FORESTRY

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GEOMETRIC MORPHOMETRIC ANALYSIS OF CONE SCALES FOR PHENOTYPIC DIFFERENTIATION OF *LARIX* SPECIES (PINACEAE)

Research article

Abstract

Methods of geometric morphometrics were used to analyze differentiation of three larch species – *Larix gmelinii*, *L. cajanderi*, and *L. sibirica*, which are the most common larch species in North Asia, by the shape of the cone scales. The samples of seed-bearing scales of mature cones were collected from 185 trees in 8 populations, which represented the different regions of the *Larix* species areas. Ten outline points on one side of the cone scales were chosen to characterize their shape. Patterns of shape variation were depicted using Generalized Procrustes Analysis (GPA). PCA results of partial warps (PW) revealed the shape differences of cone scales among the three species of *Larix.* The CVA of relative warps (PCA scores) showed that the *Larix* species were all successfully discriminated, and populations within the species were considerably differentiated. Geometric morphometrics can be used as an effective tool to analyze inter- and intra-specific differentiation of *Larix* species based on the shape of cone scales.

Keywords: Geometric morphometrics, cone scale shape*,* *Larix* taxonomy.

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ГЕОМЕТРИЧЕСКИЙ МОРФОМЕТРИЧЕСКИЙ АНАЛИЗ СЕМЕННЫХ ЧЕШУЙ ШИШЕК ДЛЯ ФЕНОТИПИЧЕСКОЙ ДИФФЕРЕНЦИАЦИИ ВИДОВ *LARIX* (PINACEAE)

Научная статья

Аннотация

Проведено тестирование геометрической морфометрии семенных чешуй шишек для внутри-и межвидовой дифференциации лиственниц на примере трех видов, наиболее распространённых на северо-востоке Азии – *Larix gmelinii*, *L. cajanderi*, and *L. sibirica.* Образцы семенных чешуй шишек собраны с 185 деревьев в 8 популяциях, которые представляют разные районы ареалов лиственниц. Десять контурных точек на одной стороне чешуй были выбраны для характеристики их формы. Особенности вариации формы чешуй были проанализированы с использованием стандартных методов геометрической морфометрии, включая анализ главных компонент (PCA) частных деформаций и канонический дискриминатный анализ (CVA) относительных деформаций. PCA результаты частных деформаций чешуй выявили различия формы чешуй среди трех исследованных видов лиственниц. Канонический анализ относительных деформаций чешуй показал, что все три вида лиственниц хорошо разделяются, а также значительно дифференцированы популяции внутри видов. Геометрическая морфометрия может быть использована в качестве эффективного инструмента для анализа внутри и межвидовой дифференциации лиственниц по форме семенных чешуй шишек.

Ключевые слова: геометрическая морфометрия, форма семенных чешуй, *Larix* таксономия.

1. Introduction

Methods of geometric morphometrics have been actively developed since the 1990s [1]. This method is based on an analysis of variation in the coordinates of landmarks and outline points that characterize the shape of morphological structures, using multivariate statistics. The standard procedure of geometric morphometric analysis, referred to as a Generalized Procrustes Analysis (GPA), followed by projection of the aligned coordinates of landmarks on a linear tangent space for multivariate analyses, and the graphical visualization of results in terms of the configurations of landmarks. A number of books [2], [3], and review articles [4], [1] provide a comprehensive theory and methods of geometric morphometrics and describe its application in biological research. The effectiveness of this approach for describing population structure of conifers was previously demonstrated in the studies of *Pinus pumila* (Pall.) Regel [5] and *Larix cajanderi* Mayr [6].

Taxonomy of the genus *Larix* Mill. (Pinaceae) remains controversial because of the high rates of interspecific hybridization and continuing processes of speciation in the regions where larch species ranges overlap [7]. Although variability and taxonomy of larch was extensively studied in the last century, that research did not provide sufficient basis for determining the status and genesis of East-Siberian and Far-Eastern taxa [8]. The most widespread larch species in Northeast Asia are *L. gmelinii* Rupr. (Rupr), *L. cajanderi*, and *L. sibirica* Ledeb., whose distribution ranges stretch from West Siberia to the coast of the Sea of Okhotsk in the east. The data on the abundance and distribution of *L. gmelinii* and *L. cajanderi* are contradictory. The status of *L. cajanderi* as the species has been supported by genetic and morphological research conducted in Russia and based on abundant factual evidence [9], [10], but this species has not been recognized until now and is regarded as the synonym of the typical variety of *L. gmelinii* (*L. gmelinii* var. *gmelinii*) [11], [12]. The differentiation of larch species in Siberia and Far-East is associated with the history of their origin and distribution in this region. It has been assumed that *L. gmelinii* emerged in East Asia shortly before the Pleistocene, and, owing to its tolerance of freezing, waterlogging, and permafrost, migrated west, displacing *L. sibirica* [13], [14], and *L. cajanderi* is a younger species, which formed in the late Pleistocene in the initial populations of *L. gmelinii* [15], [7].

In larch taxonomy, the major diagnostic markers are cone structure characters, the shape of cone scales being one of the most significant characters [16]. Studying variations in generative organs is important for understanding the taxonomic differentiation of the larch species growing in North Asia and showing exceptional polymorphism. The purpose of the present study was to test the methods of geometric morphometrics as a tool for analyzing inter- and intra-specific larch differentiation by the shape of cone scales.

2. Material and method

2.1. Samples

Three samples of cones were collected from *L. cajanderi* populations in Yakutia and Magadan Oblast; two samples of cones were collected from *L. gmelinii* populations in Evenkia and Transbaikalia, and three samples of cones were collected from *L. sibirica* populations in South Siberia (Table 1).

Table 1 – Characteristics of studied samples from *Larix* populations

Species	Geographic location of the studied populations	Geographic coordinates	Total trees/scales in the sample
L. cajanderi	Yakutia, Namsky ulus	N62º35′ E129º43'	20/96
	Magadan region, Bol. Annachag range	N62°03′ E149°09′	30/109
	Yakutia, surroundings of Chersky village (N-Kolyma)	N68º45′ E161º19′	22/86
L.gmelinii	Evenkia, surroundings of Tura village	N64°19′ E100°07′	22/110
	East Transbaikalia, valley of the Ingoda river	N51° 49′ E113° 09′	23/116
L. sibirica	Altai, Cherginsky range foothills	N51º 34′ E 85º34′	20/103
	Tyva, West Sayan, Ak-Dovurak environs	N51º 23′ E 90º 27′	22/109
	Khakasia, Kuznetskiy Alatau foothills	N 54º 59′ E89º 49′	26/133

Cones were collected from 20–30 trees in each population. Fifteen to twenty cones were collected from each tree; five largest cones were selected, and 3–5 scales were taken from their middle parts and scanned. Scanning was done using an Epson Perfection V500 Photo scanner. After scanning, 5–10 scales, which were the most representative, were selected for each tree.

2.2. Morphometric data

To characterize shape variation of cone scales using methods of geometric morphometrics, outline points were placed along the scale edges followed by analysis of partial warp scores, describing individual differences in shape of scales. Outline points were placed along the scanned scales with a TPSDig screen digitizer [17], using angular algorithm (Figure 1a). Cone scales are bilaterally symmetric structures, and, therefore, 10 outline points were placed on one side of the scales. Points 1 and 2 were placed on the axis of symmetry at the base and at the apex of the scale; point 3 corresponded to the point of curvature in the upper part of the scale in *L. cajanderi* and *L. gmelinii*, but in *L. sibirica*, it was placed at an angle of 15 degrees to the axis of symmetry. Other outline points (4, 5, 6, 7, 8, 9, and 10) were placed at angles of 30, 50, 70, 90, 110, 130, and 145 degrees to the axis of symmetry (Figure 1a).

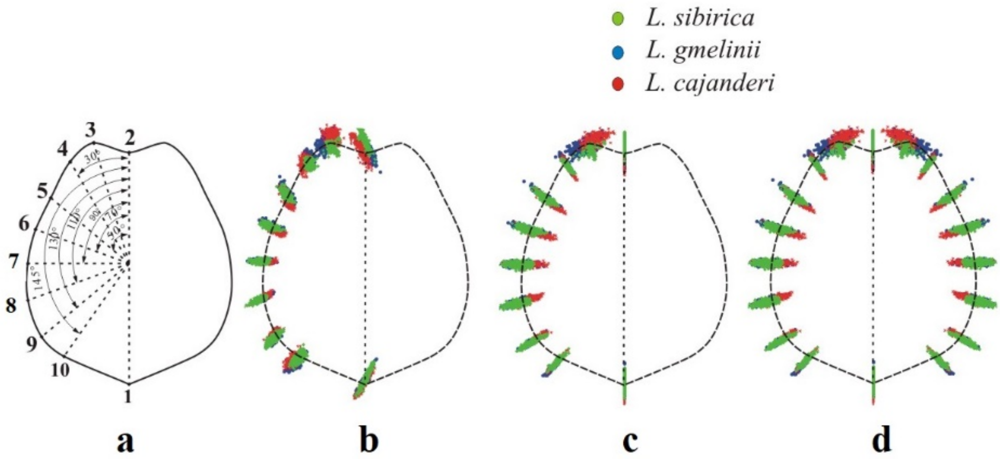

Figure 1 – Graphical representation of the morphometric analysis. *a*: outline points recorded on cone scale, *b*: Procrustes superimposed outline points of 870 cone scales from 8 populations of *Larix* species; *c*: the cone scale samples after Sliding Baseline Registration (SBR); *d*: reconstruction of the whole cone-scales by reflecting duplicated SBR-outline point coordinates across the midline

Initial coordinates of the outline points were aligned using Procrustes superimposition of the cone scale sample with the average configuration, common for the three species (Figure 1b), in the CoordGen6 program [18]. For graphical presentations of the statistical results, Sliding Baseline Registration (SBR), which prevents rotation of the symmetry axis of morphological structures, was used (Figure 1c). To visualize results of analysis, images of whole scales were obtained by duplicating the outline points coordinates and reflecting them over the axis of symmetry (Figure 1d).

2.3. Statistical analysis

The data were processed and analyzed using Integrated Morphometrics Programs software [18]. The methods of geometric morphometrics used for the present analysis are also described in Zelditch et al. [3]. The main directions of the scale shape variation were revealed using the Principal Component Analysis (PCA) of partial warp scores including uniform shape deformations in the PCAGen6N program [18]. Differences in shape of cone scales between species were determined by paired comparison of the samples in the TwoGroup6h program [18]. The Procrustes distance between means of the samples was calculated as the sum of the squared distances between corresponding outline points. To test the statistical significance of shape differences between the species, Bootstrap resampling-based Goodall's F-test (for 900 replications) was used for coordinates of contour points of cone scales in the Procrustes superimposition The differentiation of the species or populations was analyzed using Canonical Variates Analysis (CVA) based on PCA- scores [18], [3].

3. Results and discussion

PCA of partial warps of the scales revealed four main components, which accounted for 91% of the total shape variation of the cone scales for the three larch species. Vector visualization of these transformations, which characterize the main directions of scale shape variation corresponding to the maximal and minimal values of the four principal components, is shown in Figure 2.

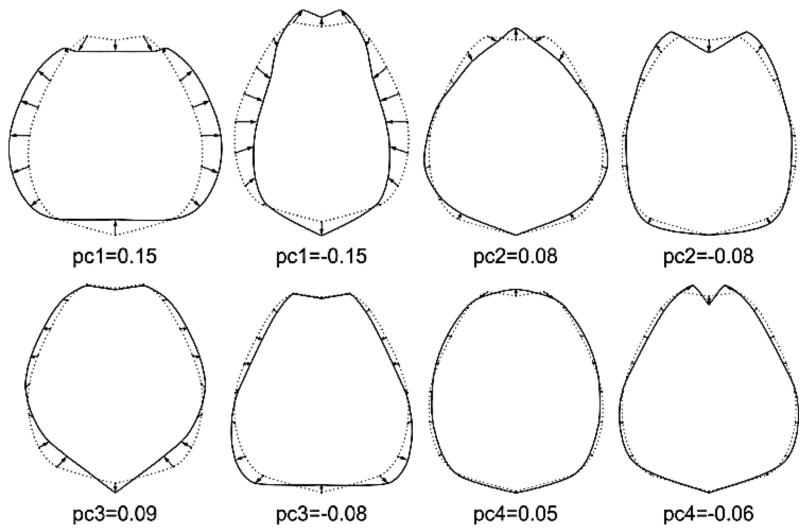

Figure 2 – Shape variation of the cone scales in the three *Larix* species. Arrows indicate the changes in position of outline points of reference (mean) scale configuration in accordance with the maximum and minimum values of the four principal components

The utmost scale shape variation in the three larch species (55.5% of the total variance in partial warp scores) was associated with the variations in the scale width and length explained by the first principal component. The second principal component (16.7% of the total variance) characterized scale shape variations from broadly ovoid scales with rounded or pointed tips to ovoid ones, with notched upper edges. The third principal component (13.7% of the total variance) accounted for variations in notched scales from the spade- to heart-shaped scales. The fourth principal component (7% of the total variance) characterized variations in the depth of the notch and the width of the upper part of the scales.

The ordination of samples on the plane of principal components gave some indication of the differences in the directions of shape variations of the scales from the three larch species (Figure 3). The *L. sibirica* sample occupied an intermediate position on PC1 and prevailed in the region of positive values on PC2, which corresponded to the presence of ovoid scales with no notch on the upper edge. The *L. gmelinii* and *L. cajanderi* samples with notched scales varied within a wide range of values of the first principal component: *L. gmelinii* prevailed in the region of positive values on PC1, which corresponded to the presence of the scales broader than those of *L. cajanderi*; the scales of *L. cajanderi* were more elongated, and it prevailed in the region of negative values on PC1.

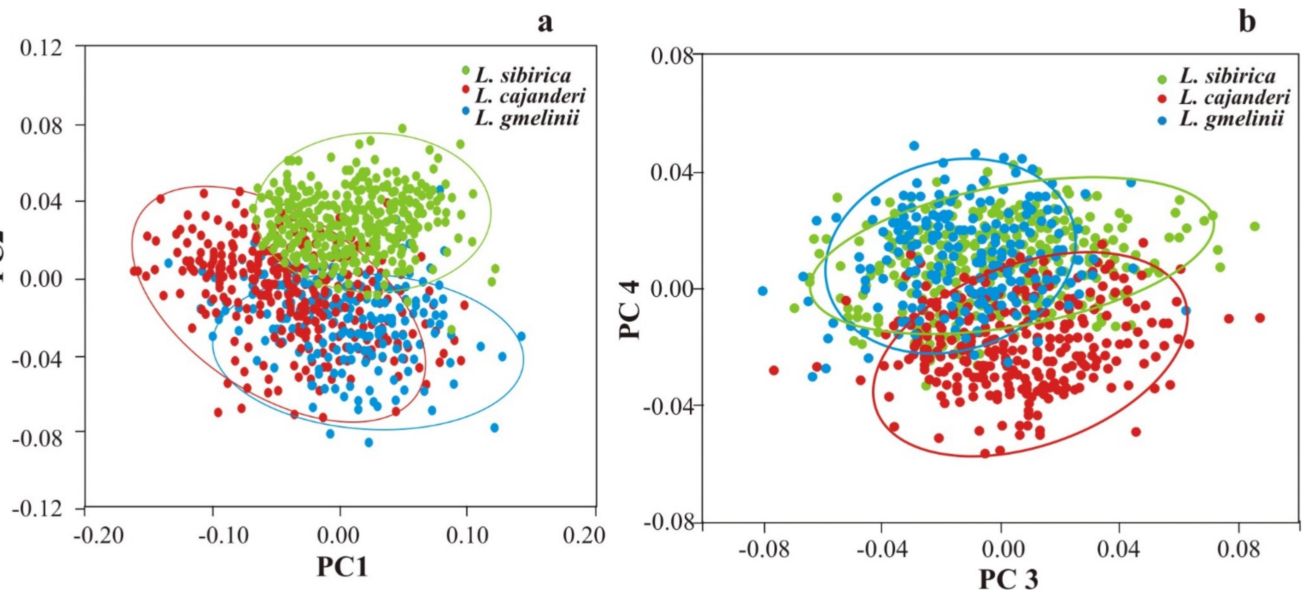

Figure 3 – PCA-ordination of larch samples based on shape of the cone scales: a) plot of PC1 (53.5% of total variation) and PC2 (16.7% variation) showing 90% confidence ellipses of *Larix* species means; b) plot of PC3 (13.7% of total variation) and PC4 (7.0% variation) showing 90% confidence ellipses of *Larix* species means

Species differentiation was also observed on the third and fourth principal components: *L. sibirica* and *L. gmelinii* samples occupied the region of positive values on the fourth principal component, which corresponded to the presence of oval scales with rounded or flat tips, and the *L. cajanderi* sample occupied the region of negative values, corresponding to the deeply notched scales. Differentiation on the third principal component was less significant: the *L. gmelinii* sample with the broader spade-shaped scales was shifted to the region of negative values, and the *L. sibirica* and *L. cajanderi* samples with heart-shaped scales were shifted to the region of positive values. Canonical variate analysis resulted in distinct differentiation between the three larch species (Figure 4).

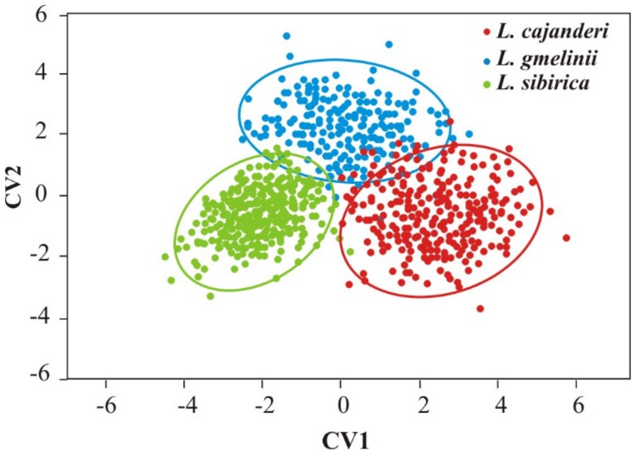

Figure 4 – Scatterplot of canonical variates axes 1 and 2 for canonical variate analysis (CVA) of PCA scores. Plot of CV1 (53.5% of total variation) and CV2 (16.7% variation) showing 90% confidence ellipses of species means of CVA axes scores

Mahalanobis and Procrustes distances confirm significant differences between species in the shape of cone scales (Table 2).

Table 2 – Differences in the cone scale shapes among the *L. cajanderi, L. gmelinii*, and *L.sibirica* species. Mahalanobis distances (right) & Procrustes distances (left): *p*-values (above); distances between species (below)

	L. cajanderi	*L. gmelinii*	*L.sibirica*	*L. cajanderi*	*L. gmelinii*	*L.sibirica*
L. cajanderi	–	<.001	<.001	–	<.001	<.001
L. gmelinii	0.0533	–	<.001	10.46	–	<.001
L.sibirica	0.0647	0.0501	–	19.89	10.29	–

Although *L. cajanderi* and *L. gmelinii* are closely related species, the distances between these species and *L. sibirica* are different: *L. cajanderi* is differentiated from *L. sibirica* to a greater extent than *L. gmelinii* (Table 2). The reason for this is that the *L. gmelinii* population from Transbaikalia (the Ingoda population) is located close to the distribution range of *L. czekanowskii* Szafer – the *L. sibirica* and *L. gmelinii* hybrid.

Canonical variate analysis of the matrices of relative deformations of scales calculated for each species showed intraspecific differentiation of larches (Figure 5).

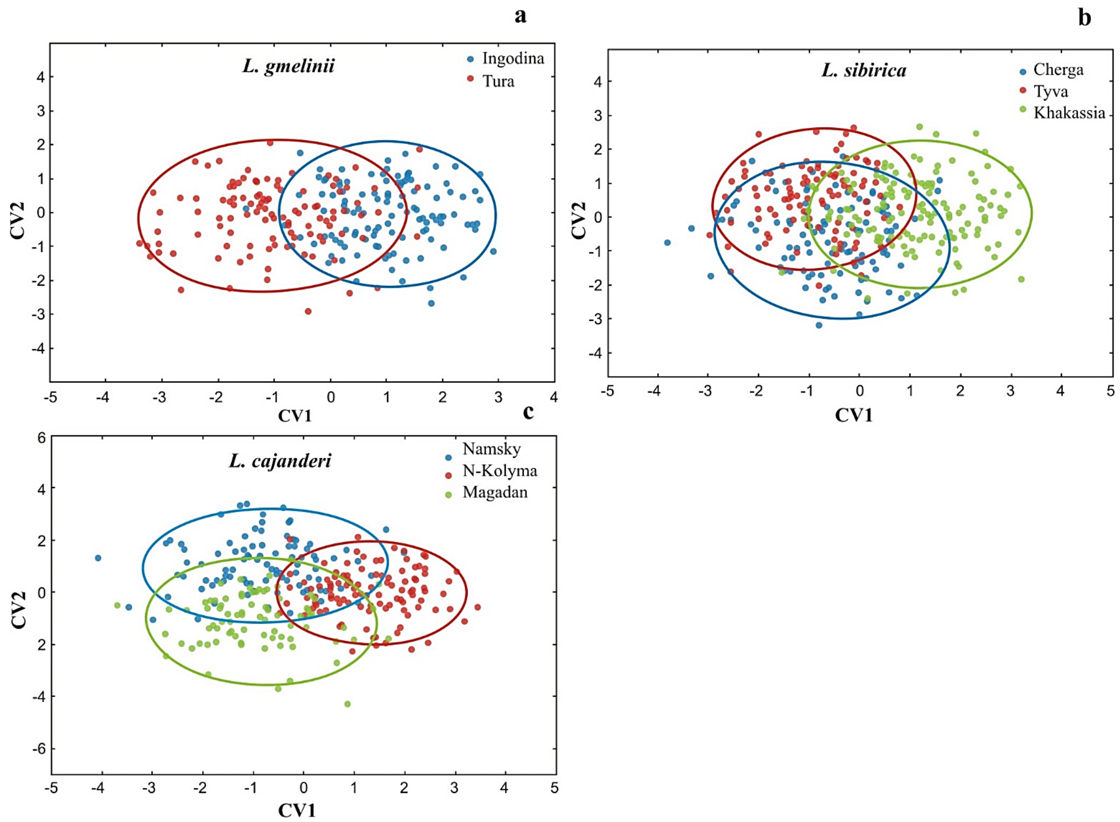

Figure 5 – Scatterplot of canonical variates axes 1 and 2 for canonical variate analysis (CVA) of *Larix* populations data. Plot of CV1 and CV2 showing 90% confidence ellipses of means of CVA axes scores for *Larix* populations: *a)* plot of *L. gmelinii* populations (CV1 59.9% and CV2 40.1% of total variation); *b)* plot of *L. sibirica* populations (CV1 90% and CV2 10% of total variation); *c)* plot of *L. cajanderi* populations (CV1 79.2% and CV2 20.8% of total variation)

Mahalanobis distances were estimated to confirm significant differences between populations of the same species in the shape of cone scales (Table 3). The highest degree of differentiation was noted for populations of *L. cajanderi*.

Table 3 – Differences in the cone scale shapes among populations of the *Larix* species.
Mahalanobis distances between populations (below); *p*-values (above)

Distances between populations of *L. cajanderi*				Distances between populations of *L. sibirica*			
	Namsky	N-Kolyma	Magadan		Altay	Tyva	Khakasia
Namsky	–	<.001	<.001	Altay	–	<.001	<.001
N-Kolyma	5.56	–	<.001	Tyva	1.59	–	<.001
Magadan	4.60	5,92	–	Khakasia	3.59	4.50	–

The *L. sibirica* sample collected at the foothills of the Kuznetskiy Alatau differed considerably from the samples of populations from Altay and Tyva (Figure 5 b, table 3), although the three *L. sibirica* populations were of the Upper-Yenisei geographic race. The high polymorphism of the Upper-Yenisei geographic race of *L. sibirica*, commonly occurring in the northeast Altay, Kuznetskiy Alatau, and the West and East Sayan Mountains was noted by N.V. Dylis [13]. The *L. gmelinii* populations from Evenkia and East Transbaikalia were significantly differentiated (Figure 5 a), Mahalanobis distance between populations of *L. gmelinii* was 4.26, p<.001. A study of allozyme variation showed the high level of genetic diversity of those *L. gmelinii* populations, which suggested that they could be considered as geographic races [19].

4. Conclusion

The study of shape variation of cone scales using methods of geometric morphometrics confirmed differentiation of the three larch species: *L. gmelinii*, *L. cajanderi*, and *L. sibirica*. PCA showed that the shape differences of cone scales were mostly associated with the scale width and length and the presence and shape of the notch on the upper edge of the scale. PCA-ordination of larch samples revealed interspecific differences in shape variations of cone scales. CVA demonstrated that the three species of the *Larix* genus were all successfully discriminated and that populations within the species were noticeably differentiated.

Geometric morphometrics of cone scales can be used as an effective tool to analyze inter- and intra-specific differentiation of *Larix* species. Geometric morphometrics is a reliable tool not only in taxonomic studies but also in further research of larch biogeography and evolution based on shape variations of morphological characters of cones.

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Conflict of Interest

None declared.

Конфликт интересов

Не указан.

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