

Tragopogon porrifolius × *T. pratensis*: the present state of an old hybrid population in Central Bohemia, the Czech Republic

Současný stav hybridogenní populace *Tragopogon porrifolius* × *T. pratensis* u Roudnice nad Labem ve středních Čechách

František Krahulec¹, Zdeněk Kaplan¹, Jan Novák²

¹Institute of Botany, Academy of Sciences of the Czech Republic, CZ-252 43 Průhonice, Czech Republic, ²Laboratory of Archaeobotany and Palaeoecology, Department of Botany, Faculty of Biological Sciences, University of South Bohemia, České Budějovice, Czech Republic

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A population of a hybrid between *Tragopogon porrifolius* and *T. pratensis* (*T. ×mirabilis*), which occurs in SW part of the town of Roudnice nad Labem, N part of Central Bohemia, was analysed with respect to its morphology, fertility, life history, ploidy level and DNA content. Both parental species vary relatively little morphologically; they are biennials (monocarpic perennials) and diploids. *T. pratensis* is a native species in the Czech Republic, *T. porrifolius* was cultivated there in the past. The hybrid plants are extremely morphologically variable, with variation ranges of some characters overlapping those of the parental species (e.g. ligules are often longer than involucral bracts, peduncles are often lanate). Only diploids were found within the hybrid population; however, they have substantially lower DNA content than both parents (18% lower than *T. pratensis*, 42% lower than *T. porrifolius*). The plants of the Roudnice hybrid population are polycarpic perennials in contrast to the monocarpic perennial (mostly biennial) parents. The distribution is described in detail; it shows that the hybrid plants are spreading and at present even occur outside the town. The long-persisting population of fertile diploid hybrid plants in Roudnice nad Labem is an alternative evolutionary pathway to that of the allotetraploid *Tragopogon* species known from North America.

Key words: *Asteraceae*, chromosome numbers, distribution, DNA content, life history, morphology, *Tragopogon*

Introduction

In the Czech Republic, there are several native species of the genus *Tragopogon*: *T. orientalis* L., *T. dubius* L., and *T. pratensis* L. [subsp. *minor* (Mill.) Wahlenb. and subsp. *pratensis*]. Another species, *T. porrifolius* L. is not native to the Czech flora (Pyšek et al. 2002). It was cultivated as a vegetable in the Middle Ages and only a few records document its rare escapes from gardens in the last two centuries. Escaped these plants survived only for a short period of time in human-made habitats close to the place of cultivation. The species is not known to occur in the Czech Republic at present.

This group of *Tragopogon* taxa is recognized in the different floras covering the Czech Republic since the beginning of the 20th century (e.g. Polívka 1901, Domin & Podpěra 1928, Dostál 1948–1950, Kaplan 2002, Kaplan 2004). The hybrid between *T. porrifolius* and *T. pratensis* was the first plant hybrid produced by K. Linné to demonstrate sexuality in plants (Novák 1922, Ownbey 1950). Hybridization between these species has been recorded in the Czech Republic only once (Novák 1922). This hybrid (*T. ×mirabilis* Rouy) is

not recorded in other countries in Central Europe, for example in recent German Floras (e.g. Jäger & Werner 2002). It is reported from England by Stace (1997) as rare and persisting together with *T. porrifolius*.

There is a different situation in North America. *T. porrifolius*, *T. pratensis* and *T. dubius* were introduced to western USA (Oregon, Idaho) where they hybridized and formed two new allotetraploid species: *T. mirus* Ownbey (based on *T. dubius* × *T. porrifolius*) and *T. miscellus* Ownbey (based on *T. pratensis* × *T. dubius*). From the time of their recognition (Ownbey 1950) these species were frequently used as model species for various studies and are the best-documented cases of the origin of new species (summarized by Novak et al. 1991 and Soltis et al. 2004).

At the end of the 1990s, Jan Novák discovered a distinct population of *Tragopogon* in Roudnice nad Labem. This population was characterized by extreme variation in flower colour, from dark yellow to whitish yellow and even dirty blue. In addition, the pubescence of the stem, capitulum size and shape of the plants also varied. Because Jan Novák was aware of the evolutionary events in the North American *Tragopogon*, he started a more detailed study. At the beginning he thought he had found a third allopolyploid, absent from North America (based on *T. pratensis* and *T. porrifolius*). However, the chromosome numbers and DNA content indicated the diploid nature of this population (F. Krahulec et al., in preparation). The determination of plants was based at the fact that *T. pratensis* is still present on the locality, and the influence of *T. porrifolius* was obvious from the flower colour. Later, we found a paper written by F. A. Novák (1922) in which he records a hybrid between *T. porrifolius* and *T. pratensis* found at the same place, growing together with both its parents. This is cited several times in Floras and determination keys (e.g. Domin & Podpěra 1928, Dostál 1948–1950, Dostál 1989). The original locality was a garden of the Secondary school of agriculture, where *T. porrifolius* was cultivated. Later on this area became part of a machine factory (Roudnické strojířny, later Ross). There is no indication that another species was cultivated there.

Both parents are diploid and the hybrid plants are invariably diploid as well. Both parents significantly differ in their DNA content, *T. pratensis* having the lower value. Surprisingly, plants from Roudnice have even less than *T. pratensis*. The value is about 18% lower than that for *T. pratensis* and 42% lower than that for *T. porrifolius* (F. Krahulec et al., in preparation).

Characterization of the hybrid population

Morphology of hybrids

The characteristic feature of this population is that it is extremely variable in most of the morphological characters. A comparison of the important characters is given in Table 1. It should be noted, that the variation ranges of several characters of the hybrid overlap those of both parents, e.g. the peduncles are often lanate, which is a character state absent in *T. pratensis* and rare in *T. porrifolius*. The leaves are extremely variable varying from narrowly linear to lanceolate, often undulate. The ligules are usually longer than the involucral bracts, while both parents have ligules shorter or equalling the bracts. The variation in flower colour and shape is illustrated in Figs 1 and 2. There is great polymorphism in the coloration of the anther tubes, with several morphotypes (Table 1, Figs 1, 2): upper half of anther tubes black with rest yellow, black with yellow stripes, yellow with black stripes (as in *T. orientalis*) or completely yellow (or pale brown).

Table 1. – Comparison of morphological characters of *Tragopogon pratensis*, *T. porrifolius* and hybrid plants from Roudnice nad Labem (*T. xmirabilis*). Data presented are partly based on treatment of *Tragopogon* in Flora of the Czech Republic (Kaplan 2004).

Character	<i>T. pratensis</i>	<i>T. xmirabilis</i>	<i>T. porrifolius</i>
Stem colour	green	green to glaucous	glaucous
Peduncles	not inflated, glabrescent	indistinctly inflated, rarely glabrous to lanate	inflated, glabrous to floccose-lanate
Stem leaves	linear-lanceolate, more or less subamplexicaul at the base	extremely variable, from narrowly linear (3 mm) and short (40 mm) to linear and long (up 200 mm) or lanceolate (18 mm) and long (250 mm), often with undulate margin	broadly-linear, widened at base
Capitulum diameter	3–4 (–5) cm	4–6 cm	5–6 cm
No. of involucre bracts	(5–) 8–12	7–10	(5–) 8–12
Length of involucre bracts (during flowering-during ripening)	2.2–3.4 cm	2.5–4.5 cm	3.5–5.0 cm
Corolla colour	pale yellow to yellow	pale yellow, yellow, whitish, dirty violet	lilac to deep violet or reddish-purple
Colour of back side of ligules	pale yellow to yellow	pale yellow or whitish with violet stripes or dirty violet	lilac to reddish-purple
Ligule length vs. involucre bract length	ligules shorter or equaling bracts	extremely variable, 5 mm shorter to 8 mm longer	ligules shorter or equaling bracts
Colour of the anther tube	upper 1/4–1/2 dark violet to black, rest pale yellow	extremely variable: usually upper half dark violet to black or striped with prevailing dark colour, rarely opposite, with narrow black stripes rarely whole black or pale yellow	upper 3/4 dark violet to black, rest violet-whitish
Length of achene corpus (achene without rostrum)	8–13 mm	8.5–10.0 mm	12–15 mm

Stems are commonly erect, but prostrate plants are not rare. It is a perennial (see below) with the stems originating from one root head and forming tussocks of erect or prostrate stems.

Due to the high variation, identification is extremely difficult and using available keys usually leads to incorrect conclusions. Some plants are identified as *T. pratensis*, some even as *T. orientalis*, especially when only the length of the ligules and involucre bracts are considered. The combination of characters is random; they are highly variable but uncorrelated with each other. It needs to be emphasized that without knowledge of the history of a hybrid population and its detailed complex investigation, the correct identification of many plants is impossible by using keys in floras. In addition, some features given in European national floras as species-diagnostic were found, in the course of cultivation, unreliable or even totally misleading for identification (Kaplan 2004).

Fertility of plants

The plants within the population studied are of highly variable fertility. Most plants are partially or fully fertile, but fully sterile plants were also noted. The germination rate of achenes collected in the field varied also from zero to 100% (depending on the maternal plant), with an average of almost 60% (for achenes collected in 2002).

Life form

The most conspicuous feature of the hybrid population in Roudnice is the life history of the plants. Both parental species are usually described as biennial, but strictly they are monocarpic perennials (Qi et al. 1996). Primary hybrids produced by artificially crossing these species in a garden, e.g. by Zdeněk Kaplan in the course of this study, were also monocarpic perennials. However, the population in Roudnice consists of perennial polycarpic plants. Root heads start to develop new stems in late summer or in autumn, soon after the flowering of stems from the previous year (Fig. 3d). Many plants in the field have remnants of several generations of flowering stems, often forming dense tussocks (Fig. 3a). After transplantation to a garden these plants continued to produce re-growths and flowered regularly in each of the four years of the study. Some of the plants form new ramets not only on the head of the main root, but also from the finer roots (Fig. 3c). Density of tussocks can be very high; Figs 3a, b show tussocks produced by two years old plants (originated as a seedling in the garden); the plant in Fig. 3a is more similar to a grass such as *Dactylis glomerata* than to *Tragopogon*.

The present distribution and habitats

The population of *T. ×mirabilis* in Roudnice nad Labem occurs at several places in SW part of the town. A high concentration of plants is still present in the area of the former garden of the Agricultural school (later Roudnické strojírný, Ross) and its vicinity. Most of the plants (our estimate is several thousands) occurred in the neighbourhood of a small train station (Roudnice-Hracholusky); in 2003 and 2004 the railway yard was treated with herbicide and most of the plants died. However, hundreds of plants survived at the periphery of this station. The other rich localities are lawns bordering the road to the station and lawns near the school. They occur scattered also in many other places in the town, even on



Fig. 1. – Capitula of *Tragopogon* taxa studied: *T. pratensis* (upper row, left; Planá u Mariánských Lázní), *T. porrifolius* subsp. *porrifolius* (upper row, middle; garden culture), and individuals from hybrid population of *T. ×mirabilis* in Roudnice nad Labem.

the top of stonewalls. One of the typical habitats is at the base of walls, fences etc. The most distant occurrence was along the road from Roudnice to the highway, i. e. some distance from the ruderal places in the town. The detailed distribution is given on Fig. 4.



Fig. 2. – Capitula of *Tragopogon xmirabilis* from Roudnice nad Labem.

Discussion

The hybrid population of *T. xmirabilis* in Roudnice nad Labem is not more than 85 years old. Prof. F. A. Novák, who came from Roudnice found one hybrid between *T. porrifolius* and *T. pratensis* there in 1921. It is unlikely he could have overlooked a larger hybrid population. At present, this population seems very unstable in many respects: it is extremely variable in many morphological characters, such as leaf shape and size, colour and size of

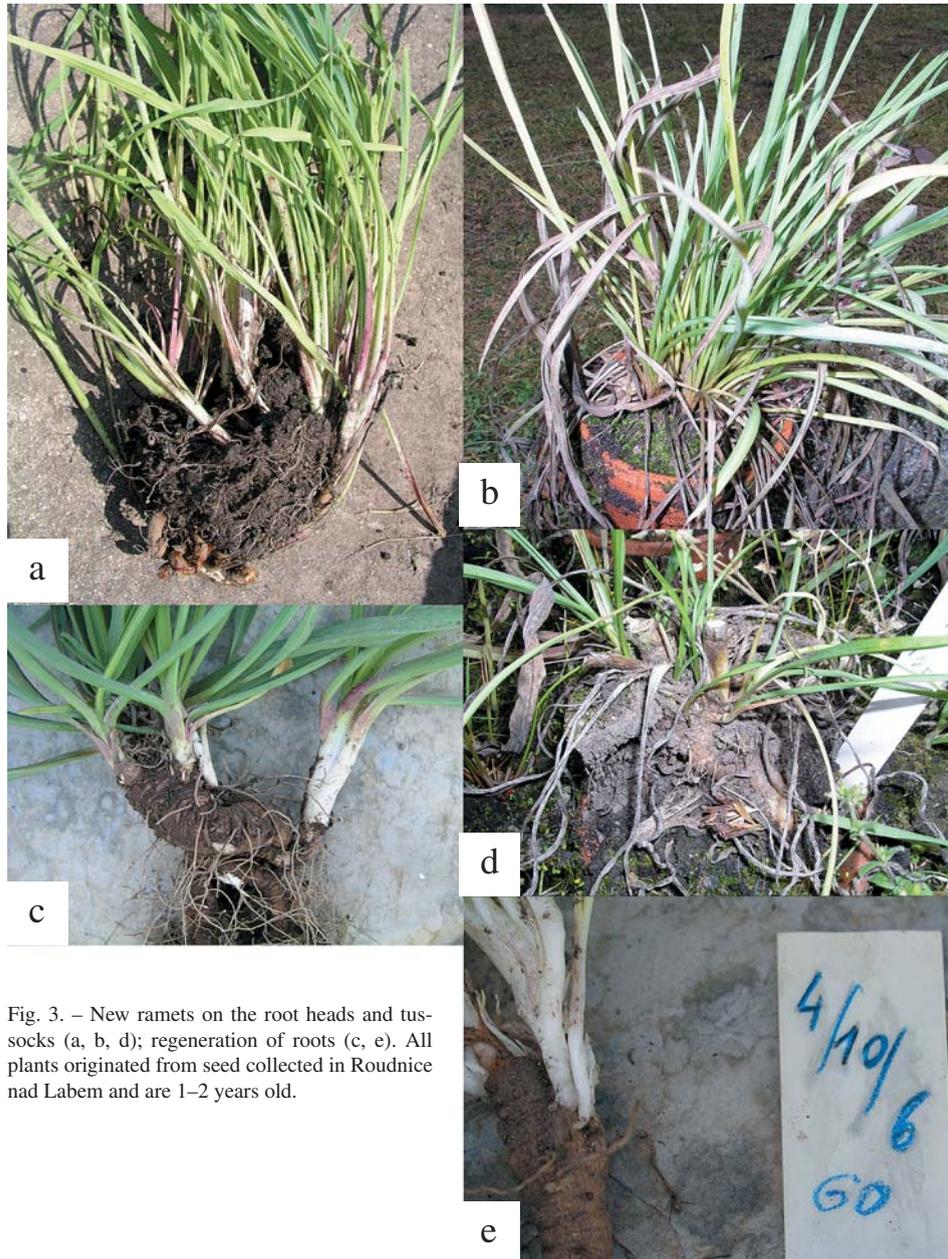


Fig. 3. – New ramets on the root heads and tussocks (a, b, d); regeneration of roots (c, e). All plants originated from seed collected in Roudnice nad Labem and are 1–2 years old.

ligules, their length with respect to length of involucral bracts, hair density on peduncles, coloration of anther tubes and in isozyme spectra (F. Krahulec et al., unpublished results). Characters directly related to fitness, such as fertility and seed germination were also highly variable. Some characters typical of at least some plants from this population seem to differ from those of both parents, such as lanate peduncles, ligules longer than

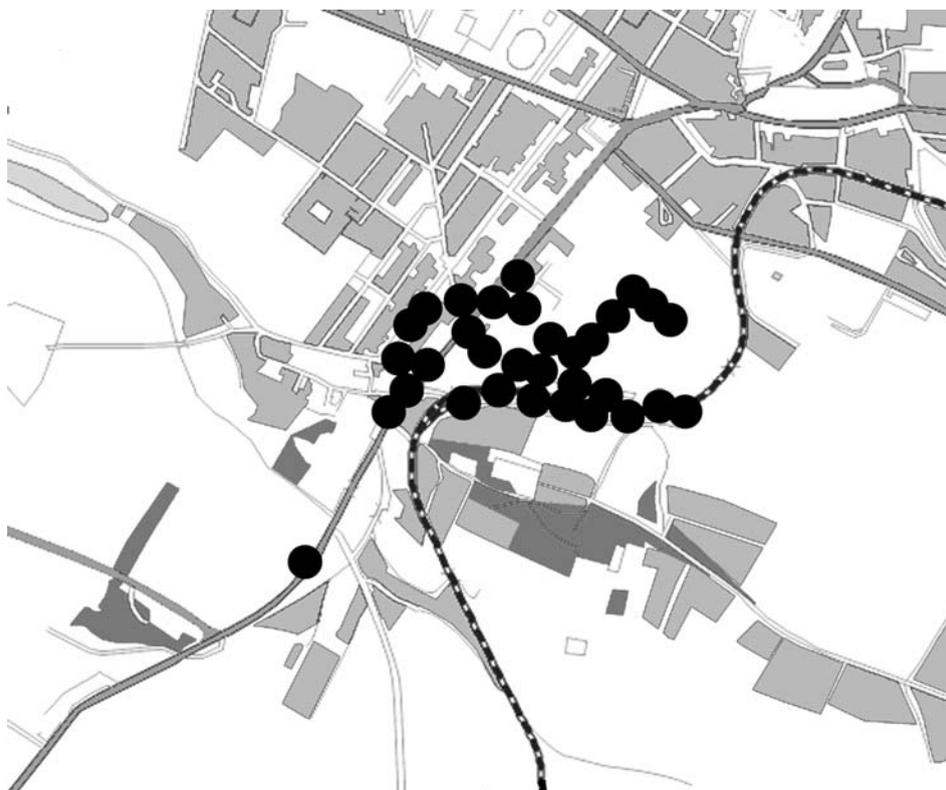


Fig. 4. – Distribution of *Tragopogon xmirabilis* in SW part of the town of Roudnice nad Labem.

involucral bracts and coloration of anther tubes. Polycarpic perenniality is a new character for *Tragopogon* in Central Europe. More than 800 plants grown from seed collected at this locality were perennials, forming new shoots on the root heads. None of the hundreds of *T. pratensis* plants in populations in western Bohemia, the area with richest population of this species in the Czech Republic, were perennial. We do not think it is a character, which appeared de novo in the hybrid plants. We think it is a reversal to the primary condition. This opinion is based on the fact that there are some perennial *Tragopogon* species such as *T. ruber* S. G. Gmelin, *T. marginifolius* Pawłowski, *T. kotschy* Boiss., *T. montanus* S. Nikitin and *T. albinerve* Freyn et Sint. The last three species were found to be the most primitive ones of *Tragopogon* in the phylogenetic analysis of the subtribe *Scorzonerinae* published by Mavrodiev et al. (2004: Fig. 5). The biennial life history (it is better to speak about monocarpic perennials, see also Qi et al. 1996) appeared independently at least two times within this subtribe, annuals at least three times. Based on the present knowledge one can only speculate about the advantages of the perennial life history for the plants in Roudnice. The richest population was at the train station, a habitat that is often occupied by annuals and biennials (as *Oenothera* sp., *Berteroa incana*, *Daucus carota*).

Tragopogon species, which originated as hybrids between *T. porrifolius* and *T. dubius* (*T. mirus*), and *T. dubius* and *T. pratensis* (*T. miscellus*), are probably the best-documented cases of the origin of allopolyploid species. All three parental species are diploids and the descendants tetraploids. Both diploid and tetraploid species are described as biennials. In this respect, the hybrid population in Roudnice represents a different evolutionary pathway. It is based on the combination of species, which are not known to produce a new allopolyploid type in North America. The population in Roudnice remained at the diploid level. Hybridogenous populations in North America are probably of the same age. *Tragopogon porrifolius* and *T. pratensis* were established there prior 1916, *T. dubius* prior 1928 (Ownbey 1950). Both the populations in North America and those in Roudnice have gone through a similar number of generations, not more than 40. The evolution of the Roudnice population could be more complicated with respect to the perennial life history: each plant may have hybridized with some others several times and even with their own progeny. In spite of the fact that *T. ×mirabilis* was found by F. A. Novák and is mentioned several times in our floras, it was not studied in detail until the end of the last century. So, the evolutionary history of this population remains unknown compared to the hybridogenous populations in North America. We hope it will be an attractive topic, especially the changed life history, for future study.

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Souhrn

V roce 1922 popsal F. A. Novák vznik křížence mezi druhy *Tragopogon porrifolius* a *T. pratensis* (*T. ×mirabilis*) v zahradě zemědělské školy v Roudnici nad Labem. Přestože byly tento hybrid i lokalita zmíněny ve všech důležitých určovacích příručkách, nikdo další tento případ hybridizace nestudoval. V současné době se na místě bývalé zahrady nachází objekt podniku Ross (dříve Roudnické strojírny). V jeho areálu stejně jako v areálu železniční stanice Roudnice-Hracholusky a v přilehlých ulicích roste velká populace hybridních kozích brad. Ty se liší celým souborem znaků od svých rodičů, v některých případech jsou i mimo rozsah variability obou rodičů. Celkově je variabilita této populace velmi vysoká, a to nejen v morfologických znacích, ale např. i ve formě vzrůstu rostlin, kde se vyskytují jak vysoké (až 1,5 m) rostliny, tak i nízké s vystoupavými lodyhami. Za nejzajímavější skutečnost považujeme to, že ač oba rodiče jsou krátkověké trvalky kvetoucí jednou za život, hybridní populaci tvoří trvalky kvetoucí opakovaně. Rostliny jsou diploidní, v průběhu hybridizace došlo ke změně obsahu DNA, který je o 18 % nižší než u *T. pratensis* a o 42 % nižší než u *T. porrifolius*. Tímto vývojem na diploidní úrovni se daná populace liší od hybridogenních populací ze Severní Ameriky, kde po křížení *T. porrifolius* a *T. dubius* vznikl tetraploidní *T. mirus*, a po křížení *T. dubius* a *T. pratensis* opět tetraploidní *T. miscellus*. Žádný z těchto nových druhů se ale nechová jako opakovaně kvetoucí trvalka. Populace v Roudnici nad Labem tedy představuje evoluční alternativu k polyploidnímu vývoji v Severní Americe.

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