

Contribution to the knowledge of the genus *Dactylorhiza* (*Orchidaceae*), and the first record of *Dactylorhiza traunsteineri* (Saut. ex Rchb.) Soó in Croatia

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Abstract

This paper provides critical notes on several taxa of the genus *Dactylorhiza* in Croatia. Flora Croatica Database (FCD) lists 12 taxa of *Dactylorhiza*, but the presence of some of them in Croatia is questionable. According to our long-term field research, after checking the relevant literature and herbaria, and discussing the problems of misidentifications in the field, which seems to be quite constant, we established that only seven species and one subspecies are present in Croatia. It appears that *D. maculata* s. str., *D. cordigera*, *D. incarnata* ssp. *ochroleuca* and *D. incarnata* ssp. *cruenta* are not present in Croatia, and we propose to remove them from the list of national flora. *Dactylorhiza saccifera* is present in Croatia, but its incidence is overestimated due to misidentification. Furthermore, it is proposed to change the nomenclature for *D. fuchsii* (Druce) Soó ssp. *transsilvanica* (Schur) S. E. Fröhner, the name currently used in the FCD, to *D. maculata* (L.) Soó ssp. *transsilvanica* (Schur) Soó, which is a more appropriate combination that is used in contemporary literature. The presence of *D. traunsteineri* in Croatia was based on old literature from 1938 that turned out to be erroneous. However, in our recent survey in 2024, we discovered an important population of this species in the Lika Region, providing the first record of this species for Croatia. From a taxonomic point of view, this species belongs to the very complex *D. traunsteineri* species group, and we briefly discuss the position of this somewhat geographically isolated Croatian population. We also discovered several plants of *D. × duftii*, a natural hybrid between *D. incarnata* and *D. traunsteineri*, which is a new taxon in the Croatian flora. Also, since the FCD does not list *Dactylorhiza* hybrids, we present and describe all known hybrids found in the literature, as well as the results of our field research.

Keywords: *Dactylorhiza traunsteineri*, *D. × aschersoniana*, *D. × kerneriorum*, *D. × duftii*, *D. × braunii*

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Sažetak

Ovaj rad donosi kritičke bilješke o nekoliko svojiti roda *Dactylorhiza* u Republici Hrvatskoj. U bazi podataka Flora Croatica Database (FCD) navedeno je 12 svojiti iz roda *Dactylorhiza*, no prisutnost nekih od njih u Republici Hrvatskoj je upitna. Prema rezultatima vlastitih terenskih istraživanja, nakon provjere relevantne literature i pregleda herbarijskih zbirki, te rasprave o problematici pogrešnog određivanja svojiti na terenu, koje je poprilično često, proizlazi da je u Republici Hrvatskoj prisutno samo sedam vrsta i jedna podvrsta roda *Dactylorhiza*. Svojite *D. maculata* s. str., *D. cordigera*, *D. incarnata* ssp. *ochroleuca* i *D. incarnata* ssp. *cruenta* nisu prisutne u Hrvatskoj te predlažemo njihovo uklanjanje s popisa hrvatske flore. Vrsta *D. saccifera* prisutna je u Republici Hrvatskoj, ali su njezina učestalost i broj nalaza preuveličani zbog krivog određivanja na terenu. Također, predlaže se promjena nomenklature za *D. fuchsii* (Druce) Soó ssp. *transsilvanica* (Schur) S. E. Fröhner, kombinaciju koja se trenutno koristi u FCD-u promjeniti u *D. maculata* (L.) Soó ssp. *transsilvanica* (Schur) Soó, što je prikladnije rješenje koje se koristi u suvremenoj literaturi. Prisutnost vrste *D. traunsteineri* u Republici Hrvatskoj temeljila se na starim literaturnim podacima iz 1938. godine, koji su se pokazali pogrešnima. Međutim, u našem nedavnom istraživanju 2024. godine pronašli smo značajnu populaciju ove vrste na području Like, što predstavlja prvi nalaz ove vrste za Republiku Hrvatsku. S taksonomskog gledišta, ona pripada vrlo složenoj skupini vrsta iz grupe *D. traunsteineri*, pa ukratko raspravljamo o položaju ove, donekle geografski izolirane, hrvatske populacije. Također smo otkrili nekoliko primjeraka *D. × duftii*, hibrida između *D. incarnata* i *D. traunsteineri*, koji predstavlja novi takson u flori Hrvatske. Budući da na popisu FCD-a nema navedenih hibrida iz roda *Dactylorhiza*, navodimo sve hibride zabilježene u literaturi, kao i rezultate osobnog terenskog istraživanja.

Ključne riječi: *Dactylorhiza traunsteineri*, *D. × aschersoniana*, *D. × kerneriorum*, *D. × duftii*, *D. × braunii*

Introduction

The monophyletic genus *Dactylorhiza* Necker ex Nevski 1937 (*Orchidaceae*) is considered a very complex and problematic group of terrestrial orchids with a vast distribution throughout Eurasia and the mountains of North Africa (Buttler 1991, Baumann et al. 2006, Delforge 2006, 2016). Several species inhabit forest edges, dry to semi-dry grasslands, and Mediterranean terraces, but a large number of taxa are wetland specialists, inhabiting wet meadows, bogs and marshes. Therefore, the genus *Dactylorhiza* is one of the most vulnerable

orchid genera due to the loss of habitats that are highly affected by human land management such as drainage and afforestation (Baumann et al. 2006, Delforge 2006, 2016, Griehl & Presser 2021). The taxonomy of the genus is complicated by high morphological intraspecific variability and frequent hybridization among species, a significant factor in its evolution (Hedrén 2001, Shipunov et al. 2005, Pillon et al. 2006, Delforge 2016). The genus contains numerous hybridogenous taxa that sometimes originate from the same parents but

have developed at different times and in different places. Occasionally, these taxa further interbreed with each other, their parental species or with other sympatric taxa, which in turn makes identification in the field challenging (Delforge 2006). Quite often hybrid swarms, showing transitional characteristics between the parent species, sometimes involving multiple taxa, or even populations in which the parent species are completely absorbed, resist or even prevent proper identification (Pedersen 1998, Pillon et al. 2006, Delforge 2006, 2011). These problems are then reflected in the very variable approaches in taxonomy and nomenclature, which are in any case diverse and unstable (Baumann et al. 2006, Delforge 2006, 2011, 2016, Griehl & Presser 2021). In Europe, different authors distinguish between 12 and 85 taxa of *Dactylorhiza* (Davis et al. 1988, Buttler 1991, Pedersen 1998, Pillon et al. 2006, Baumann et al. 2006, Delforge 2016, Griehl & Presser 2021).

In Croatia, the genus *Dactylorhiza* is not especially species-rich, and therefore the overall situation is much less intricate. According to Kranjčev (2005), the genus is represented by seven species: *Dactylorhiza sambucina* (L.) Soó, *D. romana* (Sebastiani) Soó, *D. incarnata* (L.) Soó, *D. majalis* (Rchb.) P. F. Hunt & Summerh., *D. saccifera* (Brongn.) Soó, *D. fuchsii* (Druce) Soó, *D. maculata* (L.) Soó, and one variety, *D. maculata* var. *transsilvanica* (Schur) P. Delforge. In the Flora Croatica Database, in addition to these seven species, two more are listed, namely *D. cordigera* (Fries) Soó and *D. traunsteineri* (Saut. ex Rchb.) Soó, and two additional subspecies of *D. incarnata*: *D. incarnata* (L.) Soó ssp. *cruenta* (O. F. Müll.) P. D. Sell and *D. incarnata* (L.) Soó ssp. *ochroleuca* (Wüstnei ex Boll) P. F. Hunt et Summerh. Moreover, in the FCD the taxon *D. maculata* var. *transsilvanica* is treated as a subspecies, unlike in Kranjčev (2005), and it is subordinated under *D. fuchsii*, as *D. fuchsii* (Druce) Soó ssp. *transsilvanica* (Schur) S. E. Fröhner. Therefore, according to the FCD, a total of 12 taxa (nine species and three subspecies) of the genus *Dactylorhiza* are present in the flora of Croatia

(Nikolić et al. 2025). Unfortunately, it seems that some of these taxa are problematic in terms of correct identification and their actual presence in Croatia. In addition, not a single hybrid combination is listed in the FCD. On the other hand, in Kranjčev (2005), several hybrids, both intrageneric and intergeneric, are mentioned and illustrated, although some of them seem to be problematic.

The initial objectives of this paper were to present: a) the first reliable record of *D. traunsteineri* in Croatia, b) the problem of the *D. traunsteineri* species group, which seems to be very complex, and c) a list of *Dactylorhiza* hybrids that should be included in the national flora.

However, during the writing of this paper, we have come across a lot of confusing data about the genus *Dactylorhiza* in Croatia, many erroneous representations of taxa published in various books or in the FCD gallery, and taxa that are listed in the national flora but are actually not present in the country. Thus, we have decided to expand this work with notes on several taxa that seem to be the most problematic and most often misidentified in field research. A complete revision of the genus *Dactylorhiza* in Croatia is needed, preferably a publication with identification keys and illustrations of typical representatives of each taxon, such a task lies far beyond the scope of this contribution. This paper can be considered a preliminary, preparatory work pointing in this direction.

Material and methods

The first author has been researching into the orchids of Croatia since 1998. During this period, a survey was conducted in almost all the regions of Croatia, including many of its numerous islands. The second and third authors have conducted research into the orchids of Slovenia and Croatia since 1985. We have also investigated orchids, sometimes independently, and sometimes together, in neighbouring countries like Bosnia and Herzegovina, Montenegro, Serbia, Austria, Switzerland, Italy,

Albania, Greece and France. The orchids were examined *in situ*, and depending on the genus, the particular diagnostic characters were examined in detail. In the numerous field surveys in all the countries mentioned, depending on the seasons involved, of course, we also encountered many taxa of the genus *Dactylorhiza*. We have always examined several different individual specimens in a population which is especially important in the genus *Dactylorhiza*. All foliar and floral features were examined and compared, and in the occasional situations in which hybrid plants were present, we even examined almost all the specimens in population and their eventual morphological, phenological and ecological differences in order to understand them better and to be able to identify them correctly.

The most recent field trip was carried out from May 28 to June 3, 2024, in the regions of Lika and Dalmatia, with a special emphasis on the genus *Dactylorhiza*. In Dalmatia, extremely rare and small populations of late-flowering *Dactylorhiza* species have been studied on several mountains and in river valleys. In the Lika Region, the wetlands in the southern part of the Plitvice Lakes National Park (near the village of Rudanovac) were of particular interest. The latter locality was revisited on June 3 to study the more advanced flowering stage and variability of *Dactylorhiza* populations. Several plants were carefully studied and photographed *in situ*, and herbarium material was collected and deposited in Herbarium Croaticum (ZA). Standard and specialized identification keys and iconographies were used for identification: Buttler (1991), Baumann et al. (2006), Delforge (2006, 2016) and Griehl & Presser (2021). We also reviewed the main collections of Croatian herbariums (ZA, ZAHO). Taxonomy, nomenclature and arrangement of species groups are those of Delforge (2006, 2016). Since Delforge does not use the rank of subspecies, an exception is made for *D. maculata* ssp. *transsilvanica*, which follows Baumann et al. (2006), and is therefore more in line with the FCD.

Results and discussion

***Dactylorhiza sambucina* (L.) Soó, *D. incarnata* (L.) Soó, *D. majalis* (Rchb.) P. F. Hunt & Summerh., *D. fuchsii* (Druce) Soó and *D. romana* (Sebastiani) Soó**

According to Flora Croatica Database, of the 12 taxa listed for Croatia, *Dactylorhiza sambucina*, *D. incarnata*, *D. majalis* and *D. fuchsii*, are rather common species and each of them has a significant number of records throughout the country. This is also in line with Kranjčev (2005) and our personal long-term field research. In contrast, the Mediterranean *D. romana* is a rare species in the country and has been recorded only in southern Dalmatia on the Pelješac peninsula and the islands of Korčula, Hvar (Kranjčev 2005) and Brač (authors' personal observations). Recently, a single specimen was recorded on the island of Mljet (Vedran Šegota, pers. comm.). These five species do not pose any major problem in identification and do not need any further comment.

Other taxa appear problematic due to misidentification in the field and in herbarium, and it seems that several of them have never been reliably recorded and documented in Croatia. Each of these problematic taxa is discussed separately below.

***Dactylorhiza cordigera* (Fries) Soó**

This morphologically very distinctive species of more eastern distribution, essentially a Balkan-Carpathian endemic, having Bosnia and Herzegovina as its western distribution limit, has never been mentioned in modern literature for Croatia (Buttler 1991, Delforge 2006, 2016, Griehl & Presser 2021), or is mentioned as restricted to southern Yugoslavia, but without precise locations (Davis et al. 1988). The species is mentioned for Croatia in Lakušić (1988), as part of its Yugoslavian distribution, but without any specific locations. For Croatia, it is also mentioned in Domac (2002) sub nom. *Orchis cordigera* Fr., but without any precise

distribution or named localities. In Kranjčev (2005), the species is not listed and not even mentioned, regardless of his long-term survey in Croatia.

According to the Flora Croatica Database, only three records of *D. cordigera* from Croatia are known, but all of them were recorded more than a century ago. The oldest one is a herbarium sheet with three plants (one missing a flower spike) collected by Vukotinović and Schlosser in 1852 near Skrad in the Gorski Kotar Region. The original label has been preserved, and the collected plants were named *Orchis cruenta* L. Unfortunately, after checking the relevant literature and databases, this particular combination appears to be invalid and erroneous. However, two very similar and valid combinations do exist. One is *O. cruenta* O. F. Müller, the basionym of *D. cruenta* (O. F. Müller) Soó (member of the *D. incarnata* species group), and the other *O. cruenta* Rochel, the synonym of *D. cordigera*. Further complications arise from the fact that the collected plants do not represent either *D. cruenta*, or *D. cordigera*, but the more common *D. sambucina*. The leaves are unspotted, as in *D. sambucina*, whereas the leaves in both *D. cruenta* and *D. cordigera* are heavily spotted. However, the most important characteristics are the size of the flowers and spurs. The flowers of *D. cruenta* are proportionally quite small and have shorter and smaller spurs (Delforge 2006), a description that does not correspond to the herbarium material. The flowers of *D. cordigera* are quite large, but the spurs are shorter than the lips and ovaries (Delforge 2006). In herbarium specimens from Skrad, highly diagnostic spurs are very robust, curved downwards, longer than lips and about the same length as ovaries, and perfectly match the morphology of *D. sambucina*. We can assume that Vukotinović and Schlosser were probably deceived by the epithet *cruenta* = bloody, since *D. sambucina*, in addition to yellow, also has red flowers; the two species also have very similarly shaped lips.

Some years later, the species was recorded, as *O. cordigera* Fries, in the mountain meadows of Mt Učka

(“hayfields on Mt Maggiore“) by Simonkai (1888). In his work on the flora of Učka, D. Hirc (1915) reports the presence of this species, *sub nom. Orchis cordigera*, in high-altitude meadows, rocky pastures and the highest peak of the mountain, referring to the work of Simonkai (1888). Hirc (1915) also remarks: “...and this is its only location in Istria, otherwise it grows in Bosnia and Herzegovina, and in Montenegro.“ We personally studied *D. cordigera* on Mt Jahorina and Mt Vlašić in Bosnia and Herzegovina. On both of these mountains we have found this species in the bogs, marshes and seepages, which are typical habitats for this species (Lakušić 1988, Davis et al. 1988, Buttler 1991, Delforge 2006, 2016, Tsiftsis & Antonopoulos 2017, Griebel & Presser 2021). We have also visited locations on Učka several times and the problem lies in the habitat type. The highest peak of Učka is a dry limestone ridge, while the rocky pastures and meadows that we have personally inspected are also too dry, unsuitable habitats for *D. cordigera*. These habitats are also too dry for *D. majalis*, the species most similar to *D. cordigera*, and the only recorded species of *Dactylorhiza* was again *D. sambucina*. It seems that in the era of the above-mentioned botanists, the confusion between the *D. cordigera* and *D. sambucina* was obvious, at least in this particular case in Croatia. Therefore, we do not recognise *D. cordigera* as a member of Croatian flora due to misidentifications with *D. sambucina*. If *D. cordigera* is ever to be found in Croatia, then probably the best chances for its discovery are Mt Biokovo, Mt Dinara, Mt Kamešnica or some other southern locations bordering Bosnia and Herzegovina, provided that there are appropriate habitats for this species at those places.

In addition, four photos of *D. cordigera*, correctly identified, have been entered in FCD, all of them taken on Mt Vranica, Bosnia and Herzegovina by Dubravko Šincek. Two of these photographs are also published in the Flora Croatica vol. 3 (Nikolić 2020, p. 201). Three additional herbarium sheets, collected outside Croatia, are presented in the FCD. The material on two of them was collected on

Mt Treskavica, Bosnia and Herzegovina, and they were correctly identified. One herbarium sheet contains two plants collected on Mt Vlasina, Serbia, but they are in very poor condition and cannot be accurately identified.

***Dactylorhiza saccifera* (Brongn.) Soó**

Dactylorhiza saccifera is a very rare species in Croatia. According to the available data, it seems that the main problems are the correct identification in the field, the understanding of its ecological requirements and its distribution in Croatia. This predominantly Mediterranean and sub-Mediterranean species occurs mainly in the Central and Eastern Mediterranean: Greece, Albania, Montenegro, Bosnia and Herzegovina, Croatia, Italy, North Macedonia, Bulgaria, but also penetrates deeper into the continent northwards to Serbia and Romania, and extending eastwards to Turkey (Davis et al. 1988, Buttler 1991, Baumann et al. 2006, Delforge 2016, Tsiatsis & Antonopoulos 2017, Djordjević 2021, Griebel & Presser 2021, Šabanović et al. 2021).

It is important to mention the relatively recent record of *D. saccifera* from Paklenica National Park (Mt Velebit) (Alegro 2004). Unfortunately, no photos have been published, and it is quite surprising that this finding is not included in the FCD. *Dactylorhiza saccifera* was detected in the wider area of Mala and Velika Močila, an area with a spring and seepage zones (A. Alegro, pers. comm.). On the other hand, Kranjčev (2005) reports *D. fuchsii* for Velika Paklenica. This location with a sub-Mediterranean climate and damp to wet conditions seems to be an adequate habitat for *D. saccifera* in Croatia, so it will be worth checking this record *in situ*.

In FCD, under the *D. saccifera* page, five photos from Croatia (Primorje-Gorski Kotar County) were taken by Frank Verhart, but unfortunately none of them actually represent *D. saccifera*. The floral morphology of depicted specimens clearly represents the more common *D. fuchsii*. Perhaps

the author of the photos was confused or misled by the somewhat more robust plants and longer bracts, but the morphology of the lips and spurs in the photographs is sharply different from that of *D. saccifera*. The additional 39 photos in FCD were taken by Šemso Šarić at various places in Bosnia and Herzegovina. Although 25 out of them do indeed represent *D. saccifera* with its typical characteristics, the others show plants with a short inflorescence, very dark-coloured flowers and, most importantly, a lip shape that does not correspond to that of *D. saccifera*. We can assume that these plants are probably hybrids with *D. majalis* or *D. cordigera* (both species with dark-coloured flowers). We have personally studied *D. saccifera* in Bosnia and Herzegovina and found that it is a rather common and quite distinctive species. In Kranjčev (2005, p. 68–69), three photographs were published as *D. saccifera*, but unfortunately, all without the typical morphology of the species, and in our opinion, none represents *D. saccifera*, but probably some hybrids. There is too little information to determine the parents, and with the lack of detailed and high-quality photos of habitus, leaves and flowers, determination is impossible.

According to our experience in the field, *D. saccifera* is present in the Croatian flora, and we have seen, studied and photographed this rare species in the area of Knin-Sinj, Dalmatia. These small populations in Dalmatia represent the western limit of its Balkan distribution (Griebel & Presser 2021). Outside of Dalmatia, further west and north in Croatia, in places with a continental climate, *D. saccifera* is replaced by *D. fuchsii*, one of the most common *Dactylorhiza* species in the country. In several decades of field survey in Croatia, we have never seen *D. saccifera* outside of Dalmatia, nor have we seen any published photos that truly represent it.

It is worthwhile mentioning the problem of *D. gervasiana* (Tod.) Baumann & Künkele. This taxon was originally described as *Orchis gervasiana* Tod. in 1842, from Sicily (Biagioli 2016). It was later recombined as *O. maculata* var. *gervasiana* (Tod.)

Nyman and *D. saccifera* ssp. *gervasiana* (Tod.) Kreutz, and nowadays it is considered a synonym for *D. saccifera* (Biagioli 2016, Delforge 2016). However, the latest molecular research has revealed that *D. saccifera* s. l. can be clearly divided into two clades separated by the Adriatic Sea: one eastern, Balkan, representing *D. saccifera* s. str., and a western (Italy, Sicily, Corsica, Algeria) representing *D. gervasiana* (Bateman 2021). Interestingly, Delforge, like many others, at the time of his last published field guide (2016), considered *D. gervasiana* to be synonymous with *D. saccifera*, but also writes: "...*D. gervasiana*, populations croates, italiennes et sardes..." Due to the already large number of many other trans-Adriatic orchids and other plants, it is very possible that these very rare and small Croatian populations are of trans-Adriatic origin. However, as already mentioned, *D. saccifera* is present in Greece, Albania, Serbia, Montenegro and Bosnia and Herzegovina, so the Croatian population represents only a continuum of the Balkan distribution, constituting the westernmost limit of the species' range (Griebel & Presser 2021). From a morphological point of view, the two taxa can hardly be distinguished, but on average, *D. gervasiana* has a slightly less robust spur and sometimes a less pronounced three-lobed lip. Also, *D. gervasiana* appears to be a less hygrophilous species and can be found on the forest edges, while *D. saccifera* is more water-dependent (Kreutz 2024). However, an extensive morphometric study would be required to show whether this can be applied to all populations in the entire distribution range of the two taxa. In Croatia, we found both variations, in terms of morphology and habitat preference, so that only molecular studies can definitely reveal the origin of small Dalmatian populations, and then they can be properly named according to the results.

***Dactylorhiza maculata* (L.) Soó**

***Dactylorhiza maculata* s. str.**

Of all the species of the genus *Dactylorhiza*, *D. maculata* s. str. is certainly one of the most frequently misidentified species in Croatia. Considering

the abundance of literature, specialised field guides, descriptions and keys (e. g., Davis et al. 1988, Baumann et al. 2006, Delforge 2006, 2016, Griebel & Presser 2021, etc.), the amount and the frequency of the misidentification of *D. maculata* s. str. in Croatia is astonishing! The above-mentioned authors and many others clearly define tetraploid *D. maculata* s. str. as an acidophilous species, with the lowermost leaf having an acute to subacute tip; a more orbicular to obcordate lip with the wide, rounded lateral lobes, a narrow and small middle lobe that is only very shallowly incised; and with a rather delicate spur. Its main distribution is Atlantic, boreal, mostly western and northern Europe, it extends further east towards central Siberia, and it reaches the NE Balkans via the Carpathians. On the other hand, the diploid *D. fuchsii* is mostly found on alkaline substrates; the lowermost leaf is usually wider on the distal half and has a more rounded, often obtuse tip; the lip is more deeply three-lobed, more angular, rhomboid, the middle lobe is usually deeply incised, triangular, wide and mostly longer than the lateral lobes; the spur is long and medium-thick. It has a similar Euro-Siberian distribution, but it penetrates deeper into central and southern Europe (Baumann et al. 2006, Delforge 2006, 2016, Griebel & Presser 2021). Naturally, there are some atypical plants/populations with transitional characteristics, but this is mostly the case only where the two species are sympatric, or, more rarely, when the plants grow on more acidic or atypical habitats. In cases where the floral morphology is unclear, the use of the lower leaf character is usually helpful (Delforge & Kreutz 2005).

In FCD, under the presentation page of *D. maculata*, 31 photos are posted, one of which depicts the subterranean organs, while the rest depict leaves, habitus, inflorescence or individual flowers. Fourteen of these photos were taken in Sweden by Semir Maslo, and they do indeed represent *D. maculata* s. str. Furthermore, in our opinion, the set of 13 photographs taken in Bosnia and Herzegovina by Šemso Šarić represents the coloured form of *D.*

maculata ssp. *transsilvanica*. Two additional photos, taken by the same author, show flowers with a deeply incised lip with a strong and prominent central lobe, and with a thick conical spur, and we assume that they represent hybrid plants, most likely crossed with *D. saccifera*. And finally, there is a single photo from Croatia, which was taken in the Risnjak National Park by Jasenka Topić. Unfortunately, even this photo does not represent *D. maculata* s. str. With its strongly three-lobed, deeply incised rhomboid lip and with its wide and long middle lobe, it clearly depicts the common *D. fuchsii*.

Besides these 31 photographs, more than 60 scanned herbarium sheets are presented, but unfortunately, they only add to the confusion due to many misidentifications. In these herbarium sheets, in addition to misidentified *Dactylorhiza* taxa, there are also several sheets with plants from different genera. For example, in a detailed study of the herbarium, we noticed *Platanthera bifolia* (L.) Rich., *D. sambucina*, *D. majalis*, *Coeloglossum viride* (L.) Hartm., and *Orchis mascula* (L.) L. ssp. *signifera* (Vest) Soó. Most of them are old materials, some of them collected more than a century ago and probably partially misidentified in the field. It can also be assumed that some of the labels have been mixed up or misplaced over time. Many herbarium specimens that are labelled *D. maculata* actually represent *D. fuchsii*. Even in the herbarium, it is usually possible to identify *D. fuchsii*, not only due to its more rhomboid, deeply incised three-lobed lip with a long central lobe (when visible), but also by the often obtuse, rounded tip of the lowermost leaf that is mostly broader in distal half, especially well visible if the herbarium material is well prepared and preserved.

In FCD, there are more than 100 records of *D. maculata* s. str. distributed throughout Croatia, but unfortunately, there is not a single photo from the national territory showing this species. In Kranjčev (2005, p. 62–63), seven photos were published as *D. maculata* s. str. In our opinion, photos 1, 2 and 7 represent *D. fuchsii* with its typical characteristics,

photos 3, 4 and 5 represent *D. maculata* ssp. *transsilvanica* (even though photo 5 is presented as *D. maculata* var. *transsilvanica* × *D. maculata*, due to the pink wash on the flowers), and finally photo number 6 is presented as *D. maculata* × *D. majalis*, which looks like a hybrid, but the parent formula should be *D. fuchsii* × *D. majalis*. Two photographs were published in Flora Croatica vol. 3 (Nikolić 2020, p. 199), but they are the same photos as in FCD taken in Sweden by Semir Maslo. *Dactylorhiza maculata* s. str. is not even present in the neighbouring countries such as Slovenia, Hungary and Austria (Novak 2010, Griebel & Presser 2021, Dolinar 2025). In Bosnia and Herzegovina, in our opinion, according to photographs posted in FCD, *D. maculata* s. str. appears to have been confused with the coloured form of *D. maculata* ssp. *transsilvanica*.

Many times, we have visited a number of locations where *D. maculata* s. str. has supposedly been recorded, only to find the common *D. fuchsii*, and in almost all of these visited locations, even the habitat was not appropriate for *D. maculata*. The initial suspicion about the presence of this species in Croatia turned into a clear realisation that *D. maculata* s. str. is not present in the flora of Croatia, at least not according to personal long-term field research and examined published material and collections. In Croatia, it appears that *D. fuchsii*, one of the most common *Dactylorhiza* species in the country, and the rare colour form of *D. maculata* ssp. *transsilvanica*, are the main source of confusion and the constant misidentification as *D. maculata* s. str.

***Dactylorhiza maculata* ssp. *transsilvanica* (Schur) Soó**

The relatively rare *D. maculata* ssp. *transsilvanica* belongs to a group of taxa whose identification in the field is usually easy and straightforward, but here we would like to briefly discuss its more rare coloured form, and the nomenclature solution adopted in FCD. In its floral morphology, *D. maculata* ssp. *transsilvanica* is not significantly different from *D. maculata* s. str., and roughly, the main differences

are the larger lip and the longer and thicker spur in *D. maculata* ssp. *transsilvanica*, while in the general shape and outline of the lip, it is very similar to *D. maculata* s. str., while the lowermost leaf has a subacute to obtuse tip as against the acute to subacute tip in *D. maculata* s. str. Of course, the most obvious differences are the colour of the flowers, which are usually completely white or suffused with pastel pink tones, the unspotted leaves, and a more isolated, southeastern, essentially Carpathian-Balkan distribution (Kranjčev 2005, Delforge 2016, Griebel & Presser 2021, Taraška et al. 2023).

In Croatia, we studied this taxon in the region of Gorski Kotar and Mt Žumberak, and most of the specimens we examined had completely white flowers, while specimens with a pink wash, but without loop and streak markings on the lip, were rather rare, but nevertheless present. On the other hand, in Slovenia, beside the typical white coloured individuals, we observed rare specimens with pink flowers decorated with the loop and streak markings on the lip that are typical of *D. maculata* s. str. However, these rare coloured specimens that we studied had exactly the same morphology and phenology, and grew in mixed populations with typical white coloured specimens, so we treated them as two colour forms of the same taxon (a situation somewhat analogous to *D. incarnata* f. *incarnata* and its white flowered colour form named *D. incarnata* f. *ochrantha* Landwehr, and to *D. sambucina* and *D. romana* with the two colour forms). Until recently, plants in populations containing both white and pink-decorated flowers were treated as two different taxa, *D. maculata* s. str. and *D. maculata* ssp. *transsilvanica*. These rare coloured forms of *D. maculata* ssp. *transsilvanica* are partially responsible for the confusion and erroneous identifications and records of *D. maculata* s. str. in Croatia (and Slovenia). However, in the east of its range, in the Carpathians, where *D. maculata* ssp. *transsilvanica* was originally described, both colour forms, white and pink, with the decorated lip, linked with the transitional forms, very often

occur together in the same populations (Taraška et al. 2023). In Slovenia, this situation with both coloured forms growing mixed at the same locality and with the same morphology and phenology, is also recognized and treated only as dichromic forms of the same taxon (Dolinar 2015, 2025, Kavšek 2021).

Also, if plants from the same population share the same phenology and morphology, and differ only in flower colour, they should be assigned the rank of forma, for they do not satisfy the criteria for subspecies. This only confirms that the dichromic forms in some populations of *D. maculata* ssp. *transsilvanica* represent the same taxon, which has already been accepted by Dolinar (2015, 2025), Kavšek (2021) and Taraška et al. (2023), among others.

The strategy of colour polymorphism has already been studied in nectar-rewardless orchids. For example, a study of *Orchis mascula* (L.) L., showed that when populations of purple-flowered plants contain several white-flowered specimens, the fruit set increased significantly. Pollinators quickly learn that a particular type of flower/colour, is nectar-free, and stop visiting such colour-homogenous populations, whereas populations with colour polymorphism are visited for a longer period of time, resulting in a higher pollination rate (Dormont et al. 2010). However, it seems that in the case of *D. maculata* ssp. *transsilvanica*, this colour polymorphism evolved further on, and in the west of the distribution area, Croatia and Slovenia, the white form became dominant.

Both *D. maculata* s. str. (not present in Croatia) and *D. maculata* ssp. *transsilvanica* are tetraploids, while *D. fuchsii* is a diploid (Klein & Deutsch 2005, Petrova et al. 2009, Taraška et al. 2023). Diploid *D. fuchsii* has distinct foliar and floral morphology and different ecological requirements than tetraploid *D. maculata* s. str. (Delforge 2006, 2016, Griebel & Presser 2021), and in view of all the information presented, the nomenclature concept adopted in

FCD should be modified. Therefore, we propose replacing the combination currently used in FCD, *D. fuchsii* (Druce) Soó ssp. *transsilvanica* (Schur) S. E. Fröhner, with a more logical and more commonly used combination: *D. maculata* (L.) Soó ssp. *transsilvanica* (Schur) Soó. This combination is used in almost all modern publications, for instance: Davis et al. (1988), Buttler (1991), Ravnik (2002), Baumann et al. (2006), Griehl & Presser (2021), Taraška et al. (2023), Dolinar (2025), etc. Of course, subordination under *D. maculata* is also used in Delforge (2006, 2016), but at the variety level, since Delforge belongs to the group of authors who do not use the rank of subspecies, and use the rank of variety as the highest rank below the species (for a detailed explanation of variety *sensu* Delforge, see Delforge (2010)).

***Dactylorhiza ochroleuca* (Wüstnei ex Boll)
J. Holub, *D. cruenta* (O. F. Müller) Soó and
D. traunsteineri (Saut. ex Rchb.) Soó**

In FCD, *D. ochroleuca* and *D. cruenta* are commonly treated as subspecies of *D. incarnata*, but we, as already stated, follow the nomenclature of Delforge (2006, 2016). The following three taxa: *D. incarnata* ssp. *ochroleuca*, *D. incarnata* ssp. *cruenta* and *D. traunsteineri* are listed in the FCD (Nikolić et al. 2025) and in Flora Croatica vol. 3 (Nikolić 2020), but their presence in Croatia is marked as doubtful (Hr:?). For all three of these taxa: a) there is not a single record from the country, b) there are no photographs taken in Croatia that truly represent them, and c) there is no herbarium material collected within the national borders.

Dactylorhiza ochroleuca is a rare species with yellowish flowers present in Alpine countries such as Germany, France, Austria and Switzerland, and it is also rare in Scandinavia and the Baltic countries (Delforge 2016, Griehl & Presser 2021). There is one superficially similar taxon in Croatia, and that is *D. incarnata* f. *ochrantha* Landwehr, a hypochromatic variety of *D. incarnata*. It has the same morphology as the nominate form, but the

colour of the flower and the lip range from white to yellowish, occasionally with a delicate pastel pinkish, hardly any contrasting markings on the lip (Delforge 2006). *Dactylorhiza incarnata* f. *ochrantha* can be confused with *D. ochroleuca*, which is a taller plant with shorter leaves, while the flowers have much more deeply incised lips and much deeper, stronger yellow hue, especially at the base of the lip (Delforge 2006, 2016, Griehl & Presser 2021). The form *ochrantha* is very rare in Croatia, except in one location in the vicinity of the Plitvice Lakes National Park, where it grows in a large population mixed with the other two colour forms of *D. incarnata* (Kranjčev 2005). This particular population of *D. incarnata* f. *ochrantha* is illustrated with a beautiful photograph in Kranjčev (2005, p. 396). When and if the researcher eventually encounters a hypochromatic, white/yellowish coloured *D. incarnata* s. l., a detailed examination of the plants will be needed to correctly identify the plants, without confusing *D. incarnata* f. *ochrantha* and *D. ochroleuca*. So far, there is no evidence (in the shape of field records, photographs or herbarium material) of *D. ochroleuca* from the national territory, nor is it mentioned for Croatia in contemporary literature (Buttler 1991, Baumann et al. 2006, Delforge 2016, Griehl & Presser 2021), so we do not recognize it as a member of the Croatian flora.

Dactylorhiza cruenta is another rare species with a Eurasian distribution, but in Europe it is mainly limited to the Alps and Scandinavia (Delforge 2016, Griehl & Presser 2021). It has a very similar morphology to that of *D. incarnata*, but it is a smaller species with shorter leaves that are heavily spotted on both sides, and smaller and darker coloured flowers (Delforge 2016, Griehl & Presser 2021). In Croatia, *D. incarnata*, the species that is most similar to *D. cruenta*, is moderately common, and according to the FCD distribution map, there are about 90 records, and all photos in the FCD show typical plants. In our long-term survey in Croatia, we have never even come across varieties of *D. incarnata* with spotted leaves, namely: *D. incarnata*

var. *haematodes* (Reichenbach fil.) Soó with leaves spotted only on the upper side, and *D. incarnata* var. *hyphaematodes* (Neuman) Landwehr with leaves spotted on both sides (Delforge 2006), the two taxa that can be confused for *D. cruenta*, nor *D. cruenta* itself. In Kranjčev (2005), there is no mention of *D. cruenta*, nor the varieties of *D. incarnata* with spotted leaves. The species is also not mentioned in Domac (2002). Again, as in the case of *D. ochroleuca*, there is no evidence of the existence (field records, photographs or herbarium material) of *D. cruenta* in the national territory, nor it is mentioned for Croatia in contemporary literature (Buttler 1991, Baumann et al. 2006, Delforge 2016, Griehl & Presser 2021), therefore we do not recognize it as a member of the Croatian flora.

After discussing the most problematic taxa, we came to the conclusion that several taxa have either been misidentified or misunderstood, and for some of them that have already been marked as doubtful, there is no evidence that they have ever been recorded in the national territory, so we reject their presence in the Croatian flora. Thus, we recognize only seven species and one subspecies of the genus *Dactylorhiza* in the flora of Croatia. The latest addition, the seventh species of *Dactylorhiza* in the flora of Croatia, was discovered in 2024 in Lika-Senj County: this is *D. traunsteineri*, presented in detail below.

An overview of existing data on *Dactylorhiza traunsteineri* in Croatia

The first mention of *D. traunsteineri* in Croatia appears in the Index Florae Croaticae (Hršak 2000), and is based on literature data (Heusser 1938). However, after a detailed examination of this work, it turned out that *D. traunsteineri* is not mentioned in connection with Croatia, so we consider this reference erroneous.

The species is also listed in the FCD, but without any records in the country. In FCD, under the presentation sheet of *D. traunsteineri*, nine photos were posted, and all of them represent one

and the same individual plant photographed by Semir Maslo (Gislaved, Sweden). All nine photos have the same captions: “*D. traunsteineri* (Saut. ex Rchb.) Soó, Austria, Tirol, Tuxer Alpen, Innsbruck, Obernberger See, 27. 06. 2016.” Unfortunately, the plant shown does not represent *D. traunsteineri*, but the more common, variable and widespread *D. fuchsii*. Interestingly, the same author posted two photos on FCD with exactly the same photo captions and from the same location in Austria, under the presentation page of *D. fuchsii*, and there they were correctly identified.

Unfortunately, one of these photos, taken in Austria, which effectively depicts *D. fuchsii*, was published as *D. traunsteineri* in the Flora Croatica vol. 3 (Nikolić 2020, p. 201). In the same volume, the presence of *D. traunsteineri* in Croatia is marked as doubtful (Hr:?).

The mention of *D. traunsteineri* in the Index Florae Croaticae on the basis of literature data is obviously erroneous. The photographs taken in Austria and posted in the FCD do not represent *D. traunsteineri*, and, more importantly, were not taken within the national territory. Finally, there is no herbarium material of this species deposited in any major Croatian herbaria. Therefore, we conclude that the population discovered in the Lika Region, and presented in this paper, represents the first reliable evidence of *D. traunsteineri* in Croatia so far.

The diversity of *Dactylorhiza* species in the Lika Region in May/June, 2024, and the discovery of *D. traunsteineri*

A total of three species, three colour forms and one hybrid combination were recorded in the Lika Region in May and June 2024. Therefore, we decided to present, describe and comment on the situation, with all the taxa recorded in the research area near the village of Rudanovac (Plitvice Lakes National Park) during our visit in 2024 as follows:

On May 28, we found small groups or scattered individual plants of *D. majalis* in several places, all in

the fruiting stage. This species has been documented in flower in our previous visits to the same locations, but always earlier in the season. *Dactylorhiza majalis* has very wide, heavily spotted leaves, dark purplish flowers with three-lobed lips. It is an early flowering species, usually growing in moist to marshy habitats (Baumann et al. 2006, Delforge 2006). Due to its specific morphology and early phenology, it is a species that is easy to identify in the field. In the research area, we did not notice hybrids with this species. Two intrageneric hybrids with *D. majalis* have been recorded in Croatia.

At the same time, the much more plentiful *D. incarnata* was in the middle to full flowering stage, and was represented by three colour forms. The typical colour form with a darker shade of pink or lilac flowers was the rarest. A form with very delicate, pastel pale pink coloured flowers named *D. incarnata* f. *rosea* W. Zimm, and a form with completely white flowers, or white flowers with very pale pinkish loop-shaped markings and dots on the lip, or sometimes even with slightly yellowish colour tones, named *D. incarnata* f. *ochrantha*, were represented by hundreds of plants. This last colour form is often mistakenly identified as *D. ochroleuca* (Delforge 2006). *Dactylorhiza incarnata* is usually very easy to identify due to its long, medium-wide and erect unspotted leaves that usually reach the inflorescence; the flowers are numerous, densely packed, the lip is somewhat rhomboid, entire or only slightly incised. The species inhabits damp meadows, marshes and stream banks (Baumann et al. 2006, Delforge 2016). In Croatia, *D. incarnata* forms hybrids with four other species of the genus *Dactylorhiza*.

We also discovered several very interesting *Dactylorhiza* plants with slender habitus, very narrow leaves and medium to large, richly coloured flowers. All plants were in a very early flowering stage with 1–3 open flowers. In the vicinity, more plants were found, but also all in buds or with several open flowers. So, we decided

to revisit the station again a week later, at the end of our planned expedition tour, to see and study a more advanced flowering phase, more plants and the eventual variability of this population. Nevertheless, the few flowering plants were easily identified as *D. traunsteineri*, since we had already personally seen and studied this species (complex) in several different localities in Slovenia and northern Italy.

On June 3, we visited the location near the village of Rudanovac again (Fig. 1A). This time, the situation was far more favourable due to the numerous plants in flower. Of the approximately 150–180 plants found, the majority of plants had about half or up to two-thirds of the flowers open, and some plants were in full bloom. The population appeared homogeneous with a stable and consistent morphology, and we confirmed our initial identification of these plants as *D. traunsteineri*. The syntropic *D. incarnata* was in full flower and partially past its best. Obviously, *D. traunsteineri* is a late-flowering species. In the same area, we can observe a flowering order as follows: *D. majalis* flowers at the beginning of May till mid-May, followed by *D. incarnata* flowering in mid-May till the beginning of June, and finally *D. traunsteineri* flowering from the very end of May/beginning of June till mid (end) of June. This late flowering time also explains why this species has remained overlooked, even though we have visited the same locations in the past, but usually earlier in May. However, the first author inspected a personal photo archive relating to the same area, and a single photo named “*Dactylorhiza* sp.,” taken in May 2011, was found and studied. The photo shows an inflorescence with a few opened purplish coloured flowers with a proportionally large lip (Fig. 1B). Unfortunately, the habitus and leaves have not been photographed, which are very important for correct identification, and it remained unidentified until now. This photo from 2011 is probably the first documented evidence of the presence of *D. traunsteineri* in Croatia.

Description: a very spindly plant 20–40 cm tall, stem is only slightly compressible and washed violet at the top; leaves are few, usually 3–5, mostly outspread along the stem, linear-lanceolate, 5–16 cm × 0.5–1.8 cm, pointed, keeled, erect or slightly arched outwards, unspotted or slightly spotted only on the upper side, the largest leaf is usually at its broadest close to the base; bracts are coloured and longer than the

ovary; the lax inflorescence is ovoid to nearly cylindrical 3–10 cm tall; 5–20 rather large flowers are richly purple to magenta; lip 6–10 mm × 7–13 mm is obovate to obcordate and three-lobed, often folded longitudinally, the centre is paler, decorated with dark purplish loops, streaks and dots, side lobes often turn down and then are slightly reflexed, central lobe is tooth-like and pointed; spur is rather robust, conical 7–12 mm

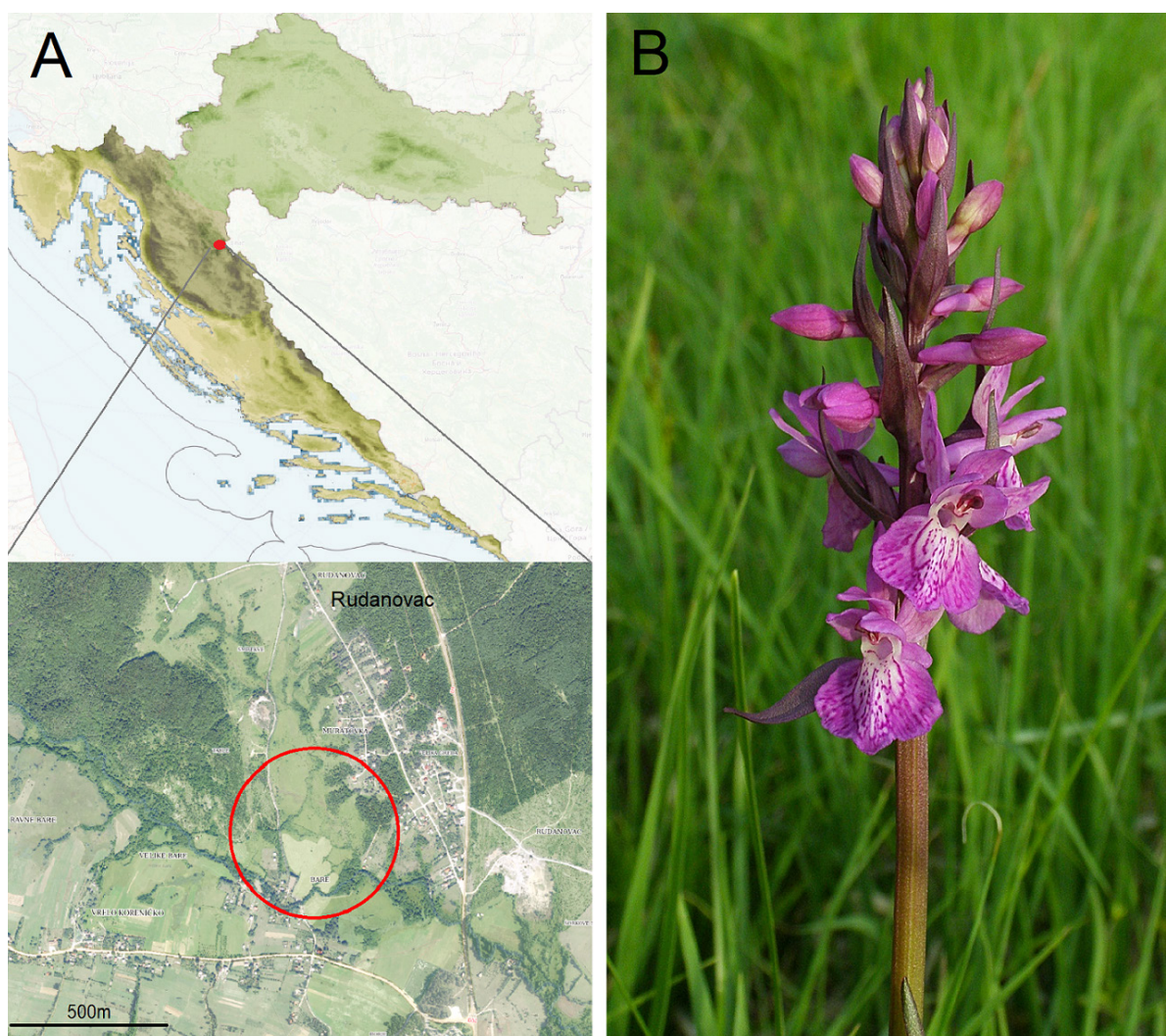


Figure 1. A – *Dactylorhiza traunsteineri* site near the village of Rudanovac, B – *D. traunsteineri*, an inflorescence, May 29, 2011 (photo by R. Čičmir).

Slika 1. A – Nalazište vrste *Dactylorhiza traunsteineri* u blizini sela Rudanovac, B – *D. traunsteineri*, cvat, 29. 5. 2011. (fotografija R. Čičmir).

× 2–3.5 mm, near horizontal, straight to slightly descending (Buttler 1991, Kreutz 2002, Ravnik 2002, Baumann et al. 2006, Delforge 2006, 2011, 2016, Griebel & Presser 2021).

The species inhabits open sunny habitats, but tolerates a slight shade. It is always found on wet, alkaline substrates, mainly in montane and alpine bogs (Baumann et al. 2006, Delforge 2006), and the



Figure 2. *Dactylorhiza traunsteineri*, June 3, 2024, Rudanovac, Croatia: A – specimens collected for the herbarium, B – details of lips and spurs, C – sparsely spotted and narrow leaves (photos by R. Čičmir).

Slika 2. *Dactylorhiza traunsteineri*, 3. 6. 2024., Rudanovac, Hrvatska: A – primjerci sakupljeni za herbarij, B – detalji usne i ostruga, C – rijetko pjegavi i uski listovi (fotografija R. Čičmir).

locality in Croatia fits this description. It is distributed mostly in the Alps and the wider mountain belt that surrounds them (Kreutz 2002, Ravnik 2002, Baumann et al. 2006, Delforge 2006, 2016).

Our own observations and measurements performed on a few plants are in accordance with this description, or have only slightly deviated in some features. In one part of the site, in loose reed stands, next to normal plants, we found several robust and unusually tall specimens, but with a floral morphology of *D. traunsteineri*, and although certainly striking, they were evaluated as an insignificant extreme. Perhaps some of the peculiar characteristics of this population are small to medium-sized plants, somewhat shorter and with weakly spotted leaves, very thick spurs, and lips with a white base extending to the centre of the lip, sometimes quite significantly (Fig. 2, 3). However, as already mentioned, we closely studied just a few plants (collected through collaboration and with permission of ZA Herbarium collection), while the entire population was only briefly examined due to time constraints. It is well known that individual plants in any *Dactylorhiza* population can vary in plant height and in the number and size of leaves and flowers. These differences are also largely dependent on the micro-location in which the plants grow. The external appearance of the plants is much affected by a wetter or drier spot in the habitat, on poor or rich soil, with dense or sparse surrounding vegetation, and the plasticity within the population is sometimes strongly expressed. However, this is more evident in the quantitative features of the plants, while qualitative characteristics are usually more stable. It is well known that in the approach to the identification of *Dactylorhiza* taxa, the emphasis should be placed more on the population level rather than on a single plant, an approach that is sometimes crucial (Delforge 2006, 2011, 2016).

At one micro-location where a smaller group of *D. traunsteineri* grew in proximity to several plants of *D. incarnata*, we discovered a couple of hybrid plants. As in many other places where two or more *Dactylorhiza* taxa are syntopic, and if their

phenology overlaps, the presence of hybrids is almost unavoidable, or at least certainly not rare. However, if the parent species have a very different morphology, as in this particular case, and if the plants are carefully examined, the identification of primary hybrids is usually simple due to intermediate foliar and floral morphology and intermediate phenology. This hybrid combination has already been recorded and formally described under the name *Dactylorhiza* × *duftii* (Hauskn.) Peitz (based on *Orchis* × *duftii* Hauskn. 1885), Peitz (1972), and represents a new taxon in the Croatian flora.

In Croatia, due to the rather small number of *Dactylorhiza* taxa, the identification of *D. traunsteineri* should not pose any major problems, provided that healthy flowering plants are inspected *in situ*. Spindly plants with very few leaves, narrower than 1.8 cm (2 cm), and medium to large, richly coloured flowers, in combination with late phenology and a wet habitat, make misidentification with other Croatian *Dactylorhiza* taxa almost impossible. Also, due to its very specific habitus, this species is relatively easy to identify in herbaria and in photographs, especially if they are accompanied by additional information such as phenology and habitat type.

Problems of the *Dactylorhiza traunsteineri* group

Dactylorhiza traunsteineri group is composed of allotetraploid and allohexaploid species, resulting from repeated but separated speciation events, and ancient hybridizations in which *D. incarnata*, *D. fuchsii*, *D. maculata*, and probably some other taxa, played a crucial role (Hedrén 1996a, 1996b, 2002, 2003, Bateman et al. 2003). Because of the hybridization process, of nearly identical, or sometimes even the same parent species formula, the general morphology of these isolated species appears very similar, and identification is complicated for field botanists and taxonomists alike (Delforge 2011, 2016). Most orchid specialists believe *D. traunsteineri* is a species present only in the Alps, in the alkaline fens of Bavaria, Austria, Switzerland and Italy. All other plants that resemble it, outside the Alpine arc, represent other related species, and/

or hybrid swarms (Klinge 1898, 1899, Vermuelen 1958, Nelson, 1976, Landwehr 1982, Reinhard et al. 1991, Delforge 2006, 2011, 2016). Some other authors,

who use the morphological species concept almost explicitly, consider it a more widespread species (Davis et al. 1988, Buttler 1991).



Figure 3. *Dactylorhiza traunsteineri*, variability in the population, June 3, 2024, Rudanovac, Croatia (photos by R. Čičmir).

Slika 3. *Dactylorhiza traunsteineri*, varijabilnost unutar populacije, 3. 6. 2024., Rudanovac, Hrvatska (fotografije R. Čičmir).

Dactylorhiza traunsteineri was originally described from an Alpine fen in the region of North Tyrol, Austria, in 1830 (Delforge 2006). Outside the Alps, it is replaced by *D. curvifolia* (F. Nylander) Czerepanov in the Baltic region and possibly further east in Russia; by *D. carpatica* (P. Batousek & Kreutz) P. Delforge in the western Carpathians; by *D. schurii* (Klinge) Averyanov in the eastern Carpathians; by *D. devillersiorum* P. Delforge in the Haute-Marne department, NE France and by *D. traunsteineroides* (Pugsley) Landwehr ex R. M. Bateman & Denholm in the British islands (Baumann et al. 2006, Delforge 2011, 2016, Griebel & Presser 2021).

In addition to these well-established species, there are several other morphologically very similar taxa, such as *D. angustata* (Arvet-Touvet) D. Tyteca & Gathoye, from the western Alps in the border zone of SE France and NW Italy; *D. turfosa* (F. Prochazka) Kreutz, from the SW Bohemia, Czech Republic and *D. bohémica* Businsky, from N Bohemia, Czech Republic, all of them sometimes considered a subspecies of *D. traunsteineri* (Delforge 2006, Griebel & Presser 2021). They all have small distribution areas and are treated differently by various authors, and probably more studies are needed to understand them properly (Delforge 2006, 2016). Recently, however, they have become more and more accepted at the species level (Griebel & Presser 2021).

In Europe, multiple species with very similar morphology have evolved separately through the various hybridization events. On the other hand, it is also possible that, at least in part of the distribution area, the once more widespread species has been reduced to separate populations due to habitat loss. Now isolated, each of them has developed particular and distinctive morphological characteristics; being thus diagnosable and isolated, they are treated as separate species (Reinhard et al. 1991, Baumann et al. 2006, Delforge 2006, 2011, 2016, Griebel & Presser 2021).

It seems that the Croatian Dinaric population of *D. traunsteineri* is more or less isolated. The closest known populations are located in neighbouring Slovenia, where the species is known from several

localities, especially in the Alpine and peri-Alpine regions of the country (Ravnik 2002, Dolinar 2015, 2025), and also perhaps in the Dinaric part of the country (Dolinar 2025). However, the correct identification of some of these records is questionable (personal field research). Also, it is quite interesting that in a few of these Slovenian populations, some foliar and floral differences are quite obvious in relation to the plants of the Croatian population. This only shows how complex this whole imbroglio named the *D. traunsteineri* species group can actually be. Nevertheless, this newly discovered Dinaric site of *D. traunsteineri* in Croatia represents the easternmost location of this species so far.

On the origin of the Croatian population of *D. traunsteineri*

The existence and the origin of the Croatian Dinaric population of *D. traunsteineri* can be explained and discussed in the framework of the following scenarios. The population of *D. traunsteineri* from the Lika Region represents: a) an unstabilized hybrid swarm, b) an original undescribed taxon and c) *D. traunsteineri* s. str.

When we encountered this relatively large population, we never had the impression that we were standing in front of an unstabilized hybrid swarm. The plants were uniform, of course, with the usual variation of the individual plants that can be found in any *Dactylorhiza* population. Also, they did not appear to be intermediate between syntopic taxa, nor was their phenology intermediate either. On the contrary, the plants looked quite homogeneous, and their morphology and phenology were distinct. We can safely rule out the scenario of an unstabilized hybrid swarm, since there are no elements to support such a theory.

A scenario proposing an original, undescribed taxon is very possible and plausible due to the geographical isolation and remoteness of the Croatian population; the small morphological differences also support it. However, as already mentioned, only a few plants have been briefly

examined, and additional study is needed to reveal possible differences that would allow separation of the Croatian population as a distinct taxon. Furthermore, a molecular study is also required to support this hypothesis and a comparative study of its habitat to complement it. Therefore, we cannot completely rule out a scenario in which the Croatian population represents an overlooked, original and undescribed taxon, but this hypothesis should be taken with caution, and should be confirmed by multidisciplinary investigation.

Finally, what remains is a scenario in which the Croatian population represents the *D. traunsteineri* s. str., and if we apply Occam's razor principle, it is the simplest and the easiest scenario to follow, and that is our current choice. We can assume that the Croatian population originated from seed dispersal from the closest sites, or at least from those sites from which favourable wind direction regimes occur, or occurred in the past. Orchid seeds are among the tiniest seeds and are easily airborne and dispersed by the wind, and adequate habitats are easily colonized (Arditti 1992, Rasmussen 1995). However, it is more likely that Croatian plants represent a relict population of *D. traunsteineri*. After the withdrawal of the ice sheet at the end of the last glaciation event, this population remained isolated. It survived and prospered in a favourable habitat, but until now it remained undiscovered or misidentified. In the current state of limited knowledge about this species in Croatia, and until further detailed multidisciplinary research is conducted, it is best to treat this particular Dinaric population as *D. traunsteineri* s. str., and if necessary, to point out its peculiar characteristics.

Future research

The population of *D. traunsteineri* presented in this paper is the only one known in Croatia. In the coming seasons, it will be very important to expand the survey to a much wider area. In addition to similar wetlands in the Lika Region, the research should be expanded to the adjacent region of Gorski Kotar,

where there are many similar wet habitats, and the presence of *D. traunsteineri* can be expected as well. These habitats must be visited during the flowering period of this species, otherwise the plants can easily remain overlooked due to the gracile habitus with a few narrow leaves, which in turn are difficult to spot in the usually dense vegetation. The time of the survey is obviously of paramount importance and must be adjusted properly. For the locations in the Lika Region, the first week or fortnight of June, according to our experience, seems to be the best time for a survey, while in the region of Gorski Kotar, a somewhat more mountainous and colder place, a shift of about a week (or two) later would probably be more appropriate.

Regardless of whether only one known population remains or additional populations of this rare species will be discovered in the future, research should not focus only on the geographical distribution in Croatia. Molecular research is becoming more accessible and is ever more often applied, so the true phylogenetic relationships between species and various populations are more properly understood, and cryptic taxa are regularly discovered. Also, the fact that numerous similar-looking taxa, all of which have been found outside the Alpine arc, have been described as separate and distinct positions the Croatian population as another extra-Alpine population that is worth reconsidering as isolated and original. However, only a multidisciplinary study would make any further taxonomic research meaningful, and that is the task for future work.

Conservation status of *Dactylorhiza traunsteineri* in Croatia

So far, only one population of *D. traunsteineri* is known in Croatia. Even though our current knowledge of the distribution area and the population size of this species is incomplete, we briefly describe the situation only to emphasize the need for urgent protection of this species and its habitat. The population in the Lika Region consists of about

180 specimens distributed in a small area. The occupancy area (AOO) is approximately estimated to be less than 2 km². This only known population of *D. traunsteineri* is located within the borders of the Plitvice Lakes National Park, and therefore it is already protected, but unfortunately, it is located on the very edge of the National Park, near the settlement where it is partially exposed to grazing and sport activities. Perhaps an even greater danger is the succession of natural vegetation, especially in the more waterlogged part of the habitat, where *Phragmites australis* forms very large and dense stands with its usual tendency to expand. In the next season, it is necessary to conduct a targeted and detailed study of the exact population size, distribution area and ecology of this species. On the basis of the data collected, the category according to the IUCN Red List of Categories and Criteria can be appropriately applied.

***Dactylorhiza* hybrids in Croatia**

Taxa of the genus *Dactylorhiza* hybridize easily. Due to backcrossing, sometimes more or less easily identifiable primary hybrids are further blurred by transitional characteristics (Delforge 2006). Even though many taxa are separated by different phenologies, every now and then, cold weather postpones the flowering of early species, and then a sudden warming or heat wave will bring early and late species to flower simultaneously, or they will overlap in their flowering just enough to hybridize. Many species are also ecologically isolated, but they are encountered in transitional habitats, and these ecotones are often the places where hybrids occur.

While the hybrids are not generally interesting to most botanists, and in many plant families and genera they are usually rare, sometimes, as in the genus *Dactylorhiza*, they are worth reporting due to the identification problems in the field. To date, more than a hundred hybrids have been formally described in Europe, which include all possible combinations between almost all known taxa. On the other hand, in Croatia, hybrids seem to be

generally neglected, overlooked or misidentified. Not a single hybrid of *Dactylorhiza* is listed in FCD, although some are mentioned, for example, in Kranjčev (2005). Therefore, an overview of hybrids of the genus *Dactylorhiza* recorded in Croatia is given below.

***D. × aschersoniana* (Hausskn.) Soó**, (*D. incarnata* × *D. majalis*), is a hybrid whose parent species both grow in wet habitats, and since they are often syntopic and their phenology overlaps, they can hybridize easily. Hybrid plants are recognizable by their intermediate foliar and floral characteristics (unspotted versus spotted leaves, smaller, lighter-coloured flowers with a near entire lip versus larger flowers with a three-lobed lip of darker colour), and intermediate phenology. This hybrid is mentioned in Kranjčev (2005). In Croatia, we found it only in the region of Gorski Kotar, although it is probably more widespread.

***D. × kerneriorum* (Soó) Soó**, (*D. incarnata* × *D. fuchsii*), is probably one of the most common *Dactylorhiza* hybrids in Croatia, but it is still rare. *Dactylorhiza incarnata* always grows in wet habitats, while *D. fuchsii* is one of the most habitat-tolerant species of *Dactylorhiza* in Croatia. It grows in dry to wet grasslands, marshes, road ditches, woodland edges and forests. Hybrid plants are usually found on the edges of wet meadows where the parent species come into contact. They can also be found on elevated, drier parts of land in wet meadows, and less often in the wet meadows themselves. Hybrid plants can be easily identified by their intermediate foliar morphology (unspotted versus spotted leaves), by their intermediate floral morphology (near entire lip versus deeply three-lobed lip with a prominent and pointed median lobe), and by their intermediate phenology. This hybrid combination is not mentioned in Kranjčev (2005), although he mentions *D. incarnata* × *D. maculata*, but due to the misidentification of *D. maculata* and *D. fuchsii* as explained elsewhere in this paper, it is obvious that the illustration in his book refers to this hybrid (Kranjčev 2005, p. 61, Figure 7). We have personally

seen this hybrid in the regions of Gorski Kotar and Lika, but it can probably be expected in other parts of the country as well.

***D. × duftii* (Hauskn.) Peitz**, (*D. incarnata* × *D. traunsteineri*), this hybrid is new to the Croatian flora, and we present it for the first time in this paper. The parent species have very different morphology and therefore the hybrid plants are easy to identify due to intermediate floral and foliar characteristics. The robust (diploid) *D. incarnata* has several very long and medium-wide unspotted leaves that reach the inflorescence, the stem is very thick, not purplish coloured at the top, or only faintly so, and the inflorescence, which is elongated, is composed of a large number of small to medium-sized densely packed pink flowers. On the other hand, the rather delicate (allotetraploid) *D. traunsteineri* is a spindly plant with a few narrow, sparsely spotted leaves, the thin stem is strongly purplish at the top, and the rather loose inflorescence is formed of medium to large, purplish flowers.

***D. × braunii* (Halácsy) Borsos & Soó**, (*D. majalis* × *D. fuchsii*), is probably one of the rarest *Dactylorhiza* hybrids in Croatia due to a significant gap in the phenology of the parent species. *Dactylorhiza majalis* flowers quite early, whereas *D. fuchsii* is a late-flowering species, so they rarely overlap at the time of flowering. Hybrid plants have intermediate foliar and floral characteristics (leaves longer and outspread along the stem vs more concentrated at the base; flowers of darker purple colour with oval mid-lobe vs pink and pointed mid-lobe). This hybrid is mentioned in Kranjčev (2005) as *D. maculata* × *D. majalis*, and is illustrated by one photograph (Kranjčev 2005, p. 63, Figure 6). We saw it only once in the region of Gorski Kotar, where it grew in the transition zone of a wet meadow and the forest edge.

Kranjčev (2005), also mentions *D. maculata* × *D. maculata* ssp. *transsilvanica* (as var. *transsilvanica*) referring to specimens with pink suffusion on white flowers. However, plants with slightly

coloured flowers represent only the coloured form of *D. maculata* ssp. *transsilvanica*. These plants with coloured flowers growing together with plants with white flowers, both of which have exactly the same morphology and phenology have always created a lot of confusion for researchers and have only recently finally been properly understood (Taraška et al. 2023).

The hybrid *D. maculata* ssp. *transsilvanica* × *D. fuchsii* is also listed in Kranjčev (2005), but it is not illustrated. The presence of this hybrid in Croatia is very possible because in several places (Gorski Kotar, Žumberak) these two taxa are sympatric and their flowering time overlaps. A very detailed examination of the putative hybrid plants must be carried out to confirm the intermediate characteristic and not to confuse the coloured individuals of *D. maculata* ssp. *transsilvanica* for hybrids. We have not personally seen this hybrid in Croatia, and until it is confirmed *in situ*, or with several high-quality photographs that illustrate important intermediate characteristics, its presence in Croatia must remain questionable.

In Kranjčev (2005), three more hybrid combinations are listed, *D. saccifera* × *D. incarnata*, *D. saccifera* × *D. majalis* and *D. saccifera* × *D. maculata*. However, due to the misidentification of *D. saccifera* itself by the same author, we also have doubts about the correct identification of these three hybrids. We have not personally seen these three hybrids, and in the very few and rare locations of *D. saccifera* in Croatia, we have not seen *D. incarnata*, *D. majalis* or *D. maculata*. Therefore, we do not recognize these three hybrid combinations for the Croatian flora.

In addition to intrageneric hybrids, Kranjčev (2005) also listed three intergeneric hybrids (without illustration). One of them, *D. maculata* × *Gymnadenia conopsea* (L.) R. Br., is a well-known hybrid in Europe, for example, see in Baumann et al. (2006) and Dolinar (2025), and the same stands for the hybrid *D. fuchsii* × *G. conopsea*. Due to misidentification of *D. maculata* with *D. fuchsii*, it is impossible to conclude

whether Kranjčev found the hybrid *D. maculata* ssp. *transsilvanica* × *G. conopsea* or *D. fuchsii* × *G. conopsea*. We have personally seen *D. fuchsii* × *G. conopsea* only in Slovenia, but not in Croatia, so the presence of this intergeneric hybrid in Croatia remains questionable. The hybrid combination *G. conopsea* × *D. saccifera*, is also problematic due to the misidentification of *D. saccifera*, thus it cannot be accepted for the Croatian flora.

The third intergeneric hybrid combination is *D. maculata* × *Orchis mascula*, the presence of this hybrid is very unlikely because it is not recognized in the modern literature. Most likely, Kranjčev misidentified some atypical plant of either of the supposed parents for the hybrid. Therefore, we do not recognize this hybrid for the Croatian flora.

It is very possible that some other intrageneric and intergeneric hybrid combinations will be recorded in Croatia. However, it is very important that the researchers inspect in detail all the characters, including the leaves, their size, position and colouration; stem thickness and colouration, flower size, colouration, shape of the lip and its ornamentation; size, thickness and direction of the spur; as well as phenology and ecological context. Before naming any plant a hybrid, it is necessary to exclude the possibility that the plant has an unusual morphology or colouration due to ecological conditions, an unusually dry year, growing on atypical soil, or due to hypochromy or hyperchromy in the flower colouration. It is very important to look for clear intermediate characteristics of plant morphology, intermediate phenology and sometimes ecology, and it is only after detailed examination that hybrids can be confirmed.

Conclusion

Dedicated research on the genus *Dactylorhiza* has never been conducted in Croatia, so this could be one of the reasons why there are so many erroneous identifications and why some taxa have remained on the list of the national flora, even though they have never been confirmed in Croatia.

Of the 12 taxa of *Dactylorhiza* listed in FCD, two species with the records in the country, *D. maculata* s. str. and *D. cordigera*, appear to be based on misidentification, and should therefore be removed from the list of the national flora. Furthermore, two taxa that are on the national list, but without field records, without photographs and herbarium material that truly represent them, *D. incarnata* ssp. *ochroleuca* and *D. incarnata* ssp. *cruenta*, should also be removed from the national flora due to the lack of evidence of their presence in Croatia. The presence of *D. traunsteineri* in Croatia was based on old literature data that turned out to be erroneous, but in May 2024, we detected one population in the Lika Region, so this species is present in Croatia. This late-flowering species belongs to the *D. traunsteineri* species group, a group made up of taxa with a very complex hybrid origin. Many taxa of this group, mostly geographically isolated populations, have been described as distinct taxons, and in this regard, the somewhat isolated Croatian population deserves multidisciplinary research in the future. We also propose one change in nomenclature, a combination currently used in FCD: *D. fuchsii* (Druce) Soó ssp. *transsilvanica* (Schur) S. E. Fröhner, should be replaced with *D. maculata* (L.) Soó ssp. *transsilvanica* (Schur) Soó, a combination used in contemporary literature. Furthermore, since nothing has been written about *Dactylorhiza* hybrids in Croatia, we have tried to summarize and briefly list all the known hybrids recorded in the national territory so far. From our observations, we conclude that Croatia still possesses a great richness of *Dactylorhiza* taxa in terms of the number of populations and their size, but it is not particularly rich in the number of taxa. According to our research, we accept seven species, one subspecies and four hybrids of *Dactylorhiza* in the flora of Croatia: *D. sambucina*, *D. romana*, *D. incarnata*, *D. majalis*, *D. saccifera*, *D. fuchsii*, *D. maculata* ssp. *transsilvanica*, *D. traunsteineri*, *D.* × *aschersoniana*, *D.* × *kerneriorum*, *D.* × *duftii* and *D.* × *braunii*. We hope that with this study and the presentation of our understanding of this genus

and its situation in Croatia, at least some of the long-standing problems concerning *Dactylorhiza* will be clarified, and that this paper will be of help to all future researchers dealing with Croatian *Dactylorhiza*.

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