

THE FLOWER ORGAN TRANSITION IN WATER LILY  
(*NYMPHAEA ALBA* S.L., NYMPHAEACEAE) UNDER CROSS-EXAMINATION  
WITH DIFFERENT MORPHOLOGICAL APPROACHES

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Received 11 January 2006; accepted 17 October 2006.

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ABSTRACT. — A classical example of petal-to-stamen transition is the flower of white water lily (*Nymphaea alba* s.l., Nymphaeaceae). The description in terms of classical plant morphology cannot reveal all morphological variation of transitional organs. Our aim was to describe transitional structures of *Nymphaea* flower using an integrated approach, which could adequately reflect the nature of transitional structures. We collected 25 water lily flowers from four regions of European Russia. All the organs of the flowers were measured (2479 organs in total). Our data were analysed graphically and by various methods of multivariate statistics. To reduce the influence of size we computed two integrated “hybrid” morphological indices. The Euclidean distances from “typical stamen” and membership coefficients of fuzzy clustering were also calculated. In addition, we tested the descriptive ability of landmark-based geometric morphometrics.

Besides traditional petal-to-stamen transition in *Nymphaea* flowers, we documented intermediate organs between sepals and petals, which were close to sepals by their morphology. Traditionally gradual petal-to-stamen shifts were postulated for *Nymphaea* flower. In spite of this postulate, our application of computing Euclidean distances method, of “hybrid” indices and of cluster membership of fuzzy clustering revealed that petals, stamens and transitional structures could be efficiently separated by their characters. The analysis of these characters shows diversity in morphology of flowers, collected from distinct regions of European Russia, which could be of taxonomic importance. It is remarkable that different morphological feature shifts, leading to substitution of sepals by petals and of petals by stamens, occur asynchronously.

Flowers were investigated as “populations”, where any separate organ represents a single “individual”. Thus methods, used in plant population biology, may be applied to flower organs. Morphological nature of these organs is better revealed via integral characteristics such as “hybrid” indices, distances and cluster membership.

KEY WORDS. — *Nymphaea*, dynamic morphology, continuum morphology, fuzzy clustering, geometric morphometrics, transitional structures.

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## INTRODUCTION

The concept of “iron triad” is the most widespread in plant morphology. According to this paradigm, all the variety of flowering plant organs could be referred to as one of three main organ types: root, stem or leaf. Following W. Goethe’s foliar theory (ARBER 1946), flower organs are metamorphosed leaves (phyllomes). This concept was placed on the cornerstone of the ABC-model of genetic regulation of flower organ type (COEN & MEYEROWITZ 1991). The ABC-model postulates vegetative leaf to be the “initial state” of organs, whereas the appendicular flower organs develop as a result of activation of genetic functions of A, B, and/or C gene groups. These changes in gene expression pattern cause certain modifications in the program of phyllome development and the initial “vegetative leaf” appears to metamorphose into the corresponding flower organ. All the variety of organs in this model is restricted to (1) vegetative leaves, (2) sepals, (3) petals, (4) stamens and (5) carpels. Thus, *a priori* assumption of the existence of distinct organ types in the flower is widespread in modern botany (TIMONIN 2002). It is accepted that one can definitely classify every flower structure to one of the five mentioned types, the “merons” *sensu* MEYEN (1973).

However, in flowering plants, organs with enormous variation in morphology are sometimes found, which are intermediate between traditional merons. These transitional structures appear both in vegetative and generative spheres. For instance, “phylloclades” of Asparagaceae, shoot-like organs of *Utricularia* (Lentibulariaceae) and phyllomorphs of *Streptocarpus* (Gesneriaceae) possess morphological characters of both axes and leaves (TIMONIN 2002). The classical example of petal-to-stamen transition is the flower of water lily (*Nymphaea*, Nymphaeaceae). The structures with partly androecial and partly perianth characters were already described in Goethe’s “Plant Metamorphosis” (ARBER 1946). The white water lily (*N. alba* L. s.l.), which is widespread in Europe, is regarded as a species with a gradual transition from petals to stamens (HESLOP-HARRISON 1955, DUBYHNA 1982).

*Nymphaea alba* has large solitary androgynous flowers with double perianth and long

peduncle. The outer perianth whorl(s) is(are) composed of three to seven (usually four) sepals. The abaxial side of sepals is green, while the adaxial side is greenish-white. The numerous petals are white. The transitional region of the flower (intermediate organs with combined androecial and corolla characters) is placed inwards the typical petals. We avoid the term “staminode” because of its morphological uncertainty (see WALKER-LARSEN & HARDER 2000). Stamens are numerous, more or less spirally arranged; they have a long connective and anthers submerged in the sterile tissue. The gynoecium consists of 5–35 laterally connate carpels with sessile stigma (HESLOP-HARRISON 1955, MOSELEY 1961, SCHNEIDER *et al.* 2003). The degree of transition between petals and stamens is considered as an important diagnostic character in *Nymphaea* taxonomy (UOTILLA 2000). However, there has been no attempt of quantitative estimation of character transgression in water lily flowers. Several botanists accept that description of transitional structures from the viewpoint of classical morphology cannot cover all their variability (SATTTLER 1996, TIMONIN 2002). Therefore, we decided to find other tools that are adequate for the exact definition of these structures.

Dynamic, or continuum morphology as suggested by SATTTLER (1966) is one appropriate approach. The main idea of dynamic morphology is the substitution of rigid system of organ types by quantitative estimation (for example, by scores) of the character expression. This approach exactly corresponds to the method of “hybrid” indices that was suggested for investigations of introgression by E. Anderson in 1949 (WILSON 1992). Different methods to compute the similarity between individual plants are even more widespread in taxonomy than “hybrid” indices (WILSON 1992, SATTTLER & RUTISHAUSER 1997). These methods are usually based on computations of different types of distances and/or principal component analysis (SATTTLER & JEUNE 1992, LACROIX *et al.* 2003).

The methods of dynamic morphology were repeatedly used by morphologists to study transitions between different types of vegetative organs (SATTTLER 1996, LACROIX *et al.* 2003),

**Table 1.** Characters recorded for each flower (the primary characters are in uppercase).

Abbreviation	Description
N.ORG	number of organ (counted from periphery to centre)
LN	length (from base to top), in millimetres
WD	maximal width, in millimetres
POS	the position of maximal width (from the base), in millimetres
LN.TH	the length of anthers (or the length of topmost narrow part of organ), in millimetres
ANGLE	the angle between thecae (0 anthers are absent, 1 thecae are nearly parallel, 2 thecae form the sharp angle, 3 thecae form right or obtuse angle)
COLOR	the colour (9 different colours are coded as the relative hue degree from HSB colour model)
VIS	the visually attributed type of organ (petal, tr1, sepal, tr2, stamen; where "tr" are transitional organs)
rel.ln	the ratio of maximum organ length to maximum width
th.ln	anthers length to maximum length of the organ ratio
pos.ln	the location of maximal width (measured from the base of the organ)
color.n	the colour code: the "G" (green) component of the RGB colour scale

whereas the dynamic morphology investigation of transitional flower structures has not yet been made (RUTISHAUSER 1989). Furthermore, this methodology is of great interest in the light of the ABC-model of flower development. Thus, the aim of this paper is to describe the transitional structures of *Nymphaea* flowers using a dynamic morphology approach.

## MATERIALS AND METHODS

We investigated flowers of *Nymphaea alba* L. sensu lato (including those often recognized as separate species *N. candida* J.Presl; see UOTILLA 2000) from four regions of European Russia: southern Kaluga (3 flowers), Tver' (13 flowers), Chelyabinsk (2 flowers), and northern North Karelia (7 flowers). All the material was collected in Jun.–Sep. 2004. In total, 2479 flower organs were analysed. We recorded all main morphological characters for all organs of each specimen, removing organs sequentially from periphery to the centre of the flower. Both qualitative and quantitative characters were recorded (Table 1). Some of them (primary characters) were measured (length, maximal width, the position of maximal width, the length of anthers); the remaining (secondary) characters were calculated from primary ones (the ratio of maximum organ length to maximum width, the ratio of anthers length to maximum length

of the organ, the location of maximal width, the colour code). The distal part of stamen, bearing anthers, and geometrically separated distal part of the transitional organ were treated equally. Despite size characters (e.g., length, maximal width) are related to growth processes, they can be used in classifications of flower parts if all analysed flowers are at the same developmental stage (mature flowers in particular).

For every flower we created virtual morphological characteristics of a "typical stamen", by calculating the median values for all the analysed stamen characteristics. After this step, the degree of dissimilarity for each organ could be based on the reference value of the "typical stamen". We calculated dissimilarity as multi-dimensional Euclidean distance between characters of the given organ and of the "typical stamen". Then, median values for all the stamens and petals from all the flowers were used as starting points for the calculations of cluster membership in fuzzy clustering. This method is widely used in multivariate data analysis and solves the problems of including (or excluding) a given object in a given class (KAUFMAN & ROUSSEEUW 1990). We used the value of cluster membership in the cluster of "typical stamens".

Similarly to well-known hybrid indices, we have proposed two integral morphological indices: each organ was characterized by two scores from one to ten (Table 2): (1) by index A, in which 1 corresponded to a typical sepal and 10 to the typical stamen and (2) by index B in which 1 corresponded to a typical petal and 10 to the typical stamen (sepals and transition organs

between sepals and petals were ignored in this case). The index A did not contain maximum width location because the value of this character for sepals is between

petals and stamens (Table 3). We computed the score of each index as the arithmetical mean between scores for all morphological characters (Table 4).

**Table 2.** The translation of the morphological characters into the scores of "hybrid" indices.

character	index A		index B	
	character values	score	character values	score
angle	anthers are lacking	1	anthers are lacking	1
	have acute angle between them	7.5	have acute angle between them	5
	almost parallel to each other	10	almost parallel to each other	10
organ colour	brown	1	...	...
	greenish-brown	2	...	...
	green	3	...	...
	whitish-green	4	whitish-green	1
	white	5	white	2
	light yellow	7	light yellow	5
	dirty-yellow	8	dirty-yellow	6
	yellow	9	yellow	8
	yellowish-orange	10	yellowish-orange	10
rel.ln	[1.4; 3]	1	[1.4; 2.4]	1
	(3; 4]	6	(2.4; 3.2]	3
	(4; 5]	7.5	(3.2; 5.0]	5
	(5; 6]	8.5	(5.0; 10.0]	7
	(6; 22]	10	(10.0; 22.0]	10
th.ln	0	1	0	1
	(0; 0.1]	6	(0; 0.2]	3
	(0.1; 0.25]	7.5	(0.2; 0.3]	5
	(0.25; 0.4]	8.5	(0.3; 0.4]	7
	(0.4; 0.7]	10	(0.4; 0.7]	10
pos.ln			(0.6; 0.9]	1
			(0.4; 0.6]	3
	...	...	(0.3; 0.4]	5
			(0.1; 0.3]	7
		[0; 0.1]	10	

**Table 3.** Typical values of morphological characters for different organ types of *Nymphaea* flowers (90% quantile range).

Organ	LN	WD	POS	LN.TH	ANGLE	rel.ln	th.ln	pos.ln	color.n
pet	25-59	10-29	13-36	0-0	0-0	2.7-2.7	0.0-0.0	0.4-0.7	0.00-0.00
spl	39-62	19-31	16-31	0-0	0-0	1.7-2.6	0.0-0.0	0.4-0.6	0.07-0.32
sta	13-28	1-5	0-9	5-11	1-2	4.0-15.7	0.3-0.5	0.0-0.5	0.13-0.18
tr1	40-61	21-32	21-35	0-0	0-0	1.8-2.6	0.0-0.0	0.5-0.6	0.28-0.32
tr2	19-30	4-10	5-14	0-12	0-2	2.5-6.6	0.0-0.4	0.2-0.6	0.00-0.16

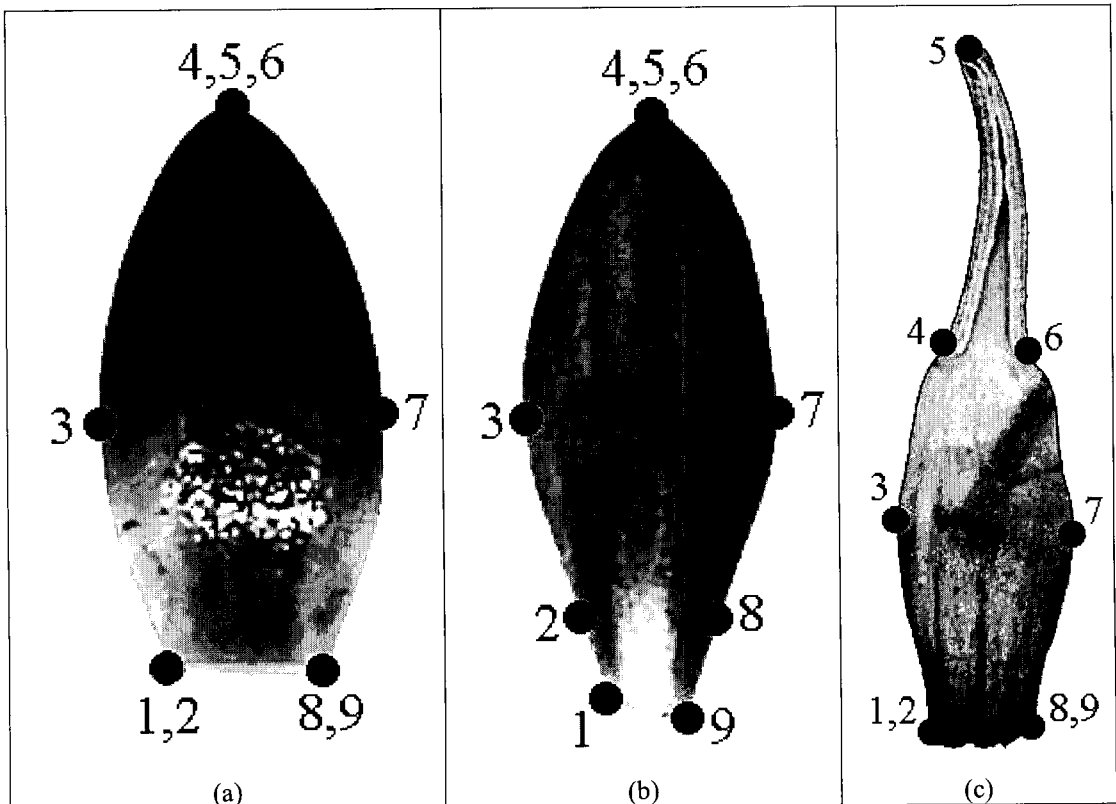
**Table 4.** The 90% quantile range of “hybrid” indices scores for different organ types.

Organ	index A	index B
pet	2.0-2.0	1.2-2.0
spl	1.0-1.5	...
sta	8.1-9.3	5.4-9.0
trl	1.5-1.8	...
tr2	3.3-9.0	1.0-2.8

Geometric morphometrics (referred hereafter as GM) helps to avoid the influence of organ size on our understanding of organ shape. This method examines the organ shape as a whole, without reference to the size (BOOKSTEIN 1991, ADAMS *et al.* 2002). The most widespread methods of GM (e.g., thin plate splines analysis, TPS; or generalized least-squares orthogonal

Procrustes analysis, GLS) use so-called “landmarks” as key points of the investigated contour. These landmarks should be homologous at least geometrically, because TPS and GLS manipulate exclusively landmark coordinates, and the differences between objects should be comparative. TPS computes the bending energy required for fitting landmarks from one specimen to another, whereas Procrustes distance is the square root of the sums of squared distances between two centred, normalized and optimally rotated configurations of landmarks. Thus, the latter is analogous to the Euclidean distance and comparable with other widely used indices of dissimilarity (PAVLINOV 2001).

We outlined each of 73 organs of flower #35 to test the possibility of applying GM methods. Nine landmarks were used for describing the shape of each organ. We used not only biological but also geometrical reasons for locating the landmarks: they were located in the points of maximum contour curvature (Fig. 1a–c).



**Fig. 1.** Positions of the landmarks for geometric morphometrics. Numbers correspond to the numbers of landmarks. A: typical sepal; B: typical petal; C: typical stamen.

The landmarks coordinates were revealed via tpsDig software (ROHLF 2004a); Procrustes distances were computed with tpsSpline (ROHLF 2004b).

The cubic spline smoothing was used for plotting of “mutation curves” which show the speed of alteration between different organ types. This method is the most appropriate when curves configuration is complex. All uni- and multivariate computations were performed in R statistical environment for WINDOWS, ver. 2.0.1 (R DEVELOPMENT CORE TEAM 2004).

## RESULTS

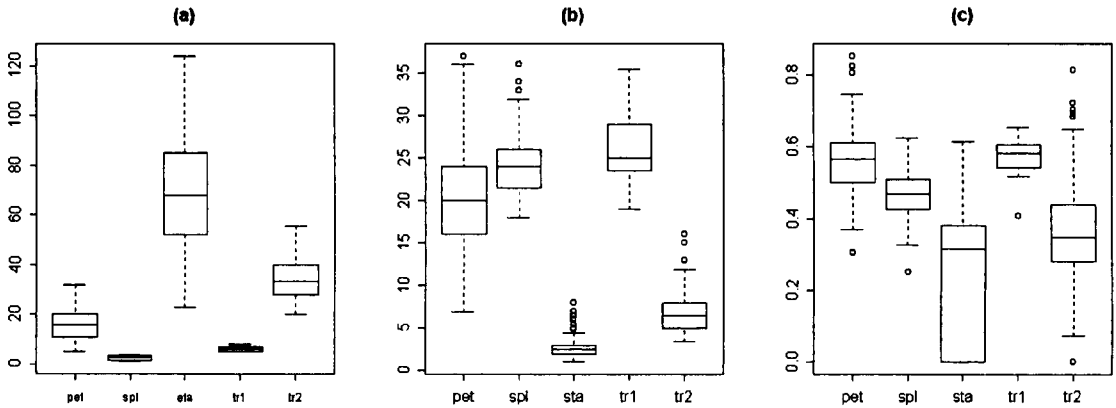
In order to make measurements easier, we classified each organ as one of five types: 1) sepals, 2) transition from sepal to petal, 3) petals, 4) transition from petal to stamen and 5) stamens. This preliminary classification was based on visual characteristics. For the transitional organs we used the following criteria. The second type (transition from sepal to petal) differs from petals by the presence of a chlorophyll band on the distal part of the abaxial side. Typical morphological characteristics of each organ type are shown in Table 3. As a rule, these organs have a more or less specific location in the flower (Fig. 2a). The visual classification (based on the classical morphological approach) appeared not to be perfect, because we found many intermediate structures even between the five mentioned types. Characteristics of organ types significantly overlap both for absolute (e.g., the width of organ) and for relative characters (e.g., the ratio between the length of organ and the relative position of maximal width) (Fig. 2b–c). The multivariate analysis (PCA) of most characters returned a graph where many points did not have a unequivocal position (Fig. 3). The sepal-to-petal transitions were morphologically close to sepals. The linear discriminant analysis showed that mean misclassification error was relatively high (26.7%) and even more (31.3%) for petal-to-stamen transitions; 26% of petal-to-stamen transitions were erroneously classified as stamens, and 2% of stamens as transitional organs.

The Procrustes distance matrix (the GM analysis of contours) and Euclidean distance matrix between organs of flower #35 (classical

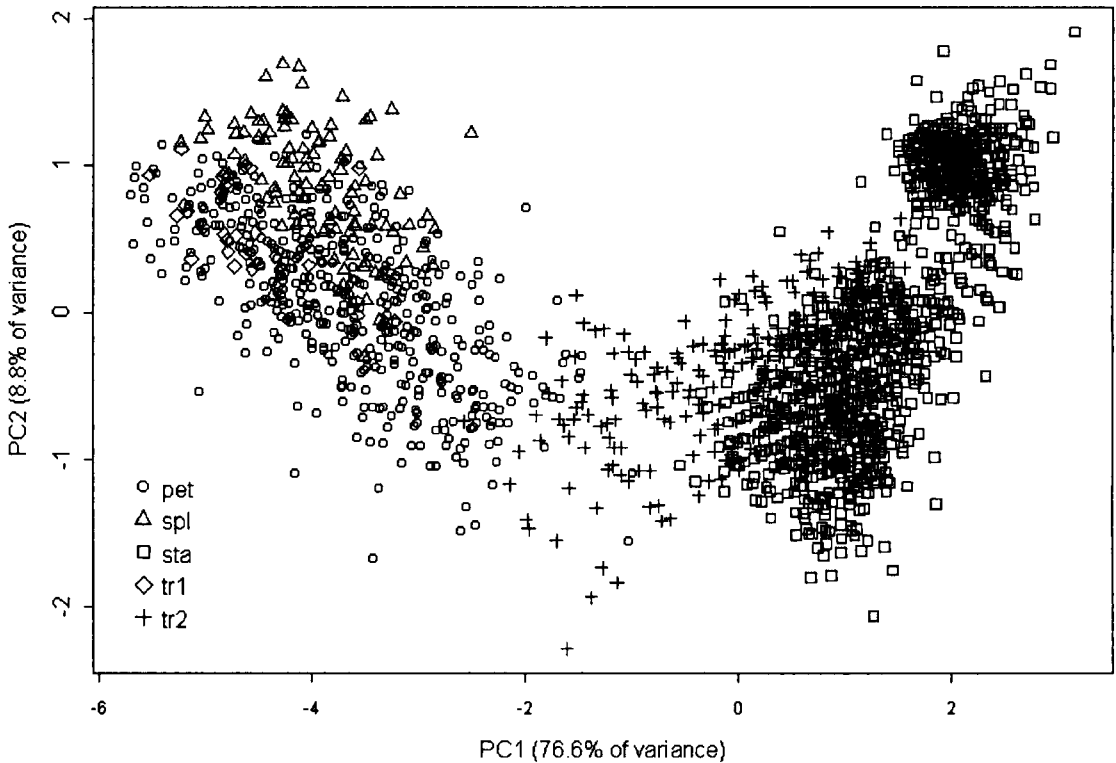
morphological data) were highly correlated (Mantel test  $r = 0.77$ ,  $P < 0.01$ ). The multidimensional scaling of GM data allowed a better separation of organ types compared to the analysis of classical morphological data, without significant overlap (Fig. 4), but gaps between clouds of points were narrow. The first dimension in this graph could be useful as a character for a dynamic analysis, but GM is extremely sensitive to sampling (PAVLINOV 2001), which makes the results of the different GM analyses incomparable.

The integrated hybrid indices showed a continuous bimodal distribution with two peaks. These indices appear to be better for the characterization of all organ types (Table 4 and Fig. 5), but they are more valuable for subsequent dynamic analyses. For the investigation of changes in distinct characters we used the smoothed splines (“mutation curves”). Surprisingly, the first extremes of different curves fall on diverse regions of the flower, and the relation between curvature and organ type appeared not to be so obvious (Fig. 6a,b). For example, in the transitional region between petals and stamens the curve extreme for the organ width falls either to the transition organs between petal and stamen, or it is not expressed (Fig. 6a), the curve extreme for position of maximal width falls either on stamens, or on the transitional organs (Fig. 6b). Therefore, the different morphological characters have different behaviours (i.e., change asynchronously) and do not allow representing the whole flower structure. Euclidean distance between the actual organ and the “typical stamen” slightly increases during the transition from sepals to petals, and essentially decreases during the transition from petals to stamens, asymptotically reaching 1 (Fig. 6c). The extremes of this curve do not always correspond with the alternation from one organ type to another.

The mutation curve of cluster membership in the cluster of “typical stamens” shows the maximal increase in the region of transitional organs, whereas the part of the curve before the steep increase corresponds to the basal border of the androecial region (Fig. 6d). The curves of sampled flowers #26 and #34 are closer in this case, which demonstrates the better quality of cluster



**Fig. 2.** Boxplots of the selected characters: (a) number of organs in the investigated flower, (b) maximal width, (c) location of maximal width. The central line in the box is median value, the box shows lower and upper quartiles, the whiskers show minimum and maximum values, small circles show outliers.



**Fig. 3.** Principal component analysis of the morphological data for all organs of all flowers (organ types highlighted: pet = petal, spl = sepal, sta = stamen, tr1 = sepal to petal transition, tr2 = petal to stamen transition).

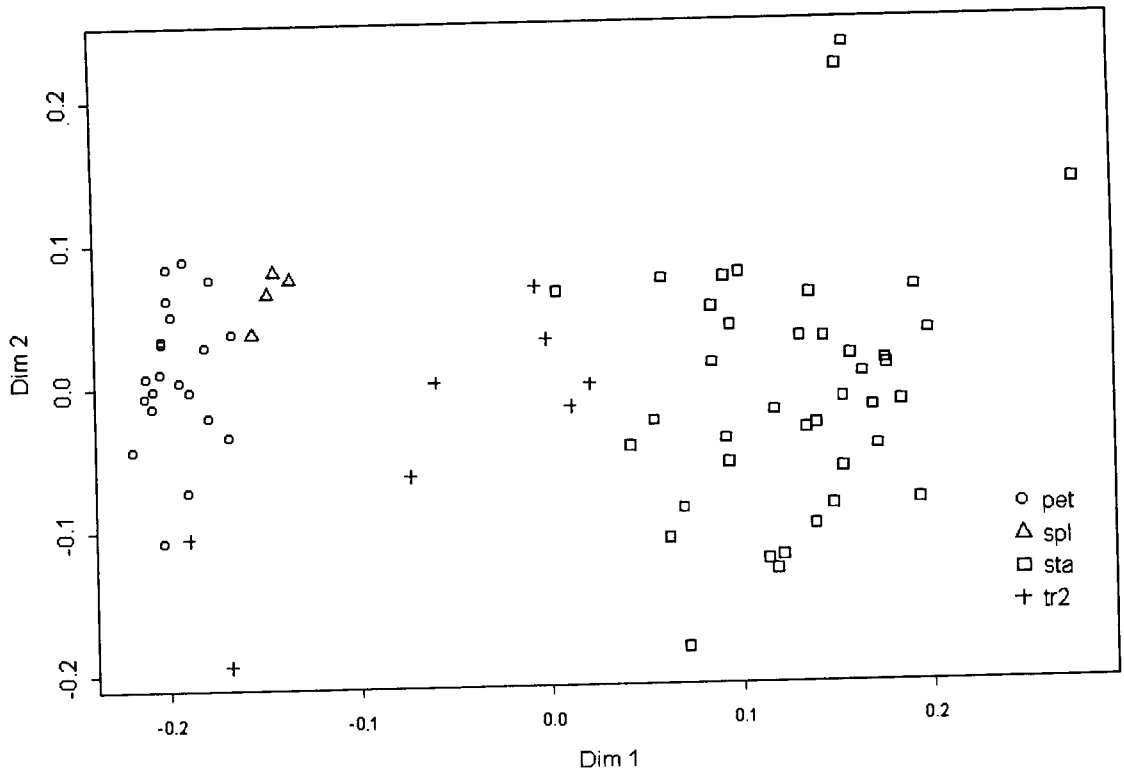


Fig. 4. The multidimensional scaling of the matrix of Procrustes distances for all organs of flower #35.

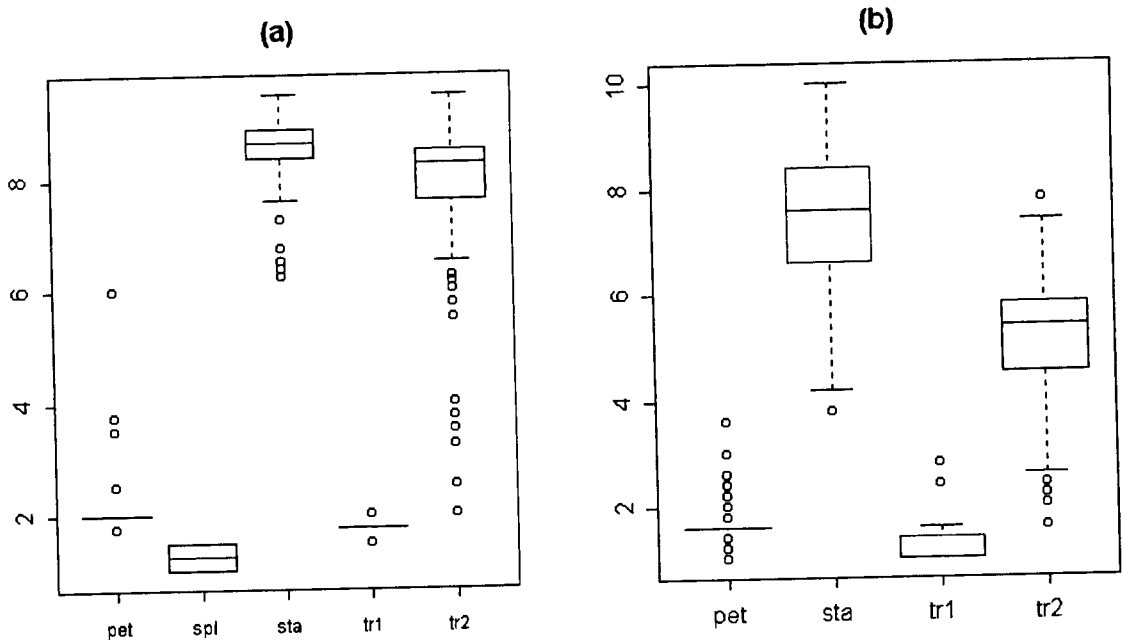
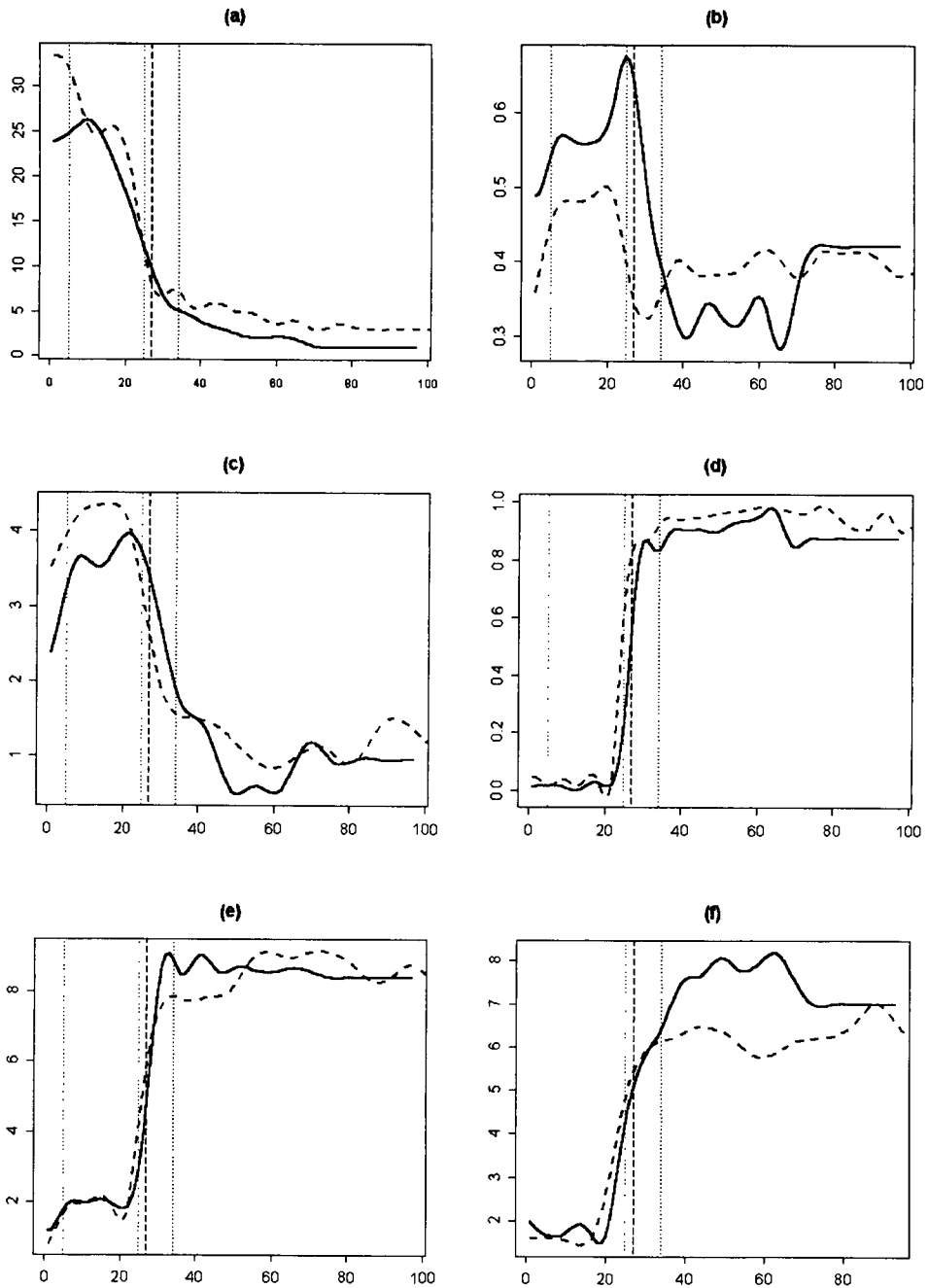


Fig. 5. Boxplots of the index A and index B values.





**Fig. 6.** The smoothed splines of the changes ("mutation curves") of selected morphological characters and integral indices for flowers #26 (North Karelia, dashed line) and #35 (Chelyabinsk region, full line): (a) maximal width, (b) location of maximal width, (c) Euclidean distance from typical stamen of each flower, (d) membership in the cluster "typical stamen" of each flower, (e) index A, (f) index B. The vertical lines represent borders between different organ types: the first two (from left to right) dotted lines represent borders between sepals and petals and between petals and petal-to-stamen transitions, respectively; the third dotted line and the dashed line represent the border between petal-to-stamen transitions and, respectively, stamens for flower #35 and #26:

membership for comparing organs in different flowers. The curve for index A has relatively simple shape with clear extremes that correspond to organ types alternations (Fig. 6e). The steep increase corresponds with the transitional organs between petals and stamens. For some flowers, this part of the graph looks almost like vertical line (not shown). The mutation curve for index B illustrates the process of transition from petals to stamens in another manner (Fig. 6f).

The investigation of dynamic features of flowers also revealed differences between flowers from different regions of Russia. In some northern populations we found that stamens were more similar to petals, than stamens of flowers from other populations of *N. alba* s.l. The flowers from Karelia were characterized by maximal width located almost in the middle of the organ (near the base in flowers from other populations), by the organ length being 4 to 6 times their width (7–11 for other populations), and by the acute angle between anthers (nearly parallel in other populations). The proportion of transitional organs between petals and stamens was quite different for these groups: 0–4% for Karelian population and 8–18% for southern ones.

## DISCUSSION

As a whole, we used six different approaches to characterize the floral organs of *Nymphaea*: (1) the visual classification; (2) PCA ordination for the primary and secondary morphological characters; (3) multidimensional scaling for matrix of Procrustes distances, revealed by GM; (4) hybrid indices A and B; (5) the membership in the cluster of “typical stamens”, revealed by fuzzy clustering and (6) the Euclidean distances between each organ and “typical stamen” of each flower. The approaches 2–6 are based on the view that flowers (and other parts of plant) can be investigated as particular “populations”, where organs can be referred to as “individuals”. This viewpoint was justified in the investigations of other (mostly vegetative) plant organs (SÄTTLER & JEUNE 1992, LACROIX *et al.* 2003).

The comparison between the traditional visual classification of *Nymphaea* organs and the classification based on the morphology performed by PCA (Fig. 3) revealed differences between these classifications for stamens and petal-to-stamen transitional organs. In contrast, the similarity of the results obtained by methods of classical and geometrical morphometry, shows that morphological indices can characterize the shape of *Nymphaea* flower organs as effectively as GM does.

The presence of transitional organs between sepals and petals in *Nymphaea* flowers, besides the existence of petal-to-stamen transitions, is a new morphological observation. These organs appeared to be widespread among the specimens from the Tver region. There are also other differences between flowers from different regions. As an example, the stamens of northern Karelia *Nymphaea* have some morphological features that are typical for the petal-to-stamen transitional organs (Table 3); the proportions of transitional organs in the flower are also different. These characteristics could be of taxonomical importance, because most of authors accept at least two different species on the territory of European Russia: *Nymphaea alba* and *N. tetragona* Georgi. However, the present uncertainty in European water lilies taxonomy (UOTILLA 2000) does not allow us to relate the observed features to species description.

The analysis of “mutation curves” for every individual morphological character showed that some of them (e.g., organ width) could not be used for attributing organ types to observed organs. The metrics from PCA (e.g., the value of PC1) or from GM (e.g., the value of the first dimension from multidimensional scaling of Procrustes distances) are also not sufficient, because they are strictly depending on the initial set of organs (this is especially significant for any type of GM analysis).

Correspondingly, the classical morphology is not a perfectly appropriate method for exact characterisation of the petal-to-stamen transition, i.e., we should use some integral characteristic, such as the “hybrid indices”, cluster membership from fuzzy clustering and Euclidean distances,

which have better “resolution” for adequate characterization of these transitions. Our results on *Nymphaea* flowers thus confirm the idea of dynamic morphology, used in previous investigations on vegetative organ transitions (SATTLER 1966, SATTLER & JEUNE 1992, SATTLER 1996, SATTLER & RUTISHAUSER 1997, LACROIX *et al.* 2003). According to Fig. 6, the best approaches are cluster membership and index A, which demonstrates the good accordance between organ type and corresponding index. Taken as a whole, different dynamic morphological approaches are effective methods for investigation of transitional generative structures of flowering plants.

The methods described could also be efficiently used for the precise examination of various transitional structures both in morphology, teratology and in genetics. For example, in *Cactaceae* flowers the features of sepals (or even of vegetative leaves), typical for the basal organs, gradually shift to petal characters in the upper part of perianth (BARTHOLOTT & HUNT 1993). The proposed methods allowed us to judge more precisely about the morphological nature of problematic organs, and solve terminological difficulties in the case of the existence of more than four classical organ types.

According to the widespread ABC-model of flower development, differentiation of petals and stamens is caused by changes in expression of B-group genes. Petals are initiated in the space with simultaneous expression of genes from the A and B classes, and stamens appear in the region with overlapping expression of genes from the B and C classes (COEN & MEYEROWITZ 1991, SOLTIS *et al.* 2002). Thus, substitution of petals by stamens is caused by substitution of expressed genes. According to the ABC-model, the expression of each gene class occurs in definite domains, which causes differentiation of sharply bordered regions of calyx, corolla, androecium and gynoecium on the floral primordium. In this case, it would be adequate to describe the structure of the flower by the means of the classical typological approach.

The orthologs of ABC-genes for *Nymphaea* are currently poorly characterized (SOLTIS *et al.* 2002). In *Nymphaea* flowers the morphology of the organs gradually changes, which suggests that

borders between zones of gene expression are not well-pronounced. The border between androecium and petals is determined by configuration of expression zones of A and C class genes (COEN & MEYEROWITZ 1991). Obviously, there are zones in *Nymphaea* flowers where gene activity of both A and C classes could be hypothesized, and the dynamic approach is more appropriate for the description of these organs. It is noticeable that the characteristic points of remarkable changes of morphology in the space of the flower seldom coincide for different features. If we suppose that all the investigated morphological features of *Nymphaea* flowers are controlled by the ABC-system, we should accept the existence of critical levels of gene expression, influencing each organ feature separately. This hypothesis can explain the non-synchronic changes of different morphological characters toward the flower centre (Fig. 6). It is possible that in other taxa changes of expressed gene classes in flower development are also not so sharp as it is supposed by the ABC-model or/and are controlled by supplementary genes, not included in the ABC-model. Our hypothesis is confirmed by findings of KRAMER & IRISH (2000), who showed that some aspects of ABC-program of basal angiosperms display a high degree of plasticity.

The dilemma of the most appropriate approach in plant morphology (typological or dynamic) remains unresolved (SATTLER 1966, SATTLER & RUTISHAUSER 1997, TIMONIN 2002). The main objection against the dynamic morphology is the necessity of choosing a typical pattern for a particular character expression to develop a scale for organ comparison. The initial patterns for the indexed scale are the meron (clearly distinguished type of structural elements) features revealed by the typological approach (TIMONIN 2002). However, we can consider morphological characters of extreme morphotypes between which transition exists, as a particular pattern of character expression. Let us imagine merons as these extreme morphotypes (because these morphotypes are merons), and the differences between classical and dynamic morphology disappear. Even when one rejects the existence of transitional forms

between merons, typological and dynamic morphology will stay complementary and coexistent approaches (SATTLER 1996).

### ACKNOWLEDGEMENTS

Most of our data were gathered during summer field practices of the Biological Department of Moscow South-West High School (headed by Dr. S.M.Glagolev). We thank O. Aleksandrova, E. Altshuler, N. Blohina, E. Chervyachkova, A. Glagolev, O. Kudina, N. Kulyhina, D. Mordvinkin and N. Velichanskaya for help in data collection.

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