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Dactylorhiza traunsteineri (Orchidaceae) in Murmansk Region (Russia)

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The current distribution of *Dactylorhiza traunsteineri* (Saut. ex Soó) Soó (= *Dactylorhiza lapponica* (Laest. ex Hartm.) Soó = *D. majalis* (Rchb.) P.F. Hunt & Summerh. subsp. *lapponica* (Laest. ex Hartm.) H. Sund.) in Murmansk Region, Russia, is limited to two occurrences. Almost all the historical herbarium specimens from the area proved to be *D. maculata* (L.) Soó. The taxonomy of the complex is discussed.

A newly discovered population of *D. traunsteineri* is described in detail. The fitness of northern populations of *D. traunsteineri* is reduced according to a variety of measures. The species is probably at the risk of extirpation in the north because of narrow phytosociological and ecological amplitudes and low seed production. The status of this species in the regional Red Data Book should be 'Critically Endangered'.

Introduction

Dactylorhiza Necker ex Nevski is a complex genus, in which natural selection and hybridization are still very active (Averyanov 1990a, Pedersen 1998, 2002, Stahlberg 2007, Bateman & al. 2003, Pillon & al. 2007, Hedrén & al. 2011, Bateman 2011). This leads to extremely high variability of all morphological parameters within a single species and even between individuals within a population. Furthermore flower traits and dimensions show discrepancy within a single inflorescence (Bateman & Rudall 2006). This complex situation creates difficulties in delimiting the scope of each taxon and in deciding the taxonomic rank.

Various authors have distinguished 12 to 75 species of *Dactylorhiza* in Europe (Pedersen 1998). Splitting at the species level, based mostly on multivariate morphometric analysis, has been common in taxonomic research on European orchids during the last 35 years (Pedersen 2010). For instance, according to the revision of the herbarium specimens of KPABG by L. V. Averyanov (Komarov Botanical Institute, St.-Petersburg) in 1980, six *Dactylorhiza*-species were recognized for Murmansk Region: *D. incarnata* (L.) Soó, *D. maculata* (L.) Soó, *D. meyeri* (Rchb.f.) Aver., *D. elodes* (Griseb.) Aver., *D. psychrophila* (Schltr.) Aver. and *D. sudetica* (Poech ex Rchb.f.) Aver. However, distinguishing characters of the new *Dactylorhiza* species described by him were overlapping and his keys had weak thresholds between taxa (Averyanov 1988, 1989, 1990b, 1991, 1992). Finally the splitting of *Dactylorhiza* in Europe resulted in taxonomic inflation (Dubois 2008).

The recently applied molecular methods along with traditional morphological approaches have traced in detail the evolutionary processes in the genus, and they have improved our understanding (Hedrén 1996, Bateman 2001, Shipunov & al. 2004, Stahlberg & Hedrén 2008). Five groups of species have been recognized and the hierarchical status of many taxa (species/subspecies) has been analyzed (Pillon & al. 2007). It seems that for many European orchids, including species of *Dactylorhiza*, the last glaciations brought about strong selective pressures (Nordström & Hedrén 2008, Stahlberg & Hedrén 2008, Blinova 2008, 2009a, Bateman 2011). Climatic changes may rapidly alter the shoot structure of orchid species (Blinova 2012).

Dactylorhiza lapponica (Laest ex Hartm.) Soó and *D. traunsteineri* (Saut. ex Rchb.) Soó have been accepted in most of the recent North European floras (Hämet-Ahti & al. 1998, Krok & Almquist 2001, Mossberg & Stenberg 2003, Lid & Lid 2005). Furthermore in most of the Nordic herbaria the specimens have been filed as *D. lapponica* and *D. traunsteineri*. However, extensive field work with subsequent statistical analyses in order to discriminate the two species (Reinhard 1985, 1990) has proved that many characteristics are intermediate not only between them, but in the whole complex of *D. majalis-lapponica-traunsteineri*. Moreover the individuals of *D. lapponica* from Swedish Lapland have mixed features of *D. traunsteineri* and *D. maculata*. The combined morphological and molecular data failed to separate *D. lapponica* from *D. traunsteineri,* which indicates that they are taxonomically conspecific (Bateman 2001, Pillon & al. 2007). The advanced molecular analyses by Nordström & Hedrén (2008, 2009) and Hedrén & al. (2011) showed that *D. traunsteineri/lapponica* is closely related to *D. majalis* (Rchb.) P.F.Hunt & Summerh., and it should be treated as a subspecies of that taxon (*D. majalis* subsp. *lapponica* (Laest. ex Hartm.) H. Sund.). By using various molecular methods they showed that it encompasses three previously accepted species, *Dactylorhiza traunsteineri* (including *D. curvifolia* (F.Nyl.) Czerep.), *D. lapponica* and *D. russowii* (Klinge) Holub.

With regard to *D. traunsteineri/lapponica,* new molecular data support the existence in Europe of three geographic areas in each of which the taxon has arisen independently (Nordström & Hedrén 2008, Paun & al. 2010, Hedrén & al. 2011), and according to Bateman & Denholm (2012) it should be recognized at specific level: *D. traunsteineri* in the Alps, *D. lapponica* in Scandinavia and *D. traunsteinerioides* (Pugsley) R.M. Bateman & Denholm in the British Isles. *D. traunsteinerioides* is accepted in the 3rd edition of "New Flora of the British Isles" (Stace 2010).

However, the results have not yet stabilized the taxonomy of this complex group (Bateman 2011), and the question remains to be settled. Morphological differences between the taxa are fairly weak, and large parts of the distribution area of the group have not been adequately studied. In our opinion it is not yet practical to split the complex, at least for conservation purposes, and in this paper the name *D. traunsteineri* in a collective sense is applied to the taxon occurring in the northern parts of Fennoscandia.

In Murmansk Region *Dactylorhiza lapponica* was regarded as an Arctic race of *D. traunsteineri*, and in Flora of Murmansk Region (Orlova 1954) only *D. traunsteineri* was accepted. Botanists of the Polar-Alpine Botanical Garden-Institute (PABGI), Apatity — M. L. Ramenskaya, N. I. Orlova, I. P. Breslina and A. A. Pokhilko — have collected and/or identified 27 herbarium specimens as *D. traunsteineri* (KPABG). Most of them were confirmed in the inventory of Ramenskaya in the 1970s (Ramenskaya 1983), but in 1980 L. V. Averyanov redetermined all the specimens and excluded this species from Murmansk Region. However, his revision was not generally accepted: for instance *D. traunsteineri* was still included in floristic lists of various parts of Murmansk Region (e.g., Belkina & al. 1991, Kostina 1995, Kostina & Berlina 2001).

Methods

Herbarium studies

Northern *Dactylorhiza* specimens from the following herbaria were examined: H, KPABG, LE, MW, the herbaria of the Lapland Nature Reserve (LAPL) and the Kandalaksha Nature Reserve (KAND). Further, information about *Dac-*

tylorhiza specimens from Murmansk Region was received from OULU, S and TROM.

Field studies of the new population

Ecological measurements. Vegetation cover was estimated using the Braun-Blanquet cover-abundance scale (Barkman & al. 1964). pH of the surface water was measured directly in the field using a PH-009 (Kelilong Instruments) pen with a 0.0 – 14.0 scale divided into units of 0.1. Soil salinity was measured using a TDS 5 (HM Digital) pen with a 0–9990mg/l scale divided into units of 1 mg/l. Illuminance of the habitat was measured using a ”Leningrad 8” photoelectrical exponometer, which has a three-step scale: 1 = 6–95 Lx, 2 = 95–18000 Lx, 3 = 12500–112000 Lx.

Counting of shoots. Flowering and non-flowering shoots were counted and their life stages estimated. Such an ontogenetic approach is widely applied in population studies in Russia (Gatsuk & al. 1980, Rabotnov 1983, 1987), including orchids (Vakhrameeva & Denissova 1983, Vakhrameeva & Tatarenko 1998). As in the case of other root-tuber orchids in Murmansk Region (Blinova 1998) all recorded shoots of *D. traunsteineri* were examined and assigned to one of the following classes or ontogenetic stages: juvenile (j), immature (im), vegetative (v), generative (g).

Measurements of seeds. In five randomly chosen capsules the seeds were counted and their sizes measured using a JJ-Optics digital Lab 2 microscope with magnification scale ×10–100, a calibration tool and a linear-measurement function. The seeds were released onto microplates comprising 1.5 × 1.5 cm wells with a thin layer of water over a 1 × 1 mm grid. The number of seeds within a grid cell was counted at three to five different places and the average obtained was multiplied by the total number of grid cells containing seeds.

Estimation of population fitness. It has been defined as the number of flowers per plant, the percentage of successfully pollinated flowers, the number of seeds per capsule, the number of seeds per plant, the number of flowering individuals and the seed production per population.

Results and discussion

Distinguishing *Dactylorhiza traunsteineri*

Due to great variability in the morphological characters generally used to distinguish *Dactylorhiza* species (e.g. leaf size and pigmentation, colour and shape of the labellum and their alteration in herbarium specimens), there have been difficulties in distinguishing *D. traunsteineri* from other species. However, there are fewer difficulties in distinguishing *Dactylorhiza* species in the field than in the herbarium. In *D. traunsteineri* the stem is relatively thick and hollow. Generative individuals possess only 2, rarely 3 narrow green leaves with weak pigmentation (Fig. 1). Small

Fig. 1. Part of the inflorescence (A) and a green leaf (B) of *Dactylorhiza traunsteineri*. Note the weakly pigmented leaf, lax inflorescence with conspicuous violet floral bracts, and relatively large flowers with wide conical spurs. Photo from the newly described population near the town of Apatity (Murmansk Region, Russia).

rounded dots may occur on the whole leaf surface above, and they do not merge with each other. Floral bracts are conspicuous, leaf-like and violet. The inflorescence is lax, and the structure of every flower is clearly visible. The spur is straight, conical and wide at the entrance (2–3 mm); the labellum has a small medial tip.

Dactylorhiza traunsteineri differs from *D. incarnata* by its pigmented leaves, larger flowers and lax inflorescence. The impressive, wide, conical spur contrasts strikingly with the narrow (1 mm), cylindrical spur of *D. maculata*.

Within its distributional range *Dactylorhiza traunsteineri* has variable traits (Bateman & Denholm 1983, Reinhard 1985, Andersson 1994, 1995, Filippov 1997, Kulikov & Filippov 1999, Bertolini & al. 2000, Kirillova 2010). Rarely the leaves have no markings. A great discrepancy can be observed between the size of individuals and the size of flowers. Also leaf shape — curved vs. fairly straight, narrow and long — may vary between different populations. In spite of the fact that there is great variation in flower parameters and leaf areas in herbarium specimens, the descriptive statistics of the shoot units (metameres) show that two characteristics — numbers of flowers and of green leaves — are more or less constant in different areas, whereas the numbers of stem bracts, height of shoot and total leaf area show plastic responses (Blinova, unpubl.).

Results of herbarium studies

Most of the old records of *Dactylorhiza traunsteineri* from Murmansk Region have proved to be erroneous. In the Russian herbaria LE, MW and KAND and the Fennoscandian herbaria OULU, S and TROM there are no specimens of *D. traunsteineri* from Murmansk Region. 40 specimens collected from Murmansk Region (27 in KPABG and 13 in H), previously labeled as *D. traunsteineri*, were all *D. maculata* except for two, one of which was *Coeloglossum viride* (L.) Hartm. (= *Dactylorhiza viridis* (L.) R. M. Bateman, Pridgeon & M. W. Chase)[1]. A similar tendency was observed for the specimens from northern Finland, preserved in H. Of 15 labeled as *D. lapponica*, six were correct (i.e. *D. traunsteineri* according to us) and nine were *D. maculata.* On the other hand only few samples identified as *D. traunsteineri* represented *D. maculata* or *D. incarnata*.

Only one specimen of *D. traunsteineri* was discovered in KPABG: *Orchis traunsteineri* Saut., [*Lapponia Imandrae* (*Lim*)], Imandra area, between Lake Chunozero and Lake Osinovoje, on the edge of a mire with *Betula nana, Vaccinium uliginosum, Potentilla erecta* and *Sphagnum* mosses. Common. 13.07.1934. Col. / det. O. Semenov-Tjan'-Shanskij. The specimen was confirmed as *Dactylorchis traunsteineri* by M. L. Ramenskaya in 1973, and renamed *Dactylorhiza maculata* by L. V. Averyanov in 1984.

During field work in 2012 the site "between Osinovoje and Lake Chuna" was visited, but no *D. traunsteineri* was found. Furthermore the area is covered by oligotrophic mires dominated by *Scheuchzeria palustris* and *Sphagnum papillosum,* and it may mean that the original site indication was not entirely accurate. The locality may nevertheless lie somewhere within the Pirenga river system, but 15 km south-west from the given site, where some calcium-rich rocks are known from a small area.

In addition, in the herbarium of Lapland Nature Reserve there is a specimen from the Monchetundra: "*Dactylorhiza traunsteineri* (Saut.)

[1]In spite of the fact that the shoot characteristics in *Coeloglossum* and *Dactylorhiza* are very similar, which indicates their close relationship, we still recognize *Coeloglossum* as a separate genus because of its unique flower characteristics, which are absent in *Dactylorhiza* species: vestigial saclike spur, presence of nectar in the spur, and the specific shape of the labellum. In Orchidaceae flower shape and the pollination syndrome are the main speciation elements. Additionally *Coeloglossum* is distinct from *Dactylorhiza* in flower phenology: successful pollination is soon followed by the spur turning black and withering; drying of the labellum and the inner perianth segments is postponed, and the outer perianth segments remain green for an extended period, almost until seed dispersal. The circumpolar distribution of *Coeloglossum* together with slight morphological variation in Europe contrasts strongly with the Eurasian range of the highly variable *Dactylorhiza*. In our opinion *Coeloglossum* is one of the oldest and distinct genera in the subtribe Orchidinae. Other arguments are given by Tyteca & Klein (2008).

Soó, Monchetundra, the middle stream of the river Korneskorr, Col. N. Syroid, 25.07.1976." It was determined by R. N. Shlyakov, 03.1997, with the remarks: "Probably ssp. *curvifolia* (Nyl.) Soó = *D. curvifolia* Nyl" and "Insufficient material!" So it appears that he had doubts about the determination. In our opinion the specimen is poorly preserved and cannot be determined as either *D. maculata* or *D. traunsteineri*. This site should be checked for confirmation of the identity of the population. Other occurrences in Chunatundra (Berlina 1997, Kostina & Berlina 2001, 2012) are based on field observations only (Berlina, personal communication), and should be checked, too.

In 1913 a site with a population of *Schoenus ferrugineus* was found between Kandalaksha and Kolvitsa (Lindberg 1914). This species is remarkably diagnostic for communities of *Caricion davallinae* Klika 1934 (see ecology below), which is also a very appropriate habitat for *D. traunsteineri*. This locality might represent a further biotope with *D. traunsteineri* in Murmansk Region. *S. ferrugineus* is known from Velikij Island in the White Sea south of Kandalaksha, but *D. traunsteineri* was not recorded there even though the place is regularly monitored since it belongs to the Kandalaksha Nature Reserve.

Range

Dactylorhiza traunsteineri is a more or less European species distributed in Scandinavia, the British Isles (as *D. traunsteinerioides*), the Alps, the Baltic countries, north-western Russia, the Karelian Republic, Central Russia and the Ural Mountains (Hultén 1971, Smoljianinova 1976, Ramenskaya 1983, Reinhard 1985, Hultén & Fries 1986, Averyanov 2000, Stace 2010, Efimov 2011). However, the range of *D. traunsteineri* requires further study, especially in the border areas, and even within the Alps from where it was described. The range seems to be fragmented into several parts, of which Fennoscandia, including the Baltic area, is the largest and most populated. Small separate enclaves are reported for the northern and southern Urals (Mamaev & al. 2004). Very little is known about the distribution pattern and the borders of the species in central Russia (Averyanov 2000). The species has also been mentioned, as *D. russowii*, from western and central Siberia (Ivanova 1987).

As to the northern limit of this species in Europe, misidentifications have led to many mistakes in published maps (e.g., Hultén 1971, Hultén & Fries 1986) where at least 9 dots are marked for the species in Murmansk Region. The actual distribution of this species in Murmansk Region is limited to two sites, both in *Lapponia Imandrae* (Fig. 2). The first is based on Semenov-Tjan'-Shanskij's specimen (see above). The second is based on a new population found in 2011 at a site 3 km east of the town of Apatity (~67°32' N, 33°28' E) at an altitude of 174 m (06.07.2011 Blinova; KPABG). South of Murmansk Region and the Arctic Circle, *D. traunsteineri* is rare in the Karelian Republic but found in all provinces (Markovskaya 2004, Dyachkova & al. 2004, Kravchenko & Kuznetsov 2009).

Ecology and phytocoenology

European populations of *Dactylorhiza traunsteineri* occur in base-rich habitats (Andersson, 1994, Øien & Moen 2002, Aeschimann & al. 2004, Hanhela 2008, Šefferová Stanová & al. 2008, Nordström & Hedrén 2008, Landolt & al. 2010, Stace 2010, Efimov 2011, Bateman 2011). However, some authors (Vakhrameeva & Tatarenko 2001, Vakhrameeva & al. 2008) believe that the species grows on acidic soils.

The narrow ecological amplitude of *D. traunsteineri* also helps to recognize it in the field and to review the herbarium collections. Especially in northern Europe, calcareous fens occupy very restricted areas, often limited to sites supplied with water from a calcium-rich spring. Such "islands" with a specific and rich plant composition may occur unexpectedly within extensive acidic biotopes, which predominate everywhere within the Baltic Shield. However, if no calcareous rocks are known for the region, field measurements indicate acidic soil, and no characteristic species have been found at the site, it is very unlikely that a population of *Dactylorhiza* in such a place will be *D. traunsteineri.*

The area of the plant community containing the newly discovered population of *D. traunsteineri* near Apatity is 470 m^2. Ecological factors (ac-

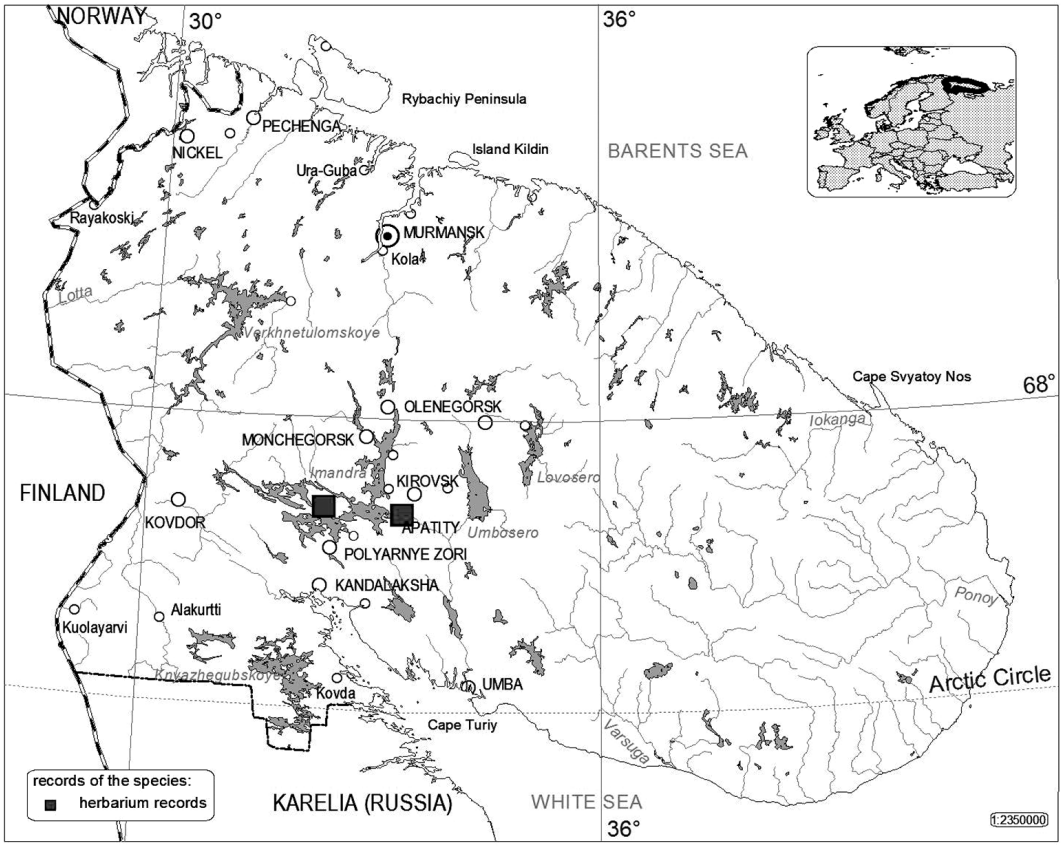

Fig. 2. The localities of *Dactylorhiza traunsteineri* in Murmansk Region, Russia.

cording to Landolt & al. 2010) are the following: light 4–5 (illuminance 75000 Lx), water availability 5 (very wet), soil reaction 3 (pH=6.8), soil aeration 1–2 (from low to middle) and soil salinity 30.8 mg/l.

The site represents a rich fen. The vegetation cover corresponds to the alliance *Caricion davallianae* Klika 1934 with such diagnostic species as *Carex flava, C. hostiana, Dactylorhiza traunsteineri, Eleocharis quinqueflora, Eriophorum latifolium, Pinguicula vulgaris, Fissidens osmundoides, Campylium stellatum, Limprichtia cossonii* (Table 1).

Seasonal development

In Murmansk Region the seasonal development of *Dactylorhiza traunsteineri* lasts for about three months, from June until early September. Flowering begins in the first week of July and lasts about ten days. There is only one flowering peak in the population, and all individuals enter this phase synchronously. Flowers start withering in the middle of July. The capsules are developing from the end of July to the end of August. The ripe capsules turn brownish and dry out. Seeds change colour from white to brownish when they are ripe. Seed dispersal takes place at the end of August or in early September. The shoots die back in early September.

The short flowering period and low number of flowers in the inflorescence make it difficult to detect the species in the field. In Murmansk Region the best time to search for populations seems to be between July 5 and July 15. The length of the flowering period was reported to be 2–4 weeks in Central Norway, where there are large populations of 400–500 flowering individuals (Sletvold & al. 2010a).

Table 1. The description of vegetation cover in the plant community with *Dactylorhiza traunsteineri*. Nomenclature according to Czerepanov (1995) and Ignatov & Afonina (1992). Explanation of symbols: "r" = 1–3 individuals; "+" = less than 1%, "1" = 1–5 %, "2a" = 5–15%, "2b" = 15–25%, "3" = 25–50%, "4" = 50–75%, "5" = 75–100%.

Total cover (%)	100
Field layer (%)	95
Moss layer (%)	100
Total number of species	64
Vascular plants	55
Mosses	9
Tree layer:	
Betula subarctica	+
Pinus friesiana	+
Shrub layer:	
Betula nana	1
Juniperus sibirica	r
Salix myrsinites	1
Field layer:	
Andromeda polifolia	+
Angelica sylvestris	+
Antennaria dioica	+
Baeothryon alpinum	1
Bartsia alpina	+
Carex adelostoma	1
Carex dioica	1
Carex flava	1
Carex hostiana	1
Carex lasiocarpa	2a
Carex rariflora	+
Carex vaginata	1
Cirsium heterophyllum	1
Chamaenerion angustifolium	+
Dactylorhiza maculata	+
Dactylorhiza traunsteineri	1
Deschampsia cespitosa	1
Eleocharis quinqueflora	2a
Equisetum hyemale	1
Equisetum palustre	1
Epilobium palustre	r
Eriophorum latifolium	+
Eriophorum polystachion	2a
Eriophorum vaginatum	1
Festuca ovina	1
Galium uliginosum	+
Geranium sylvaticum	+
Geum rivale	+
Gymnadenia conopsea	+
Hieracium sp.	+
Listera ovata	1
Melica nutans	+
Menyanthes trifoliata	+
Molinia caerulea	2a
Moneses uniflora	+
Parnassia palustris	+
Pinguicula alpina	+
Pinguicula vulgaris	+
Potentilla erecta	1
Ranunculus acris	1
Sanguisorba polygama	1
Saussurea alpina	+
Saxifraga aizoides	+
Selaginella selaginoides	+
Solidago lapponica	1
Thalictrum alpinum	1
Trientalis europaea	+
Triglochin palustre	+
Vaccinium uliginosum	r
Viola montana	+
Moss layer:	
Aulacomnium palustre	+
Campylium stellatum	1
Dicranum spadiceum	+
Fissidens osmundoides	r
Philonotis fontana	r
Limprichtia cossonii	2b
Limprichtia revolvens	2a
Scorpidium scorpioides	2a
Rhizomnium pseudopunctatum	1
Sphagnum capillifolium	2b
Sphagnum warnstorfii	2b
Rhytidiadelphus triquetrus	+
Tomenthypnum nitens	1

Life cycle

In Murmansk Region seeds of *Dactylorhiza traunsteineri* are released from the fruits at the end of the growing period. On average the seed length is 0.89±0.14 mm and the seed width is 0.27±0.09 mm. The volume of the embryo is ca. 0.003 mm^3. However, only some of the seeds develop (Fig. 3). Very little is known about the germination of *D. traunsteineri.* The time between germination and appearance of the first above-ground shoot is unknown, but it is assumed to be at least two years.

In Murmansk Region the following ontogenetic stages have been distinguished in the field:

Juvenile (j). Individuals having small shoots with 1 leaf up to 2–3 cm long and 3–6 mm wide, with 1–3 leaf ribs.

Immature (*im*). Individuals intermediate between juveniles and adults, having shoots with 1 or 2 leaves, 3–5 cm long and 6–8 mm wide, with 6–8 leaf ribs.

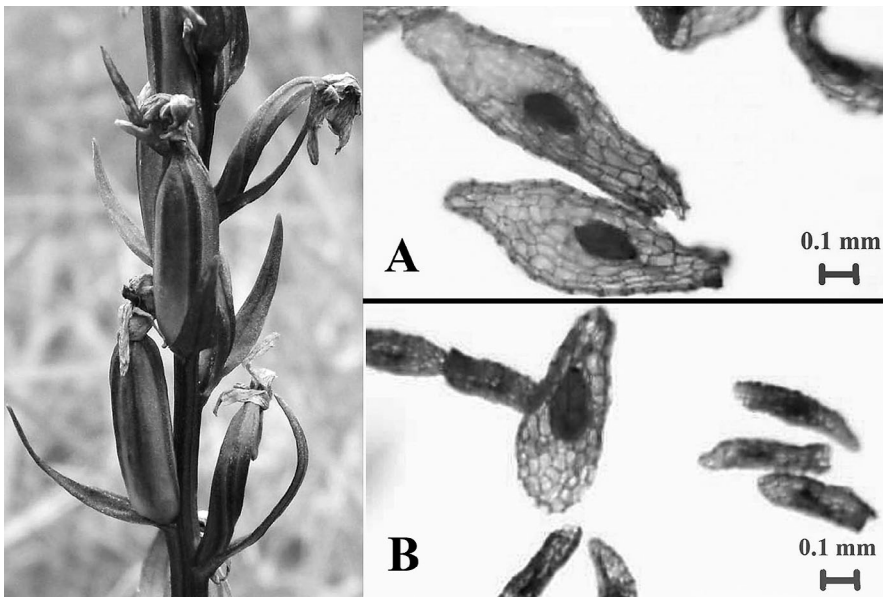

Fig. 3. Fruits (left) and seeds (right) from two different seed capsules (A, B) of *Dactylorhiza traunsteineri* from the population near Apatity (Murmansk Region, Russia). During fruiting leaf-like violet floral bracts are conspicuous. Some capsules may have many undeveloped seeds (B).

Vegetative (v). Individuals including a mixed group with temporary non-flowering shoots and post-immature individuals having shoots with 1 or 2 leaves, 4–7 cm long and 8–11 mm wide, with 6–8 leaf ribs.

Generative (g). Flowering individuals having shoots with 2 or 3 leaves, 4–6 cm long and 8–12 mm wide, with 8–16 leaf ribs, and 4–12 flowers in the inflorescence.

Senile (s). These individuals were never found in our populations because many root-tuber orchids die after the generative stage without passing through the senile stage (Vakhrameeva & Denissova 1990), and therefore they were not relevant to this study.

We estimate that the life cycle of *D. traunsteineri* in Murmansk Region lasts about ten years. Further detailed studies are required.

Population performance

The area of occupancy of the population of *Dactylorhiza traunsteineri* in Murmansk Region is ca. 100 m^2, and it is restricted to one part of the biotope, ca. 470 m^2 in size. The individuals were at some distance from each other. There were one or two young, vegetative plants near each flowering individual and there were no clumps of flowering or vegetative individuals.

In 2011 the size of the population was only 48 individuals, 23 of which were at the generative stage (Fig. 4). In 2012 the population size was still smaller: 32 individuals, 18 of them at the generative stage. In comparison with populations in Central Norway, where 400–500 flowering individuals have been counted (Øien & Moen 2002; Øien & al. 2008; Sletvold & al. 2010b), the effective size of the population in the Murmansk Region is about 1/20 of their size.

According to the data collected in 2011–2012 the fitness of the *D. traunsteineri* population in Murmansk Region has decreased in many ways. The population has a small area of occupancy in the biotope, small number of individuals, and small effective size. The individuals have a low number of flowers (8.2 flowers per shoot).

The species seems to be insect-pollinated in Murmansk Region. Among the visitors and potential pollinators, flies from the family Ulidiidae and *Stenodema holsata* (Fabricius 1787) from the family Miridae (Heteroptera) have been noted in the flowers of *D. traunsteineri*. The polli-

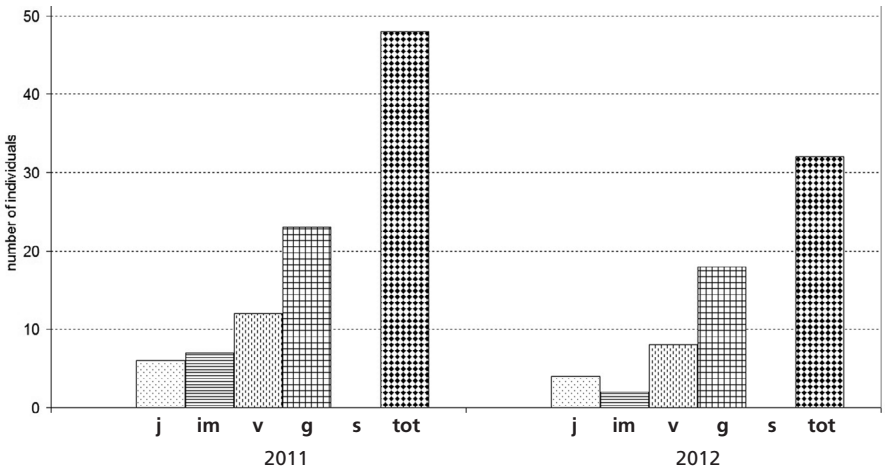

Fig. 4. Ontogenetic stages in the *Dactylorhiza traunsteineri* population in Murmansk Region.

j = juveniles
im = immatures
v = vegetatives
g = generatives
s = seniles
tot = total

nation success is rather low. The number of capsules per shoot is 1.9 on average, so the fruiting rate is about 23 %.

Several *Bombus* species have been observed pollinating flowers of *D. traunsteineri* in Central Norway (Sletvold & al. 2010a). This group represents the classical pollinator vector for orchids in general (Van der Pjil & Dodson 1966). However, the average fruit set in Central Norway was similar to Murmansk Region and amounted to 20–30 % (Sletvold & al. 2010a). Moreover 16 % of fruits were damaged by herbivory. Various groups of insects were observed in the consortiums of *D. traunsteineri* in the southern Urals (reported as *D. russowii*) with Diptera as the main pollinators and a high (ca. 67 %) fruiting rate (Krivosheev 2009).

In Murmansk Region the number of seeds per capsule of *D. traunsteineri* is on average 1200. In comparison with other *Dactylorhiza* species in the Region, such seed production per capsule is low. *D. maculata*, which is also insect-pollinated in Murmansk Region, has on average about 2300 seeds per capsule. *D. incarnata* has about 5000 seeds per capsule, and it is self-pollinated. The low value of seed set might indicate higher vulnerability of related species.

However, the importance of high seed production in orchids requires further study and is not well understood. How heavy a seed rain is sufficient to support the life cycle? In spite of relatively high seed production in *D. incarnata* compared with *D. maculata*, the former species became vulnerable in Murmansk Region on account of narrow ecological amplitude and a specific population behavior strategy. Populations of *D. incarnata* in the north comprise fragments which appear, flower once (rarely more often) and then disappear (Blinova 2009b). Each population remains within the same plant community but because of monocarpy the short-lived flowering clusters ”migrate” through the community. That is why the higher investment in seed production is more important for survival in the case of *D. incarnata* than in *D. maculata,* in which generative individuals are polycarpic and occupy the site in the long-term. Other bottlenecks in the life cycle are seed viability and germination rate. In Norway the germination probability for *D. traunsteineri* was about 11 % and seeds were short-lived, less than one year (Øien & al. 2008). The average number of juvenile plants in the population of this species in Murmansk Region equals five. It implies that mortality in the early stages of development is very high.

Population size, the number of flowering individuals and the seed production differ markedly between *Dactylorhiza* populations in Murmansk Region (Table 2). *D. traunsteineri* is the most vulnerable species. The small number of flowers in the inflorescence is not even compensated by the transition to self-pollination, as happened in *D. incarnata*, to meet the costs of short-lived flowering clusters. Finally the seed production per population in *D. traunsteineri* is about 28 times smaller than in *D. incarnata* and 6 times smaller than in *D. maculata.* Moreover the frequency of regional populations declines abruptly from *D. maculata* to *D. traunsteineri.*

Table 2. Some reproductive characteristics of *Dactylorhiza* species in Murmansk Region, Russia. The data are averaged over populations monitored in the long-term (Blinova 2009c).

Parameter / Species	Number of flowers	Fruiting rate, %	Number of seeds per capsule	Number of seeds per shoot	Number of flowering individuals in population	Population seed production
Dactylorhiza incarnata	13.2	68	5000	45000	26	1170000
Dactylorhiza maculata	15.4	41	2300	15000	18	270000
Dactylorhiza traunsteineri	8.2	23	1200	2000	21	42000

Note. Less attention has been given to *Dactylorhiza maculata,* which occurs frequently in Murmansk Region. The census of flowering individuals was carried out during relatively cold years (1992–1996). Rapid population growth has been observed since 1998 but it was not measured for this species.

Vulnerability and protection

Dactylorhiza traunsteineri is one of four orchid species in Murmansk Region included in the Red Data Book of the Russian Federation (Bardunov & Novikov 2008) and in the Red Data Book of Murmansk Region (Blinova 2003).

Both *Dactylorhiza lapponica* and *D. traunsteineri*, in different threat categories, are included in the Red Data Book of East Fennoscandia (Kotiranta & al. 1998) and in the books of threatened plants in Finland (Ryttäri & Kettunen 1997, Ryttäri & al. 2012). Reconsideration of the situation is required for Finnish Lapland, where 60% of the specimens previously named *D. lapponica* were in fact *D. maculata*.

It seems that the northern border of the range of *Dactylorhiza traunsteineri* in Fennoscandia approximately coincides with the Arctic Circle. In the north there are several isolated populations (fewer than indicated in all known European distribution maps), and only two of them are known from the northeastern part of Fennoscandia (Murmansk Region).

The IUCN Red List categories have been applied to the species, and 'Critically Endangered' is the appropriate status in Murmansk Region, rather than 'Vulnerable' (see Blinova & Uotila 2011). The details concerning population fitness presented here, in comparison with other *Dactylorhiza* species, support that proposal.

The establishment of small protected areas for every biotope where this species occurs could help to protect *D. traunsteineri* in subarctic latitudes.

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