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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-

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ловое размножение известно. Детальный анализ гербарного материала по *Taraxacum kolymense* Khokhryakov с использованием данных о размерах пыльцы и морфологии семянок выявили наличие полового размножения у этого уникального представителя секции *Borealia*. В статье обозначен лектотип *T. kolymense* и приведено новое сводное описание вида.

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

The impact of mating systems on the organization of genetic diversity in *Taraxacum*

Mating system	Frequency of heterozygotes	Genotype diversity
allogamous sexual	Hardy-Weinberg equilibrium	very high
autogamous sexual	very low	low to moderate
agamospermous	very high, fixed	very low

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, ± bordered, 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 sexual reproduction, assigned to *T.* sect. *Ceratophora* by Tzvelev, Yurtzev, 1984, in fact belong to *T.* sect. *Arctica*).

On the other hand, plants close to *T.* sect. *Borealia* or intermediate between *T.* sect. *Borealia* and *T.* sect. *Mongolica* and distributed in the Kuriles and on Hokkaido, Japan, often exhibit features indicating sexuality (Kitamura, 1957; Morita, 1980).

As regards the North American members of *T.* sect. *Borealia*, there are admirably meticulous studies by Haglund (1946, 1948, 1949), with the taxonomy based on a very representative material; G. E. Haglund did not intend to study the reproductive behaviour of his plants but cultivated dozens of samples, and sexuality would be clearly indicated by an extensive variation among siblings in cultivation. Plants reported under the name *T. ceratophorum* from the Rocky Mountains, USA, obviously are sexual (Brock, 2004); probable sexuals were described from the same region under the name *T. fasciculatum* A. Nelson.

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 proof – 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.

Taraxacum kolymense Khokhryakov, 1973, Byull. Glavn. Bot. Sada 88: 47.

Lectotype (designated here): [Russian Federation, The Far East] "Magadan Region, Srednekansk [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]).

Protologue citation: "Typus: regio Magadanica, distr. Seimczan, in glareosis ad ripam fl. Kolyma, 5 km infra Ustj-Srednekan. 29 VII 1969. M. T. Mazurenko et A. P. Khokhrjakov. In herbarium Horti Botanici Principalis conservatur".

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-oblanceolate, 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 (indumentum 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 thick horn to ca. 1 mm long; inner phyllaries 10–12 mm long, corniculate. 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 distionguished by its ovate-lanceolate, broader outer phyllaries, much longer cone and ± glabrous scapes. *Taraxacum badzhalense* Worosch. et Schlotg. 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, involucre 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*,

T. leucocarpum Jurtzev et Tzvelev (2*n* = 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.

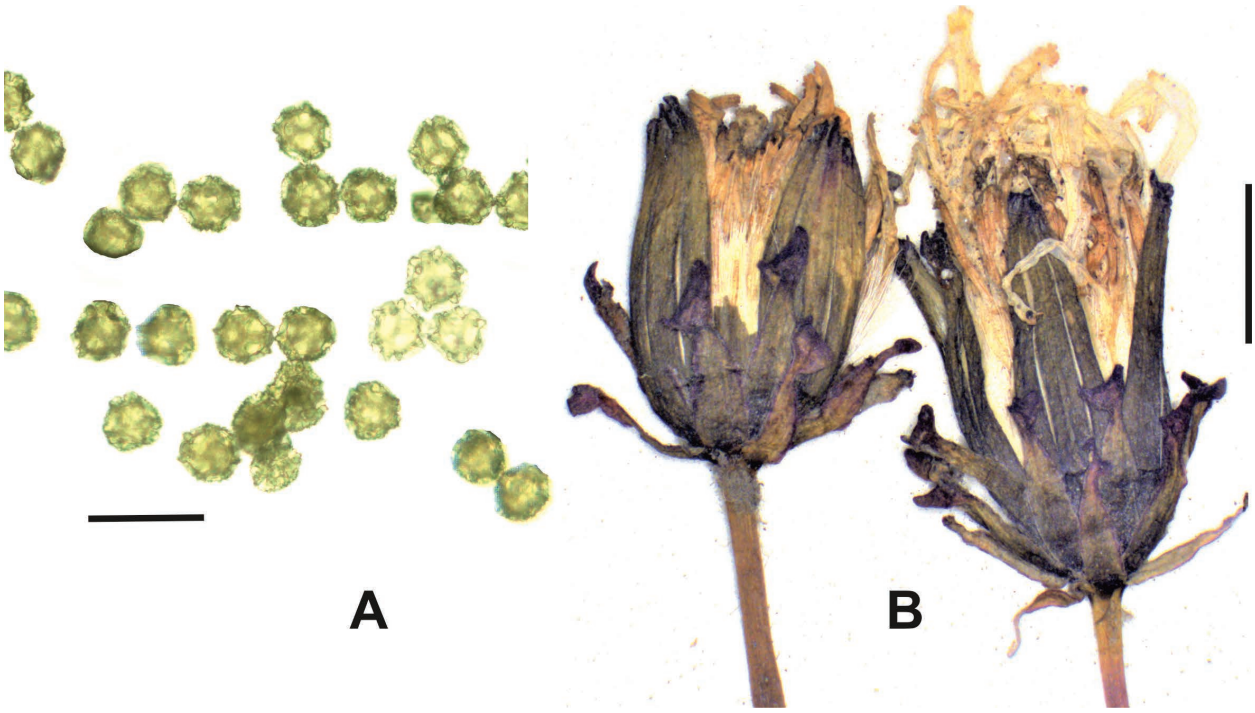

Fig. 1. *Taraxacum kolymense*; A – pollen from the lectotype specimen. Note the ± uniform size of pollen grains, a relatively safe indicator of sexuality. Composed of three separate images and cleared in CorelDraw. Scale bar = 40 µm. B – a detail of flower head (MHA0033873). Scale bar = 5 mm.

Fig. 2. *Taraxacum kolymense*. Examples of general habit: A – MHA0033875; B – MHA0033873; C – MHA0033871. Scale bars = 2 cm.

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.

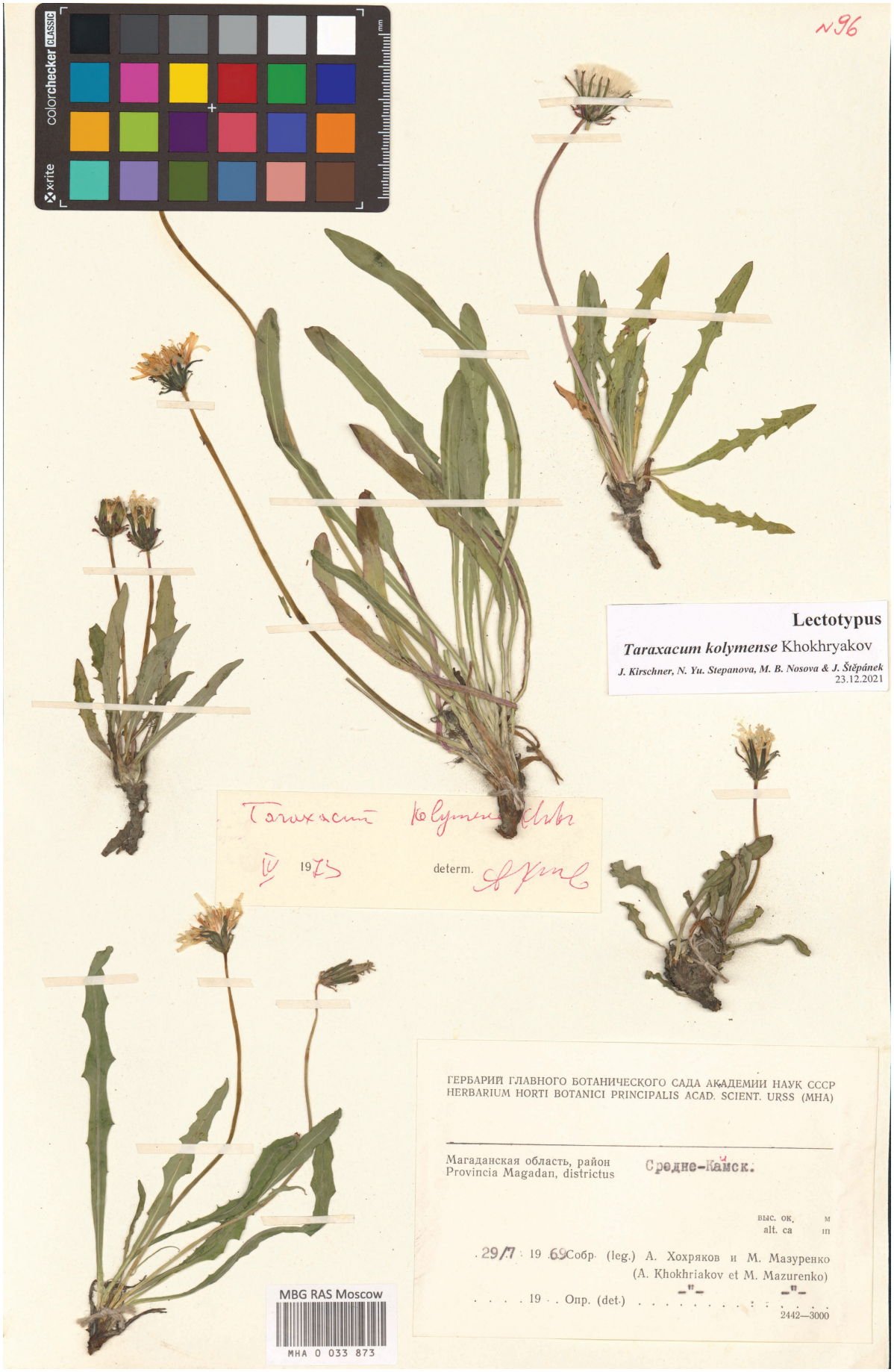

Fig. 3. *Taraxacum kolymense* Khokhryakov. The lectotype (MHA0033873).

If we compare the data for *T.* sections *Arctica* and *Borealia* (including *T. kolymense*), 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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