Sexual reproduction in *Taraxacum* sect. *Borealia* (Asteraceae, *Crepidinae*)

*first documented in the continental Russian Far East*

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**Summary.** Modes of reproduction vary considerably in the genus *Taraxacum*. In particular, the extent and distribution of sexuality are decisive criteria for the evaluation of variation and the taxonomic conclusions in this complicated genus. *Taraxacum* sect. *Borealia* is widespread in the Arctic and Subarctic regions of the Asiatic part of Russia, but sexual reproduction has not been known to occur there, unlike *T.* sect. *Arctica* with a number of sexually reproducing species in the continental Far East. A detailed analysis of the herbarium material of *Taraxacum kolymense* Khokhryakov, using pollen size analysis and achene set examination, revealed sexuality in this distinctive member of *T.* sect. *Borealia*. The lectotype is selected for *T. kolymense* from a rich type gathering consisting of seven herbarium specimens, and a new consolidated description was compiled.

Половое размножение, впервые выявленное у одуванчика секции *Borealia* (Asteraceae, *Crepidinae*) с континентальной части российского Дальнего Востока

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**Ключевые слова:** агамоспермия, Азиатская Россия, половое размножение, *Taraxacum kolymense*, *Taraxacum* sect. *Borealia*.

**Аннотация.** В роде *Taraxacum* встречаются виды с различными способами размножения. В частности, частота и распространение полового размножения являются решающими критериями при оценке изменчивости и принятии таксономических решений в этом сложном роде. Секция *Borealia* рода *Taraxacum* широко распространена в арктических и субарктических регионах Азиатской России, но для нее ранее не было известно полового размножения, в отличие от sect. *Arctica*, в которой для некоторых дальневосточных видов по-
Introduction

A within-genus variation in the mode of reproduction is not a rare phenomenon in plants (Richards, 1997). Boundaries between the diverse reproduction systems and mechanisms are not clear-cut, moreover, and, although the majority of cases are unequivocal, there are relatively frequent various unstable or intermediate reproductive phenomena. Sexuality, however, is generally the most frequent reproduction among plants while asexual reproduction is often considered as an aberrant, temporary feature (Asker, Jerling, 1992; Ozias-Akins, van Dijk, 2007). In Taraxacum, however, we can demonstrate that the variation and shifts in modes of reproduction represent a major phenomenon in microevolution and speciation, both generally and geographically or ecospatially (Hörandl, 2006).

An outline of sexual reproduction in Taraxacum

Taraxacum L. is an almost cosmopolitan genus usually divided into ca. 60 sections (with approximately 2500 species, see Kirschner et al., 2020). Even the taxonomic distribution of sexuality in Taraxacum is remarkable: out of the 60 sections, 32 involves sexuality (but only eight sections are exclusively sexual: Kirschner et al., 2020).

As regards the geographical distribution of sexuality, it is very uneven. Sexuality predominates among native dandelions in the Southern Hemisphere (South America, Australia, New Zealand, see Uhlemann et al., 2004); it is very common in Southern Europe and the Mediterranean, and sexual populations are common in Japan, China and Taiwan (Ge et al., 2011). A scattered to rare occurrence of native sexual dandelions was reported from the northernmost North America (Elvén, 2021), and sexuality is relatively widespread in Middle Asia (sensu Cowan, 2007). A special attention is paid, in the present paper, to the dandelion sexuality center in the broad Beringian area, although it is only scarcely documented from the American side.

After having summarized the taxonomic and geographical distributions of dandelion sexuality, we should mention features of spatial coexistence of sexuality and agamospermy at the population level. Agamospermous entities relatively frequently coexist with sexuals at the local scale, usually as stable microspecies with a gene flow being very restricted or even blocked but sometimes with a gene flow being well documented and presumably relatively common (Nijs et al., 1990; de Kovel, de Jong, 2000; Mártonfiová, 2006, 2015).

Consequences of the varied modes of reproduction in Taraxacum at the species level

In Taraxacum, the variation is controlled by a combination of mating systems, ploidy levels and ancient, fixed hybridity. Polyploidy is associated with agamospermy (with very few exceptions), as is fixed hybridity. These phenomena and processes operate both generally, at the level of taxonomic entities, and in a spatially specific manner.

Three main mating systems in Taraxacum are allogamy, autogamy and agamospermy. The main consequence of varied modes of reproduction and variation patterns is that Taraxacum species are remarkably different, when their population heterozygosity and genotype diversity are considered (after Hughes, Richards, 1988; Richards, 1997) (table).

Table

<table>
<thead>
<tr>
<th>Mating system</th>
<th>Frequency of heterozygotes</th>
<th>Genotype diversity</th>
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<tbody>
<tr>
<td>allogamous sexual</td>
<td>Hardy-Weinberg equilibrium</td>
<td>very high</td>
</tr>
<tr>
<td>autogamous sexual</td>
<td>very low</td>
<td>low to moderate</td>
</tr>
<tr>
<td>agamospermous</td>
<td>very high, fixed</td>
<td>very low</td>
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</table>

The three main systems of reproduction roughly correspond to the “types” of species. Other factors to be considered are (a) history of the population structure, (b) spatial and phylogenetic proximity of sexual and agamospermous entities, and (c) ecological differentiation among species (and sections).
On this basis, we recognize allogamous, variable sexual species, such as *T. erythrospermum* Bess. s. str. or *T. serotinum* (W. et K.) Fisch., or distinctive autogamous species, such as *T. besarabicum* (Hornem.) Hand.-Mazz. or *T. aristum* Markl., or diplosporous agamospermous species (the absolute majority of polyploids in *Taraxacum*).

A clear conclusion to be made on the basis of these facts is that the knowledge of the occurrence and distribution of sexual reproduction is essential for understanding the variability of dandelions.

**Basic features of *Taraxacum* sect. *Borealia***

*Taraxacum* sect. *Borealia* Hand.-Mazz., often referred to as *T.* sect. *Ceratophora* Dahlst. or *T. ceratophorum* agg., is a group of species distributed in an Arctic-Alpidic pattern, with a circumpolar main part of its distribution range, and a scattered occurrence in the temperate mountains (Ge et al., 2011; Kirschner et al., 2014; Kirschner et al., 2020).

In general, *T.* sect. *Borealia* is characterized by a relatively robust growth, leaves with broadly winged petioles and ± patent lateral segments, scapes often growing from outside the leaf rosettes, outer phyllaries numerous, appressed to erect-patent, ± borde-red, with horns near their apex, and achenes most often with a conical to subconical cone and a long beak.

Members of *T.* sect. *Borealia* in Europe (Scandinavia and the Alps) and the continental Asia were known to have asexual, agamospermous reproduction (the continental Far East species with a diploid chromosome number, 2n = 16, and therefore sexu-chromosome number), or intermediate between sexual species, such as *T. erythrospermum* Bess. and *T. ceratophorum*. Thus, we consider the sexual behaviour of *T. kolymense* as a proven fact (Fig. 1a).

According to the data available, *Taraxacum* sect. *Borealia* appeared as completely agamospermous in the continental Asiatic Russia.

**Materials and methods**

**An analysis of *Taraxacum* kolymense**

As pointed out above, in the continental Asiatic Russia, until now, sexual reproduction has not been known in *Taraxacum* sect. *Borealia*. It was not until we studied a rich type gathering of *T. kolymense* Khokhryakov that we realised there are indicators of sexuality, indicators that proved to be reliable in other *Taraxacum* groups (Kirschner, Štěpánek, unpublished). These first, indirect features pointing to possible sexuality include:

(i) variable colour of well developed, ripe achenes within a gathering;

(ii) frequent occurrence of sterile, whitish achenes;

(iii) a very narrow involucre (4–6 mm wide);

(iv) a narrowly obconical involucre base (i. e., not rounded as in most of other taxa).

As the herbarium material of *T. kolymense* was collected more than fifty years ago, we are left with a single, feasible method of a sexual reproduction pro- of – the pollen size variability analysis (den Nijs et al., 1990, Gürdal et al., 2018). This approach is based on the fact that the *Taraxacum* diplospory is confined to megasporogenesis, while microsporogenesis leads to the irregular distribution of chromosomes and therefore variable pollen. The simple method, as described in the latter works, includes a direct binocular lens observation of pollen on stigmas (or on a slide under the microscope) with the evaluation of whether the pollen grains are ± of the same size (sexuality) or clearly variable in size (probable agamospermy, or recent hybridity).

The analysis of pollen grains of *T. kolymense* was performed by two of the present authors (MN and NS), and it confirmed a perfectly regular pollen size. Thus, we consider the sexual behaviour of *T. kolymense* as a proven fact (Fig. 1a).

**A brief outline of *Taraxacum* kolymense**

The protologue description of *T. kolymense* (Khokhryakov, 1973) is inadequate (the achene description is based on sterile, whitish achenes, beak length is not included, pappus length is inaccurate, pollen presence/absence data and stigma colour are missing), not corresponding to the generally adopted standards, and we therefore provide a detailed description of the original material. The protologue designation of the holotype, moreover, refers to the
whole gathering, which consists of seven herbarium duplicates, so according to Art. 40.2, Note 1, Ex. 3 of the Shenzhen code (Turland et al., 2018), we select the most representative herbarium specimen as the lectotype.


**Lectotype** (designated here): [Russian Federation, The Far East] “Magadan Region, Srednekanšk [Ust'-Srednekan]. 29 VII 1969. A. Khokhryakov, M. Mazurenko s. n.” [Originally in Russian] (MHA! [MHA0033873], Fig. 3; isolecto – MHA! [MHA0033870; MHA0033871; MHA0033872; MHA0033874; MHA0033875; MHA0033876]).


**Distribution:** Known from a single macrolocality along the Kolyma River, Magadan Region, Russia.

Plants slender, ca. 12–23 cm tall. Petiole long, narrow, narrowly winged, pale greenish, sometimes suffused purple, subglabrous. Leaves light green, ± glabrous, linear to linear-oblancculate, usually 6–13 × 0.6–1.0 cm, undivided, most often with remote, very short teeth, or wholly entire, only seldom sinuate-dentate, with more numerous, patent to recurved teeth, seldom leaves pinnatisect, with 2–3 pairs of patent, narrowly deltoid entire lateral segments; mid-vein usually pale green. Scapes light green to light brownish green, later often suffused purplish, sparsely to densely arachnoid below capitulum (indicating whitish or greyish), ± equalling leaves. Capitulum yellow, ca. 2.5 cm wide. Involucre olivaceous-green, ca. 4–6 mm wide and ± narrowly obconical at base. Outer phyllaries 10–13(15), appressed to loosely appressed, some ± erect, subimbricate, linear-lanceolate to narrowly lanceolate, usually 5–7 × 1.2–1.5(–2.0) mm, ± light olivaceous green to deep grey-green, with a ± gradual transition into a paler light greenish border ca. 0.1(–0.3) mm wide (sometimes border not visible or purplish), margin subglabrous, apex with a thin horn to ca. 1 mm long; inner phyllaries 10–12 mm long, conciliolate. Outer ligules flat to canaliculate, striped very light purplish outside. Stigmas discoloured. Pollen present, regular in size. Achene set with a significant, relatively high proportion of sterile achenes, usually slender, to 0.5 mm thick, whitish grey or otherwise paler than fully developed achenes. Achenes red-brown or greyish light brown (with a light pinkish hue) when well developed, 4.3–4.7 × 0.8–1.0 mm, sparsely to densely spinulose in upper 1/5–1/4, gradually narrowing into a short, subcylindrical cone ca. 0.3–0.5 mm long; beak thin, ca. (4.5–)7 mm long, pappus yellowish white, ca. 5.5–6 mm long. – Sexual (Fig. 1, 2, 3).

**Diagnostic notes:** The basic features show the distinctiveness of *T. kolymense*: the very narrow, narrowly, inconspicuously bordered outer phyllaries with distinct horns, narrow, usually linear, mostly undivided leaves, obconical involucre base, and achenes with a short cone are diagnostic. It may be compared with *T. lenense* Tzvelev with deep grey or deep grey-olivaceous achenes spinulose and tuberculate throughout, outer ligules striped grey-purple outside, deeply lobed leaves, involucre broader and rounded at base. *Taraxacum lateritium* Dahlst. can be distiguished by its ovate-lanceolate, broader outer phyllaries, much longer cone and ± glabrous scapes. *Taraxacum badzhalense* Worosch. et Schlott. differs from *T. kolymense* in a totally different leaf shape, longer inner phyllaries and longer beak. And last, *T. macilentum* is distinct from *T. kolymense* in having lanceolate, broader outer phyllaries, light greyish stramineous brown achenes with a longer cone, and a longer beak.

**Discussion**

It is not only *Taraxacum* sect. *Borealia* indicates the importance of the Beringian area and adjacent regions for the evolutionary diversification in *Taraxacum*. Another group, also having a circumpolar distribution with an Arctic-Alpidic pattern, is *T.* sect. *Arctica*. It is comprised of slender, small, usually ± glabrous plants with very narrow petioles, involucr with a low number of outer phyllaries of a broad shape, usually without paler border or with an indistinct, extremely narrow border, and achenes of various colours, very often only sparsely spinulose or tuberculate, a short ± conical cone, and a short beak.

Sexuality in *T.* sect. *Arctica* is known to a greater extent than that in *T.* sect. *Borealia*. The Beringian region is dominated by a widespread sexual species centred in the southern half of Kamchatka and radiating to the Aleutians and the adjacent Alaska in the east, and to Magadan Region in the west. It is *T. kamtschaticum* Dahlst., with very similar sexual populations described as *T. subalternilobum* Khokhr. and *T. nigrocephalum* Khokhr. from the Magadan Region (see also Kirschner et al., 2015). Another sexual taxon, a marginal member of *T.* sect. *Arctica,
*Taraxacum leucocarpum* Jurtzev et Tzvelev (*2n = 16*, Tzvelev, Yurtzev, 1984), described from Chukotka, and yet another probable sexual, a rather marginal member of *T.* sect. *Arctica* is *T. lineare* Worosch. et Schaga from the Khabarovsk Region (the type has ± regular pollen, frequently sterile achenes and a very narrow obconical involucre). Last, *T. soczavae* Tzvelev, a species with purplish pink flowers, is also regarded as sexual, on the basis of indirect indicators.

The reproductive behaviour of *T.* sect. *Arctica* on the American side is rather imperfectly known. However, there is a remarkable relictual sexual species of nunataks in the northernmost Canada (Ellesmere Island) and the northernmost Greenland, *T. holmenianum* Sahlin, and a sexual species probably belonging to *T.* sect. *Arctica*, *T. scopulorum* (A. Gray) Rydberg, described from the Rocky Mountains.
If we compare the data for T. sections Arctica and Borealia (including T. kolympense), it is obvious that the broad Beringian area and adjacent regions of the Far East and the easternmost Siberia, and the insular regions from northern Japan to Sakhalin, harbour a widely distributed but geographically and taxonomically structured dandelion sexuality. For T. sect. Borealia, northern T. sect. Mongolica, and particularly for T. sect. Arctica the above territory represents a “melting pot” for speciation and sectional diversification or reticulation.

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