

## MORPHOLOGICAL AND ANATOMICAL RELATIONSHIPS IN ALPINE-DINARIC POPULATIONS OF THE GENUS *IRIS* L., PALLIDAE SERIES (A. KERN.) TRINAJSTIĆ (IRIDACEAE)

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### ABSTRACT

The relationships within the Alpine-Dinaric and cultivated populations of the genus *Iris*, Pallidae series, have been analysed. Seven morphological characteristics (stem length, length of the largest leaf, greatest width of the largest leaf, length of the smallest leaf, greatest width of the smallest leaf, the number of leaves and the number of flowers) and seven leaf anatomical (length and width of stomata, length and width of epidermal cells, number of stomata and epidermal cells per mm<sup>2</sup> and length of styloids) have been used for this purpose. Relationships between populations were analysed by methods of multivariate statistics (Cluster, PCA and MST analyses). The results of Cluster and PCA analyses showed that, owing to leaf anatomical features, five main groups of the populations could be distinguished within the Pallidae series. Four of them belong to the species *I. pallida*, *I. cengialti*, *I. illyrica* and *I. pseudopallida*. The MST analyses showed that the fifth group contained mixed populations of *I. illyrica* and *I. pseudopallida*. The results point at the lack of taxonomic usefulness of the leaf anatomical features analysed and indicate that they caused successive geographical differentiation of the populations of the Pallidae series.

KEY WORD: Genus *Iris* L., Pallidae series (A. Kern.) Trinajstić, Alpine-Dinaric populations, morphological and anatomical relationships.

### INTRODUCTION

Within the genus *Iris* L. (Iridaceae) section *Iris* (Lawrence 1953), one of the most important and interesting series in Southeast Europe is the Pallidae series (A. Kern.) Trinajstić (Kerner 1871, Trinajstić 1976). This series was named on the basis of the cultivated species *Iris pallida* Lam., characterised by dry-skinned, snow-white spathe and pale blue flowers (Lamarck 1789).

Indigenous Alpine-Dinaric populations of the series, which are also characterised by dry-skinned spathe and pale to deep blue or violet coloured perigonium, were intensively investigated, with different taxonomic interpretations, in the 19th and at the beginning of the 20th century (Reichenbach 1840; Bertoloni 1842; Visiani 1842; Reichenbach 1847; Ambrosi 1854; Schlosser and Vukotinović 1869; Cesati et al. 1871; Kerner 1871; Tommasini 1875; Visiani 1877; Arcangeli 1882; Nyman 1882; Stapf 1887; Arcangeli 1894; Fiori 1896; Fritsch 1897; Marchesetti 1897; Ascherson and Graebner 1898/99; Gelmi 1900; Ascherson and Graebner 1906; Dalla Torre and Sarnthein 1906; Pampanini 1908, 1909; Dykes 1913; Paulin 1917; Diels 1930; Hayek 1933; Degen 1936).

Because of the morphological variability of these populations, botanists have expressed different opinions about the taxonomic positions of individual population groups of the

complex of related species of *Iris pallida* Lam. s.l. Some authors have admitted to this complex only one cultivated and naturalised variable species *I. pallida* Lam. (Hegi and Dünzinger 1909; Randolph and Rechner 1954; Ehrendorfer 1973; Webb and Chater 1980; Mathew 1981; Wraber 1998, 1999). Others have accepted two (Pampanini 1909; Dykes 1913; Hayek 1933; Mayer 1952; Lawrence 1953; Pignatti 1982), three (Köhlein 1981; Schulze 1988; Domac 1994; Scortegagna et al. 1996; Trpin and Vreš 1995) or numerous species of dry-skinned spathe irises in the Alpine-Dinaric area (Rac and Lovrić 1990).

Trinajstić (1976, 1983) was the first author to put the Alpine-Dinaric populations into the separate Pallidae series (A. Kern.) Trinajstić, with four species: *I. pallida* Lam. (distinguished as a horticultural species), *I. cengialti* Ambr. (endemic in the Alpine region), *I. illyrica* Tømm. (endemic to the northern Croatian Littoral and the Dinaric mountains) and *I. pseudopallida* Trinajstić (endemic to the southern Croatian Littoral). Recently, morphological analyses of the indigenous Alpine-Dinaric and horticultural populations, in which the morphological features did not show phenotypic plasticity, have provided confirmation for this view that there are four species in the Pallidae series (Mitić et al. 1999; Mitić and Pavletić 1999).

Some preliminary investigations showed that also anatomical features of leaves could be of diagnostic significance for the Pallidae series (Nikolić and Mitić 1991; Mitić and Pavlečić 1995). It is known that anatomical characteristics could be of great importance for the taxonomy of the genus *Iris* and the family Iridaceae (Goldblatt et al. 1984; Wu and Cutler 1985; Rudall 1986, 1994), as well as for other plants (Wallis 1965; Meidner and Mansfield 1968; Wilkinson 1979; Metcalfe 1985; Standley 1987; Fahn 1990; Hoot 1991; Franceschinelli and Yamamoto 1993; Splett et al. 1993). But know is also the existence of phenotypic plasticity of anatomical features, which depends on different factors, especially on ecological conditions of habitat (Meidner and Mansfield 1968; Cutter 1978; Wilkinson 1979) or sometimes on polyploidy (Aalders and Hall 1962; Wilkinson 1979; Brandham and Cutler 1981).

In this research we combined the results of quantitative morphological and leaf anatomical morphometry of the Pallidae series populations, with the intention of further explaining of the relationships within the series and to determine possible diagnostically valuable leaf anatomical features.

### MATERIALS AND METHODS

Twenty-five populations were sampled. Each population was represented by 2-20 specimens, depending on the extent of the populations (Fig. 1, Table 1). A total of 418 specimens from 21 populations collected from all over the Alpine-Dinaric area were analysed, as well as four control populations

of the species *I. pallida* of horticultural origin (Ble, Sam, Zdu and ZZr – for abbreviations see Table 1). The samples were collected from 1992 to 1997, only during the flowering time, to make the materials comparable.

For morphological analyses the plants were prepared by being pressed and dried in a steriliser at 47°C. Morphological features for morphometry were used according to Melkó (1976) and Mitić et al. (1999) and included: stem length (without flowers) (cm), length of the largest leaf (cm), greatest width of the largest leaf (cm), length of the smallest leaf (cm), greatest width of the smallest leaf (cm), the number of leaves and the number of flowers.

For anatomical analysis the whole leaves were prepared by fixing in FAA mixture (Cutler 1978). Leaf surface preparations were made by the scraping method (Cutler 1978), in the middle parts of the leaves. The following epidermal features were performed: length and width of stomata (µm), length and width of epidermal cells (µm), number of stomata and epidermal cells per mm<sup>2</sup>. Also, length of styloids was measured (elongated, prism – shaped crystals of calcium oxalate in the mesophyll layer, but visible through the epidermis). Twenty measurements of each parameter were made on every specimen by an ocular micrometer. The arithmetical means of every feature per population were taken as a valid value for every population (OTU).

For statistical analysis, we used 14 variables: seven morphological and seven leaf anatomical features (see below).

The row data matrix with 25 OTU-s (populations) and 14 variables were standardised by variables. The means of each variable were subtracted. The differences were then divided by

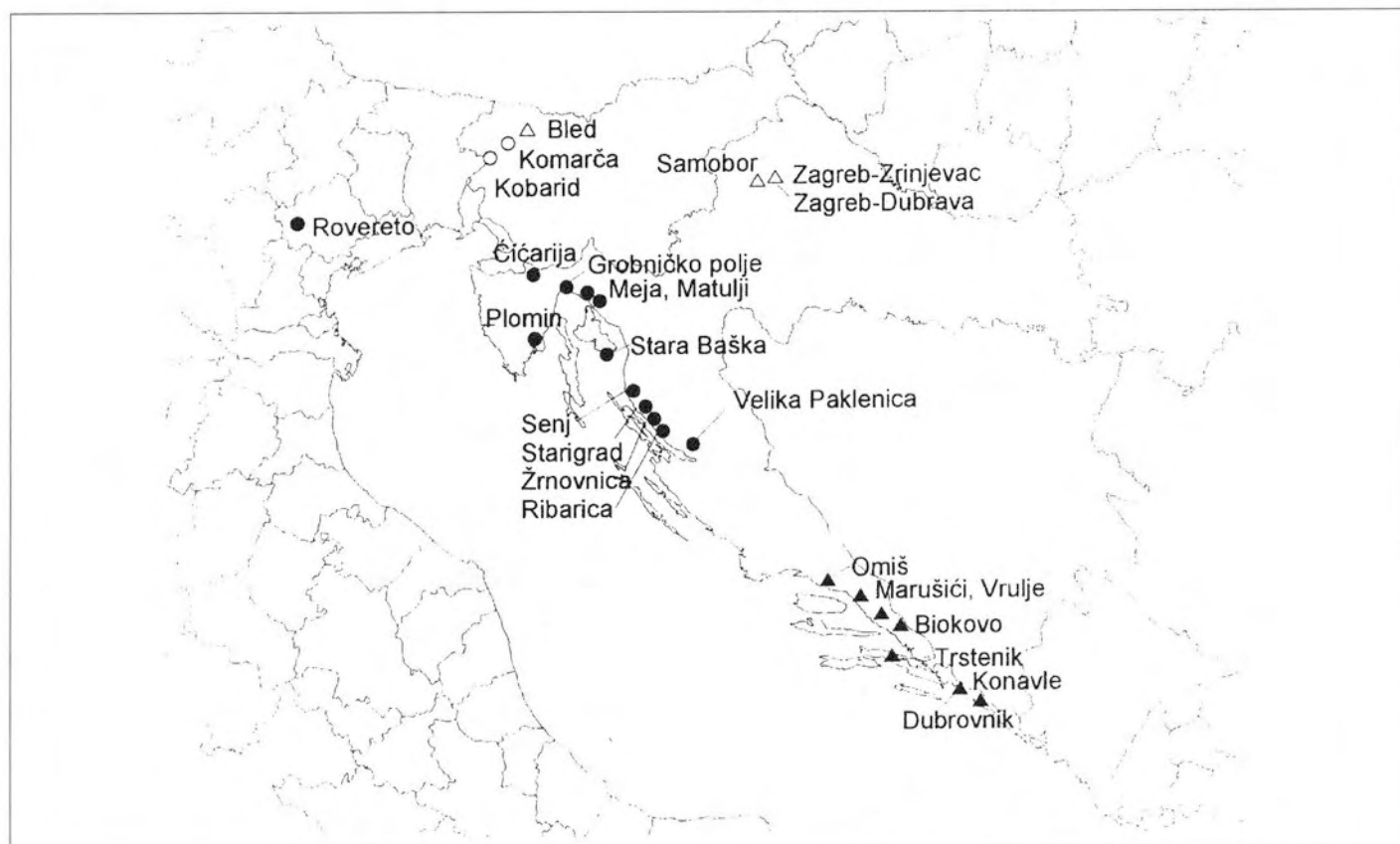


Fig. 1. The sampled populations of the Pallidae series:

- – *I. cengialti*
- – *I. illyrica*
- ▲ – *I. pseudopallida*
- △ – *I. pallida*

TABLE 1. The sampled populations of the Pallidae series: name of locality (with abbreviations); co-ordinates: Latitude (N) and Longitude (E); no. morph. – number of specimens morphologically analysed; no. anat. – number of specimens anatomically analysed.

| Locality (mark)                | Latitude (N) | Longitude (E) | no. morph. | no. anat. |
|--------------------------------|--------------|---------------|------------|-----------|
| Biokovo (Bio)                  | 43° 17' 18"  | 17° 03' 22"   | 20         | 20        |
| Bled (Ble)                     | 46° 21' 00"  | 14° 06' 55"   | 2          | 2         |
| Čičarija (Cic)                 | 45° 27' 12"  | 14° 01' 00"   | 5          | 5         |
| Dubrovnik (Dub)                | 42° 38' 13"  | 18° 08' 20"   | 20         | 20        |
| Grobničko polje (Gro)          | 45° 22' 13"  | 14° 28' 48"   | 10         | 10        |
| Kobarid (Kob)                  | 46° 16' 30"  | 13° 33' 05"   | 15         | 15        |
| Komarča (Kom)                  | 46° 17' 47"  | 13° 47' 40"   | 10         | 10        |
| Konavle (Kon)                  | 42° 32' 18"  | 18° 17' 32"   | 10         | 10        |
| Marušići (Mar)                 | 43° 24' 50"  | 16° 46' 42"   | 9          | 9         |
| Matulji (Mat)                  | 45° 21' 50"  | 14° 20' 05"   | 7          | 7         |
| Meja (Mej)                     | 45° 17' 40"  | 14° 36' 38"   | 5          | 5         |
| Omiš (Omi)                     | 43° 27' 03"  | 16° 42' 00"   | 5          | 5         |
| Plomin (Plo)                   | 45° 08' 22"  | 14° 10' 50"   | 5          | 5         |
| Ribarica (Rib)                 | 44° 33' 06"  | 15° 03' 07"   | 20         | 20        |
| Rovereto (Rov)                 | 45° 45' 30"  | 11° 40' 00"   | 2          | 6         |
| Samobor (Sam)                  | 45° 48' 05"  | 15° 43' 30"   | 20         | 20        |
| Senj (Sen)                     | 44° 49' 00"  | 14° 44' 59"   | 16         | 16        |
| Stara Baška (Stb)              | 44° 57' 26"  | 14° 41' 37"   | 20         | 20        |
| Starigrad (Stg)                | 44° 46' 07"  | 14° 54' 00"   | 20         | 20        |
| Trstenik (Trs)                 | 42° 55' 03"  | 17° 24' 58"   | 10         | 10        |
| Velika Paklenica (Vpa)         | 44° 18' 08"  | 15° 28' 47"   | 15         | 15        |
| Vrulje (Vru)                   | 43° 24' 10"  | 16° 53' 12"   | 12         | 12        |
| Zagreb-Dubrava (cult.) (Zdu)   | 45° 49' 55"  | 16° 03' 30"   | 20         | 20        |
| Zagreb-Zrinjevac (cult.) (ZZr) | 45° 53' 42"  | 16° 03' 00"   | 20         | 20        |
| Žrnovnica (Zrn)                | 45° 06' 35"  | 14° 51' 00"   | 20         | 20        |

the standard deviation. A standardised data matrix was the input matrix for cluster and principal component analyses (PCA).

Cluster analysis was done by calculating the average taxonomic distance. The clustering method was UPGMA (Unweighted pair-group method, arithmetic average). The results were presented as a dendrogram.

PCA was carried out by computing eigenvalues and eigenvectors from the variables correlation matrix. The three dimensions were retained. The eigenvectors matrix and the eigenvalues, their percentages, and their cumulative percentages are listed. The results, the spatial relationships between populations, are presented in the form of a 3D-scatter diagram, each axis according to three principal components. Minimum spanning tree (MST) was used to detect local distortion – pairs of points which look close together in a plot, but actually are more distant if other dimensions – MST tree – are superimposed on the 3D PCA scatter diagram.

All calculating was done by the NtSys-pc 1.6 package (Rohlf 1990).

## RESULTS

The arithmetical means of the measurements of epidermal characteristics and length of styloids for each of population are shown in Table 2.

Morphometry of seven analysed morphological features was taken from Mitić et al. (1999).

The results of the hierarchical cluster analysis obtained on the basis of 14 variables (seven quantitative morphological and seven quantitative leaf anatomical features) are shown in a dendrogram (Fig. 2), which reveals five main groups of populations (marks A-E in Fig. 2).

At step one, all cultivated populations (mark A in Fig. 2) were separated from the whole sample, with coefficient of

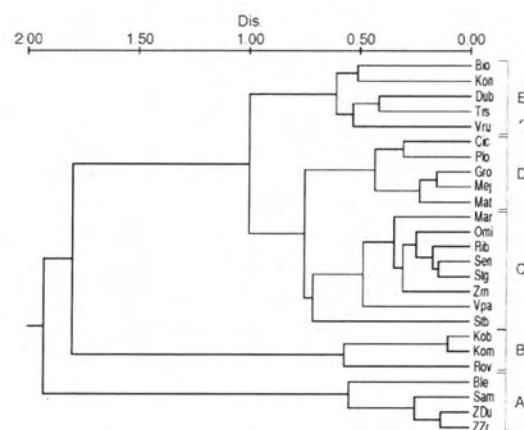


Fig. 2. UPGMA dendrogram based on seven quantitative morphological and seven quantitative leaf anatomical variables in 25 populations (OTUs) of the Pallidae series (A-E population groups; A – cultivated populations, B – Alpine populations; C – miscellaneous northern and central Adriatic populations; D – northern Adriatic Littoral populations and E – southern Adriatic Littoral populations).

distance  $D = 1.92$ . In the rest of the sample the Alpine populations (mark B in Fig. 2) were clearly separated from the group of Croatian Littoral populations (marks C-E in Fig. 2), with coefficient of distance  $D = 1.79$ .

Croatian Littoral populations comprised three main clusters. Southern Adriatic populations (mark E in Fig. 2) were first split off from the remaining populations ( $D = 1.0$ ). Northern Croatian Littoral populations (mark D in Fig. 2) diverged from the cluster of miscellaneous populations from the northern (Stb, Sen, Stg, Zrn, Rib and Vpa) and central (Omi, Mar) Adriatic coast (mark C in Fig. 2) with coefficient of distance  $D = 0.74$ .

The results of PCA on the whole confirmed the results of cluster analysis (Table 3, Fig. 3). The total variability of the first PC axis contributed as much as 55.84% of the total inter-species variability, and the first three PC axes contributed as much as 94.23% of the cumulative variabilities, which indicated a good representation of the relationships among the populations, that is, the reliability of PC analysis. Other dimensions explained very little additional variation and could probably be ignored. The distribution along the first PC axis is in a large measure contributed to by the length of stomata, the greatest width of the largest leaf, number of epidermal cells per mm<sup>2</sup>, length of the largest leaf and length of epidermal cells. The number of leaves, length of the smallest leaf, width of epidermal cells and stem length are most correlated with the second PC axis, and the number of leaves and width of stomata with the third.

The presence of the five groups of populations within the Pallidae series (marks A-E in Fig. 3), shown by PCA scatter diagram (Fig. 3) was the same as in cluster analysis (Fig. 2). Group C contained populations from different geographical regions, i.e. from the north and central Adriatic coast. Superimposed MST analyses showed the transitional characteristics of group C. The population of Velika Paklenica (Vpa) was joined to the population of Grobnik (Gro) and was responsible for the connection of group C with the northern Croatian Littoral populations (group D). The population of Marušići (Mar) was joined to the population of Vrulje (Vru) and was responsible for the connection with the group of the southern Croatian Littoral populations (group E).

## DISCUSSION

Multivariate analysis, on the basis of 14 quantitative morphological and leaf anatomical characteristics (Table 3, Figs

2, 3), revealed the presence of five groups within the Pallidae series. To differentiate the groups established, in PCA analysis the most significant features turned out to be: length of stomata, the greatest width of the largest leaf, number of epidermal cells per mm<sup>2</sup>, length of the largest leaf and length of epidermal cells.

The length of stomata, the greatest width of the largest leaf, the number of epidermal cells per mm<sup>2</sup>, length of the largest leaf and length of epidermal cells (Table 3) mostly brought about a separation of cultivated irises (mark A in Figs 2, 3) and Alpine (mark B in Figs 2, 3) from the rest of the sample. The longest lengths of stomata and epidermal cells and the lowest numbers of epidermal cells per mm<sup>2</sup> (Table 2) were in the cultivated (group A) and Alpine populations (group B), and the south Dalmatian populations had values opposite to those parameters (group E). The values of the morphological characteristics of the same populations – length and the greatest width of the largest leaf were the highest in the cultivated populations and also very high in the Alpine populations (cf. Mitić et al. 1999).

The features that contributed most to the separation of all five groups (marks A-E in Figs 2, 3) were the number of leaves, length of the smallest leaf and width of epidermal cells and stem length (Table 3). Cultivated populations had the highest values of the named morphological features in the whole sample (cf. Mitić et al. 1999), but Alpine populations had the widest epidermal cells (Table 2).

The better separation of all the Adriatic populations (marks C-E in Figs 2, 3) was caused mostly by number of leaves and width of stomata (Table 3). Southern and central Croatian Littoral populations had more leaves than the northern populations (cf. Mitić et al. 1999), but northern and central Croatian Littoral populations had straighter stomata than southern populations (Table 2).

TABLE 2. Arithmetical means of the leaf anatomical features of the 25 populations of the Pallidae series (LS – length of stomata, WS – width of stomata, LE – length of epidermal cells, WE – width of epidermal cells, NS – number of stomata per mm<sup>2</sup>, NE – number of epidermal cells per mm<sup>2</sup>, S – length of styloids).

| Population   | LS (μm) | WS (μm) | LE (μm) | WE (μm) | NS    | NE     | S (μm) |
|--------------|---------|---------|---------|---------|-------|--------|--------|
| Biokovo      | 46.74   | 45.23   | 279.56  | 44.26   | 68.62 | 104.63 | 127.66 |
| Bled         | 50.90   | 49.68   | 299.02  | 49.98   | 48.60 | 74.60  | 169.53 |
| Čičarija     | 47.97   | 42.78   | 301.76  | 49.03   | 57.16 | 79.46  | 157.06 |
| Dubrovnik    | 44.74   | 44.96   | 225.32  | 40.68   | 76.82 | 112.34 | 121.74 |
| Grobnik      | 46.10   | 43.94   | 275.66  | 46.62   | 60.37 | 86.86  | 155.13 |
| Kobarid      | 52.72   | 57.15   | 330.53  | 57.52   | 44.45 | 69.59  | 168.10 |
| Komarča      | 52.84   | 57.19   | 334.91  | 56.84   | 44.17 | 69.91  | 167.12 |
| Konavle      | 45.36   | 44.77   | 267.38  | 42.23   | 73.52 | 109.64 | 119.20 |
| Marušići     | 43.98   | 44.11   | 246.40  | 42.35   | 70.54 | 109.99 | 121.79 |
| Matulji      | 44.82   | 43.38   | 275.93  | 46.87   | 60.45 | 87.60  | 154.87 |
| Meja         | 46.19   | 44.70   | 272.80  | 45.08   | 59.67 | 86.35  | 153.62 |
| Omiš         | 45.35   | 43.65   | 253.65  | 44.09   | 68.20 | 107.12 | 122.64 |
| Plomin       | 46.64   | 43.56   | 295.08  | 47.83   | 60.77 | 86.32  | 155.47 |
| Ribarica     | 44.43   | 44.16   | 251.92  | 43.41   | 65.83 | 105.49 | 125.89 |
| Rovereto     | 53.91   | 53.14   | 358.46  | 63.31   | 41.42 | 73.12  | 176.22 |
| Samobor      | 51.71   | 50.65   | 324.61  | 50.83   | 50.77 | 70.91  | 162.10 |
| Senj         | 44.28   | 43.90   | 253.68  | 43.74   | 64.98 | 105.32 | 127.73 |
| Stara Baška  | 43.60   | 43.67   | 233.53  | 43.46   | 65.78 | 104.76 | 133.31 |
| Starigrad    | 44.25   | 44.02   | 246.66  | 43.73   | 65.39 | 105.47 | 124.35 |
| Trstenik     | 43.75   | 44.52   | 234.52  | 41.28   | 75.58 | 110.53 | 121.91 |
| V. Paklenica | 46.51   | 44.08   | 296.61  | 44.91   | 61.82 | 99.88  | 122.16 |
| Vrulje       | 44.17   | 44.24   | 228.30  | 41.52   | 72.17 | 109.56 | 121.79 |
| Zagreb (Zdu) | 50.57   | 49.71   | 321.56  | 48.48   | 53.30 | 74.11  | 153.69 |
| Zagreb (ZZr) | 51.53   | 50.39   | 320.44  | 48.82   | 53.25 | 74.15  | 154.44 |
| Žrnovnica    | 44.35   | 43.80   | 230.11  | 43.89   | 65.71 | 105.32 | 124.78 |



(Meidner and Mansfield 1968; Esau 1977; Cutter 1978; Wilkinson 1979; Wilder 1985 etc.). Bačić (1982) has shown that the number and dimension of stomata varied depending on the influence of light and the age of plants. Nikolić (1997) has cited the phenotypic plasticity of the width of epidermal cells, caused by different light conditions. According to Pazourek (1970) the stomatal frequency decreases with the decrease of light intensity. Knecht and O'Leary (1972) observed the development of a higher number of stomata with increased light intensity, Lucansky and Clough (1986) have stated the dependence of leaf anatomical features on xeromorphy and mesomorphy of habitat etc.

Leaf anatomical characteristics of the Pallidae series were possibly correlated with geographical co-ordinates and the related climatic conditions, especially the gradient of habitat xeromorphy or mesomorphy (*I. pallida* and *I. cengialti* are continental and *I. illyrica* and *I. pseudopallida* Mediterranean species). The populations of *I. pallida* were collected from a continental, typically mesomorphic area, as were those of *I. cengialti*, picked on high Alpine Mountains. The littoral, xeromorphous species *I. illyrica* and *I. pseudopallida* were grouped, due to leaf anatomical features, in three groups. Group D contained typical sub-mediterranean populations of the northern part of the Croatian Littoral, from the range of the species *I. illyrica*, with the smallest xeromorphous effect in Littoral populations. Group E consisted of typical Mediterranean populations of extreme xeromorphous southern part of Croatian Littoral, from the range of the species *I. pseudopallida*. Group C was represented with mixed Mediterranean populations from moderate xeromorphous stands of both species.

Thus successive geographical differentiation of populations of the Pallidae series revealed ecological clinal variability within the series, which indicates the lack of taxonomic usefulness of the anatomical features analysed.

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MORFOLOGICZNE I ANATOMICZNE ZALEŻNOŚCI  
MIĘDZY ALPEJSKO-DYNARSKIMI POPULACJAMI  
Z RODZAJU *IRIS* L., SERIA *PALLIAE* (A. KERN.) TRINAJSTIĆ (*IRIDACEAE*)

STRESZCZENIE

Analizowano zależności między alpejsko-dynarskimi i hodowanymi populacjami z rodzaju *Iris*, seria *Palliae*. Badano siedem cech morfologicznych oraz siedem cech anatomicznych. Podobieństwa między populacjami analizowano metodami statystycznymi wielozmiennymi (PCA, MST). Wyniki analiz statystycznych pokazują, że dzięki cechom anatomicznym liścia można było wyodrębnić pięć głównych grup populacji w ramach serii *Palliae*. Cztery z nich należą do gatunków *I. pallida*, *I. cengialti*, *I. illyrica* i *I. pseudopallida*. Analizy MTS wykazały, że piąta grupa zawierała populację mieszaną *I. illyrica* oraz *I. pseudopallida*. Uzyskane wyniki wskazują na brak taksonomicznej użyteczności analizowanych cech anatomicznych liścia, oraz że są one ważne dla sukcesywnego różnicowania geograficznego populacji z serii *Palliae*.

SŁOWA KLUCZOWE: rodzaj *Iris*, seria *Pallidae*, populacje alpejsko-dynarskie, zależności morfologiczne i anatomiczne.