches to upper edge of segment of capsule. Capsule from 2,7 (2,8) to 3 mm long with beak at apex (0,2—0,3 mm) long, which is dark brown. Subepidermal sclerenchymatic blocks in stem link up with phloem only in some secondary vascular bundles. Sclerenchymatic sheath in primary vascular bundles continuous and markedly enlarged on side of xylem. Epidermis is bent and forms riblike ridges.

d) vergent subulifloroides Křísa

Syn.: *J. subuliflorus* Drejer, Fl. excurs. Hafn., 127, 1838. — *J. Leersii* Marss. *var. subuliflorus* (Drejer) Buchenau, l.c., 233, 1890. — *J. conglomeratus* L. B. II. *subuliflorus* A. et G., 446, 1904.

Main marks: inflorescence contracted or only slightly overhanging, branches of flower anthelas from 1—2 to 4 cm long. Perianth segments mostly of equal length as capsule and sometimes markedly long acute (effusoid mark). Capsule about 3 mm long with dark coloured beak. Subepidermal sclerenchymatic blocks never reach vascular bundles, and the sclerenchymatic sheath in some of the vascular bundles is earlike protracted at place of change over of phloem and xylem, but is mostly not compact. Epidermis strongly bent.

Graebner in Ascherson et Graebner (1904) mentions further varieties of the species *J. conglomeratus* L.: *var. viridiflorus* A. et G., l.c., 1904 and *var. umbrosus* A. et G., l.c., 1904. They are evaluated according to the colour of the perigone, which is a very changeable mark and which is characteristic rather for juvenile stages.

On the basis of the above mentioned marks it is not possible to determine an intermediate hybrid between both species, as the variability of the whole complex makes it possible to attach such a type to any vergent. Therefore the hybrid *Juncus brueggeri* Domin 1936 (syn.: *J. Haussknechtii* P. Fourn. non Ruhm.) is only a component part of the whole hybrid complex.

Attached there is a table giving a brief survey of diacritical marks of transitional vergents between both parent types and a graphic illustration of the phenophases of both species.

In conclusion I should like to express my gratitude to Dr. R. Hendrych, C.Sc. for his painstaking reading of the manuscript.

Survey of the variability of the hybrid complex of *Juncus effusus* L. s. l.

Main marks	*Juncus effusus* L. s. s.	vergent proliferoides	vergent compactoides	vergent laxoides	vergent subulifloroides	*Juncus conglomeratus* L. s. s.
Morphological: inflorescence	spread, overhanging branches 5 to 10 cm and longer	overhanging branches 5—7—10 cm long	slightly overhanging, branches of anthelas 3—4 to 6 cm long	sparse, prolonged, branches of flower anthelas 2—4 to 6 cm	contracted or little overhanging, 1—2 to 4 cm long	contracted, headlike, branches of flower anthelas at most 2 cm long
perigone	P 2.2—2.8 mm long outer little longer than inner and exceeding capsule	P of equal length or only slightly longer than capsule	P of equal length as capsule	P reaching only to upper edge of segment of capsule	P ± length of capsule and markedly pointed	P linearly lanceolate with scarious margins and with central green keel
capsule	on apex blunt without point of style	2.5—2.7 mm long, on apex strongly pressed inside	2.6—2.8 mm long, blunt edge of segment slightly pressed inside	2.7 (2.8)—3 mm long at apex protuberance (0.2 to 0.3 mm)	3 mm long, at apex dark beak	obovate ± overhanging perigone and on top with marked point
Anatomical: subepidermal sclerenchymatic blocks in stem	enveloping phloem part of vascular bundles	reaching phloem only in secondary vascular bundles	reach phloem only in some secondary bundles	rarely reaching phloem of vascular bundles	never reach vascular bundles	never touch vascular bundles
sclerenchymatic sheath round vascular bundles	continuous and equally strong in xylem and phloem	equally strong in primary and secondary vascular bundles	equally strong only in primary vascular bundles	continuous, but enlarged on side of xylem	earlike protracted at place of change over of xylem and phloem	earlike protracted at place of tracheas in xylem
epidermis	slightly corrugated	strongly corrugated	slightly bent	forms riblike ridges	strongly bent	strongly bent

Position of varieties and hybrids mentioned in literature

Juncus brueggeri ←——→

var. *umbrosus* ←——→

var. *viridiflorus* ←——→

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Author's address: Bohdan Kříša, katedra botaniky přírodovědecké fakulty University Karlovy, Benátská 2, Praha 2, Czechoslovakia.