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M O N O C O T S   II

MODULARITY IN HELOBIAL FLOWERS

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Abstract

We have previously proposed that the flowers of helobial monocotyledons are derived from assemblages of primitive unisexual units. The main reason for the proposal lies in the different and partly independent developmental patterns of the perianth/androecial and the gynoecial components of the flower. In many cases in the Zosterales, e.g. *Triglochin, Lilaea, Potamogeton,* and *Scheuchzeria,* there is stamen/tepal superposition: each stamen is formed above a perianth member in a way suggesting an axillary relationship, and the sets of organs occur in whorls of different numbers according to the taxon. Similarly, in the Alismataceae and related families, the perianth members occur in whorls of three, and there is commonly an association between a petal and a superposed pair of stamens which develop in assocation with it, often from what appears to be a common primordium. Further stamens may be initiated above (some Alismataceae) or below (*Hydrocleis*) the first-formed stamens. In all these cases carpels are initiated in what seems initially to be a whorled pattern above the androecium, with the numbers in a whorl corresponding to those in the perianth. However, it has been shown in *Potamogeton* and *Ruppia* that carpel positioning is more flexible and appears to operate like an ordinary phyllotactic system. The flowers can be seen as being made up of two different types of module, one being the perianth/stamen complex, and the other the carpel. We now have additional data for floral development in two genera of Alismataceae, *Luronium* and *Wiesneria,* which complement older data and seem to reinforce the concept of independence of development in the two regions. Phylogenetic analysis indicates these genera are in interesting positions within the Alismataceae: *Luronium* is near other genera showing some range of gynoecial organisation, and *Wiesneria* is part of a complex including *Sagittaria* which shows extreme variation in meristic complexity.

Key words: Helobial, flowers, development, evolution, Alismatidae, Alismataceae, monocots

INTRODUCTION

The helobial monocotyledons, nowadays grouped in the subclass Alismatidae, are a particularly interesting study in evolution. In spite of an enormous diversity of floral and vegetative structures, accentuated by a variety of adaptations to an aquatic environment and sometimes extreme reduction, they have long been considered to be a natural group (e.g. Hutchinson 1959; Tomlinson 1982). More recently phylogenetic investigations have reinforced this view (Les and Haynes 1995; Les *et al.* 1997) and

they have also shown that the Alismatidae are an ancient lineage of angiosperms which are a sister group to the aroids (Chase *et al.* 1993, 1995a, b; Les and Schneider 1995; Stevenson and Loconte 1995). These recent investigations provide a new background against which floral construction and evolution among the Alismatidae must be considered.

Floral evolution in the Alismatidae has been the subject of considerable speculation at times, fuelled by some of the unorthodox elements of construction such as the superposition of stamen
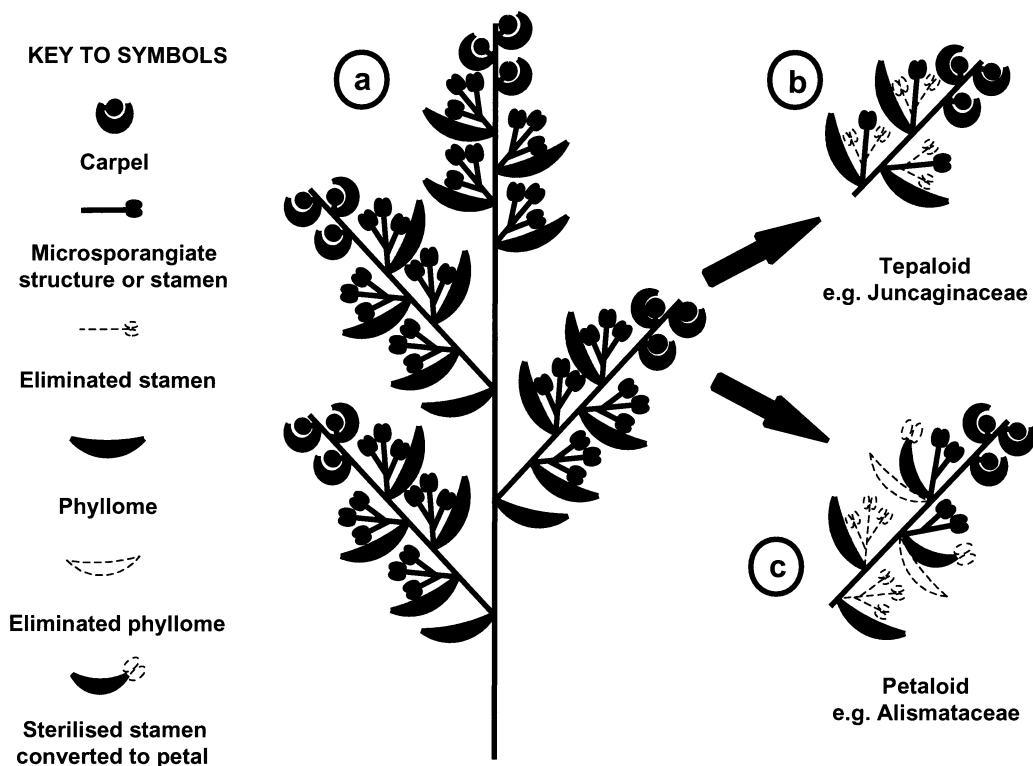
KEY TO SYMBOLS

Carpel

Microsporangiate
structure or stamen

Eliminated stamen

Phyllome

Eliminated phyllome

Sterilised stamen
converted to petal

Tepaloid
e.g. Juncaginaceae

Petaloid
e.g. Alismataceae

Fig. 1. Schematic diagram of possible original multiaxial reproductive structure of helobial monocotyledons (a) with derivation of tepaloid forms (b) and petaloid forms (c) by modification and suppression of some components. This diagram is intended to be illustrative and not a definitive view of helobial flower evolution.

over tepal which is found in the Potamogetonaceae and elsewhere, and can readily be seen as an axillary structure and its subtending foliar member. As far back as 1841 Kunth interpreted the flower of *Potamogeton* as a condensed inflorescence branch, i.e. as a pseudanthium; Miki (1937) also made this suggestion; in 1947 Uhl extended and refined this interpretation to a number of other cases such as *Scheuchzeria, Triglochin,* etc. Also, Sattler (1965) and Posluszny and Sattler (1974) concluded that the flowers of *Potamogeton* had features of both 'flower' and 'inflorescence' in the traditional sense. The field of speculation was widened considerably when it was suggested that the inflorescences of *Triglochin* (Charlton 1981), *Lilaea* (Posluszny *et al.* 1986), and *Potamogeton* (Charlton and Posluszny 1991) had developmental features which were more commonly associated with floral than inflorescence development, such as initiation of lateral structures without subtending bracts, whorled arrangements of laterals, and presence of a residual meristem at the tip of the inflorescence.

Posluszny and Charlton (1993) saw the Alismatidae as falling into two distinct groups of families, which they called the 'petaloid' and 'tepaloid' types, and a third residual group which they called the 'extra-simple' types. The 'petaloid' Alismatidae have a perianth which is normally divided into distinct calyx and corolla. This group comprises Alismataceae, Butomaceae, Hydrocharitaceae and Limnocharitaceae. The 'tepaloid' Alismatidae have a perianth which is not divisible into calyx and corolla, and is usually sepal-like. These taxa include Juncaginaceae, Lilaeaceae, Scheuchzeriaceae, Potamogetonaceae, Aponogetonaceae and Zosteraceae. They often have unorthodox floral morphol-

ogy, including stamen/perianth superposition, and it was from this group that previous authors had developed the pseudanthial hypotheses mentioned above. The 'extra-simple' types were a residual group containing taxa in which reproductive structures, particularly the perianth, were so simple and/or reduced that their relationships to the other groups were not evident.

Posluszny and Charlton (1993) then produced an evolutionary hypothesis which proposed that the present reproductive structures of Alismatidae in general could have arisen by the partitioning in different ways of an original multiaxial reproductive structure from a pre-floral state into what are now seen as 'flower' and 'inflorescence'. A possible form of this archetypal construction, loosely based on Meeuse (1966), is shown in Fig. 1a.

For the tepaloid types, in its essentials this hypothesis incorporated much of the earlier 'pseudanthial' hypotheses of Kunth, Miki, and Uhl, as it used the proposition that the stamen/tepal superposition represented a bract subtending a microsporangiate member consisting of a single stamen (Fig. 1b). This was considered to be one of the basic components of the original multiaxial structure. It also built on the suggestion of Uhl (1947) that the gynoecium of these flowers represented either a single female flower or a number of female flowers each reduced to a single carpel, and took the carpel to be another basic component of the multiaxial structure. It then proposed that the main axis of the original structure became differentiated into 'inflorescence' and the lateral axes into 'flowers'. Finally, if 'flower' and 'inflorescence' were seen as being derived from the same original complex structure, then it is not unreasonable that each should show some features of the other.

For the petaloid types it was proposed that all the axes of the original multiaxial structure became differentiated distally into 'flower' and proximally into 'inflorescence'. The components of the 'flower' differ from those of the tepaloid types, but if it is assumed that the two groups are of common origin, then the reproductive structures must be initially comparable. It was suggested that the petal and stamen were homologous in the petaloid types; that the association of a pair of stamens with a petal seen in many cases represented a partially-sterilised stamen fascicle; stamens also could occur as individuals, not in fascicles. Since there is no foliar structure subtending a stamen or stamen fascicle, it was proposed that the subtending structure had probably been lost. The sepals were seen as phyllomes which no longer subtended lateral structures. On this interpretation the perianth/androecial component of petaloid types is derived from phyllomes subtending microsporangiate structures (Fig. 1c), as are the same components in tepaloid types (Fig. 1b). The gynoecium can be seen simply as an assemblage of carpels, as in the tepaloid types, superimposed over the perianth/androecium component of the flower.

It is tempting to see some of the 'extra-simple' types, and even the occasional tepaloid type, as still existing in a pre-floral state, but the balance of comparative morphology generally suggests these are reduced forms. Molecular phylogenetic data now makes it abundantly clear that these are derived forms: consider the position in the most recently published phylogeny of the Alismatidae (Fig. 2 in Les *et al.* 1997) of a few specific cases in which floral structure is extremely simple or reduced. They are all close or indeed very close to taxa with quite adequate flowers. *Zannichellia*, in which the male 'flower' is only a single stamen, and the female 'flower' is a spathe surrounding a cluster of carpels, is seen to be quite closely related to the Potamogetonaceae. *Lilaea*, in which the reproductive structures were seen by Posluszny *et al.* (1986) as being neither clearly 'inflorescence' or 'flower' but rather being in a 'pre-floral' state, seems to be closely related to *Triglochin*. In fact it is more closely related to *Triglochin* even than *Cycnogeton*, which itself has been included in *Triglochin*. Since *Triglochin* and *Cycnogeton* have quite respectable trimerous flowers, *Lilaea* must be seen as a derived case. *Najas* is seen to belong among the Hydrocharitaceae (confirming Shaffer-Fehre's (1991a, b) astute placement of *Najas* on the basis of seed-coat structure). In fact any taxon that would have been placed among the extra-simple types can now be placed among either the tepaloid or petaloid types on the basis of the molecular data.

The proposed original multiaxial reproductive structure for the Alismatidae was seen as bisexual even though the male and female components could themselves have been of different morphological derivations. Consequently the scheme for floral evolution would consider any present case of unisexual flowers as derived, although this was not specifically stated. The phylogenetic analyses of Les *et al.* (1997) show in an equally direct way that unisexuality is a derived state within the group.

A general morphological evolutionary scheme of this nature must, however, remain hypothetical until all the links in the chain are demonstrated. That may never happen: the most recent phylogeny based on molecular data (Les *et al.* 1997) makes it clear that the petaloid and tepaloid groups of Alismatidae form two very distinct major lineages in the subclass, and evidence for the nature of the steps of divergence could only come now from the fossil record. Nevertheless the morphological and developmental relationships of the extant taxa can be assessed further or re-assessed with the added benefit of the new light of the molecular phylogenetic data.

The unified view which we have developed of the flower of the Alismatidae is really a modular one. Barlow (1989) defined three levels of constructional unit: merophyte, module and metamer. A merophyte is a unit derived from one cell produced by division of an initial cell. A metamer is a single macroscopic unit produced by an apical meristem, such as a leaf and associated node and internode. A module is a unit of construction made up of a number of metamers produced by the same apical meristem. In Barlow's original version a flower would probably be seen as a module. In our context we need to modify Barlow's definition of a module to some extent: to us a module must be a construction made up of a number of metamers of the same fundamental nature. In the unified view of the basic flower of the Alismatidae, therefore, the flower consists of a perianth/androecial module containing a number of metamers derived from a bract and a subtended microsporangiate unit (and, strictly speaking, the associated portions of receptacle), and a gynoecial module which contains a number of metamers which each consist of a carpel and associated portion of receptacle. We will refer to these modules as the PA module and the G module respectively.

We presume that development of these floral modules, and the metamers within them, is subject to the genetic control mechanisms found in other plants (e.g. Weigel 1995). The variations within these modules, the divergence of development of the metamers, and the variations in the relationships between the modules and metamers make up much of the substance of floral evolution. This is also a matter which would ultimately be susceptible to genetic analysis, since it will be possible to examine the evolutionary changes which occur in the genes controlling floral development (Frohlich and Meyerowitz 1997). It would certainly be interesting to see if and how the currently accepted ABC model of floral development would apply to these flowers. For now it is a matter which we can examine in developmental/morphological terms. It would be inappropriate to attempt a comprehensive review of the Alismatidae at this stage, but we can consider some particular cases where the modular concept of the flowers is easy and consistent to apply, and some cases where problems may be encountered. We use here material which has already been published and some material which was unpublished (Charlton 1999a, 1999b, in press) at the time of this symposium. Where specific sources are not mentioned, general morphological information is taken from Tomlinson (1982). All methodology is described in previous publications.

MODULES, METAMERS, PHYLLOTAXIS, AND ESCAPES FROM CONSTRAINT IN TEPALOID TYPES

Flowers in many of the families in the tepaloid Alismatidae are bisexual with well-marked tepal/stamen superposition, and the number of members in a whorl tends to be constant from perianth to gynoecium, i.e. across what we are now calling the PA and G modules. This condition is found in Potamogetonaceae (tetramerous) and Lilaeaceae (monomerous), Juncaginaceae

(trimerous in two whorls, or tetramerous) and Scheuchzeriaceae (trimerous in two whorls), and when considered in the light of the cladogram of Les *et al.* (1997) the condition appears to be a rather fundamental feature of the group. We can also include Zosteraceae in this statement, as a form with monomerous flowers which are sessile and incorporated into a dorsiventral inflorescence axis, since it is extremely closely related to *Potamogeton* and some members do show stamen/tepal superposition if the retinacula are accepted as perianth segments (Soros-Pottruff and Posluszny 1994, 1995). However, sometimes the flowers have lost some of these attributes, for instance in *Lilaea* the flowers grade from unisexual female in the lower part of the inflorescence through perfect flowers in the middle to unisexual male at the top. But, though the female flowers generally consist of only a single carpel, stamen/tepal superposition is normally present in the perfect and male flowers. In other families in the group the flowers diverge more markedly. Given the concept of modular organisation of the flowers, can we see the divergences from the basic plan as recognisable specific kinds of departure from the constraints of modular organisation? First it is neccessary to consider what kind of constraints are likely to be operating in the basic plan.

The variability in floral construction in the genus *Potamogeton* (Potamogetonaceae), reported by Charlton and Posluszny (1991), provided the clearest evidence of the difference in organisation of the PA and G modules. Flowers of many *Potamogeton* spp. are normally completely tetramerous, with a whorl of four perianth members and four superposed stamens, and a whorl of four carpels alternating with the stamens. In modular terms, the PA module is invariably tetramerous (except in flowers derived from small floral buds at the tip of the inflorescence, or large floral buds at the junction of parastichies of flowers in the inflorescence) and the superposition of stamen and tepal is as stable. The G module is also as stable in some species.

In other species of *Potamogeton* carpel number is increased or decreased, and different mechanisms seem to be responsible for increase versus decrease. When floral development was compared in species with four carpels and those with more, it was found that the floral meristem kept growing after the initiation of the first four carpels, providing space for more to be initiated. These were formed above and alternating with the first four, but not necessarily in a whorled pattern. *P. compressus* and *P. zosteriformis* have only one to three carpels: this situation seems to have arisen by a shift in the size relationships between the PA and G modules such that the carpel primordia are larger in relation to the available space on the floral meristem and consequently only a reduced number can be formed. In these cases too the carpel primordia occurred in sites alternating with, and above, the stamen primordia.

The observations on *Potamogeton* led to the hypothesis that the perianth/androecial component of the flower, the PA module, was developmentally very stable, and in the gynoecial phase, the G module, the carpel primordia were simply positioned by phyllotactic means so that usually the carpels appeared in a whorl of four alternating with the stamens. Consequently, when the relative size of carpel primordia was changed, or the floral apex continued to grow and produced more space in which carpel primordia could be initiated, carpel number could be varied and whorled appearance lost.

It is a simplistic suggestion, but most or all of the variation in floral make-up of the tepaloid Alismatidae could result from variations on these themes. In forms which show meristic constancy, i.e. *Triglochin*, *Scheuchzeria*, many *Potamogeton*, *Zostera*, the pattern is set up in the PA module and perpetuated phyllotactically. In terms of metamers the PA module has a very stable number (though variable across taxa) and positioning of metamers in one or two whorls, which each consist of a tepal and superposed stamen. The number of metamers in the G module is determined by size relationships of the metamers, i.e. the carpel primordia, and the floral apex, while the positioning of metamers in the G module is determined phyllotactically by the PA module at first but, if development of the G module is extended, positioning is determined by phyllotactic considerations only within the G module. This basic modular construction forms an innate set of constraints which still operate even when the flowers show meristic change. More marked changes in organisation demand escape from these constraints. For instance, unisexual flowers could arise by partial or complete suppression of development of one of the modules. Both possibilities occur in *Phyllospadix*, where the stamens are reduced to staminodes in female plants, but there are no vestigial carpels in male plants (Soros-Pottruff and Posluszny 1994). There is also the possibility that the perianth can be reduced or eliminated, and it could be argued that elimination has occurred in Zosteraceae without retinacula.

In unisexual flowers where only one module develops at all meristic comparability between the two forms of flower presumably will only be maintained when the size relationships of floral meristem and primordia remain comparable. This is presumably the case in Cymodoceaceae where both sexes of flower appear to be dimerous (Tomlinson and Posluszny 1978). On the other hand, there is only a single stamen (or perhaps two fused) in the male flowers of Zannichelliaceae, while there are one to three carpels in *Althenia* and *Lepilaena* and four or more in *Zannichellia* (Posluszny and Sattler 1976; Posluszny and Tomlinson 1977). However, unisexuality is rather a feature of the forms earlier called 'extra-simple' and in these there is the additional variation that the perianth is reduced or absent, as indeed is the case in Cymodoceaceae and Zannichelliaceae. *Posidonia* and *Ruppia* have bisexual flowers but also appear to lack perianth. *Ruppia* has a dimerous androecium and a gynoecium in which the first carpels are inserted in a dimerous pattern following on from the androecium, but further carpels are simply added alternating with the earlier ones in a way which may maintain the dimerous pattern or may not (Kaul 1993) – thus, *Ruppia* shows the same behaviour as *Potamogeton* can, in allowing the G module to prolong development and to form carpels in any convenient phyllotactic arrangement. *Posidonia* has a trimerous androecium and monomerous gynoecium: in the G module it probably has the reverse modification to that of *Ruppia* – probably the carpel primordium simply uses up the available floral apex. There are no developmental observations on *Posidonia*.

Finally among the tepaloid types there is the case of *Aponogeton*. Morphologically this is hard to place, but on molecular grounds it is clearly a member of the tepaloid group. There is a perianth,

which may consist of 1–3 members according to species (Tomlinson 1982). Development has only been studied in *A. natans* and *A. undulatum* (Singh and Sattler 1977b). Stamens occur in two trimerous whorls in *A. undulatum* and *A. natans*, but the stamens are not superposed over perianth members, rather they alternate with them in a more conventional pattern. Then a whorl of three carpels alternates with the upper whorl of stamens. In some other species up to 23 stamens have been found, arrangement not clear, and 4 carpels are common. In *Aponogeton*, then, in the PA module, the constraint of the stamen/perianth association has been lost, in both positional and numerical terms. Perhaps it would be advisable to see the PA module as dissociated into a perianth component, with a reduced number of metamers, followed by an androecial component in which the number of metamers is liable to increase. It would be interesting to examine the positioning of extra stamens – are they in trimerous whorls as in the species with small numbers of stamens, or do spiral, non-whorled, patterns occur? In the G module it is clear that where there are three carpels over trimerous whorls of stamens, as in *A. natans* and *A. undulatus*, the carpels alternate with the last whorl of stamens as in many other cases. However, again it would be interesting to examine the relationship between carpel and stamen positioning in cases with large numbers of stamens.

MODULES, METAMERS, PHYLLOTAXIS, AND ESCAPES FROM CONSTRAINT IN PETALOID TYPES

All the families in the petaloid group include representatives which have flowers with conspicuous trimerous perianth divided into calyx and corolla. This is almost universal in the Alismataceae and Limnocharitaceae. It is common in the Hydrocharitaceae, in which family it is evident from phylogenetic analysis (Les *et al.* 1997) and on morphological grounds (Sculthorpe 1967) that the forms which have departed from a 'petaloid' appearance are derived, and modified in relation to various forms of hydrophilous floral biology. *Butomus*, the single representative of the Butomaceae, has a perianth with two petaloid whorls but the two whorls are not identical. The trimerous differentiated perianth is probably fundamental in the petaloid group, but it is unclear how it relates to the undifferentiated perianth of the tepaloid group. Posluszny and Charlton (1993), on the basis of their proposed original polyaxial reproductive structure, suggested that the sepals probably represented phyllomes which had originally subtended androecial structures, but no longer did so. They would therefore be homologous with the perianth members of tepaloid types, and they certainly resemble them. It was proposed that petals and stamens were homologous (i.e. petals represented sterilised stamens). A developmental relationship has been perceived between a petal and a pair of stamens in a number of Alismataceae and also in *Hydrocleis* in the Limnocharitaceae and *Butomus* in the Butomaceae (see review by Sattler and Singh 1978), and this led to the suggestion that the association could be derived from a stamen fascicle in which one stamen had been sterilised and transformed into a petal (Posluszny and Charlton 1993), although the additional stamens present in some taxa were seen as being inserted singly above the fascicles. Since that review was written floral development has been studied in more Alismataceae and it may be time to revise this view of the petal/stamen pair association, and also of the petal itself. Stamens can occur in pairs in the

Hydrocharitaceae (e.g. Kaul 1968b) but there has been no suggestion here that the pairs are specifically associated with perianth members. It would be satisfying if a unified view could be arrived at which would encompass these cases too.

Sometimes in Alismataceae and related cases the stamens and petal are preceded by what appears to be a common primordium which was called a CA primordium (after Singh and Sattler 1972) but in other cases the association between stamen pair and petal is only one of timing. There are two cases where CA primordia can sometimes but not invariably be discerned before the petals and stamens are initiated. In *Ranalisma* (Charlton 1991) floral development is to some extent unidirectional, i.e. development of appendages occurs consistently earlier on one side of the flower than the other. On the 'earlier' side of the flower the floral meristem takes on the appearance of two CA primordia before the petal and stamen pairs are initiated: but on the 'later' side the petal and stamen primordia are initiated directly on the floral meristem without a preceding bulge. In *Luronium* some floral apices develop a prominent three-cornered appearance which could represent three CA primordia (Fig. 2), and the petal/stamen pairs are initiated on these (Fig. 3), but other apices remain round in outline at this stage (Fig. 4) and therefore cannot be considered to produce CA primordia. These cases provide evidence that a 'CA primordium' is not a prerequisite for stamen and petal initiation, even if it can sometimes be discerned. The appearance of CA primordia seems to arise simply from changes in shape of the floral apex after sepal initiation, and they are not really primordia as such. Both in *Luronium* and *Ranalisma* (irrespective of the appearance of CA primordia) pairs of stamen primordia can be discerned in the sense that the members of each pair are initiated simultaneously but the three pairs are not necessarily initiated simultaneously. However, the six stamens of the three 'pairs' are evenly spaced around the floral apex (e.g. Figs 3, 4) in a whorl and it might well be that the difference in timing of initiation of the 'pairs' simply implies that the members of the whorl are not initiated simultaneously, which is quite a common condition in floral development in any case.

However, there are problems in other cases in interpreting the six stamens simply as a whorl: in *Butomus*, for instance, the stamens of a 'pair' are inserted over the edges of the associated petal – and this results in the curious situation that the two members of a 'pair' here are considerably further apart than the two adjacent stamens of adjacent 'pairs' which occur opposite to an outer perianth member. In fact Payer (1857), followed by Salisbury (1926) and others, recognised pairs in these more closely approximated stamens in various taxa. Salisbury even proposed that these 'pairs' had arisen by dédoublement from an original single stamen. Sattler and Singh (1978) consequently had to make clear the distinction between the antipetalous 'pairs' of stamens which they could discern on a developmental basis even if this were only a matter of timing, and the antisepalous pairs which earlier workers had discerned on a positional basis. Nevertheless a 'positional' matter must have a developmental basis also. Sattler and Singh (1978) suggested that the stamens of their 'pairs' could be displaced further apart (i.e. towards the antisepalous position and making a Salisbury 'pair' prominent) by increase in size of the petal primordium. This certainly seems to be the case in *Butomus*.
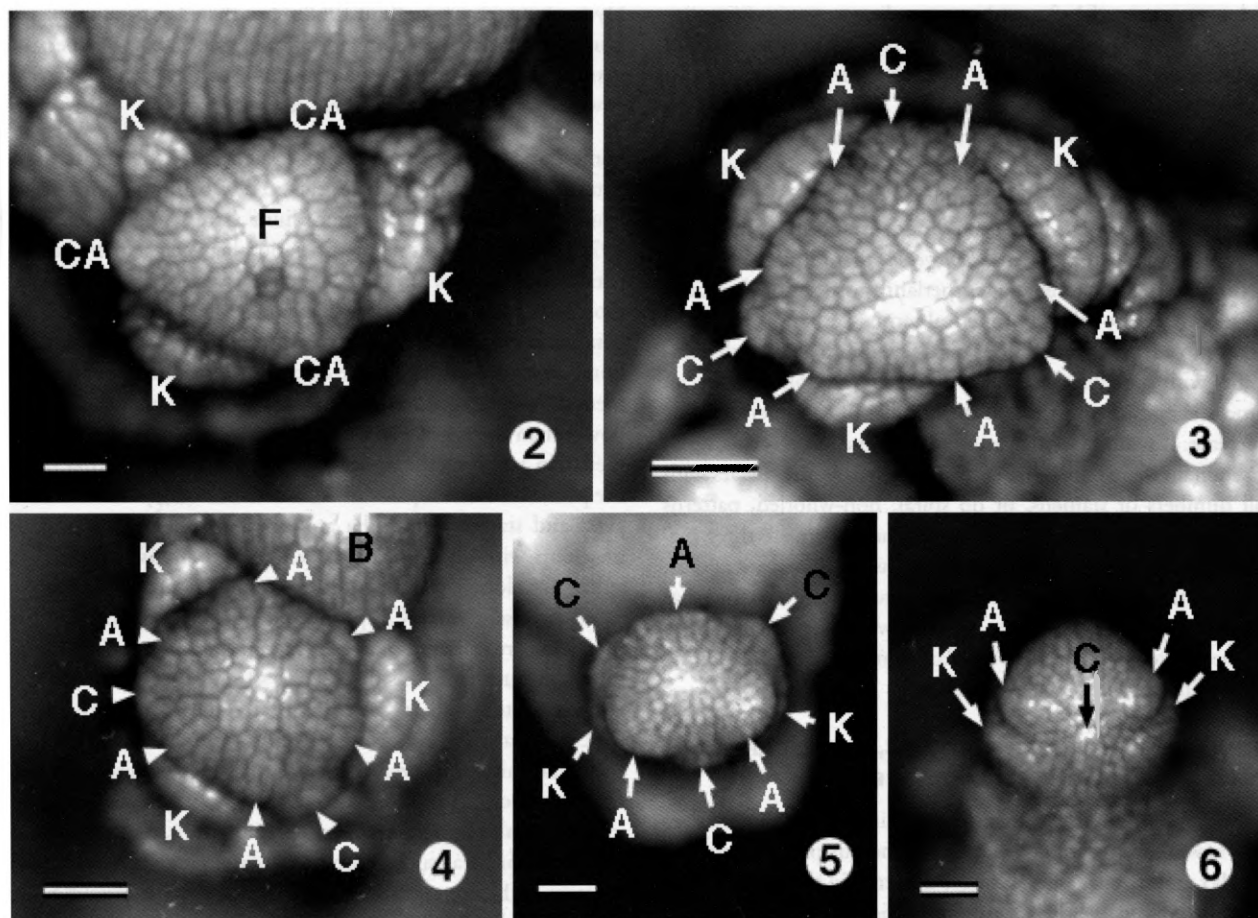
Figs. 2–6. Early stages in flower development of *Luronium natans* (Figs. 2–4) and *Wiesneria triandra* (Figs. 5 and 6). A = stamen primordium, B = bract, C = petal primordium, CA = common primordium which will give rise to a petal and a pair of stamens, K = sepal primordium. Scale bar = 50 μm. **Fig. 2.** Top view of *L. natans* bud showing sepal primordia which are well-developed and the floral apex which has become triangular in outline with prominent outgrowths of CA primordia at the corners. **Fig. 3.** A slightly older stage of a developing *L. natans* floral bud in which two pairs of stamen primordia have become quite prominent (lower left and top of photograph) and the third is less well-advanced (lower right). Petal primordia are present at all three sites. **Fig. 4.** Floral bud of *L. natans* with a rounded outline, and all three stamen pairs present at the same early stage of development. **Fig. 5.** A slightly oblique top view of a female floral bud of *W. triandra* showing the outgrowth of petal primordia between and below the staminode primordia. **Fig. 6.** Side view of the same flower shown in Fig. 5.

Decraene and Smets (1995) produced an extension of the argument of Sattler and Singh (1978) in the opposite direction. Taking the case of *Sagittaria* they saw the 'pairs' of Sattler and Singh becoming more noticeable as the relative size of the petal primordium decreased. In a general sense they considered the six stamens of the stamen 'pairs' in the Alismataceae and similar cases as representing a hexamerous whorl (an alternative view which was recognised by Sattler and Singh in 1978) in which the relative positioning was dependent on the size relationships of the perianth primordia. Their view of the 'pairs' of stamens which may be detected in this whorl can be seen as basically a phyllotactic one, in which the positioning of the stamen primordia was determined by the proximity of both sepal and petal primordia when the petal primordia are small in relation to the sepals, or by the petals alone if their primordia were large. Expanding this 'phyllotactic' view, when the petal and sepal primordia are both small and the stamens arise between the petal and the edge of the sepal they will appear closely approximated to the petals, appearing as antipetalous pairs associated with the petals. If the petal

primordia are large the six stamens will have to be inserted above and between them, and in this case the stamens will appear as antisepalous pairs. The case of *Wiesneria*, unique among the Alismataceae in having only three stamens, is very interesting in this context. Although the petal primordia are small, the three large stamen primordia arise in positions alternating with the petals (Figs 5, 6) as would be expected. There is no need to consider hypothetical means of deriving the three stamens from three pairs of stamens, a change in size relationships is enough to make the change. *Wiesneria* has unisexual flowers with the three stamen primordia developed as staminodes in female flowers, and it is interesting that the primordia are similar in size and position in male and female flowers.

If the concept of a specific association between stamen pairs and petals is discarded, perhaps the suggestion of derivation of the petal from a sterilised stamen should also be discarded. The petal could then be viewed as a phyllome comparable to the sepal. However, we continue to view the petal as derived from a sterilised stamen. There is evidence that stamen and petal are to some
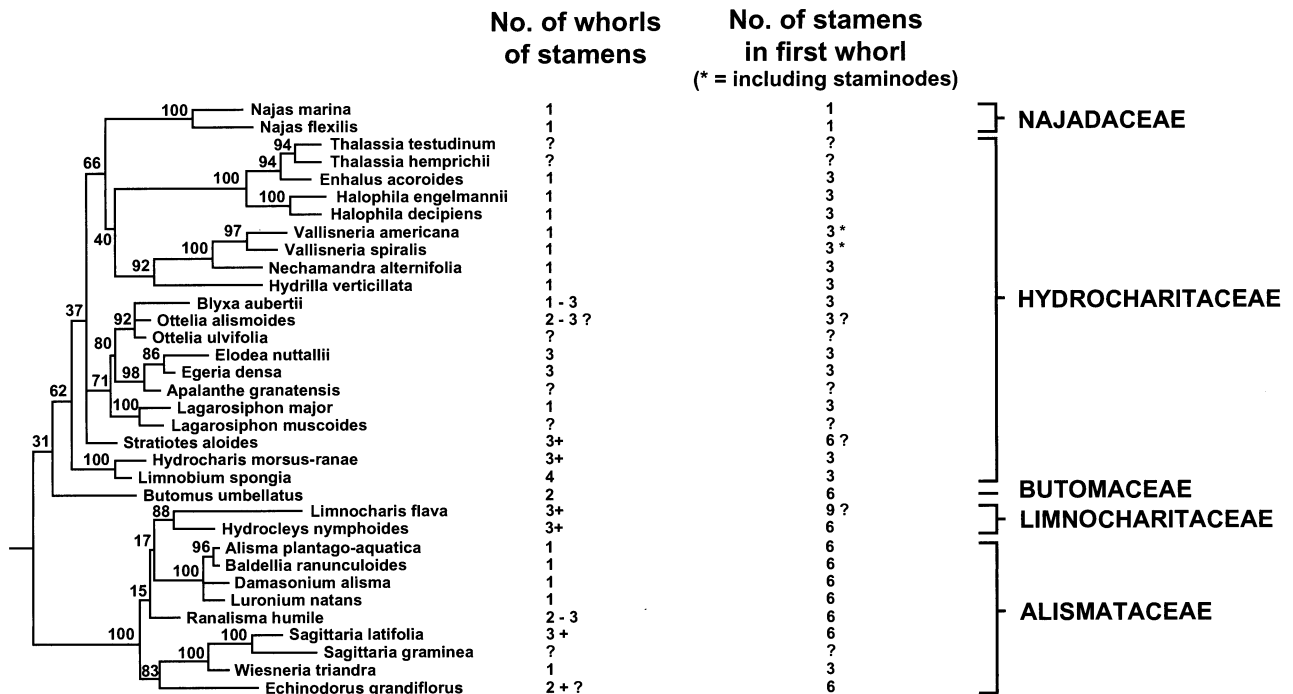
Fig. 7. Portion of the cladogram from Les et al. (1997) showing the number of whorls of stamens and number of stamens in the first whorl in species of five petaloid families; Najadaceae, Hydrocharitaceae, Butomaceae, Limnocharitaceae and Alismataceae.

Species	No. of whorls of stamens	No. of stamens in first whorl (* = including staminodes)	Family
Najas marina	1	1	NAJADACEAE
Najas flexilis	1	1	
Thalassia testudinum	?	?	HYDROCHARITACEAE
Thalassia hemprichii	?	?	
Enhalus acoroides	1	3	
Halophila engelmannii	1	3	
Halophila decipiens	1	3	
Vallisneria americana	1	3 *	
Vallisneria spiralis	1	3 *	
Nechamandra alternifolia	1	3	
Hydrilla verticillata	1	3	
Blyxa aubertii	1 - 3	3	
Ottelia alismoides	2 - 3 ?	3 ?	
Ottelia ulvifolia	?	?	
Elodea nuttallii	3	3	
Egeria densa	3	3	
Apalanthe granatensis	?	?	
Lagarosiphon major	1	3	
Lagarosiphon muscoides	?	?	
Stratiotes aloides	3+	6 ?	
Hydrocharis morsus-ranae	3+	3	
Limnobium spongia	4	3	
Butomus umbellatus	2	6	BUTOMACEAE
Limnocharis flava	3+	9 ?	LIMNOCHARITACEAE
Hydrocleys nymphoides	3+	6	
Alisma plantago-aquatica	1	6	ALISMATACEAE
Baldellia ranunculoides	1	6	
Damasonium alisma	1	6	
Luronium natans	1	6	
Ranalisma humile	2 - 3	6	
Sagittaria latifolia	3 +	6	
Sagittaria graminea	?	?	
Wiesneria triandra	1	3	
Echinodorus grandiflorus	2 + ?	6	

extent interchangeable, e.g. petals can replace stamens in *Ranalisma* (Charlton 1979, 1991) and a stamen can replace a petal plus stamen pair in *Luronium* (Posluszny and Charlton 1993). But in terms of process morphology (Sattler 1990, 1992) the petal is equivalent to a phyllome, and the principle of complementarity (Rutishauser and Sattler 1985) allows us to see it both as a phyllomic element of floral construction and as a derivative of a microsporangiate organ of uncertain ancestry.

When the concept of stamen fascicles, or stamen pairs as anything other than a phyllotactic effect, is discarded for the Alismataceae there is no need to see the first six stamens differently from any that follow. If the stamen pairs that have been detected in other petaloid types are also treated as phyllotactic effects (and this is a matter which would repay developmental investigation) it becomes possible to view the perianth and androecium of all the petaloid types in much the same way. In summary, in the petaloid types, the component of the flower which corresponds to that conveniently called the PA module in tepaloid types is more highly diversified so that (a) the two whorls of perianth have become differentiated, whatever the exact nature of the perianth, and (b) formation of stamens is dissociated from the formation of phyllomic appendages, except in a general phyllotactic sense. The alternation of the whorls of perianth presumably arises from a phyllotactic effect also. Androecial construction varies much more in the petaloid types than it does in the tepaloid ones, while the perianth is meristically very stable, and it is likely that this has been enabled by the dissociation of stamen and perianth, i.e. by release of a developmental constraint.

It is also possible to view the variation in androecial construction as arising in the same way as the variation in gynoecial construction in tepaloid types. The positioning of the first whorl of sta-

mens is determined phyllotactically by the preceding perianth, and the number in the whorl is determined by the size relationships of the stamen primordia to the rest of the apex. More stamens can be formed if the floral apex remains committed to the PA phase. In most cases further stamens are initiated above and alternating with the first whorl, and whorled centripetal androecial development results. In *Hydrocleis* (Kaul 1968a; Sattler and Singh 1973) and *Limnocharis* (Kaul 1967b; Sattler and Singh 1977) there is centrifugal androecial development and this appears to be made possible by a sort of intercalary growth of the floral apex below the first stamens producing more area on which stamen initiation occurs; these authors perceived it as a means of secondary increase of stamen number.

It is interesting to examine variation in androecial construction in the context of the phylogeny of the petaloid taxa using the relevant part of the cladogram from Les *et al.* (1997)(Fig. 7). There are only two basic features for which enough data are available from the literature to put against the phylogenetic information. These are: number of whorls of stamens, and number of stamens in the first whorl (neglecting stamen pairs however perceived). Data for total number of stamens are available but are not useful since they represent a combination of the preceding two features with others.

The number of stamens in the lowermost whorl is either three or six, with very few exceptions (Fig. 7). In the hydrocharit taxa, three is the norm. *Najas* can be considered to have one, but is unquestionably reduced. Only *Ottelia* and *Stratiotes* apparently have six or more, and these genera need re-evaluating, as developmental information is scanty. The Alismataceae, Limnocharitaceae and *Butomus* have six stamens in the first whorl, with exceptions only in *Wiesneria*, with three, and *Limnocharis* in
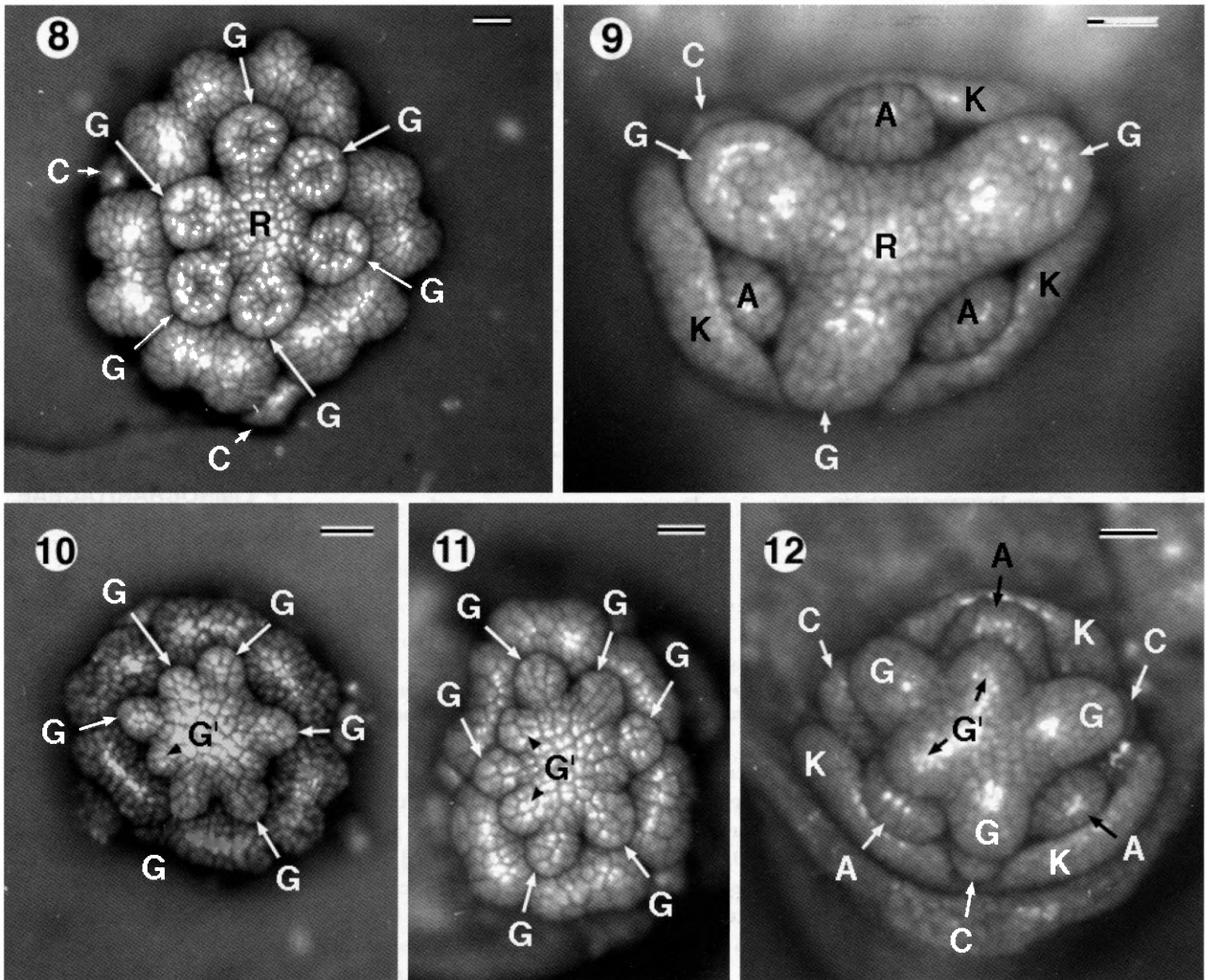
Figs. 8–12. Gynoecial initiation and development in flowers of *Luronium natans* (Figs. 8, 10 and 11) and *Wiesneria triandra* (Figs. 9 and 12). A = stamen primordium, C = petal primordium, G = carpel or its primordium, K = sepal primordium, R = residual floral meristem. Scale bar = 50 μm. **Fig. 8.** A flower bud of *L. natans* which finished carpel initiation after six carpel primordia had formed, leaving a prominent residual meristem. **Fig. 9.** Female flower bud of *W. triandra* with three carpel primordia which have now become peltate. **Fig. 10.** Top view of the gynoecium of *L. natans* showing six carpel primordia (G) which alternate with stamens and a seventh (G') that has formed later between and slightly above two of them. The stamens are developing the appearance of two thecae. **Fig. 11.** A similar stage as that in Fig. 10 showing the initiation of two more carpel primordia (G') in sites above and between the first six (G). **Fig. 12.** A female flower bud of *W. triandra* with three carpel primordia (G) alternating with the staminodes and two additional carpel primordia (G') positioned above the first three.

which the first stamens appear as three groups of three. However, if the petals of the alismad group are seen as sterilised stamens, the first whorl would actually be trimerous in the vast majority, and trimery would be the fundamental state. The alismads would therefore have undergone a secondary increase in number of stamens per whorl, at least in the lowermost whorl of true stamens (further whorls may have only three members), but this condition is basic within that group.

The number of whorls of stamens is more varied, but there is still a consistent pattern when the data are put against the phylogeny (Fig. 7). The marine hydrocharits (with the probable exception of *Thalassia*), *Vallisneria*, *Nechamandra* and *Hydrilla* have basically three stamens in one whorl (*Thalassia* has more stamens in an irregular arrangement) and *Najas* has only one stamen therefore one 'whorl'. In the rest of the hydrocharits there is normally

more than one whorl, up to three or four; *Lagarosiphon* has only one. In the alismad group, including *Butomus*, there is generally more than one whorl of stamens. Cases with only one include *Wiesneria*, and the subgroup of genera including *Alisma*. However, the general distribution of number of whorls suggests that the presence of more than one whorl is a basic feature of the petaloid group, and the subset with only one whorl is derived.

The distribution of staminodes is interesting. Stamens are absent or reduced to staminodes in cases with unisexual flowers, which is unexceptional. However, they also occur in perfect flowers, and they occur particularly in cases with relatively numerous stamens: the limnocharits and some Hydrocharitaceae, e.g. *Hydrocharis*, *Stratiotes* male flowers, *Ottelia*. Perhaps the prolongation of the phase of stamen initiation also involves a loss of the sharpness of the switch-over to the gynoecial phase so that the

determination of lateral structures as fertile stamens is diminished, but there is also an adaptive context, since the staminodes function as nectaries in some cases.

In most cases in the petaloid group, though, the shift into the gynoecial phase of development occurs after the initiation of a whorl of staminal structures, even if these are staminodes. The G module begins with a clean slate, as one might say. The relationships between the G module and the preceding PA module, and within the G module, are relatively easy to evaluate in the alismads and *Butomus* with their hypogynous flowers. However, the epigynous situation in the hydrocharits is more difficult for various reasons. There have been few adequate developmental studies; most of the hydrocharits have unisexual flowers in which the androecium is reduced; it is more difficult to follow the development of the inferior gynoecium in any case. At least the few recent developmental studies (Kaul 1969; Scribailo and Posluszny 1985) indicate quite clearly that the early stages of development of the primordia of the gynoecium are quite comparable with those of other Alismatidae.

Among the alismads and *Butomus*, the lowermost carpels normally alternate with the preceding stamens. This makes an evident whorl when the number is low, e.g. *Luronium* (Fig. 8) and female flowers of *Wiesneria* (Fig. 9). If subsequent carpels are formed they alternate with earlier ones, but whorls are not necessarily formed, e.g. *Luronium* (Figs 10, 11) and *Wiesneria* (Fig 12). Where carpel number is high the alternation is normally present but whorled arrangement is not neccessarily visible, e.g. *Sagittaria* spp. (Kaul 1967a; Singh and Sattler 1973, 1977a), *Echinodorus amazonicus* (Sattler and Singh 1978), *Ranalisma humile* (Charlton 1991). All these cases can be viewed in a similar light to the gynoecia of tepaloid types such as *Potamogeton* and *Ruppia*. In this view the carpel primordia are positioned phyllotactically over the stamens and their size relationships determine the number formed in the first cycle or whorl; more carpel primordia can be initited in a continued phyllotactic sequence, if there is space available on the floral apex. Where there are numerous small carpel primordia (*Sagittaria*, *Echinodorus*, *Ranalisma*) the floral apex is generally domed before carpel initiation starts and there is plenty of space for carpel initiation to occur in. *Luronium* and *Wiesneria*, cases with few relatively large carpel primordia, resemble more the situation in *Potamogeton* (Charlton and Posluszny 1991) where continued carpel initiation after the first whorl appeared to depend on further growth of the floral apex to produce more space for initiation. On this view the G module simply forms carpels in a phyllotactic sequence which is dependent on the prior positioning of the stamens, and any effects of the size relationships of the carpel primordia are superposed on this.

There are some cases with relatively numerous carpels which, as described, would not be seen in this light. In *Alisma triviale* (Singh and Sattler 1972), probably other *Alisma* spp., and *Limnocharis flava* (Sattler and Singh 1977) carpel initiation was described as beginning in three antisepalous regions on the floral meristem, and then more carpels were initiated in single file around the apex from these points, ultimately forming a single ring of 20 or so. We are inclined to see these cases as having a single whorl of carpels, and suggest that the appearance of carpel primordia is simply delayed in antipetalous regions. There are other cases in helobial reproductive structures where the appearance or development of some primordia is delayed in otherwise normal phyllotactic systems, e.g. in inflorescences of *Potamogeton* (Charlton and Posluszny 1991) and *Triglochin* (Charlton 1981). Carpel initiation leaves a rather large residual floral meristem in *Alisma* and *Limnocharis*, and one wonders why further carpel primordia are not formed on it. In the context of the phylogeny of the Alismatidae, it seems to be a derived state of uncertain significance. However, residual meristems are not uncommon in flowers in general and probably indicate that floral organogenesis has been positively terminated by some developmental control mechanism.

MODULAR VARIATION AND PHYLOGENY IN THE ALISMATACEAE

Although new developmental information from *Luronium* and *Wiesneria* has been used in the general arguments together with older information from the family, there is enough similar information for other members to make it worth considering this family more specifically.

The phylogeny of Les *et al.* (1997) shows that *Luronium* is closely related to *Alisma*, *Baldellia*, and *Damasonium*. This subgroup is extremely consistent in some ways and extremely varied in others. The androecium is very consistent in having only six stamens. The gynoecium varies greatly. The 20 or so carpels in *Alisma* are inserted in a single whorl but the first carpels arise initially in three regions of the floral meristem. *Luronium* always has a whorl of six, and commonly has additional carpels superposed. There are regularly six carpels in *Damasonium*, developmental sequence unknown as yet. There are about 20–30 carpels in *Baldellia*, which are not obviously regularly arranged at maturity, but are patently not in a single whorl. Variation in floral development in this sub-set is therefore concentrated in the G module, while the PA module is very stable.

Wiesneria is closely associated with *Sagittaria* and rather less closely with *Echinodorus*. This subset is much more diverse than the one containing *Alisma* and *Luronium*, meristically and also in that unisexual flowers occur in all the genera except *Echinodorus*. Unisexuality is arrived at by suppression of development of stamen or carpel primordia after initiation in *Sagittaria* (Kaul 1967a; Singh and Sattler 1973, 1977a) and *Wiesneria*.

Development of the androecium in *Wiesneria* involves the initiation of a whorl of three large stamen primordia, but in the other genera a first set of six smaller stamen primordia is formed. In *Echinodorus amazonicus* these are followed only by another set of three stamens alternating with the first six, but more are formed in *E. grandiflorus* (Leins and Stadler 1973) and the precise arrangement in this case needs further investigation. In *Sagittaria* (male) further whorls of six or three are formed, with the number per whorl and the degree of regularity diminishing more upwards.

The gynoecial phase in *Wiesneria* begins with the initiation of three carpel primordia alternating with the stamen (staminode) primordia, and then a few more carpel primordia may be initiated in alternating positions, but not necessarily forming a whorl. Carpel initiation in *Echinodorus* occurs at first in three antisepalous areas and further primordia appear between resulting in a whorl of approximately twelve alternating with the stamen primordia,

then further primordia alternate, and the arrangement becomes less regular as the summit of the floral apex is reached. In *Sagittaria* the first carpels arise in a whorl of six alternating with stamen (staminode) primordia and further carpels alternate, with the arrangement appearing less regular upwards.

In the *Wiesneria/Sagittaria/Echinodorus* subset, then, there is variation in the androecial part of the PA module, in number of stamens per whorl and in number of whorls: towards lower numbers per whorl in *Wiesneria*, and higher numbers of whorls particularly in *Sagittaria*. In the G module there are trends in various directions: towards lower numbers per whorl in *Wiesneria*, and higher numbers in *Echinodorus*; the phase of carpel initiation is strongly prolonged in *Echinodorus* and *Sagittaria* so that several cycles of carpels are formed, but it is much more restricted in *Wiesneria* so that only one complete whorl of carpels is normally formed.

Consequently, the phylogenetic divergence between these two subsets of the Alismataceae is matched by divergence in the ways in which the modular structure of the flower develops, both between the PA and G modules and within them. Changes within the PA and G modules are, again, largely independent.

GENERAL DISCUSSION

The phylogenetic data of Les *et al.* (1997) place all the taxa which Posluszny and Charlton (1993) called the 'extra-simple types' firmly into the tepaloid group of the Alismatidae, with the exception of *Najas* which belongs among the petaloid group. When data for floral morphology and development and for phylogeny are considered together it is abundantly clear that the divergence between the petaloid and tepaloid groups is extremely marked, but, echoing Tomlinson (1982), the Alismatidae are clearly a natural group. Does our 'modular' approach to floral structure help in understanding the divergence? We feel that it does, in the sense that it enables the divergence to be broken down into smaller developmental components which, when conceptually isolated, can be seen operating elsewhere within the two groups. Dissociation of the stamen/tepal association in the PA module of the petaloid group has enabled greater androecial diversity. Decoupling has made it possible for number of stamens to diversify readily without accompanying change in the perianth. Increasing the number of stamens per whorl from three to six is one means, particularly in the alismad group, and this probably operates by changes in the size relationships of stamen primordia and floral apex (e.g. *Wiesneria*). Varying the number of whorls is another means and this probably operates by prolonging the androecial phase of development. Very similar effects of the same dissociation can be seen to have occurred in *Aponogeton* in the tepaloid group.

The stamen/tepal relationship can certainly be seen in other ways. We have taken it as a basic feature of the Alismatidae which has been eliminated in the petaloid group. On the other hand, one could even see the relationship arising *de novo* in *Wiesneria*, since the large stamen/staminode primordia are conspicuously superposed over the sepal primordia, while the petal primordia are very small. Decraene and Smets (1995) also saw perianth/stamen associations as derived states which have appeared several times among the monocotyledons. Endress

(1995) noted that what he called 'cohesiveness of floral sectors' is more common in monocotyledons than dicotyledons. By this expression he meant the tendency for organs in different whorls to remain associated so that meristic change affected both simultaneously – this is what seems to happen in the tepaloid types with stamen/tepal superposition. He suggested that this was perhaps caused by the lower meristic state of monocotyledons so that individual floral organs occupied larger sectors of the floral apex at initiation, providing more stability for their association.

We have considered the Alismatidae as a case of evolution without taking any account of the wider context of other monocotyledons. Decraene and Smets (1995) considered androecial evolution in monocotyledons in general, but they made considerable use of features of the Alismatidae in their arguments. They saw a continuum in the pattern of arrangement of the first six stamens, and subsequent stamens if present, which ranged from cases as in the Alismataceae to cases in the Hydrocharitaceae, and they suggested that the androecium of Alismatales (which in their terms equates with our 'petaloid' group) was originally polycyclic, i.e. it had several whorls of stamens, and subsequently some of the whorls had been lost. They considered that the basic androecial configuration of the monocotyledons was similar to what they proposed for the Alismatales, i.e. polycyclic, with alternating whorls of three or six stamens, the lowermost whorl arranged as three pairs. Our view of the petaloid group is not very different from theirs, but it does not carry the context that it is primitive for the monocotyledons as a whole, since we view it as derived from the condition of the tepaloid types with stamen/tepal superposition.

Endress (1995) surveyed features of floral construction in monocotyledons from an evolutionary point of view without being greatly concerned with detailed problems of phylogeny. However, he made some interesting general points. He commented that one would probably see the basal state of the monocotyledon flower as trimerous, whether the Lilianae or the Alismatanae were taken to represent the basal monocotyledon clade. This is a point which we have rather avoided in a context within the Alismatidae, since we are faced there with trimery as the main form of symmetry in the petaloid types, but a range of symmetries among the tepaloid types with no clear indication from morphology or phylogeny what might be the basal condition. On a consensus basis of monocotyledons, perhaps trimery could be accepted as the basal state in the tepaloid types.

Given the consensus that the aroids are a sister group to the Alismatidae (Chase *et al.* 1993, 1995a, b; Les and Schneider 1995; Stevenson and Loconte 1995) the view of the tepaloid types as being archetypal is very appropriate in view of the fact that, like aroids, they never have a differentiated perianth, and when present it is never petaloid. It is interesting that when the perianth is present the flowers usually have dimerous or trimerous whorls of organs but that when it is absent the organ number is much more varied (Endress 1995). Floral development in aroids has been relatively little studied. Comprehensive data on floral development and morphology for the Araceae could provide a wider comparative basis for the understanding of floral evolution in the monocotyledons as a whole and also within the Alismatidae.

Finally, it is extremely appropriate to consider the features of the Alismatidae against the oldest fossil monocotyledon flower known which has recently been described (Gandolfo *et al.* 1998). This flower is unisexual, male, and has surprisingly little in common with present Alismatidae, tepaloid or petaloid. It has apparently a single hexamerous whorl of tepaloid perianth, and three stamens. It has not been shown whether there is stamen/tepal superposition. There are no vestigial gynoecial components. It does not resemble the phyllome and subtended microsporangiate structure suggested as a component of an archetypal pseudanthial 'flower' for the Alismatidae. Its meristic makeup suggests that it is not of that derivation itself, and also differs from anything found in the Alismatidae. It is not evident whether its unisexuality is fundamental or derived, but in having no vestige of a gynoecium it certainly differs significantly from any flower of the Alismatidae of similar complexity. It appears that the fossil record is still too incomplete to offer much insight into floral evolution in monocotyledons.

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