A continuum between open and closed inflorescences?
Inflorescence tip variation in *Potamogeton*
(Potamogetonaceae: Alismatales)

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Summary: Quantitative and qualitative data on variation of inflorescence tip in two species of *Potamogeton* are presented. Partial inflorescences of both species are spikes. Flowers in spikes are arranged in alternating whorls. In the lower and middle part of an inflorescence, most flowers have a structure that is typical for *Potamogeton*, i.e., four tepals, four stamens and four carpels. The frequency of flowers of anomalous morphology increases toward the inflorescence tip. In the material examined of *P. natans*, flowers of the final whorl almost always (96.7%) deviated from the typical groundplan. In contrast, in *P. lucens* only about 40% of examined flowers of the final whorl were anomalous. In all populations examined (two populations of *P. lucens* and a population of *P. natans*), more than 15% of examined spikes possessed a terminal structure (i.e., a flower-like structure, a filamentous structure or a tubular structure). Morphological variation of terminal structures (at least of oligomerous terminal structures) closely approached the variation range of lateral flowers. Considerable difficulties in distinguishing terminal pseudanthia from terminal flowers are highlighted. A morphological continuum is proposed between open (without a terminal flower) and closed (with a terminal flower) inflorescences in *Potamogeton* and / or (partial) loss of flower identity at the tip of some inflorescences. Different spikes developing on the same individual can possess an entirely different architecture at the distal region. This strongly suggests that the presence or absence of terminal structures and their morphology is not directly linked with certain genetic mutations. Rather, the variation of the inflorescence tip structure is a result of high developmental lability. Spatial constraint hypothesis of regulation of inflorescence tip development is discussed.

Keywords: evo-devo, flower identity, inflorescence, morphological variation, *Potamogeton*, peloria, pseudanthium, spatial constraint hypothesis, terminal flower

Presence or absence of terminal flowers is traditionally used as one of the major features of inflorescence morphology. This character plays a key role in descriptive terminology of inflorescence architecture (e.g., Troll 1964; Weberling 1989). Truncation or loss of a terminal flower has been discussed as a possible evolutionary pathway linking closed inflorescences (i.e., those with a terminal flower) and open inflorescences, which lack a terminal flower (Sell 1969; Maresquelle 1970; Kusnetzova 1985, 1986, 1988, 1998; Weberling 1989).

The two most popular model plants, *Arabidopsis* and *Antirrhinum*, both possess open inflorescences, but mutants that develop terminal flowers have been produced and analyzed, and relevant regulatory genes studied (e.g., Alvarez et al. 1992; Bradley et al. 1996; Ezhova & Penin 2001; Penin et al. 2004). These studies have shown that terminal structures in inflorescences of different individual mutant plants differ from each other as well as – to a greater or less extent – from wild-type lateral flowers of the same species (reviewed in Penin et al. 2004). Sometimes the inflorescence tip develops a structure that could be interpreted as a fusion product of several

uppermost flowers. Flower-like terminal structures[1] similar to those described in laboratory-induced mutants of model organisms can be found in plants from natural populations of many different angiosperms (reviewed in Sokoloff et al. 2006). In particular, flower-like terminal structures are found in inflorescences of early-divergent monocots, such as *Acorus* and *Potamogeton* (Buzgo & Endress 2000; Buzgo et al. 2004; Remizowa & Sokoloff 2004; Sokoloff et al. 2006). Comparative analyses of the diversity of terminal flower-like structures in wild material of various angiosperms and in laboratory-induced mutants of model organisms might help in understanding common mechanisms of regulation of morphogenesis. Flower-like terminal structures of *Potamogeton* (Potamogetonaceae) are of potential interest because members of the closely related and much more specialized family Zannichelliaceae (e.g., Posluszny & Sattler 1976; Posluszny & Tomlinson 1977; Mavrodiev & Sokoloff 1998) consistently possess structures commonly described as terminal flowers. Sokoloff et al. (2006) speculated that terminal flowers in Zannichelliaceae could be homologous with the terminal structures that occur occasionally in inflorescences of *Potamogeton*. They suggested that both, truncation and the opposite process, terminalization, play a role in angiosperm inflorescence evolution.

Partial inflorescences of *Potamogeton* are spikes. Flower arrangement along the spike axis is most commonly verticillate (e.g., Sattler 1965; Posluszny & Sattler 1974; Sun et al. 2000; Sokoloff et al. 2006). The structure of the inflorescence tip varies in natural populations of *Potamogeton* (Remizowa & Sokoloff 2004; Sokoloff et al. 2006). Typically, the inflorescence is terminated by several lateral flowers, but sometimes a flower-like terminal structure is formed. At least some terminal structures of *Potamogeton* could be interpreted as terminal pseudanthia[2]; i.e., as fusion products of several uppermost lateral flowers, though other interpretations are also possible. Furthermore, organs of unusual morphology can be sometimes found at the inflorescence tip. Those include filamentous and tubular structures (Remizowa & Sokoloff 2004; Sokoloff et al. 2006).

Sokoloff et al. (2006) suggested that the diversity of inflorescence tip structure is caused by morphogenetic lability of inflorescence development rather than genetic heterogeneity of the material they examined. They proposed the following preliminary hypothesis (called here 'spatial constraint hypothesis') regarding the regulation of inflorescence tip development in *Potamogeton natans*. Elongation of the inflorescence apex and initiation of the lateral flowers are controlled by two independent developmental programmes. Elongation of the inflorescence apex commences first, but proceeds more slowly than formation of lateral flower primordia, which occurs in an acropetal pattern. Sometimes the flower primordia of the final whorl have (by chance) just sufficient space for their formation at the inflorescence apex, which is then completely exhausted.

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1) The term 'flower-like terminal structure' is partly overlapping with the term 'peloria' (see, for example, Arber 1932; Endress 1994, 2001; Bateman & Rudall 2006). Peloriae are usually considered as cases of restoration of polysymmetry in normally monosymmetric flowers, regardless of their position in the inflorescence. Terminal peloria is a polysymmetric structure at the inflorescence tip in plants that normally possess only lateral monosymmetric flowers (e.g., in *Delphinium, Digitalis, Linaria*). Some authors consider terminal peloriae as pseudanthia.

2) Many authors suggested that lateral 'flowers' of *Potamogeton* in fact represent pseudanthia, with each of the four stamens belonging to individual male flowers and four carpels belonging to either a female flower or four individual female flowers (this view is discussed in Uhl 1947; Eames 1961; Posluszny & Charlton 1993; Endress 1995; Mavrodiev & Sokoloff 1998; Posluszny et al. 2000; Rudall 2003). Throughout the paper, we describe lateral structures in spikes of *Potamogeton* as flowers. In this paper, the term 'pseudanthium' is used only when congenital fusion of two or more such flowers is assumed.

However, this is often not the case, because the inflorescence apex may be longer than it is necessary for insertion of the final-whorl primordia. According to the spatial constraint hypothesis, if considerable space remains on the apex after formation of the final whorl of free flower primordia, a compound floral primordium is initiated at the inflorescence apex. Depending on the space available, this compound terminal primordium gives rise to what could easily be interpreted as a pseudanthium or an almost completely flower-like structure. In contrast, when the remaining space at the apex is smaller than the size of a typical flower primordium (or the shape of the space is atypical), unusual filamentous or tubular structures are initiated at the inflorescence apex (Sokoloff et al. 2006). This hypothesis should be further tested by empirical data.

Many aspects of inflorescence tip variation in *Potamogeton* remain unexplored. Sokoloff et al. (2006) presented only qualitative data on variation of the inflorescence tip, and their study mainly concentrated on *Potamogeton natans*. Quantitative data on inflorescence tip variation and comparative data on inflorescences of different species are desirable, but lacking so far. Charlton & Posluszny (1991) presented a detailed quantitative study of meristic variation in *Potamogeton* flowers, but they did not specifically address the diversity of terminal flower-like structures.

In this paper, we present comparative data on inflorescence tip variation in two species common in Central Russia, *Potamogeton natans* L. and *Potamogeton lucens* L.

Materials and methods

Inflorescences of *Potamogeton natans* and *P. lucens* were collected between 18.06.2006 and 26.06.2006 in Usmanka River near the Biological Teaching and Scientific Centre 'Venevitinovo' of Voronezh State University (Novousmansky distr., Voronezh prov., Russia). Additional material of both species has been collected in the same locality in June 2009, but it was used for qualitative studies only. Besides, *P. lucens* was collected in July 2007 in Moscow River near Zvenigorod Biological Station of Moscow State University (Odintsovsky distr., Moscow prov., Russia). Preliminary observations showed that inflorescences immediately after anthesis are most useful for examination of their morphology. In earlier stages, flowers are densely packed, so that it is virtually impossible to distinguish flower-subtending bracts. Only inflorescences on appropriate stages were selected for analysis. Among the collected material, we selected for quantitative studies 141 spikes of *P. lucens* and 150 spikes of *P. natans* from Usmanka River and 50 spikes of *P. lucens* from Moscow River. As far as known, *P. lucens* and *P. natans* possess perennial subterranean rhizomes that produce annual shoot systems situated in the water medium. Most spikes examined belonged to different annual shoot systems. Some annual shoot systems possessed more than one spike on stages that allowed their detailed investigation. These cases were specifically documented to understand if a given genotype can produce different morphological types of inflorescence tip structure. There is no guarantee, however, that spikes collected from different annual shoot systems belonged to different plant individuals and, moreover, to plants with different genotypes, because *Potamogeton* plants can propagate vegetatively.

For every spike the number of whorls of flowers on the inflorescence axis and flower number per whorl were calculated. Diagrams of the upper part of each inflorescence were produced. The upper part of the inflorescence was defined as three uppermost whorls of flowers (if a terminal structure was absent) or a terminal structure plus two uppermost whorls of lateral flowers.

Results

General morphology of inflorescences

In examined material of *Potamogeton natans* the number of whorls of flowers per inflorescence varied between 12 and 23 though most inflorescences possessed 15 to 18 whorls. Normally, flowers of *P. natans* are all arranged in regularly alternating trimerous whorls, so that flowers of all even whorls form three orthostichies and flowers of all odd whorls form another three orthostichies. Therefore, the typical number of orthostichies is six. Sometimes, regular whorl alternation is altered by insertion of an unusually oriented whorl. For example, in a spike illustrated in Figure 1A most flowers can be assigned to six orthostichies, but flowers of the fifth whorl are inserted between adjacent orthostichies. In a spike illustrated in Figure 1B a similar phenomenon can be seen: flowers of the second whorl are inserted between adjacent orthostichies. Another unusual feature illustrated in Figure 1B is the presence of a flower that cannot be assigned to any whorl. In some of the examined inflorescences of *P. natans*, the final whorl possessed only two flowers (but other whorls of these inflorescences were trimerous). Among all inflorescences counted the mean number of flowers in the final whorl was 2.9 (see Table 1).

In examined material of *P. lucens* the whorls were commonly tetra- or pentamerous and rarely hexamerous in the middle part of an inflorescence. The merism of the whorls, however, sometimes changes along an inflorescence. There are often fewer flowers per whorl in the lower and / or in the upper part of an inflorescence than in its middle part. The uppermost whorls are often trimerous in *P. lucens*. Among all inflorescences counted the mean number of flowers in the final whorl was 3.3 (see Table 1). The number of whorls per inflorescence varied between 12 and 25 in *P. lucens*, but most inflorescences possessed 16 to 20 whorls. Therefore, *P. lucens* is close to *P. natans* in the variation of whorl number per inflorescence.

In both species examined flowers of the same whorl are often attached to the inflorescence axis at slightly different levels (Fig. 2). This phenomenon causes some technical problems in recognizing – and counting – the whorls of flowers. However, careful examination almost always allowed clear recognizing of regularly alternating whorls of flowers throughout the length of a spike. Only nine spikes of *P. lucens* were really problematic, and their anthotaxis was indeed not whorled and should be viewed as either spiral or chaotic. These nine spikes are not counted in Tables 1–4. It should be noted that the nine inflorescences of *P. lucens* that lacked a clearly whorled anthotaxis were generally the richest in occurrence of flowers deviating from the flower groundplan typical for *Potamogeton*.

Variation of lateral flowers

We did not find any inflorescence of *P. natans* where all flowers of the three uppermost whorls or at least all flowers of the final whorl were characterized as typical for the *Potamogeton* groundplan,

Table 1. Mean flower number in distal whorls of a spike in two species of *Potamogeton* (material from Usmanka river).

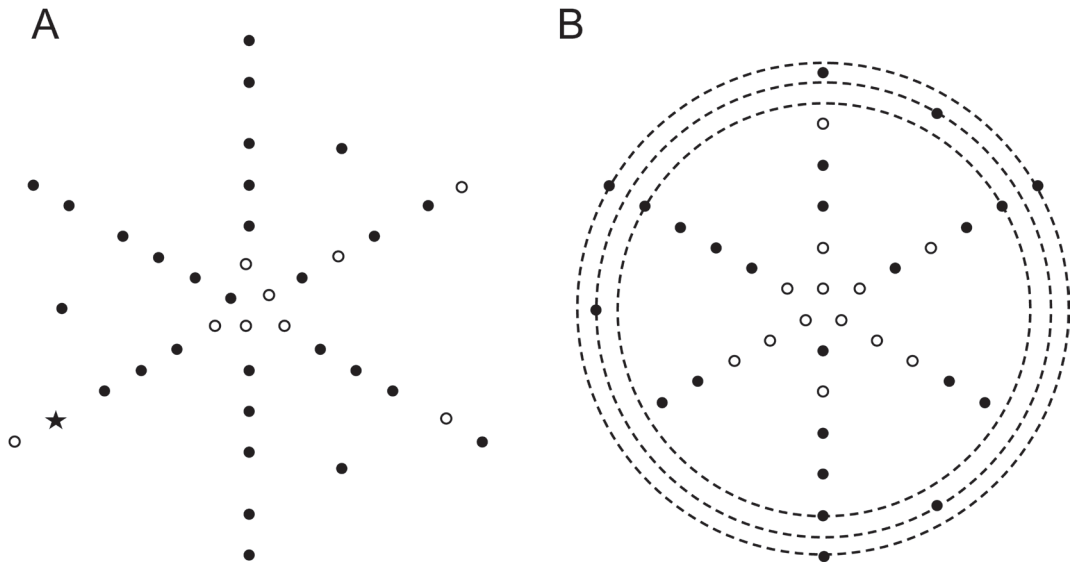| Whorl of flowers	*Potamogeton lucens*	*Potamogeton natans*
Final whorl	3.3	2.9
Second whorl from the tip of a spike	3.5	3.0
Third whorl from the tip of a spike	3.9	3.0

Figure 1. Diagrams of flower arrangement in two spikes of *Potamogeton natans*. Black circles = flowers with four tepals, four stamens and four carpels; open circles = flowers with four tepals, four stamens and less than four carpels; asterisk = flower with seven tepals, seven stamens and five carpels. Flower-subtending bracts are not drawn. Distance from a circle to the center of each figure is proportional to the distance from a flower to the inflorescence apex. Flowers form alternating trimerous whorls in both spikes. In the spike illustrated in A, the fifth whorl has an unusual orientation. In the spike illustrated in B, the second whorl has an unusual orientation. Besides, there is an additional flower inserted between the first and the second whorl in the spike illustrated in B. To make presence of this additional flower obvious, flowers of outermost whorls are connected by dashed lines in B. Flowers are usually inserted at slightly different levels within each whorl in *P. natans*. This phenomenon is not considered here, but illustrated in Figure 2.
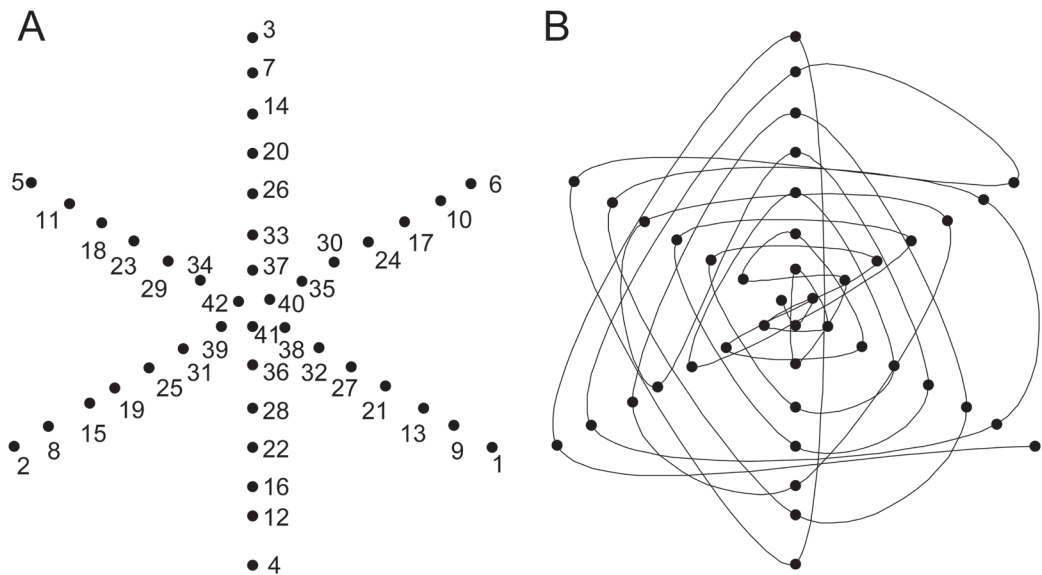

Figure 2. Diagram of flower arrangement in a spike of *Potamogeton natans*. Circles = flowers. Distance from a circle to the center of the figure is proportional to the distance from a flower to the inflorescence apex. In this figure, insertion of flowers at slightly different levels within a whorl is considered. In A, all flowers are numbered sequentially according to their insertion levels along the inflorescence axis. In B, a line connecting flowers in the sequence of their insertion levels is drawn. It is clear that flower arrangement cannot be regarded as modified spiral. Rather, it can be interpreted as whorled.

Table 2. Percentage of different flower types in different whorls of distal part of a spike (material from Usmanka river).

Flower morphology	Third whorl from the tip of a spike, %		Second whorl from the tip of a spike, %		Final whorl, %	
	P. lucens	*P. natans*	*P. lucens*	*P. natans*	*P. lucens*	*P. natans*
Flowers typical for *Potamogeton* (12 organs: four tepals, four stamens, four carpels)	98.0	21.5	96.5	14.6	60.2	3.3
Bisexual flowers with less than 12 organs	1.0	78.5	2.0	84.9	17.6	64.2
Male flowers	-	-	0.2	0.5	9.4	28.3
Flowers without carpels and stamens (tepals only)	-	-	1.3	-	5.3	3.4
Tubular and filamentous structures	-	-	-	-	4.1	0.5
United flowers	1.0	-	-	-	3.4	0.2

i.e., four tepals, four stamens, four carpels (see Fig. 3). In some inflorescences of *P. natans*, all flowers of the three uppermost whorls possessed four tepals and four stamens, but not all flowers possessed four carpels (carpel number ranged between one and four). In *P. lucens*, inflorescences where all flowers possessed typical for *Potamogeton* number of parts (four tepals, four stamens, and four carpels) were not rare.

In both species examined flowers with a groundplan typical for *Potamogeton* were especially rare in the final whorl (Table 2). The percentage of flowers with four tepals, four stamens and four carpels was significantly higher in second and third whorls from the tip of a spike. Although the general tendency of decreasing frequencies of such flowers towards the spike tip was the same in both species, the tendency was much more pronounced in *P. natans* than in *P. lucens*. Indeed, among all examined final whorl flowers of *P. lucens*, 60.2% had four tepals, four stamens and four carpels. In *P. natans*, only 3.3% of examined final whorl flowers had a groundplan typical for *Potamogeton* (Table 1). Figure 1 illustrates variation of flower structure along two spikes of *P. natans*.

In the material examined almost all flowers that did not fit the typical *Potamogeton* groundplan possessed fewer organs than typical flowers[3]. All flower types found can be arranged in a more or less continuous morphological series, ranging from typical *Potamogeton* flowers with 12 organs to flowers with much fewer organs (see Fig. 3). Our data support the results of Charlton & Posluszny (1991) that variation in stamen number in *Potamogeton* is highly correlated with variation in tepal number, so that in a given flower the tepal number is generally the same as stamen number. We did not find male flowers without a perianth. Variation of carpel number is more independent from variation of tepal number.

In both species examined here the most frequent deviation from the flower groundplan typical for *Potamogeton* was a decreased carpel number in flowers with four tepals and four stamens (for example, among eight flowers with four tepals and four stamens illustrated in Figure 3A, only two

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3) Flowers with an increased organ number were very rare in our material. For example, the inflorescence illustrated in Figure 1A has only one flower with increased organ number, and such flowers are totally absent in the inflorescence in Figure 1B.
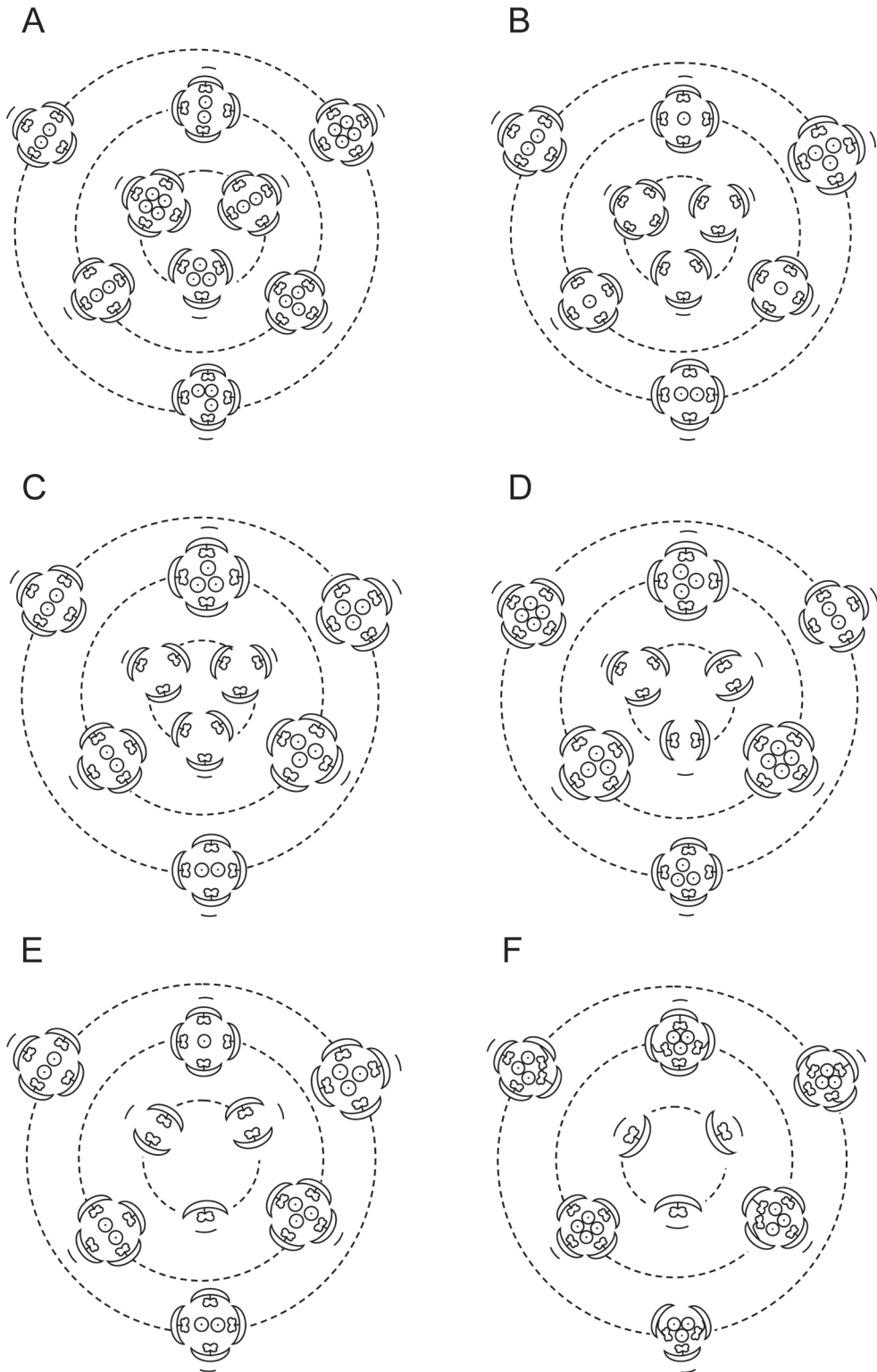
Figure 3. *Potamogeton natans.* Diagrams of three uppermost whorls of flowers in six inflorescences. Each whorl has three flowers. Each flower is subtended by a bract. Figures A–F illustrate a morphological series where last members possess fewer parts in flowers of the uppermost whorl. In this and subsequent figures, flowers of the same whorl are connected by dashed lines to make whorls more obvious.

flowers have four carpels). In other cases decreased carpel number was accompanied by decreased tepal and stamen numbers. In both species we found some flowers without any carpel. Stamen (and tepal) number in male flowers ranged from four to one, so that in some male flowers just one tepal and one stamen were present (Fig. 3B–F). In 30 spikes of *P. natans* (20% of examined inflorescences) all flowers of the final whorl were male (e.g., Fig. 2). In contrast, male flowers were not observed in the third whorl from the top of an inflorescence; they were extremely rare in the second whorl (Table 2). In *P. lucens*, like in *P. natans*, male flowers were never observed in the third whorl of flowers from the top of an inflorescence. Male flowers were extremely rare in the second whorl and more frequent in the final whorl in *P. lucens* (Table 2). Therefore, in both species examined almost all male flowers were confined to the final whorl. Also male flowers were more than twice more common in *P. natans* than in *P. lucens* (Table 2). In contrast to *P. natans* we never observed a final whorl composed exclusively by male flowers in *P. lucens.*

Although we found many male flowers, female flowers were almost completely absent in the material examined; we found only one example of a female flower (see Fig. 4).

Some flowers examined of both species lacked both gynoecium and androecium. These flowers possessed tepals only, and their tepal number was always less than four (ranging from three to one). In spikes of both species, flowers without stamens and carpels were found in the final whorl only (Table 2).

In two inflorescences of *P. natans*, a tubular structure was developed instead of a flower of the final whorl. In *P. lucens* both filamentous and tubular structures were observed, along with organs morphologically intermediate between tubular and filamentous structures. In total we found 16 spikes of *P. lucens* with tubular, filamentous or intermediate structure replacing position of a flower in the final whorl of flowers. Besides, we found one inflorescence of *P. lucens* with a tubular structure developed below the lowermost whorl of flowers in a spike.

Our data show that tubular structures might be considered as highly modified homologues of tepals, because we observed different kinds of longitudinal folding of tepals in flowers that lacked both, stamens and carpels.
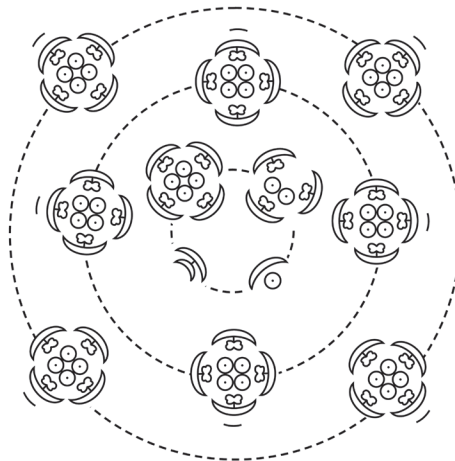

Figure 4. *Potamogeton lucens.* Inflorescence tip with four flowers in the uppermost whorl. Two flowers of the uppermost whorl have quite reduced structure. One of them (lower-right in the figure) has one tepal and one carpel (small circle). None of the flowers of the final whorl possess subtending bracts.

Variation in terminal structures

Many terminal structures observed in this study were surrounded by two or three bracts. These bracts were morphologically identical to subtending bracts of lateral flowers. Presence of several bracts was the main reason in identification of terminal structures as pseudanthia (Sokoloff et al. 2006). Structures that appear to be inserted at the top of the inflorescence but possess only one subtending bract might be regarded as lateral flowers shifted into pseudoterminal position; such structures seemingly cannot be regarded morphologically terminal. Apart from terminal structures surrounded by several bracts (similar to those illustrated in Figure 5), this study revealed the presence of terminal structures that did not possess any bract (Fig. 6). Theoretically such structures might represent terminal flowers. However, the presence and number of bracts do
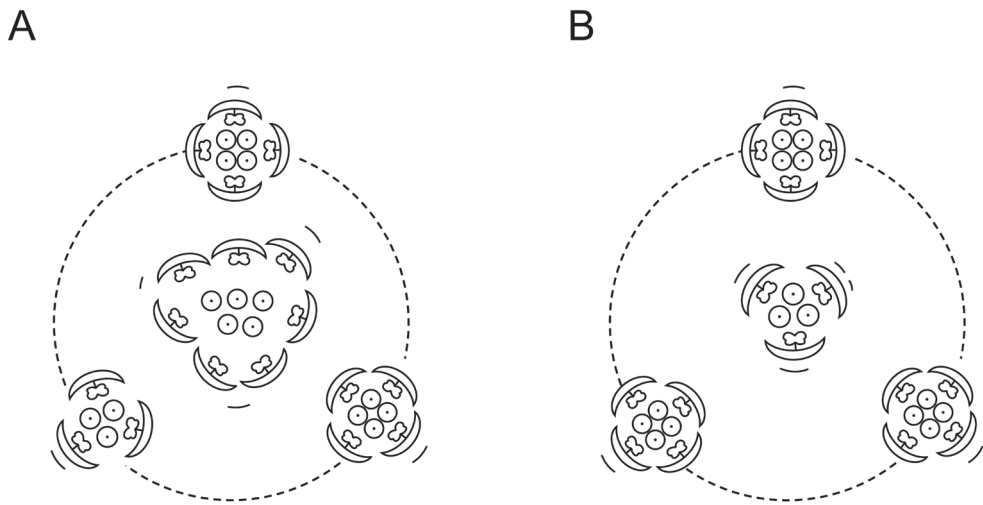

Figure 5. *Potamogeton natans*. Inflorescence tips with terminal flower-like structures surrounded by three bracts. Material from Moscow river (D. D. Sokoloff, unpubl. data).
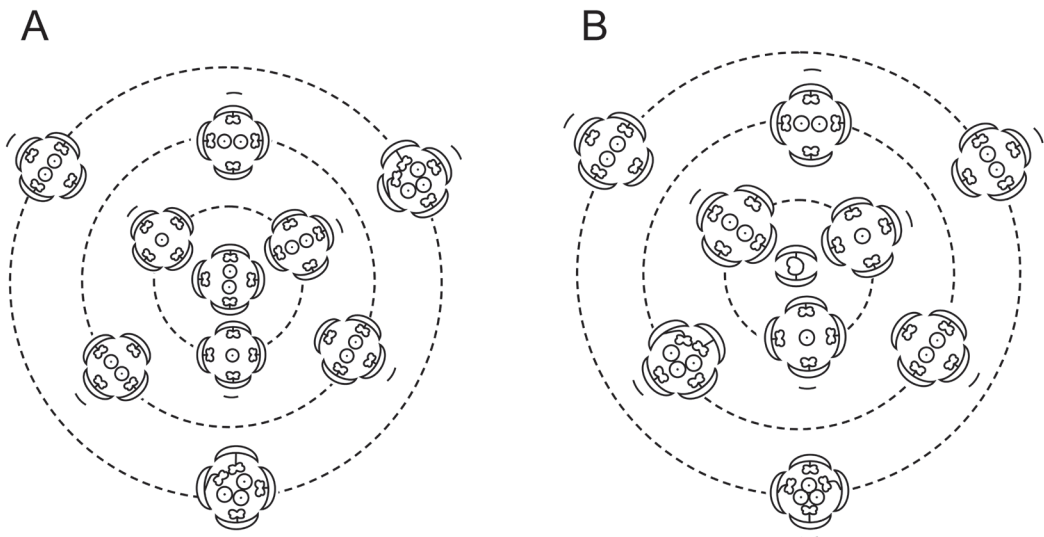

Figure 6. *Potamogeton natans*. Inflorescence tips with terminal structures not surrounded by bracts.
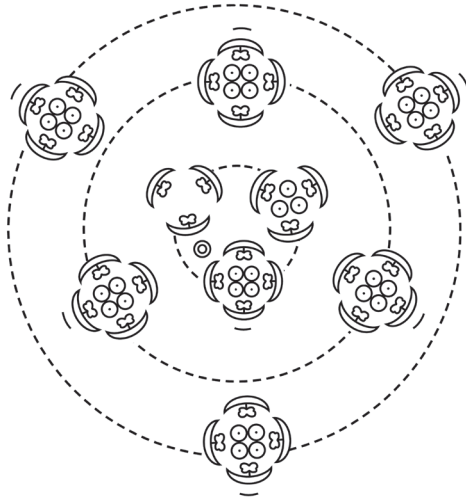
Figure 7. *Potamogeton lucens.* Inflorescence tip where two of three flowers of the uppermost whorl do not have bracts, besides, a tubular structure is present (illustrated as a double circle).

not represent the final argument in deciding whether a structure (1) is really terminal and (2) really represents a flower. Our doubts are due to the following observations. We found a number of inflorescences of *P. lucens* where none of three flowers of the final whorl was subtended by a bract (Fig. 4) or where only one of three flowers of the final whorl was subtended by a bract (Fig. 7). Sometimes (though very rarely) we failed to find subtending bracts in all flowers of an inflorescence.

The percentage of spikes that possessed a terminal structure (either surrounded by several bracts or lacking any bract) was different in the two species examined and in the two populations of *P. lucens* (Tables 3 and 4). However, in any case not less than 17% of spikes possessed any kind
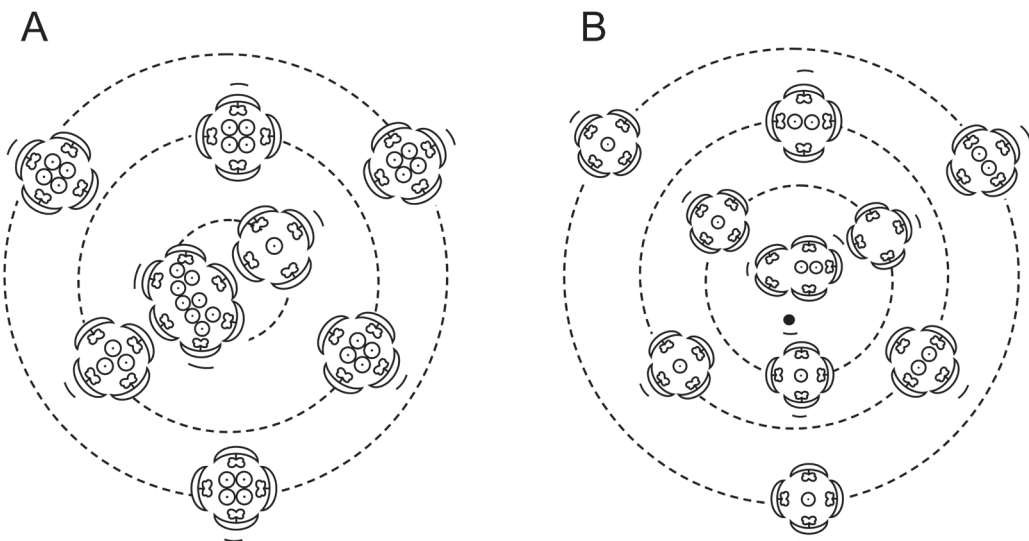

Figure 8. *Potamogeton natans.* Inflorescence tips where two of three flowers of the final whorl are united. In A, the third flower of the final whorl has nine organs. In B, the third flower is replaced by a filamentous structure (black dot).

Table 3. Occurrence of different types of terminal structures in spikes of two *Potamogeton* species (material from Usmanka river).

Morphology of terminal structure	*Potamogeton lucens*		*Potamogeton natans*	
	Number of spikes examined	%	Number of spikes examined	%
Terminal structure with organ composition as in flowers typical for *Potamogeton* (12 organs: four tepals, four stamens, four carpels)	2	1.5	1	0.7
Bisexual terminal structure with less than 12 organs	5	3.8	4	2.7
Male terminal structure	5	3.8	10	6.7
Terminal structure without stamens and carpels (tepals only)	4	3	9	6
Terminal structure with more than 12 organs	2	1.5	6	4
Terminal tubular or filamentous structure	4	3	3	2
Terminal structure absent	110	83	117	78
Total	132	100	150	100

of terminal structure. We stress that spikes used for these calculations were selected randomly from plants in natural populations, so that the figures in Tables 3 and 4 should give an idea of frequencies of occurrence of terminal structures and their different types.

All terminal structures found in this study can be arranged in a morphological series from polymerous bisexual structures that included more organs than in typical *Potamogeton* flowers to oligomerous structures that included only a few tepals and stamens and often lacked a gynoecium. When a polymerous terminal structure was supported by two bracts, the number of its organs approached a double set of organs that is present in a typical flower (i.e., $2 \times 4 = 8$ tepals, 8 stamens and 8 carpels, 24 organs). When a polymerous structure was supported by three bracts, it approached a triple set of organs. However, in all cases examined the number of organs

Table 4. Occurrence of different types of terminal structures in spikes of *Potamogeton lucens* collected in two populations.

|	Usmanka river		Moscow river	
	Number of spikes examined	%	Number of spikes examined	%
Terminal structure with organ composition as in flowers typical for *Potamogeton* (12 organs: four tepals, four stamens, four carpels)	2	1.5	3	6.0
Terminal structure with more than 12 organs	2	1.5	8	16.0
Terminal flower-like structure with less than 12 organs	14	10.6	8	16.0
Terminal tubular or filamentous structure	4	3	0	0
Terminal structure absent	110	83.3	31	62.0
Total	132	100	50	100
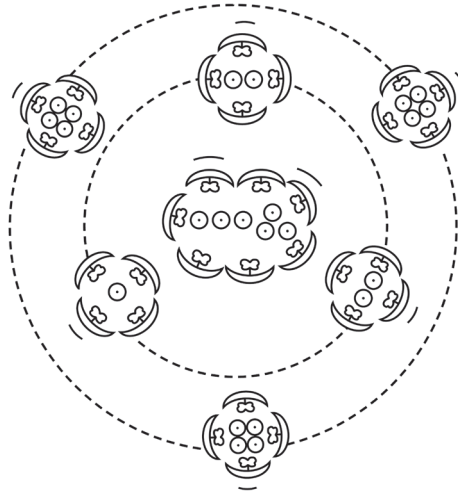
Figure 9. *Potamogeton natans*. Inflorescence with a terminal (?) structure represented by two united flowers. The fact that their subtending bracts are inserted closer to one side suggests that this inflorescence might represent a final member of a morphological series started with Figure 8A and followed by Figure 8B.

did not reach the theoretical value of 24 or 36 organs. The difference with the theoretical value was especially significant in polymerous terminal structures with three bracts. United flowers very similar to polymerous terminal structures were also found in lateral position. For example, Figure 8A shows a spike where two of three flowers of a final whorl are united while the third flower is free. In another inflorescence illustrated in Figure 8B, two flowers of the final whorl are united while the third flower is replaced by a filamentous structure. Complete loss of the third flower may effect in a terminal (or pseudoterminal?) structure illustrated in Figure 9.

Some terminal structures (in both species) possessed four or five tepals, four or five stamens and a number of carpels. These terminal structures were morphologically very similar to (often indistinguishable from) *flowers* typical for *Potamogeton*. However, these terminal structures were
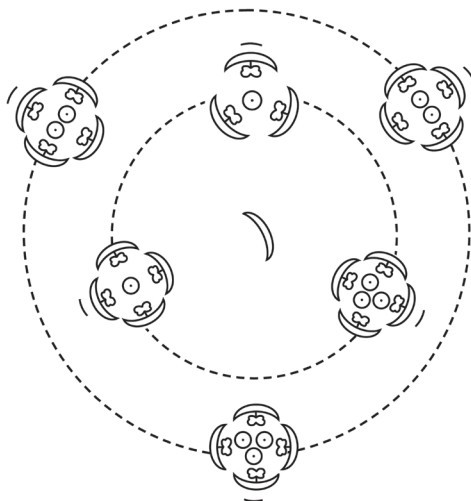

Figure 10. *Potamogeton natans*. Inflorescence tip with a tepal in an apparently terminal position.
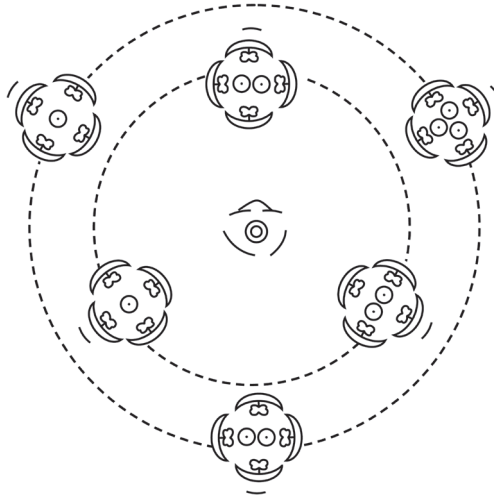
Figure 11. *Potamogeton natans.* Inflorescence tip with terminal tubular structure surrounded by three bracts.

normally surrounded by two or three bracts – a feature suggesting their homology with two or three united reduced flowers.

The variation range of oligomerous terminal structures was similar to that of lateral flowers (see above). Highly reduced terminal structures represented by solitary tepal were found. They resembled reduced lateral flowers composed just of one tepal (see above) but lacked a subtending bract and apparently occupied terminal position in a spike (Fig. 10).

We found several inflorescences of *P. natans* and *P. lucens* with terminal tubular or filamentous structures (Table 3). In one of these inflorescences a terminal tubular structure was surrounded by three bracts (Fig. 11); one of three bracts was pronouncedly bifid. Positionally, this tubular structure appears to be homologous to a terminal pseudanthium.
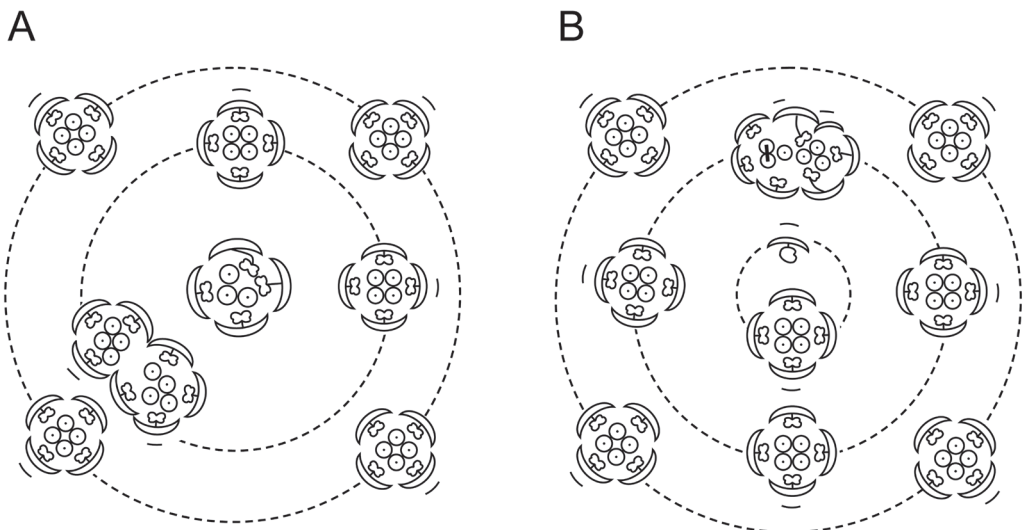

Figure 12. *Potamogeton lucens.* Diagrams of distal parts of two inflorescences belonging to the same individual.

We found a number of annual shoot systems that developed two or more spikes at stages appropriate for comparative analysis (e.g., Fig. 12). In many cases morphology of the inflorescence tip was significantly different in different spikes of the same plant. For example, when a spike possessed a terminal structure, another spike of the same plant often had only lateral flowers. The number of whorls also often differed considerably between spikes of the same plant.

Discussion

Our data on variation in lateral flower structure in two species of *Potamogeton* are congruent with results presented in the detailed studies of Posluszny & Sattler (1974) and Charlton & Posluszny (1991). In particular, we found largely independent variation in carpel and stamen number and strong correlation between stamen and tepal number. Also as in previous studies (e.g., Sattler 1965; Posluszny & Sattler 1974; Charlton & Posluszny 1991) our investigation revealed that the frequency of flowers of anomalous morphology increases toward the inflorescence tip. This study allowed quantitative comparative analysis of the distribution of anomalous flowers in inflorescences of two *Potamogeton* species. In the material examined of *P. natans* flowers of the final whorl almost always (96.7%) deviated from the typical groundplan. In contrast, in *P. lucens* only about 40% of examined flowers of the final whorl were anomalous. These differences are clearly significant, but more data are needed to test whether they characterize the species or their particular populations. The latter option might be possible because Charlton & Posluszny (1991) found considerable differences in variation in flower morphology between different populations of the same species of *Potamogeton*.

This is the first study allowing estimation of frequencies of spikes with terminal structures in *Potamogeton* plants from natural populations. In all populations examined (two populations of *P. lucens* and a population of *P. natans*) more than 15% of examined spikes possessed a terminal structure (i.e., a flower-like structure, a filamentous structure or a tubular structure). In our material, morphological variation of terminal structures (at least of oligomerous terminal structures) closely approached the variation range of lateral flowers.

We found considerable difficulties in distinguishing between terminal flowers, pseudoterminal flowers and terminal pseudanthia. Sokoloff et al. (2006) provided a review of features that are traditionally used or could be helpful in identifying these structures. Although many features should be considered, the main criterion is the presence and number of subtending bracts and physical position of a structure at the very top of an inflorescence. This study showed that the use of bracts is problematic in *Potamogeton*. Indeed, among essentially very similar terminal structures some were surrounded by several bracts (indicating a pseudanthial identity) while others lacked bracts entirely (indicating a terminal *flower* identity). Furthermore, although flower-subtending bracts are normally present in all lateral flowers, we found a few cases where all flowers of the final whorl lacked subtending bracts. Our results might be interpreted in several ways. (1) There is a continuum in *Potamogeton* between open inflorescences (lacking a terminal flower) and closed inflorescences, which possess a terminal flower. (2) Use of characters other than bract arrangement (e.g., vascular supply) could allow easier distinction between terminal vs. pseudoterminal structures and flowers vs. pseudanthia, but we consider this possibility unlikely. (3) Loss of flower identity could occur at the inflorescence tip, at least in some spikes of *Potamogeton*. In fact, hypotheses

(1) and (3) are very close to each other. When discussing possible pseudanthial interpretation of terminal flower-like structures in racemose inflorescences, Sokoloff et al. (2006) highlighted the occurrence of two principal types of pseudanthia (see also Prenner et al. 2009; Rudall et al. 2009). In the first type, the pseudanthium contains a number of closely associated and sometimes even fused flowers, but individual flowers are recognizable units, despite their reduced nature and / or connation with other flowers. In the second group, loss of flower individuality occurs. In extreme cases certain organs (e.g., stamens, carpels) cannot be assigned to individual flowers. Terminal pseudanthia of *Potamogeton* are of the second type (Sokoloff et al. 2006). Formation of the second type of pseudanthia is very similar to the phenomenon of fasciation (Sokoloff et al. 2006, 2007; Rudall et al. 2009); it might be also viewed as a (partial) loss of flower identity.

Our study has revealed that different spikes developing on the same individual can possess entirely different architecture in the distal region. For example, when a spike has a terminal flower-like structure, another spike produced by the same plant often has only lateral flowers. This supports the idea of Sokoloff et al. (2006) that the presence or absence of terminal structures and their morphology may not be directly linked with certain genetic mutations. Rather, variation in inflorescence tip structure is a result of high developmental lability. On the other hand, our results do not support the spatial constraint hypothesis that aimed to explain the underlying mechanics of this developmental lability. As outlined above, Sokoloff et al. (2006) viewed spatial constraints as the primary cause of variation in inflorescence tip morphology. They suggested that if flower primordia of the final whorl have (by chance) just sufficient space for their formation at the inflorescence apex, then a terminal structure is not formed. If the space remaining on the inflorescence apex after formation of the final whorl is insufficient for initiation of another whorl, then a terminal structure is formed, explaining why compound terminal structures possess fewer organs than could be estimated in two or three united flowers of typical morphology (i.e., 24 or 36 organs, respectively). Three observations contradict the spatial constraints hypothesis of Sokoloff et al. (2006) or at least imply that additional factors are operating. (1) The number of whorls per spike is highly variable in both species examined. Although not stated explicitly in Sokoloff et al. (2006), their hypothesis implies the presence of only slight variation in the length of the inflorescence meristem in *Potamogeton*, allowing initiation of, e.g., n-1, n, n+1 whorls of flowers depending on the length. (2) The spatial constraints hypothesis approximates the inflorescence meristem to a cylinder until its distalmost region. However, a significant decrease in the number of flowers per whorl in *P. lucens* (but not in *P. natans*!) toward the tip of a spike shows that narrowing the meristem apparently occurs earlier than at the level of the final whorl. (3) The most significant argument is that the number of organs per flower decreases significantly toward the tip of the inflorescence, and this phenomenon can be detected even in the second and the third whorls from the top of the inflorescence. Therefore, the mean size of the flower initiation zone decreases considerably toward the inflorescence tip. Moreover, when the space at the inflorescence meristem apex is apparently much smaller than necessary for initiation of a complete whorl of full-size flowers, then a whorl of distinct reduced flowers can be formed. The most intriguing question is whether in some cases inflorescences develop a terminal flower-like structure while in other cases they possess a final whorl of reduced flowers. A comprehensive theory of regulation of inflorescence development in *Potamogeton* should explain the source of this variation.

Acknowledgements

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