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Flower-like terminal structures in racemose inflorescences: a tool in morphogenetic and evolutionary research

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Abstract

Terminal flower-like structures (TFLS) occur in many angiosperms that possess indeterminate inflorescences such as spikes, racemes, or spadices. We describe and review TFLS in early-divergent angiosperms, especially the magnoliid order Piperales and the monocot order Alismatales, in which floral interpretation is controversial. Essentially similar TFLS occur in a wide range of taxa. Among magnoliids, they occur in some Piperales (Saururaceae and a few Piperaceae), but are absent from Chloranthaceae. Among monocots, they occur in some early-divergent families such as Acoraceae, Aponogetonaceae, Juncaginaceae, Potamogetonaceae, and Ruppiaceae. Similar TFLS with obscure organ identity are recorded in mutants of *Arabidopsis*. TFLS can often be interpreted as pseudanthia (close aggregations of reduced flowers), but in some cases the entire terminal pseudanthium is very similar to a true flower. In some cases, elaborated TFLS could therefore have given rise to what are normally termed 'true' (i.e. euanthial) flowers. Data presented here on terminal pseudanthia in *Potamogeton* and *Ruppia* support a pseudanthial evolutionary origin of reproductive units in the alismatid families Zannichelliaceae and Cymodoceaceae. Furthermore, in some alismatid species, either the entire inflorescence apex or an individual primordium at or near the inflorescence tip can be transformed into a filamentous or tubular (or intermediate) structure. A tubular structure enclosing stamens and carpels is described in *Piper*. This indicates that pseudanthium formation can provoke morphological novelties, per-haps due to new patterns of overlap between expression zones of regulatory genes and/or new spatial constraints.

Introduction

The spontaneous occurrence of atypical terminal flower-like structures (TFLS) in inflorescences that are otherwise indeterminate has long been considered important for understanding the morphogenesis and evolution of the inflorescence and flower. Interest in such structures has increased following discovery of the genes responsible for terminal flower formation in laboratory-induced mutants of model organisms such as *Arabidopsis* and *Antirrhinum* (Coen and Nugent, 1994; Bradley *et al.*, 1996, 1997; Cremer *et al.*, 2001; Ezhova and Penin, 2001; Penin *et al.*, 2004; see also Ordidge *et al.*, 2005). Terminal peloria are polysymmetric terminal flowers occurring in plants that normally possess only lateral monosymmetric flowers (reviewed by Rudall and Bateman, 2003). For example, they are common in Lamiales (the *Antirrhinum* clade), in which flowers are typically monosymmetric. However, they are absent from many other monosymmetric-flowered groups, such as Orchidaceae. Atypical terminal structures also occur in some plants that normally possess polysymmetric flowers; these can be interpreted either as peloria or sometimes as pseudanthia (aggregations of several flowers integrated together). The degree of distinction between

terminal peloria and terminal pseudanthia is ambiguous (Rohweder and Treu-Koene, 1971; Rudall and Bateman, 2003). Both types of TFLS result in a determinate inflorescence in a species that typically possesses indeterminate inflorescences. Even indeterminate inflorescences eventually become exhausted, and sometimes a terminal protrusion of the transformed apex (apical residuum) is present.

Evaluation of comparative empirical observations on spontaneous variability in inflorescence tip structure in a phylogenetic context can enhance our understanding of floral evolution. This is a complementary approach to research in developmental genetics. In particular, examination of TFLS in early-divergent angiosperms, in which many morphogenetic patterns are relatively labile, will ultimately allow questions to be addressed about the origin of the flower. Reproductive units of several early-divergent species (including some basal monocots) have been interpreted as pseudanthia (Kunth, 1841; Wettstein, 1907; Uhl, 1947; Prokhanov, 1974; Burger, 1977; Hickey and Taylor, 1996; see also Rudall, 2003) although this has been challenged by others (Singh, 1965; Posluszny and Sattler 1973, 1974a, b; Endress, 1995; Takhtajan, 1997; Mavrodiev and Sokoloff, 1998). Some authors (Nozeran, 1955; Meeuse, 1975; Kusnetzova, 1986) have postulated that some terminal structures on inflorescences (e.g. in some Saururaceae: *Anemopsis* and *Houttuynia*) represent a 'pre-floral state', implying a primitive condition in angiosperms. However, it is currently widely believed that the presence of flowers rather than a 'pre-floral state' is plesiomorphic in angiosperms, based on data from extant species (Endress, 2001) or early Cretaceous fossil angiosperms (Friis *et al.*, 2000, 2003). Here, terminal structures in racemose inflorescences (spikes, racemes, or spadices) of early-divergent angiosperms, especially the magnoliid order Piperales and the early-divergent monocot order Alismatales, are reviewed and compared. Although not closely related, these both represent early-divergent angiosperm lineages. Both orders have long been the subject of controversy regarding interpretation of their reproductive structures. The present report contributes to this ongoing discussion and examines whether studies of terminal pseudanthia and associated phenomena (including anomalous filamentous and tubular structures) can help in understanding evolutionary patterns and processes.

Structures that are usually termed pseudanthia fall into two distinct types that are not necessarily evolutionarily related to each other. In the first type (reviewed by Claßen Bockhoff, 1990, 1991), 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. Capitula of Asteraceae can be referred to this type. In the second group, loss of flower individuality occurs. In extreme cases, certain organs (e.g. stamens, carpels) cannot be assigned to individual flowers. All the terminal pseudanthia discussed herein are of the second type.

Materials and methods

The following species were examined: *Piper arboreum* Aubl. (Piperaceae), cultivated in the Princess of Wales Conservatory at the Royal Botanic Gardens, Kew and herbarium material (K); *Potamogeton natans* L. and *P. lucens* L. (Potamogetonaceae), collected in 2003–2005 by DD Sokoloff, MV Remizowa, and students of the Biological Faculty at Zvenigorod Biological Station of Moscow University, Moscow province, Russia; *Ruppia maritima* L. (Ruppiaceae), *Triglochin maritima* L., and *T. palustris* L. (Juncaginaceae), collected in July 2003 and July 2004 by DD Sokoloff and MV Remizowa, at the White Sea Biological Station of Moscow State University in N Karelia, Russia; *Triglochin bulbosa* L., collected in March 2004 by DD Sokoloff and AP Seregin, Akrotiri, Cyprus; *Tofieldia* and other genera of Tofieldiaceae, from all available herbarium material at Kew, Komarov Botanical Institute, St Petersburg, and Moscow State University, Moscow, plus living material listed in Remizowa *et al.* (2006).

Living material was fixed in either FAA or 70% ethanol. For scanning electron microscope (SEM) examination, material was dissected in 70% ethanol and dehydrated in an ethanol series. Dehydrated material was then critical-point dried, mounted onto SEM stubs using double-sided adhesive tape, coated with platinum or gold using a sputter coater, and examined using a Hitachi cold field emission SEM S-4700-II (2 kV) and a Hitachi SEM S-405A (15 kV).

Taxonomic distribution of terminal structures in early-divergent angiosperms

Among magnoliids, spikes and spadices are typical for both perianthless Piperales (Saururaceae and Piperaceae) and Chloranthaceae (Chloranthales). However, TFLS are absent from Chloranthaceae (Endress, 1987; Kong *et al.*, 2002), although Leroy (1983) interpreted the entire spike of male flowers in *Hedyosmum* as a flower-like structure. *Anemopsis* and *Houttuynia* (Saururaceae) possess showy bracts below the spicate inflorescence, resulting in a flower-like appearance; in addition, there is frequently a peculiar terminal structure. The TFLS of *Houttuynia* can include a terminal gynoecium surrounded by stamens and reduced male flowers; in other cases, the gynoecium is absent (Nozeran, 1955; Rohweder and Treu-Koene, 1971; Tucker, 1981; Liang and Tucker, 1990). Apical residua are present rather than TFLS in some Saururaceae and most Piperaceae (Tucker, 1979, 1980, 1982; Liang and Tucker, 1989). Thus far, TFLS are known in only two species of Piperaceae. In *Peperomia fraseri*, one or two carpels often develop at the tip of the spadix (Remizowa *et al.*, 2005). Among plants of
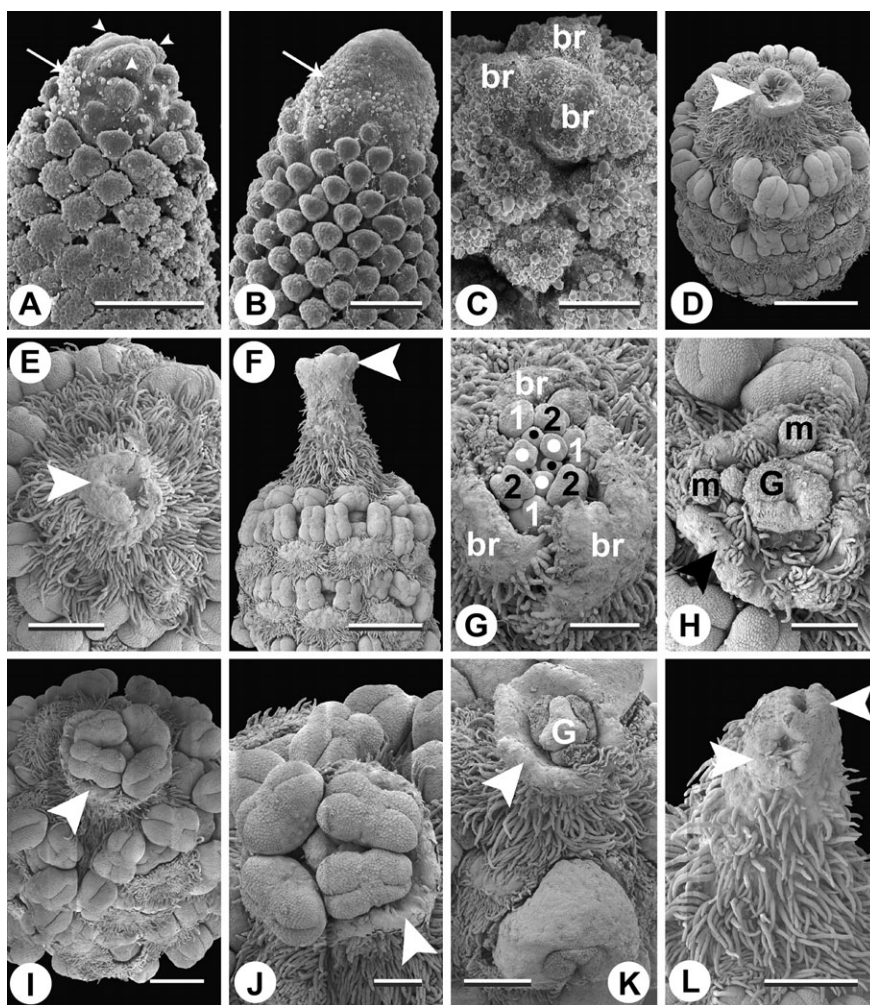
Fig. 1. SEM micrographs showing terminal structures in inflorescences of *Piper arboreum*. The structure is variable in different spikes in this specimen. (A) Three large bracts are formed at the top of the inflorescence (white arrowheads); hairs are initiated instead of bracts on one side of the inflorescence (arrow). Development of flower-subtending bracts is delayed in the uppermost portion of the young spadix. Bract primordia of the last whorl are fewer (three) but larger than those of the preceding whorl. (B) Hairs (arrow) are initiated after the last formed flower-subtending bracts. The inflorescence apex remains meristematic, and ready to produce a TFLS. (C) Three bracts (br) encircling a small apical residuum. The spadix in (C) is older than those in (A) and (B), and shows a third structural type. All space on the inflorescence axis is occupied by bracts except for a very small distalmost portion of apical meristem surrounded by a whorl of three bracts. In one young spadix (not shown), a continuous meristematic ring surrounding an apical depression was observed. (D–K) Most mature inflorescences possess a distal tubular structure that encircles the inflorescence apex. Epidermal features of the tubular structure and normal bracts are similar (e.g. presence of numerous stomata). There is often a portion of main axis below the tubular structure bearing reduced bracts and/or multicellular hairs rather than normal flowers (F). (D–F) Inflorescences with distal tubular structures (white arrowheads) that bear no stamens or carpels inside. (G) A terminal structure with three almost free bract-like organs and four trimerous alternating stamen whorls (marked 1, 2, white dots, black dots). Stamens are young but seem to be normal. It is not clear if a gynoecium would be formed in the centre of this structure. (H) A terminal tricarpellate gynoecium (G) surrounded by several microstamens (m) and a three-lobed tubular structure. This inflorescence lacks the flowerless region below the tubular structure, which is situated just above the final whorl of normal flowers. Sometimes microstamens and normal fertile stamens co-occur in the same terminal structure (not shown). (I, J) A terminal structure very similar to normal lateral flowers (i.e. four stamens and a central gynoecium) surrounded by tubular structures. (K) A tubular structure encircles three stamens (fallen off). A rudimentary terminal gynoecium (G) of three united carpels occupies the inflorescence apex. (L) At the apex of one spadix two tubular structures were united side by side. Scale bars: A, H=300 μm, B=200 μm, C=120 μm. D, F=1 mm, G, J=250 μm, E, I, K, L=500 μm.

Piper arboreum in the Kew living collections, we found one individual that produced TFLS in all inflorescences (Fig. 1), whereas other individuals produce only apical residua.

Among monocots, Buzgo and Endres (2000) and Buzgo *et al.* (2004) described TFLS in *Acorus*, and noted a similarity with *Anemopsis* and *Houttuynia*. The taxonomically isolated genus *Acorus* is putatively sister to all other

monocots, with Alismatales (Araceae, Tofieldiaceae, plus 12 families of aquatic alismatids) as sister to all monocots except *Acorus*. Terminal structures occur in many members of Alismatales. Either an apical residuum or a terminal flower is present in the racemose inflorescences of Tofieldiaceae (unpublished data). TFLS are mostly absent from Araceae (Buzgo, 2001), but present in *Calla palustris* as a cluster of stamens that cannot be assigned to individual

flowers (Lehmann and Sattler, 1992). However, it is the aquatic alismatids (formerly Helobieae) that display the widest range of TFLS. Terminal flowers (often peloric) or pairs of united flowers are present in spadices of at least some Aponogetonaceae. In Juncaginaceae, terminal or subterminal male flowers similar to the lateral male flowers have been described for *Lilaea* (Posluszny *et al.*, 1986). Bisexual terminal flowers are common in *Triglochin* (Buzgo *et al.*, 2006). Other types of terminal structure also occur in *T. maritima* (Fig. 2; see also Charlton, 1980). TFLS are extremely diverse in *Potamogeton* (Figs 3, 4; see also Charlton and Posluszny, 1991), although they do not occur in every inflorescence. *Ruppia* (Ruppiaceae) possesses two-flowered spikes, but the flowers are sometimes united (Fig. 5).

Morphological nature of terminal structures

Three basic types of terminal structure are recognized, although intermediates exist: (i) a true terminal flower; (ii) a morphologically lateral flower shifted into a pseudoterminal position; and (iii) a pseudanthium formed by united uppermost lateral flowers. (A similar phenomenon, of atypical 'double' flowers occurring in the lower or middle part of a racemose inflorescence, has also been recorded. However, united flowers in a terminal position are of particular interest because they could be mistaken for or give rise to true terminal flowers.)

There are several criteria that can be used to distinguish between these three types. (i) A true terminal flower opens before other flowers in an inflorescence, at least before the upper lateral flowers, which may be reduced (Goebel,
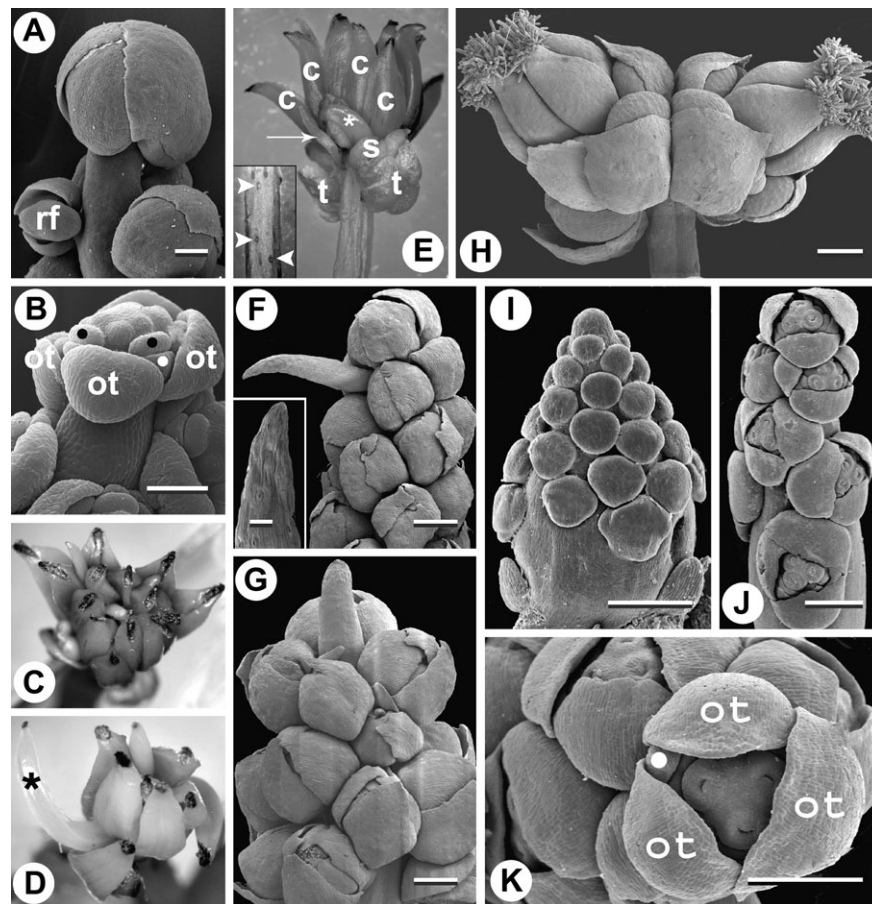

Fig. 2. SEM (A, B, F–K) and light microscope (C–E) micrographs showing terminal structures in inflorescences of *Triglochin* (*T. maritima* A–H, material from N Karelia, Russia; *T. bulbosa* I–K, material from Cyprus). (A) Distal part of the inflorescence before anthesis, with a large terminal flower bud, a small bud of a rudimentary upper lateral flower (rf), and a bud of an apparently normal lateral flower. (B) A developing tetramerous terminal flower (ot, outer whorl tepals; white dots, inner whorl tepals; black dots, inner whorl stamens). (C) A bisexual terminal structure with a gynoecium of 14 carpels and two further carpel-like structures. (D) A bisexual terminal structure with a gynoecium of seven carpels and two further carpel-like structures, one (asterisked) much longer than a normal carpel. (E) A bisexual terminal structure with increased carpel number; a further carpel-like structure (asterisk) and a filamentous structure (arrow) are visible. A long portion of the inflorescence axis below the terminal 'flower' bears short protuberances rather than lateral flowers (inset: lowermost part of this region). (F) An inflorescence tip with a lateral filamentous structure inserted below the terminal flower (inset: enlarged tip of the filamentous structure). (G) An almost terminal filamentous structure. (H) Two closely associated lateral flowers at the inflorescence tip. (I) A very young inflorescence with lateral floral primordia just before terminal flower initiation. (J) A young inflorescence with a terminal flower. (K) Top view of a terminal flower; ot, outer whorl tepals; white dot, inner whorl tepal (only one of three inner tepals is visible). Scale bars: in A, I, K=300 μm, in B=100 μm, in F–H=500 μm, in J=400 μm.
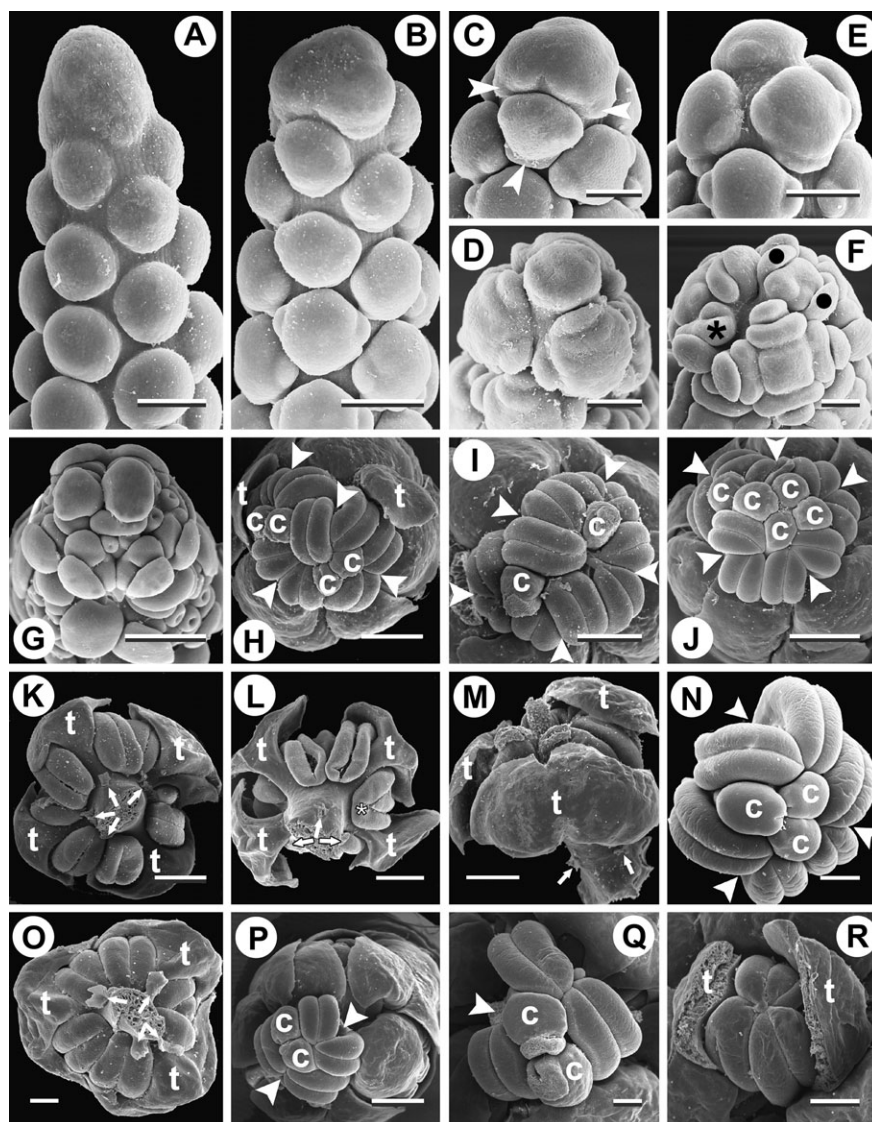
Fig. 3. SEM micrographs showing an inflorescence tip in *Potamogeton* (all *P. natans*, except *P. lucens* in N, both species collected near Moscow in Russia). A–F show variation in inflorescence tip development. (A) The fate of the tip is still not clear, but a terminal structure would probably form. (B and C) Three uppermost floral primordia are united. Arrowheads indicate flower-subtending bracts. (D) A terminal structure primordium is much smaller than three lateral flowers of the last whorl, and delayed developmentally. (E) The uppermost flower is slightly shifted to one side of the inflorescence. (F) The uppermost flower is shifted to one side of the inflorescence; it has two tepals (black dots) and a central portion that may develop into two united stamens. One of the upper lateral flowers has an unusually large stamen (asterisked) with an outgrowth of ambiguous nature. G–R show various kinds of TFLS. Their pseudanthial nature is supported by the presence of more than one flower-subtending bract. G–J, N, P–R, top view; K, L, O, terminal structure removed from inflorescence and viewed from below to show bracts; M, side view. c, carpel; t, tepal; arrow, bract; arrowhead, place of tepal attachment when tepal was removed during dissection; the asterisk indicates the place where thecae of two different stamens are united. Scale bars: in A, C, E, F=100 µm; in B, D=150 µm; in G, N, O, Q=300 µm; in R=500 µm; in H–M, P=1 mm.

1931; Weberling, 1989). This criterion is problematic for inflorescences in which flowers open simultaneously, and inapplicable in cases where the inflorescence is reduced to a single flower. (ii) The internode of the inflorescence axis below a terminal flower (termed the 'final internode' by Weberling, 1989) is often different in length from other internodes (either longer or shorter). This criterion in particular suggests that the terminal structures of *Triglochin* (Buzgo *et al.*, 2006) and *P. arboreum* are true flowers. (iii) The presence of more than one bract surrounding a

terminal structure indicates a pseudanthium, as in some material of *Potamogeton* (Fig. 3C, K–M, O) and *Piper* (Fig. 1, in which three bract homologues are united into a tubular structure). In contrast, the presence of only one bract indicates a pseudoterminal flower, as in some inflorescences of *Potamogeton lucens*. However, a complicating factor is that many angiosperms possess sterile bracts below a true terminal flower; these are possibly derived from suppressed uppermost lateral flowers (Weberling, 1989; Kusnetzova, 1995). Furthermore, some inflorescences
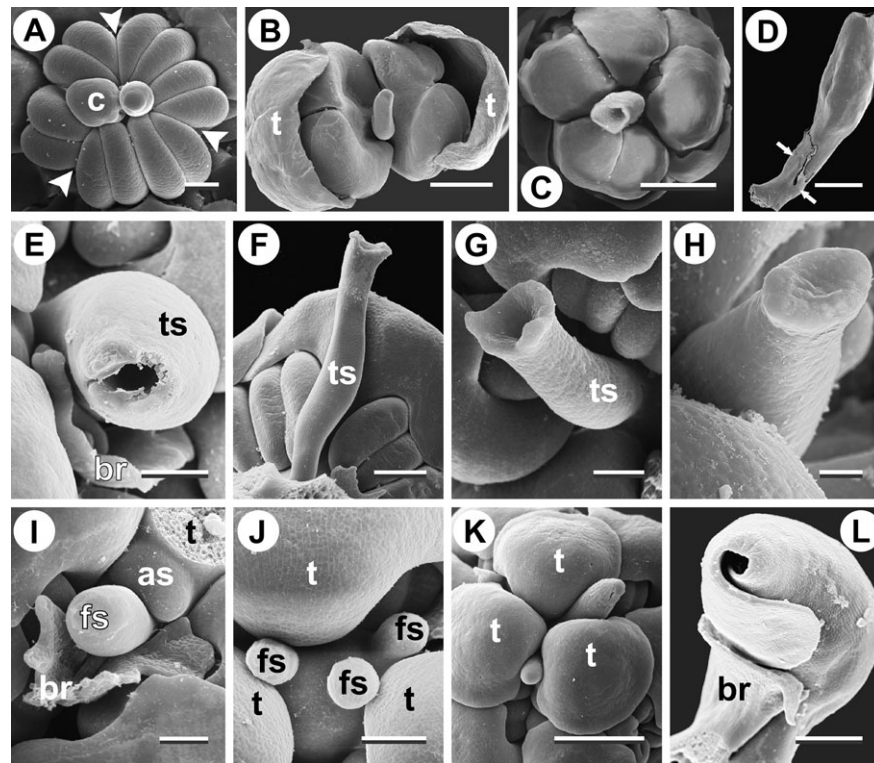
Fig. 4. SEM micrographs showing unusual organs at the inflorescence tip in *Potamogeton natans* (A, C, G, H, J) and *P. lucens* (B, D–F, I, K, L). (A) A terminal structure with three tepals (removed), three stamens, a normal carpel, and a central organ of ambiguous identity. (B) A terminal structure with two tepals, two stamens, and a central organ of ambiguous identity. (C) A terminal tubular structure surrounded by three normal lateral flowers whose tepals are visible on the figure. (D) A terminal tubular structure removed from the inflorescence to show bracts (arrows). (E) A tubular structure subtended by a bract. (F) An abracteate tubular structure. (G, H) Organs transitional between tubular and filamentous structures. (I) An inflorescence tip with a tepal (removed) associated with what could be interpreted as a sterile stamen and a short filamentous structure in the axil of a well-developed bract. (J) Three filamentous structures at the inflorescence top alternating with three uppermost lateral flowers (only their adaxial tepals are visible in the figure). The right hand filamentous structure has a subtending bract (mostly cut off in the figure). (K) Two filamentous structures alternating with uppermost lateral flowers (only their adaxial tepals are visible). (L) A twisted tepal-like structure in the axil of a bract. as, abortive stamen (?); br, bract; c, carpel; fs, filamentous structure; t, tepal; ts, tubular structure; arrow, bract; arrowhead, place of tepal attachment when the tepal was removed during dissection. Scale bars: in A, F, K, L=300 μm; in B=800 μm; in C, D=1 mm; in E, H, J=100 μm; in G=30 μm.

lack bracts entirely (as in *Triglochin*, *Ruppia*). [When lateral flowers possess bracteole(s), or prophyll(s)—which is not the case in perianthless Piperales and tepaloid Alismatales—these structures are absent from the terminal flower by definition, for example, Goebel (1931). The presence of a terminal flower in the dense bractless capitula of Asteraceae is discussed by Teeri *et al.* (2006).] (iv) Based on data both from mutants of model organisms, and a review of various angiosperms, Penin *et al.* (2004) concluded that perianth-bearing true terminal flowers cannot occur in abracteate inflorescences. If so, perianth-bearing terminal structures in abracteate inflorescences must be either pseudoterminal flowers or pseudanthia. This is the case in *Triglochin* (Fig. 2A–E, J–K). (v) Terminal flowers often differ in merosity or symmetry from lateral ones (Kusnetzova, 1985; Rudall and Bateman, 2003; Penin *et al.*, 2004). However, the same should be expected from terminal pseudanthia. (vi) Fedorova (2004) found that in compact inflorescences with unisexual or partly unisexual flowers, a terminal flower (if present) is either bisexual or female. If

the terminal flower is absent, then the uppermost lateral flowers are either male or bisexual. This suggests that the uppermost flower of *Lilaea* (Posluszny *et al.*, 1986) (which is male) is pseudoterminal rather than terminal. (vii) Preliminary (unpublished) observations on vascular anatomy of terminal structures in *Potamogeton natans* indicate that vasculature could represent an additional criterion, since the vascular supply of TFLS is different from what could be expected for just three united uppermost flowers. Rudall (2003) also discussed vasculature in relation to pseudanthia in Triuridaceae, in which vascular traces depart from the axial vascular cylinder in a manner similar to a condensed branching axis with very short internodes. (viii) The presence of an apical residuum at the top of the inflorescence proves absence of a terminal flower. However, an apical residuum is sometimes entirely absent even if all flowers are lateral. Also, an apical residuum may be present in true flowers (e.g. in *Nymphaea*).

Most data suggest a pseudanthial nature for the terminal flower-like structures of *Potamogeton* and *Ruppia*
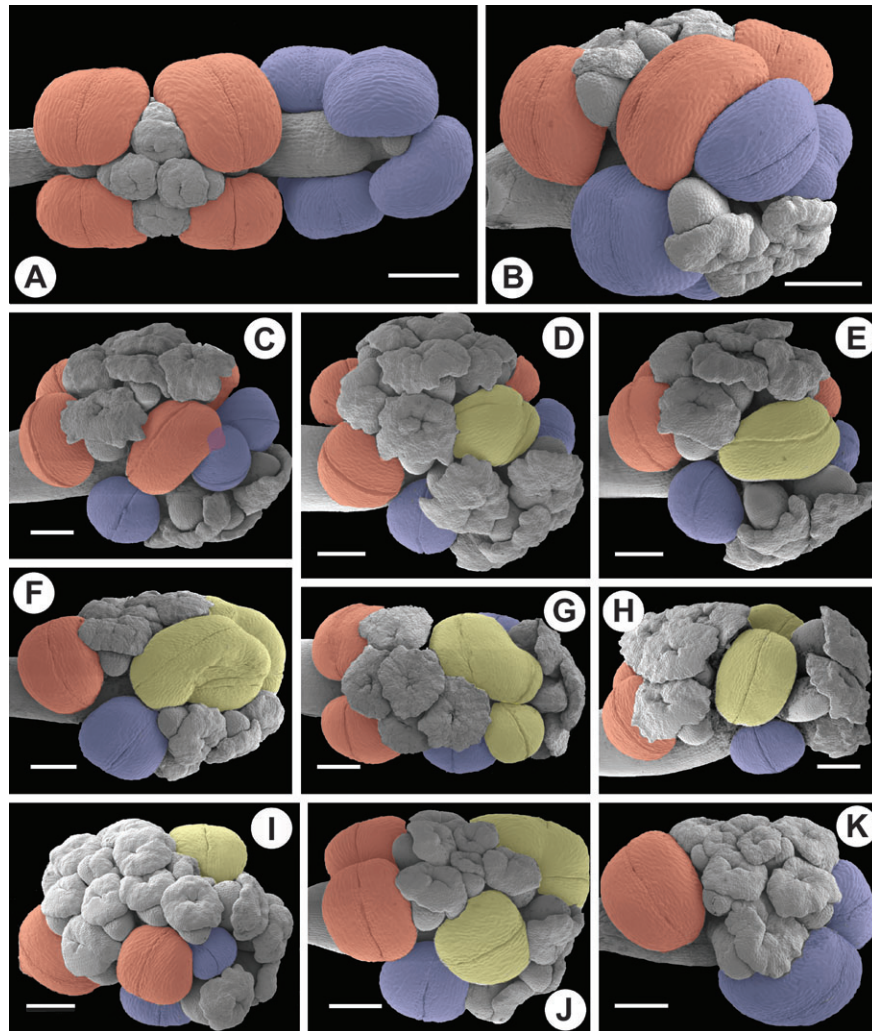
Fig. 5. SEM micrographs showing variation in the structure of two-flowered spikes of *Ruppia maritima* (material from N Karelia, Russia). Stamen thecae of the lower flower are coloured red, stamen thecae of the upper flower are in blue, and thecae of hybrid origin (amalgamated thecae belonging to adaxial stamens of different flowers) are in yellow. Carpels are not coloured. (A) Two widely spaced flowers. (B) Two flowers that are closely associated, but free. (C–J) A series showing increasing degree of amalgamation between the two flowers; only one theca of the abaxial (free) blue stamen is visible (another one is on the opposite side). In (F and I), only one theca of the abaxial (free) red stamen is visible (another one is on the opposite side). (K) Two flowers are completely amalgamated, and the entire structure resembles a solitary terminal flower. Only one theca of a red stamen is visible (another one is on the opposite side). Scale bars: in A=300 µm; in B–K=250 µm.

(Figs 3, 5). However, interpretation of these structures in *Peperomia fraseri* (Remizowa *et al.*, 2005), *Piper arboreum* (Fig. 1), and *Triglochin* (Fig. 2) is more problematic as the different criteria provide conflicting evidence. It is possible that there is a series of intermediate forms in nature (at least in certain plant groups) between a true terminal flower and a terminal pseudanthium (see also Charlton, 1980). In evolutionary terms, this may mean that an elaborated terminal pseudanthium can give rise to what is normally termed a true flower. A further possibility—for example, in polymerous TFLS of *Triglochin*—is loss of flower identity. Since possession of 'true' flowers probably represents the primitive condition in angiosperms, loss of flower identity is most probably a derived condition that occurred many times during the course of evolution of terminal structures

in various species. Similar phenomena have been described in mutants of different model organisms.

All the terminal pseudanthia discussed here represent a phenomenon that is similar to fasciation, with the important distinction that fasciation is normally believed to be derived from a discrete structure (e.g. flower or vegetative shoot) that has incompletely multiplied. For example, Worsdell (1915) defined fasciation as 'multiple forking of an axis'. Thus, the pseudanthia here represent the opposite phenomenon, assuming their homology with several independent flowers. However, a broader definition of fasciation which includes both cases is also possible, although perhaps less useful. For example, Masters (1869) cited cases in which buds are pressed together and become fused during development.

Unusual floral organs

An apparently novel observation from this investigation is that both tubular and filamentous structures sometimes occur at the inflorescence apex in wild-source material in species of at least two alismatid monocot families, Potamogetonaceae and Juncaginaceae (Figs 2E–G, 3C–K). There are also intermediate forms between the two structures, indicating that they represent different manifestations of the same morphogenetic phenomenon. The tubular structures in *Potamogeton* are essentially similar in morphology and position to the club-shaped organs described in *Acorus* (Buzgo and Endress, 2000). Filamentous structures also occur in wild-source material of another alismatid monocot, *Scheuchzeria* (Scheuchzeriaceae: M Remizowa and D Sokoloff, unpublished data).

Unusual filamentous structures are of special interest because they have been described in inflorescences of some *Arabidopsis* mutants, especially in *fil* (Sawa *et al.*, 1999) and *ufo* (Levin and Meyerowitz, 1995; Wilkinson and Haughn, 1995). Although filamentous structures are more common, tubular structures that are apparently homologous to filamentous ones have also been described for *Arabidopsis* mutants such as *lfy-6 fl54*. Levin and Meyerowitz (1995) searched for precedents for the natural formation of filamentous structures in plants other than *Arabidopsis*. They listed such examples as filiform leaves of aquatic plants as well as spines and tendrils.

Filamentous and tubular structures of both *Arabidopsis* mutants and alismatid monocots often develop in the position of flowers. Since flower-subtending bracts are absent in wild-type *Arabidopsis*, it is problematic to decide whether filamentous structures represent reduced, modified flowers or partially de-suppressed bracts (with flowers completely suppressed). Levin and Meyerowitz (1995) observed that a filamentous structure sometimes subtends the lowermost flower(s) in inflorescences of *Arabidopsis ufo* mutants, and concluded a likely bract homology for filamentous structures, although a flower homology could not be excluded. Sawa *et al.* (1999) suggested that filamentous structures of *fil* mutants represent underdeveloped flowers that form a pedicel but lack a receptacle and floral organs. Watanabe and Okada (2003) showed that *FIL* plays a role in specifying the abaxial side tissues in the development of lateral organs such as cotyledons, leaves, young flower buds, and flower organs. In *Potamogeton*, apparently normal flower-subtending bracts often subtend tubular and filamentous structures; thus, they are apparently of floral nature. The developmental mechanism responsible for unusual structure formation may not be the same in *Arabidopsis* mutants and Alismatales.

Tubular structures described here in *Piper arboreum*, a periantheless member of Piperales, differ significantly from the tubular structures of alismatid monocots. In some inflorescences, the final-whorl bracts are almost free (Fig. 1G),

indicating that the tubular structure in *P. arboreum* is probably homologous with three congenitally united flower-subtending bracts of the final whorl. Furthermore, it often contains reproductive organs (Fig. 1H–K); these are often sterile, although stamens are occasionally fertile. Interestingly, some terminal structures of *Piper* resemble flowers of Aristolochiaceae, a perianth-bearing family of Piperales in which flowers are in a terminal position. The three-lobed tubular structure of *Piper* resembles a perianth of Aristolochiaceae that is often composed of three united members. Reproductive organs inside the tubular structure often show a trimerous pattern, which is also the case in Aristolochiaceae.

Use of terminal structures in understanding inflorescence and flower morphogenesis

We propose some preliminary hypotheses regarding regulation of development in *Potamogeton natans*. Elongation of the inflorescence apex and initiation of lateral flowers are apparently controlled by two independent developmental programmes. Elongation of the inflorescence apex commences first, but proceeds more slowly than the formation of lateral flower primordia, which occurs in an acropetal pattern. The flower primordia are usually initiated in regular alternating whorls (of two, three, or four) up to the tip of the developing inflorescence (see also Posluszny and Charlton, 1983). 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. However, this is often not the case, because the inflorescence apex may be longer or shorter than is necessary for insertion of the final-whorl primordia. Another factor is the change in inflorescence shape from cylindrical throughout its length to hemispherical at the tip; this may also cause problems with proper patterning of the final-whorl primordia. 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 (Fig. 3B, C). Depending on the space available, this compound terminal primordium gives rise to what could easily be interpreted as a pseudanthium (Fig. 3G) or an almost completely flower-like structure (Fig. 3M). 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. Thus, it seems likely that, in *Potamogeton*, abnormalities are due to spatial problems. Despite the fact that there is insufficient space to initiate a flower of typical structure, expression of genes responsible for flower initiation still occurs. In this case, unusual patterns of overlap between expression zones of regulatory genes may result in the formation of unusual organs (e.g. tubular structures). Studies of terminal

structures in *Potamogeton* may therefore help in understanding the 'mass effect' in flower formation (Tucker, 1979). There is apparently a minimum size of flower primordium that can produce flower-bearing structures of 'normal' organ identity (tepals, stamens, carpels). If the floral primordium size is smaller than this threshold, flower morphogenesis is shifted entirely, and a tubular or filamentous structure is formed. These unusual structures do not merely represent suppressed flowers, but result from activity of an entirely different developmental programme. In mature inflorescences, these structures are often much longer than normal flowers.

We propose a similar pattern for the terminal structures of *Peperomia fraseri*, a species of perianthless Piperales (Remizowa *et al.*, 2005). However, among Piperales, inflorescence morphogenesis in *Piper* is quite different from that of *Potamogeton*. In wild-type *P. arboreum*, as well as in many other Piperaceae (Tucker, 1980, 1982) and other Piperales such as *Saururus* (Tucker, 1979), an apical residuum occurs at the inflorescence tip. A critical point is that the overall size of this residuum is larger than the space necessary for flower initiation. Thus, cessation of growth is an active process, and genes responsible for flower initiation are no longer active here at the appropriate time. This could represent an adaptation to prevent formation of organs with unusual identity and to unify floral structure in the inflorescence. In an anomalous plant of *P. arboreum* that bears terminal structures, pattern formation of the terminal structures probably occurs prior to patterning of the upper lateral floral primordia. There is often sufficient space on the inflorescence meristem to initiate more flowers immediately below the terminal structure. The fact that these flowers are not initiated must be due to active inhibition, as in apical residua of most Piperaceae and *Saururus*. Interestingly, hairs are formed instead of flowers in both *P. arboreum* (Fig. 1A, B, D, F, L) and *Saururus* (Tucker, 1979).

In summary, it is important to emphasize the differences between elaborated apical residua (as in some perianthless Piperales) and terminal filamentous structures (in some inflorescences of *Potamogeton* and *Triglochin*). The former reflect canalization and stability in inflorescence morphogenesis, whereas the latter result from unstable morphogenesis of the inflorescence tip. Apical residua have been described in a wide range of angiosperms (Troll, 1964). These observations may need re-investigation in the light of this new evidence.

Pseudanthial origin of reproductive units in Zannichelliaceae and Cymodoceaceae

Relationships within Alismatales have long been problematic. The submerged aquatic families Zannichelliaceae and Cymodoceaceae have traditionally been considered closely related (Dahlgren *et al.*, 1985; Takhtajan, 1997) or even treated as a single family (Eckardt, 1964), but molecular phylogenetic analyses indicate that Zannichelliaceae are closely related to (and could be synonymized with) Potamogetonaceae s.str. (Les *et al.*, 1997; APG, 2003; Chen *et al.*, 2004) whereas Cymodoceaceae are allied with Ruppiaceae (Les *et al.*, 1997). Apart from features obviously connected with submerged growth and underwater pollination, Zannichelliaceae and Cymodoceaceae share a cymose pattern of flower arrangement, although inflorescences of many Cymodoceaceae are reduced and sometimes single flowered (Irmisch, 1851; Eckardt, 1964; Kay, 1971; Posluszny and Sattler, 1976; Posluszny and Tomlinson, 1977; Tomlinson and Posluszny, 1978; Dahlgren *et al.*, 1985; Takhtajan, 1997; Mavrodiev and Sokoloff, 1998). In contrast, Potamogetonaceae and Ruppiaceae possess flowers arranged in open spikes.

Mavrodiev and Sokoloff (1998) drew attention to the essential similarity of general inflorescence architecture between Zannichelliaceae, Ruppiaceae, and Potamogetonaceae (see Supplementary Figs 1 and 2 available at JXB online), but with the important difference that the basic inflorescence units of Zannichelliaceae are flowers and those of Ruppiaceae and Potamogetonaceae are open spikes of flowers. They hypothesized that entire spikes of *Potamogeton* and *Ruppia* may be homologous to individual flowers of Zannichelliaceae. They emphasized that one of two observations could prove this hypothesis: either flowers of Zannichelliaceae are morphologically lateral but shifted to a terminal position, or spikes of *Potamogeton* sometimes bear a terminal flower. However, at that time, they did not observe any of these phenomena. Now we have found considerable diversity of flower-like terminal structures in *Potamogeton*, which should be termed terminal pseudanthia rather than true terminal flowers. We postulate that reproductive units of Zannichelliaceae could be derived from such terminal pseudanthia. One possible objection is that terminal pseudanthia (and terminal peloria) are mostly present at the ends of long, many-flowered racemes or spikes, whereas the present hypothesis implies that the entire spike in Zannichelliaceae was taken up by terminal pseudanthium formation. However, we have also observed this phenomenon in two-flowered spikes of *Ruppia* (Fig. 5), which demonstrates the possibility of use of the entire spike for formation of a terminal flower-like structure.

With a few exceptions (e.g. *Syringodium filiforme*), inflorescences of Cymodoceaceae (see Supplementary Fig. 3 available at JXB online) are mostly reduced and few-flowered, but the basic pattern is cymose (Tomlinson and Posluszny, 1978). The inflorescence of *S. filiforme* is essentially similar to that of *Ruppia*, except that the basic unit of *Syringodium* is commonly described as a flower whereas *Ruppia* possesses two-flowered spikes. Since amalgamation between flowers has been observed in

Ruppia, we suggest a pseudanthial origin of reproductive structures in Cymodoceaceae.

Authors who have interpreted the female units of Zannichelliaceae and Cymodoceaceae as pseudanthial (Prillieux, 1864; Uhl, 1947; Ducker and Knox, 1976) have regarded each carpel as a naked female flower. However, although we agree with a pseudanthial origin of the terminal structures of these plants, the end-product of amalgamation of two or three flowers can be quite an integrated structure, and it is futile to search for parts that precisely correspond to those of the initial flowers. This is especially the case for the gynoecium. For example, if the terminal structure of *Potamogeton* illustrated in Fig. 3M is a pseudanthium, each of the three carpels belongs to the entire pseudanthium, not to particular individual flowers. Flowers in two-flowered inflorescences of *Ruppia* (Kaul, 1993) and *Potamogeton densus* (Posluszny and Sattler, 1973) are in the median plane of the two subopposite leaves situated below the spike (see Supplementary Fig. 4 available at JXB online), thus continuing the distichy of the vegetative part of the shoot into the inflorescence. In Zannichelliaceae (Posluszny and Sattler, 1976) and Cymodoceaceae (Tomlinson and Posluszny, 1978), when female units are bicarpellate, carpels are in the transverse plane of distichy of the vegetative part of the shoot (see Supplementary Fig. 4 available at JXB online). These carpels cannot be assigned to individual flowers.

There are interesting morphological parallels between some terminal structures of *Potamogeton* and *Ruppia* and reproductive units of Cymodoceaceae and Zannichelliaceae. In all Cymodoceaceae and Zannichelliaceae, the male unit contains a single anther that frequently possesses more than four microsporangia and has hence been interpreted as a fusion product of different stamens. Terminal structures of *Ruppia* and *Potamogeton* also show a tendency for stamen connation. The structure of *P. lucens* illustrated in Fig. 3R (with four united thecae) resembles male flowers of some Zannichelliaceae. Interestingly, it possesses an apical appendage, a feature common in both Cymodoceaceae and Zannichelliaceae but not present in normal flowers of *P. lucens*. This probably illustrates how morphological novelty can arise during pseudanthium formation. In contrast to stamens, united carpels have not been observed in terminal structures of *Potamogeton* and *Ruppia*. This is also the case in reproductive structures of Zannichelliaceae and Cymodoceaceae. Thus, there is apparently a constraint against carpel connation in all four families, as they are among very few monocots bearing free carpels (Igersheim *et al.*, 2001). In *Zannichellia*, there is a tubular envelope surrounding the female unit. Despite extensive discussion in the literature, its origin remains unclear. However, it is morphologically comparable with the terminal tubular structures that we observed in *Piper arboreum* (Fig. 1H–K); the two species are not closely related, but the example of *Piper* demonstrates how such a morphological novelty can arise.

Terminalization versus truncation in evolution of flower arrangement in angiosperms

Evolutionary relationships between monotelic and polytelic types of flower arrangement (i.e. with and without a terminal flower; Weberling, 1989) or, more precisely, between types of flower arrangement with different axiality, have long been debated. Axiality can be defined as minimum branch order (within an architectural unit of branching system) that can be terminated by a flower (reviewed in Notov and Kusnetzova, 2004). For example, plants with terminal monotelic synflorescences are monoaxial (e.g. *Ranunculus* and Zannichelliaceae), plants with terminal open racemes, spikes, or umbels are diaxial (e.g. *Arabidopsis, Antirrhinum*, *Ruppia*, and *Potamogeton*), and plants with lateral spikes or racemes are triaxial (e.g. *Pisum* and many other legumes).

Many authors have emphasized the importance of truncation (Sell, 1969; Kusnetzova, 1988, 1998; Weberling, 1989), or evolutionary loss of a terminal flower. This transformation results in an evolutionary transition from monotelic to polytelic synflorescences, or (in more general terms) in increased axiality. When putatively primitive members of a natural group bear clearly polytelic synflorescences while putatively advanced members bear what appears to be a terminal flower, closer inspection usually shows that it is either not terminal (i.e. a lateral flower shifted into a pseudoterminal position) or a pseudanthium rather than a flower. In Zannichelliaceae and Cymodoceaceae, we have demonstrated the pseudanthial origin of terminal reproductive units. This raises the question of whether an elaborated terminal pseudanthium could give rise to a 'true' flower. This is probably so in cases such as Cymodoceaceae and Zannichelliaceae, in which the terminal structure is derived from two or more united flowers but cannot be subdivided into parts corresponding to putative individual flowers. If it is accepted that the reproductive units of these two families are flowers derived from pseudanthia, then an evolutionary change that is the opposite to truncation could be proposed. This phenomenon, which we term 'terminalization', can result in an evolutionary shift from polytelic to monetelic synflorescences and in decreased axiality.

Terminalization does not necessarily occur via formation of terminal pseudanthia, but could arise by saltation. As mentioned above, several well-known mutants differ from the wild type in the consistent presence of terminal flowers, although the question remains of whether such an apparently simple mechanism could occur during the course of evolution (see also Singer *et al.*, 1999). An example of terminalization that does not necessarily involve pseudanthium formation was described by Endress (1970, 1978) in Hamamelidaceae. In perianth-bearing Hamamelidaceae (e.g. *Parrotia*), flowers are organized into spikes that are themselves arranged in panicles. Spikes lack either a terminal

flower or a TFLS. In periantless Hamamelidaceae (e.g. *Distylium*), solitary terminal flowers occur in paniculate inflorescences instead of spikes. There is robust evidence that the ramification pattern in periantless Hamamelidaceae represents a derived condition (Endress, 1970, 1978).

Similarities between the conditions in Alismatales and Hamamelidaceae include the following (for Hamamelidaceae, see Endress, 1970, 1978; Li *et al.*, 1999). (i) Terminalization is the most likely evolutionary explanation of recent diversity in flower arrangement. (ii) In both groups terminalization is associated with loss of a perianth. (iii) Terminal flowers in derived taxa differ from lateral flowers in primitive taxa in the structure of the androecium and gynoecium (an unusual Bauplan of terminal structures is also typical for mutants of model organisms such as *Arabidopsis*). (iv) In both Alismatales and Hamamelidaceae, species with monotelic synflorescences have previously often been considered as forming natural groups, but in both cases molecular analyses have indicated polyphyly, which suggests non-unique terminalization events.

Conclusions and perspective

The present study highlights the considerable difficulties that exist in distinguishing between some elaborated terminal pseudanthia (i.e. closely associated and integrated uppermost lateral flowers) and terminal flowers. These difficulties are linked with a more general question on the homologies between lateral flowers and (true) terminal flowers, including both serial and historical homologies (Rutishauser and Moline, 2005). In turn, this homology issue is at least partially comparable with Meeuse's (1975) ideas on the differences between (holo)anthocormoids (essentially terminal and two-axial) and anthoids (essentially lateral and uniaxial) (see also Krassilov, 1989).

Application of traditional homology criteria could help to compare terminal and lateral flowers, though even these can be problematic. Remane's (1956) three basic homology criteria (reviewed by Mamkaev, 2001; Rutishauser and Moline, 2005) are: (i) position; (ii) special quality of structures (including genetic control); and (iii) linkage by intermediate forms. The position criterion (i) is usually considered the most important, but it does not work when comparing terminal and lateral flowers.

Criterion (ii) is also unlikely to help in establishing flower identity, since male, female, perianthless, and even sterile flowers exist among various flowering plants and are commonly accepted as flowers. It is relatively straightforward to list features that occur only in pseudanthia (e.g. presence of more than one gynoecium, carpels facing each other via their dorsal sides) but it is almost impossible to indicate any feature that exclusively characterizes an individual flower. Furthermore, studies of genes responsi-ble for regulation of flower development can be of limited help in establishing morphological homologies. For example, flowers of *Althenia* and *Lepilaena* (both Zannichelliaceae) possess a tripartite 'perianth' around the male and female reproductive structures. Expression of A-class genes in these structures would test their possible bract homology. However, evidence of tepal identity does not refute either the euanthial or pseudanthial interpretations. In addition, expression of some floral organ identity genes can occur in non-floral regions, even in leaves (see Buzgo *et al.*, 2006, for expression of *AP3* in *Triglochin*). There are several examples in which orthologous genes show a similar expression pattern and key morphogenetic function in structures that are clearly non-homologous. Converse examples show that morphogenesis of homologous structures can be controlled by different genes in different taxa (Nielsen and Martinez, 2003; Theißen and Becker, 2004; Rutishauser and Moline, 2005; see also Rautian, 1988; Wagner 1989; Baum and Donoghue, 2002). Finally, an elaborated end-product of amalgamation between individual flowers could be as similar to a single true flower at the molecular level as it is sometimes similar morphologically.

The occurrence of intermediate forms (criterion iii) is probably the only criterion that can give substantive grounds for homologizing terminal and lateral flowers, although even this does not guarantee a correct conclusion. Series of intermediate structures could be due to amalgamation of developmental pathways leading to 'developmental mosaics' between structures that are normally assumed to have different identities (Rutishauser and Moline, 2005; see also Lodkina, 1983; Sattler, 1988; Baum and Donoghue, 2002). In particular, structures with long-debated pseudanthial or euanthial interpretation in various angiosperm groups (e.g. Piperales and Alismatales) could have evolved as a result of overlap between the developmental programmes of a typical flower and inflorescence (Posluszny and Charlton, 1993). Some terminal structures described here should also be described in terms of loss of flower identity (e.g. TFLS of *Triglochin* with multiple carpels).

Within Alismatales, future research on flower and inflorescence evolution would benefit from a more explicitly phylogenetic approach. An important test of our hypothesis will lie in more extensive comparative and developmental studies of a wider range of species. More broadly, studies of terminal structures offer an opportunity to understand the possible morphological consequences of loss of flower identity. An important conclusion from the present investigation is that pseudanthium formation following loss of floral identity can provoke morphological novelties (including unusual tubular and filamentous structures, and unusual patterns of connation). These could be the result of either new patterns of overlap between expression zones of regulatory genes, or new spatial constraints in developing reproductive structures.

Supplementary data

Supplementary data can be found at JXB online.

Acknowledgements

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