Phylogenetics of Papaver and Related Genera Based on DNA Sequences from ITS Nuclear Ribosomal DNA and Plastid trnL Intron and trnL–F Intergenic Spacers

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INTRODUCTION

Papaver L. is the largest genus of subfamily Papaveroideae of Papaveraeae sensu Kadereit (1993a). Based on morphological considerations, subfamily Papaveroideae, including subfamily Platystemonoideae, can be divided into two major clades (Kadereit et al., 1997; Schwarzbach and Kadereit 1999). These are a New World clade containing Arctomecon Torr. et Frem., Argeomene L., Romneya Harv., Canbya Parry, Platsystemon Benth., Meconella Nutt. and Hesperomecon Greene, and a largely Old World clade with Papaver, Meconopsis Vign., Stylomecon Benth. and Roemeria Medic. The latter group shares characters such as saccamplietylrospus ovules and a seed coat with a fine layer of crystals. Additionally, meconic acid is found only in species of these four genera (Cordell, 1981). Determining relationships among these four genera of Papaveroideae is the primary focus of this paper.

Papaver consists of approximately 80 annual, biennial and perennial herbs distributed in central and south-western Asia, central and southern Europe and northern Africa (Kadereit, 1988a). Papaver sect. Meconella has a panarctic–alpine distribution that includes north-eastern North America. Papaver aculeatum Thunb. (sect. Horrida) is indigenous to South Africa, and P. californicum A. Gray (sect. Californicum) is indigenous to western North America. Papaver is characterized by the absence of a style and the possession of stigmatic tissue arranged radially on a sessile stigmatic disc crowning the ovary. The latest taxonomic revision of Papaver (Kadereit, 1988a) recognized 11 sections (Argemonidium Spach.; Carinatae Fedde; Californicum Kadereit; Horrida Elk.; Oxytoma Bernh.; Meconidium Bernh.; Meconella Spach; Papaver L.; Pilosa Prantl; Pseudopilosa Gunther; Rheoadium Bernh.). Detailed taxonomic accounts of many of the sections have been published (Goldblatt, 1974; Kadereit, 1986a, b, 1987, 1988b, c, 1989, 1993b, 1996). The separation of species into sections is based on a combination of characters, including mode of capsule dehiscence (through valves or pores), colour of anthers and filaments (pale or dark), and general capsule characteristics such as size, shape and indumentum. Based on these characters, Kadereit (1988a) recognized four groups of sections within Papaver. The first group consists of sects. Californicum, Meconella and Meconidium and is characterized by pale filiform filaments and anthers, and valvate capsule dehiscence. The second group consists of sect. Argeronomidium alone and is characterized by dark clavate filaments and anthers and poricidal capsule dehiscence. The third group comprises sects. Horrida, Pilosa and Pseudopilosa and is characterized by pale filiform filaments and anthers and poricidal capsule dehiscence. Finally, group four comprises sects. Carinatae, Oxytoma, Papaver and Rheoadium and is

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Papaver is considered to be distinct from the only European representative of the genus. Meconopsis comprises approximately 50 perennial monocarpic or polycarpic herbs, distributed primarily in southern central Asia. Meconopsis cambria (L.) Vig. is the only European representative of the genus. Meconopsis is considered to be distinct from Papaver based on the possession of stigmatic tissue borne on top of a style (although species without styles do exist). Roemeria comprises three annual species distributed mainly in southwestern and central Asia and Europe. It has long, linear, bristly capsules with sessile stigmas borne directly on top of the ovary. Stylomecon is a monotypic genus comprising the annual S. heterophylla (Benth.) G. Taylor native to western North America and is characterized by the possession of stigmatic tissue borne on top of a style. Although it is similar to Meconopsis in capsule characteristics, it is recognized as a distinct genus primarily based on its annual habit and geographical distribution (Taylor, 1930; Kadereit et al., 1997).

Delimitation of taxa into their respective genera (Papaver, Meconopsis, Stylomecon, Roemeria) seems straightforward based on the distinction of capsule characteristics. Previous molecular phylogenetic analyses of these genera (Kadereit and Sytsma, 1992; Kadereit et al., 1997), however, demonstrated that they form a monophyletic group within Papaveroidea (Kadereit, 1993a) and provided evidence that Papaver sensu Kadereit (1988a) is not monophyletic. These molecular analyses included a restriction site analysis of plastid DNA (Kadereit and Sytsma, 1992) and an RFLP analysis of the plastid trnK region (Kadereit et al., 1997). It was demonstrated that Roemeria was sister to P. sect. Argemonidium and Stylomecon was sister to P. sect. Californicum, indicating that Papaver was monophyletic only if these genera were included in Papaver. In addition, the European Meconopsis cambria did not group with the Asian species of this genus. Meconopsis cambria resolved as sister to a group of sections of Papaver including Carinatae, Meconidium, Oxytona, Papaver, Pilosa, Pseudopilosa and Roehocodium, leading Kadereit et al. (1997) to view these sections as Papaver s.s. Determining the interrelationships of these sections was limited by the small number of species sampled in their study. Generally, only a single species was used to represent sections, and single individuals were used to represent species. The non-monophyly of Papaver s.l. indicates that the stigmatic disc typical for the genus may have arisen several times independently. To define Papaver based on a single character that has multiple origins would be taxonomically and phylogenetically unsound. The results of these molecular analyses also demonstrated that some of the infrageneric taxonomic groupings suggested by Kadereit (1988a) were artificial.

The objective of this paper is to examine phylogenetic relationships within Papaver and allied genera by comparing nucleotide sequences obtained from plastid and nuclear ribosomal sequences. The two molecular regions used were the internally transcribed spacer region (ITS) of 18S–26S nuclear ribosomal DNA (Sun et al., 1994; Baldwin et al., 1995) and the trnL intron and the trnF–trnL intergenic spacer region of plastid DNA (Taberlet et al., 1991). All regions are relatively small in size (i.e. trnL–trnF ~500–900 bp; and ITS ~700 bp), which facilitates successful amplification and sequencing (Taberlet et al., 1991; Baldwin et al., 1995; Kelchner, 2000).

Combining sequences from different genomes (nuclear, plastid and mitochondrial) is common in molecular phylogenetics, as long as they produce congruent results, and has resulted in greater understanding of relationships within a wide range of plant groups (see Savolainen and Chase, 2003). Both DNA regions used here have proven useful at similar taxonomic levels in other plant groups (e.g. Gielly et al., 1994; Sun et al., 1994; Baldwin et al., 1995; Wendel et al., 1995; Gielly and Taberlet, 1996; Wendel and Doyle, 1998; Kelchner, 2000; Hodkinson et al., 2002). However, these DNA regions and their subsequent combination have not been applied to Papaver phylogenetics. The topology of the trees obtained here from the comparative analysis of the ITS and trnL–F regions is interpreted in terms of morphological, chemotaxonomic and geographical similarities.

**MATERIALS AND METHODS**

**Specimens**

Material was obtained from various botanical gardens and commercial sources and grown to maturity either at the National Botanic Garden, Glasnevin, Ireland, or in the glasshouse of the Department of Pharmacognosy, University of Dublin, Trinity College, Ireland. DNA obtained from herbarium material was also used. Voucher specimens were kept for each accession and stored in the Herbarium of the Department of Botany, Trinity College Dublin, Ireland (TCD). DNA was stored at the Department of Botany, TCD, DNA Bank. Voucher specimens for each accession and sequences obtained from GenBank are listed in Table 1.

**Outgroup selection**

Outgroup taxa were selected on the basis of the plastid DNA restriction site analysis of Kadereit and Sytsma (1992) and the morphological work of Kadereit (1993a). Eomecon chionantha Hance (Papaveraceae subfamily Chelidioideae) was chosen as an outgroup taxon owing to its position as given in previous studies. Argemone mexicana L. (Papaveraceae subfamily Papaveroideae) and Chelidonium majus L. (Papaveraceae subfamily Chelidioideae) were also included as outgroups.

**DNA extraction**

DNA was extracted from 0.5–1.0 g of fresh leaf material using a modified 2 % CTAB procedure of Doyle and Doyle (1987), precipitated using 100 % ethanol or isopropanol for at least 48 h at −20 °C, pelleted and washed with 70 % ethanol and purified via the Concert™ Rapid PCR Purification System (Life Technologies, Gaithersburg, MD, USA).
### Table 1. Species and associated voucher specimens used in the study

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<th>Taxon</th>
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<th>Voucher or reference</th>
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*ID numbers are GenBank Accession Numbers.*
DNA was then stored in TE buffer (10 mm Tris/HCl, 1 mm EDTA, pH 8.0) at −80°C until required.

DNA sequencing

For amplification and sequencing of the ITS region the forward and reverse primers of Sun et al. (1994) were used. The trnL intron and the trnL–trnF spacer (hereafter the trnL–F region) were amplified and sequenced as one segment using primers ‘c’ and ‘f’ of Taberlet et al. (1991). Difficulties were encountered when attempting to amplify certain sequence regions from herbarium specimens. Their successful amplification and sequencing was achieved using the internal primers (2 and 3) for ITS of Baldwin et al. (1995) and the internal primers (d and e) for the trnL intron and the trnL–F region (Taberlet et al., 1991).

PCR reactions for both regions were carried out in 50-μL reactions using 1% PCR buffer (Promega, Madison, WI, USA), 2.5 mm MgCl2, 0.2 μM of each primer, 0.2 μM of each dNTP, 1 U Taq polymerase (Promega) and approximately 50 ng template DNA. Reaction conditions for the trnL–F region were: denaturation at 94°C for 3 min followed by 30 cycles of 1 min at 94°C, 1 min at 51°C, 1 min at 72°C and a final extension at 72°C for 7 min in a Peltier thermal cycler (PTC 200; MJ Research). PCR amplification of the ITS region was achieved using a touchdown PCR strategy involving denaturation at 94°C for 3 min followed by 30 cycles of 1 min at 94°C, 1 min at 60–52°C (over the first eight cycles with the remaining cycles at 52°C), 1 min at 72°C and a final extension at 72°C for 7 min. Successfully amplified DNA fragments were purified using the Concert™ Rapid PCR Purification System (Life Technologies) and sequenced using Big Dye Terminator Cycle Sequencing Kits v1.1 (Applied Biosystems, Foster City, CA, USA) on an Applied Biosystems 310 or 377 automated DNA sequencer, all according to the manufacturer’s protocols and with the same primers as used for the initial amplification.

Sequence analysis and phylogenetic reconstruction

Forward and reverse sequence reads were assembled using Sequencher™ version 3.1 (Gene Codes Corporation, 1998) to obtain a contiguous sequence for the target DNA region. Consensus sequences for all accessions were imported into SE-Al v2.0 (sequence-alignment, Rambaut, 2001) in which sequences were aligned by inserting gaps manually within the data matrix following the guidelines of Kelchner (2000). The aligned matrix was imported into PAUP v4.0b for phylogenetic analysis (Swofford, 2003). Gaps were treated as missing data. Regions of the sequence alignment that contained a substantial number of alignment gaps were omitted from the analyses because the positional homology within these regions is uncertain (Swofford et al., 1996). Omitted regions included 12-, 53- and 38-bp highly variable regions of the ITS aligned matrix (corresponding to positions 138–150, 240–293 and 478–516, respectively) and the initial 14 and final 65 nucleotides of the trnL–F aligned matrix. Independent phylogenetic analysis of the trnL intron and the trnL–trnF spacer regions yielded broadly congruent trees (results not shown). If incongruence was found it was not supported by bootstrap analysis (soft incongruence; Seelanan et al., 1997). For the purposes of this study both regions were combined for parsimony analysis. These are part of the non-recombining plastid genome and are frequently combined for phylogenetic reconstruction (e.g. Hopper et al., 1999; Chase et al., 2000; Hodkinson et al., 2002) because they should have the same phylogenetic history.

Maximum parsimony (MP) trees were obtained from the resulting matrices using heuristic search options. Searches included 1000 replicates of random addition sequence (saving no more than 30 trees per replicate to reduce time spent swapping large islands of trees) with the tree bisection reconnection (TBR) branch-swapping algorithm and MulTrees on (keeping multiple equally most-parsimonious trees). Internal support was assessed using 1000 bootstrap replicates (Felsenstein, 1985), simple addition sequence, TBR swapping and MulTrees on (holding 30 trees per replicate; see Salamin et al., 2003). Groups with bootstrap percentages (BP) of 90–100 were considered to be strongly supported, 80–89 moderately supported and 50–79 weakly supported. Only groups with BP >50 that are consistent with the strict consensus tree are shown.

No major conflicts (hard incongruence) between the separate trees were identified between single-region analyses. Accordingly, the trnL–F data were joined with the ITS data in a combined analysis. The incongruence length difference (ILD) test (or similar congruence tests) was not applied as this can be ineffective in identifying combinability of data and in some cases has been shown to be misleading (Yoder et al., 2001). Our decision to combine was based on the pattern of major clades and their respective bootstrap
percentages. The combined analysis of trnL–F and ITS data was also performed using the same parameters as stated above for the single gene region analyses.

RESULTS

Analysis of ITS

The lengths of ITS1, ITS2 and 5.8S were confirmed using a comparative alignment of *Papaver rhoes* ITS1, ITS2 and 5.8S obtained from GenBank (Schwarzbach and Kadereit, 1999; accession no. AF098920). The 5.8S region ranged from 157 to 169 bp across all accessions used in this study. Relatively little variation was encountered within the 5.8S region, with only 10 of the 171 nucleotides (5.8% of the final aligned matrix) being variable, but all were potentially parsimony-informative. The ITS1 and ITS2 spacers ranged in length from 218 to 260 bp and from 216 to 257 bp, respectively. A considerable proportion of both regions were variable. Of the 189 variable sites within the aligned ITS1 (66.5% of the aligned ITS1 region), 152 were potentially parsimony-informative. Of the 171 variable sites found within the aligned ITS2 (50.4% of the ITS2 region) 128 were potentially parsimony-informative. The G+C content of both ITS1 and ITS2 ranged from 50.5 to 60.2% and 55.3 to 63.8%, respectively. Independent analysis of the ITS1 and ITS2 spacers yielded broadly congruent trees (results not shown; Carolan, 2004). For the purposes of this study both regions plus the 5.8S gene were combined for parsimony analysis. The entire aligned ITS matrix (ITS1, 5.8S and ITS2) was 705 bp long; 324 sites were variable, and 235 of these were potentially parsimony-informative. Figure 1 shows one of 151 equally most-parsimonious trees from the ITS analysis. It has 826 steps, with a consistency index (CI) of 0.57 and a retention index (RI) of 0.83.

Two distinct clades were found within the ITS tree (Fig. 1). Clade 1 comprises sects. *Argemondium*, *Meconella* and the Asian representatives of *Meconopsis*. This clade is sister to all other sections of *Papaver* in all equally most-parsimonious trees but is itself weakly supported with only 56% bootstrap support (bootstrap percentage; BP).

Roem eria refracta groups with the species of sect. *Argemondium* (97 BP). Within clade 1, sect. *Meconella* forms a well-supported group (98 BP). The Asian representatives of *Meconopsis* are resolved as sister to sect. *Meconella* in all equally most-parsimonious trees (83 BP).

Clade 2 (53 BP) comprises the remaining sections of *Papaver*, including *Meconopsis cambria* and *Stylomecon heterophylla*. *Papaver aculeatum* (sect. *Horrida*) and a group comprising sect. *Californicum* and *Stylomecon heterophylla* resolve independently but sister to the remaining sections of clade 2 (53 and 69 BP, respectively). The positioning of *Stylomecon heterophylla* as sister to *P. californicum* is well supported (98 BP). *Meconopsis cambria* and the remaining sections of *Papaver* form a well-supported group (97 BP). Sections *Papaver* and *Rhoeodium* are not monophyletic in this tree, as indicated by the grouping of *Papaver glaucum* (sect. *Papaver*) with representatives of sect. *Rhoeodium* (including sect. *Carinatae*; <50 BP) and the grouping of *P. dubium* ssp. *erosum* (sect. *Rhoeodium*) with *Papaver somniferum* (sect. *Papaver*; 88 BP). However, there is also little evidence contradicting their monophyly. Within clade 2, sect. *Pseudopilosa* is characterized by the possession of a number of unique indels. These include a 4-bp indel at positions 75–78 (A, Fig. 1; Table 2) and a 4-bp indel at positions 216–219 (B, Fig. 1; Table 2) of the aligned ITS matrix. Omitting these indels (gapped sites) from the analysis did not affect the sister group position of *Pseudopilosa* (with respect to the majority but not all of clade 2).

Analysis of trnL–F

The total lengths of the trnL intron and the trnL–F spacer were confirmed using a comparative alignment of the *Meconopsis betonicifolia* trnL intron, trnL–F spacer and the 3′ trnL exon sequence obtained from GenBank (Y. M. Yuan et al., unpubl. data, Zhongshan University, P. R. China; accession AY328263). Little variation was encountered within the 3′ trnL exon region (50 bp long, including one parsimony informative character). The unaligned trnL intron and trnL–F spacer regions ranged in length from 467 to 505 bp and 384 to 422 bp, respectively. The final aligned matrix had a total length of 951 characters (539, 50 and 362 sites for the trnL intron, the 3′ trnL exon and the trnL–F spacer, respectively). The 128 variable sites found within the aligned trnL intron (representing 23.7% of the trnL intron) consisted of 74 potentially parsimony-informative characters, and the trnL–F spacer contained 165 variable characters (representing 45.5% of the spacer), of which 103 were potentially parsimony informative. The G+C content of both the trnL intron and the trnL–F spacer ranged from 32 to 36.5% and 33.6 to 41.4%, respectively. In total the aligned trnL–F matrix was 951 bp long; 294 sites were variable, and 176 of these were potentially parsimony informative. Phylogenetic analysis of the trnL–F matrix produced eight equally most-parsimonious trees (468 steps, CI = 0.77, RI = 0.91; Fig. 2).

Three main clades are present in the trnL–F trees, which (Fig. 2) are broadly congruent with the ITS analysis. The separation of *P. sect. Argemondium* and *Roem eria refracta* (clade 3, 74 BP) and *Meconella* (clade 1, 100 BP) from the main group containing the remaining sections of *Papaver* (clade 2, 69 BP) is evident. Section *Argemondium* is well supported (100 BP). The Asian representatives of *Meconopsis* (excluding *M. aculeata*) form a well-supported group (90 BP) and are sister to representatives of sect. *Meconella* (55 BP). Members of sect. *Meconella* possessed two characteristic 4-bp indels at positions 162 and 261 (D and F, Fig. 2; Table 2), which are also present in the outlying sections of clade 2, such as *P. sects. Californicum*, *Horrida*, *Stylomecon heterophylla* and Asian *Meconopsis*. *Papaver argemo nes*, *P. apulum* and *P. hybridum* share a 10-bp deletion at positions 644–653 (G, Fig. 2; Table 2), which is not found in *P. pavonius*.

The remainder of the sections form a weakly supported group (clade 2; 69 BP). *Papaver* sects. *Horrida*, *Californicum* and *Meconopsis cambria* are resolved independently.
Fig. 1. One of 151 equally most-parsimonious trees generated from the ITS sequences. Support for each node is represented by bootstrap percentages (BP) below the branch (shown only when >50% and consistent with the strict consensus tree). An arrow indicates clades that did not appear in the strict consensus tree. Numbers above each branch indicate the numbers of character changes along each lineage (accelerated transformation, ACCTRAN, optimization).

Groups that possess characteristic indels are indicated using letters (refer to Table 2).
but sister to the main group in clade 2 with similar topologies to the ITS trees. *Papaver californicum* and *Stylomecon heterophylla* form a well-supported group (100 BP). Within clade 2, a group comprising sects. *Carinatae*, *Meconidium*, *Oxytoma*, *Papaver*, *Pilosa*, *Pseudopilosa* and *Rhoeadium* was resolved (97 BP). Section *Oxytoma* groups with sect. *Meconidium* (58 BP), with sect. *Pilosa* as sister to these (92 BP). The sampled species of section *Pseudopilosa* are well supported (99 BP). The members of sect. *Rhoeadium* do not form a monophyletic group; *P. dubium* (excluding *P. dubium* ssp. *erosum*) groups more closely with *Papaver somniferum* (sect. *Papaver*) than other members of sect. *Rhoeadium* (83 bp). In addition, *P. dubium* (excluding *P. dubium* ssp. *erosum*) does not possess a 5-bp indel at positions 186–190 (E, Fig. 2; Table 2) that the other members of sect. *Rhoeadium* share. *Papaver glaucum* groups within the main *P. rhoesas* clade (83 BP) and shares the indel (E, Fig. 2) with these *Rhoeadium* species.

### Analysis of combined ITS and trnL–F

The combined *trnL–F* and ITS matrix was 1659 bp long. Parsimony analysis of the matrix generated eight equally most-parsimonious trees of 1332 steps with a CI of 0.63 and an RI of 0.84 (Fig. 3). The combination of the ITS and *trnL–F* data sets showed increased bootstrap support for the majority of groupings compared with those found in the individual analyses. Three clades are resolved. Clade 1 (90 BP) comprises *P. sect. Meconella* (100 BP) and Asian *Meconopsis* (99 BP). Clade 2 (81 BP) comprises the remaining sections of *Papaver*, *Meconopsis cambrica* and *Stylomecon heterophylla*. Section *Horrida* (100 BP) is sister to the rest of clade 2. The single representative of sect. *Californicum* (*P. californicum*) shares a close affinity with *Stylomecon heterophylla* (100 BP). Within clade 2, the main group of sections (*Carinatae*, *Meconidium*, *Oxytoma*, *Papaver*, *Pilosa*, *Pseudopilosa* and *Rhoeadium*) is evident and well supported (99 BP). Of these, sect. *Pseudopilosa* is most divergent and monophyletic within *Papaver* (100 BP).

Support for the positioning of *Meconopsis cambrica* as sister to the core sections of clade 2 and its separation from the other representatives of *Meconopsis* increased to 99 BP in comparison with 97 BP in the ITS tree and 58 BP in the *trnL–F* tree.

Sections *Meconidium* (99 BP), *Oxytoma* (98 BP) and *Pilosa* (94 BP) form a well-supported clade (84 BP). Sections *Papaver* and *Rhoeadium* are not monophyletic. *Papaver glaucum* (sect. *Papaver*) groups with species of sects. *Rhoeadium* and *Carinatae* (56 BP; *P. commutatum*, *P. dubium* ssp. *erosum*, *P. macrostomum* and *P. rhoesas*) and not with the other representatives of sect. *Papaver*. Finally, clade 3 comprises sect. *Argemonidium* plus *Roemeria refracta* (100 BP).

### DISCUSSION

**Phylogenetics of Papaver and related genera**

The combination of nuclear ribosomal ITS and plastid *trnL–F* nucleotide sequences in a phylogenetic analysis resulted in well-resolved and well-supported trees. Three main lineages can be identified (clades 1, 2 and 3; Fig. 3). The results also show that *Papaver* is only monophyletic if *Roemeria*, *Stylomecon heterophylla* and *Meconopsis cambrica* are included in this genus. This is consistent with the molecular studies of Kadereit and Sytsma (1992) and Kadereit *et al.* (1997). Evidently, the topologies and major groupings of the phylogenetic trees produced in this analysis are incongruent with the generally accepted definitions of these closely interrelated genera. The major groupings found in this analysis are discussed below and interpreted in light of their morphology and biogeography.

**Papaver sect. Argenonidium and Roemeria**. Kadereit (1986a) revised *Papaver sect. Argenonidium* and concluded that it contains four annual, half-rosette species, *P. apulum*, *P. argemone*, *P. hybridum* and *P. pavonium*. *Papaver apulum*, *P. argemone* and *P. pavonium* are closely related and occur allopatrically from around the Adriatic Sea through Turkey–Iran to the Himalayas. The fourth species, *P. hybridum*, occupies a wide range from the Macaronesian Islands towards the Himalayas (Kadereit, 1986a, 1988a). The four species of this section are well differentiated in capsule and petal characters (Kadereit, 1986a) but are clearly closely related to each other as demonstrated by the groupings within the molecular phylogenetic trees (clade 3; 97 BP; Fig. 3). Within sect. *Argemonidium*, *P. apulum* and *P. hybridum* are sister species in both the ITS and the *trnL–F* analyses. In all analyses sect. *Argemonidium* is distinct from the other sections of *Papaver* and has characteristic indels (Table 2). The molecular distinctness of sect. *Argemonidium* is also supported by morphological differences (Fedde, 1909; Ernst, 1962; Cullen, 1965; Kadereit, 1986a; Markgraf, 1958), which

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**Table 2. Insertions/deletions in the ITS and trnL–F regions for representatives used in this study**

<table>
<thead>
<tr>
<th>Region and start points</th>
<th>Diagnostic indel or sequence</th>
<th>Tree annotation</th>
<th>Taxon</th>
</tr>
</thead>
<tbody>
<tr>
<td>ITS 75</td>
<td>TATA indel</td>
<td>A</td>
<td>Sect. <em>Pseudo-pilosa</em></td>
</tr>
<tr>
<td>ITS 216</td>
<td>TCTC indel</td>
<td>B</td>
<td>Sect. <em>Pseudo-pilosa</em></td>
</tr>
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<td>ITS 695</td>
<td>T indel</td>
<td>C</td>
<td>Sect. <em>Argemonidium</em>; <em>Roemeria refracta</em></td>
</tr>
<tr>
<td><em>trnL–F</em> 162</td>
<td>TATA indel</td>
<td>D</td>
<td>Sects. <em>Californicium</em>; <em>Horrida</em>; <em>Meconella</em>; Asian <em>Meconopsis</em>; <em>Stylomecon heterophylla</em></td>
</tr>
<tr>
<td><em>trnL–F</em> 186</td>
<td>TAGAG intel</td>
<td>E</td>
<td><em>Papaver commutatum</em>; <em>P. dubium</em> ssp. <em>erosum</em>; <em>P. glaucum</em>; <em>P. macrostomum</em>; <em>P. rhoesas</em></td>
</tr>
<tr>
<td><em>trnL–F</em> 261</td>
<td>GCCC indel</td>
<td>F</td>
<td>Sects. <em>Californicium</em>; <em>Horrida</em>; <em>Meconella</em>; Asian <em>Meconopsis</em>; <em>Stylomecon heterophylla</em></td>
</tr>
<tr>
<td><em>trnL–F</em> 643</td>
<td>10-bp deletion</td>
<td>G</td>
<td>Sect. <em>Argemonidium</em> (excluding <em>P. pavonium</em>)</td>
</tr>
</tbody>
</table>

| Table 2. Insertions/deletions in the ITS and trnL–F regions for representatives used in this study |

Start points of the indel are based on the aligned matrix for that given region. Characters mapped onto phylogenetic trees are given as letters.
FIG. 2. One of eight equally most-parsimonious trees generated from the trnL–F sequences using maximum parsimony. Support for each node is represented by bootstrap percentages (BP) below the branch (shown only when >50% and consistent with the strict consensus tree). Numbers above each branch indicate the numbers of character changes along each lineage (ACCTRAN optimization). An arrow indicates branches that did not appear in the strict consensus tree. Groups that possess characteristic indels are indicated using letters (refer to Table 2).
**Fig. 3.** One of eight equally most-parsimonious trees generated from the combined ITS and trnL–F data sets using maximum parsimony. Support for each node is represented by bootstrap percentages (BP) below the branch (shown only when $>50\%$ and consistent with the strict consensus tree). Numbers above each branch indicate the numbers of character changes along each lineage (ACCTRAN optimization). An arrow indicates branches that did not appear in the strict consensus tree.
include presence of an apical plug in the capsules, long internodes above the basal leaf rosette, polyporate pollen grains, bristly capsules and sepal morphology.

From a taxonomic point of view the most significant relationship involving sect. Argegonidium is the close grouping of its members with the genus Roemeria. In all analyses sect. Argegonidium and Roemeria are sister to each other. This affinity has been suggested by previous authors based on morphological observations (Günther, 1975; Morales Torres et al., 1988) and has been supported by previous molecular analyses (Kadereit and Sytsma, 1992; Kadereit et al., 1997). Some of the morphological characters that separate sect. Argegonidium from Papaver are shared with Roemeria, including polyporate pollen grains, sepal morphology and long internodes above the basal leaf rosette (shared with R. hybrida). Relationships within the Argegonidium–Roemeria group are unclear owing to incongruence between the ITS and trnL–F phylogenetic trees and also between these results and previous molecular analyses by Kadereit and Sytsma (1992) and Kadereit et al. (1997). The trees resulting from ITS sequences clearly show P. pavonium ssp. pavonium and Roemeria refracta as sister species (99 BP). This placement was also demonstrated by Kadereit and Sytsma (1992) and Kadereit et al. (1997). Based on the molecular similarity between P. pavonium and R. refracta and the fact that P. pavonium has a similar geographical distribution to R. refracta and R. hybrida, Kadereit and Sytsma (1992) and Kadereit et al. (1997) postulated that Roemeria had arisen from within sect. Argegonidium and most probably directly from Papaver pavonium or an ancestor of this species. However, in the analyses of the maternally inherited trnL–F region (Fig. 2), sect. Argegonidium and Roemeria are sister groups, indicating that Roemeria can be considered distinct from sect. Argegonidium but not distinct from Papaver. Incongruence of trees generated from these differently inherited DNA regions is sometimes attributed to hybridization. Given that the two species in question are both diploid (Podleck and Dieterle, 1969; Kadereit, 1986a), allopolyploidy cannot explain the different topologies of the ITS and trnL–F trees. However, hybridization or introgression could explain these differences. Divergence of ITS repeat types could also have occurred before the divergence of the Argegonidium–Roemeria group. Paralogy could therefore also explain the pattern, with one ITS repeat type retained in the P. pavonium–Roemeria group and an alternative type in the others.

The current taxonomy of Papaver and relatives does not take account of the distinctiveness of sect. Argegonidium and its close relationship to Roemeria. We here suggest a re-classification accommodating our molecular results. Elevation of sect. Argegonidium to genus level or a combination of sect. Argegonidium as a subgenus of Roemeria would be appropriate taxonomic treatments of these groups. We favour the former option because of the substantial morphological differences between sect. Argegonidium and Roemeria.

Papaver sect. Meconella and Meconopsis (excluding M. cambrica). The scapose, perennial species of Papaver sect. Meconella (represented in this study by Papaver alpinum, P. anomalum, P. croceum, P. miyabeana and P. radicatum) form a monophyletic group (100 BP in the trnL–F and combined analyses and 98 BP in the ITS analysis; Figs 1–3). Section Meconella is widely distributed across central, inner and eastern Asia, Siberia, Scandinavia through Greenland and northern Canada, with representatives found also in mountainous regions of Europe and the Rocky Mountains in North America (Rändel, 1974; Kadereit, 1988a). The species included in this study represent a limited sample from this distribution (five of 30 species; Rändel, 1974; Kadereit, 1988a).

The distinctness of this section from Papaver (excluding sect. Argegonidium) is also supported, as is its placement with Meconopsis excluding M. cambrica (Fig. 3; clade 1; 90 BP). A number of morphological characters have been used to define sect. Meconella (Hanelt, 1969; Rändel, 1974; Kadereit, 1988a). These include bristly, valvate capsules, simple or dissected pinnatisect leaves, pale anthers and filaments, and yellow, orange or white petals.

The species of sect. Meconella can be divided into two groups based on the degree of leaf dissection (finely dissected leaves: Papaver alpinum, P. miyabeana and P. radicatum; broad leaf lobes: Papaver anomalum and P. croceum), but such a grouping is not supported by our molecular analysis. This morphological character has been discussed previously by Kadereit (1990) and Kadereit and Sytsma (1992) with reference to P. alpinum. The authors of these studies regarded finely dissected leaves to be a primitive character in sect. Meconella and suggested that this character may support a relationship to sect. Argegonidium with species of similar leaf morphology. Although P. alpinum is sister to the remaining Meconella species in the combined analysis, the other representatives of sect. Meconella with finely dissected leaves group more closely with species possessing broad leaf lobes. In addition, a molecular analysis of P. alpinum s.l. by Bittkau and Kadereit (2002) found that within this species broad leaf lobes are ancestral.

The position of sect. Meconella is not fully congruent with topologies obtained from earlier molecular analyses (Kadereit and Sytsma, 1992; Kadereit et al., 1997). The results from those analyses indicated that Meconella is sister to all sections of Papaver (Kadereit and Sytsma, 1992) or that sections Meconella and Argegonidium were resolved as sister to each other (Kadereit et al., 1997). However, bootstrap support for the sister-group relationship of these two sections (in the latter study) was low (<50 BP). Based on the topology of the major clades in our molecular trees, it can be concluded that sect. Meconella (and probably Meconopsis) is derived from a lineage that separated earlier from that giving rise to most other sections of Papaver (excluding Argegonidium).

The Asian representatives of Meconopsis were resolved as sister to sect. Meconella and share the diagnostic indels of sect. Meconella (D and F; Table 2). This grouping is incongruent with results of previous molecular analyses (Jork and Kadereit, 1995; Kadereit et al., 1997). The results of those analyses demonstrated that within Asian Meconopsis two distinct clades existed (based on an RFLP analysis of plastid
DNA fragments). The first clade comprised species such as *Meconopsis chelidonifolia* and *M. villosa* that are sister to the other representatives of Asian *Meconopsis* (clade 2) plus the remaining Old World Papaveroideae (*Meconopsis cambrica*, *Papaver*, *Roemeria*, *Stylomecon*) used in that analysis. Only representatives of this second clade were included in the analyses reported here.

A significant amount of morphological difference exists between sect. *Meconella* and *Papaver s.s.* (clade 2). Although species of sect. *Meconella* possess a sessile stigmatic disc similar to the stigmatic discs typical of *Papaver*, it has been noted (Rändel, 1977; Kadereit et al., 1997) that the stigmatic discs of sect. *Meconella* may not be homologous to those found in other sections of *Papaver* (excluding *Argemonidium*). The stigmatic discs of *Meconella* consist in some cases of stigmatic tissue only, or there are deep incisions between the stigmatic rays. In addition, certain species of *Meconella* have polyporate instead of tricolpate pollen grains, a characteristic also found in some species of *Meconopsis* and *Papaver* sect. *Argemonidium*. No species of *Meconella* with polyporate pollen were included in this study.

If the current circumscription of *Papaver* is followed and sect. *Meconella* is retained within *Papaver*, a strict interpretation of the trees produced in this analysis would imply that *Meconopsis* should also be considered to be a member of *Papaver*. To retain *Meconopsis* as a genus would require a separation of sect. *Meconella* from *Papaver*. For example, it could either be raised to genus rank or included in *Meconopsis*. *Meconella* is therefore treated as a subgenus of *Papaver*, recognizing the distinction between *Meconella* and other *Papaver* subgenera but also recognizing that evidence exists for the amalgamation of *Papaver* and *Meconopsis*.

*Papaver* sects. *Californicum* and *Horrida*. *Papaver* sects. *Californicum* and *Horrida* are distributed outside the main geographical range of *Papaver*. *Papaver aculeatum* (sect. *Horrida*) is native to South Africa and is characterized by an indumentum of relatively long bristles, poricidal capsules, and pale filiform filaments and anthers. All green parts of the plant are covered with patent bristles (Kadereit, 1988c). *Papaver californicum* (sect. *Californicum*) is native to the west coast of North America and has a slender, ribbed, glabrous capsule, a many-flowered racemose inflorescence, pale anthers and filaments, and valvate capsule dehiscence (Kadereit, 1988b). Both species are annuals. In the ITS, *trnL–F* and combined trees both sections are attached to basal nodes within the main clade of *Papaver* (clade 2; Figs 1–3), and sect. *Californicum* is sister to the ‘core’ group of *Papaver* (sects. *Carinatae*, *Meconidium*, *Oxytoma*, *Papaver*, *Pilosia*, *Pseudopilosa* and *Rhoeadium*) and *Meconopsis cambrica*. *Papaver aculeatum* shares morphological and cytological characteristics with sects. *Pilosia* and *Papaver*. Similarities between *P. aculeatum* and *P. somniferum* (sect. *Papaver*) include auriculate–amplexicaulous leaves and a chromosome base number of *n* = 11, both characteristics found only in these two species. However, both these characters appear to have evolved in parallel (Figs 1–3). Similarities between sects. *Horrida* and *Pilosia* include racemose inflorescences, pale filiform filaments and the possession of long capsules with flat stigmatic discs (Kadereit, 1988c). However, these two sections do not associate in the molecular analysis presented here, and convergence is therefore also implied to explain the similarity in morphology. *Papaver californicum* shares characteristics with sect. *Meconidium*, including valvate capsule dehiscence and pale filiform filaments, but species of these two groups are geographically widely separated and do not associate in the molecular trees.

The results from the molecular analysis support the view of Kadereit et al. (1997) that *Stylomecon heterophylla* arose from within *Papaver* and should not be considered a separate genus. *Stylomecon heterophylla* and *P. californicum* are both native to California and grow in similar habitats (Kadereit, 1988b). Morphological similarities between these species include leaf shape, glabrous/globose buds, orange petals, and pale anthers and filiform filaments (Ernst, 1962; Kadereit, 1988b). The two species are differentiated by capsular morphology, with *S. heterophylla* possessing a distinct style that is similar to those found in many representatives of *Meconopsis*. In the ITS, *trnL–F* and combined analysis, *S. heterophylla* and *P. californicum* form a well-supported group (100 BP in the *trnL–F* and combined trees, Figs 2 and 3; 96 BP in the ITS trees, Fig. 1). The two species appear to have diverged relatively recently. *Stylomecon heterophylla* possesses the 4-bp indel diagnostic for sects. *Meconella*, *Californicum* and *Horrida* (incl. *Asian Meconopsis*) at positions 261–265 in the *trnL–F* region (F, Fig. 2; Table 2). The separation of *S. heterophylla* from *Papaver* therefore is not justified based solely on differences in capsule characteristics.

The results of the molecular analysis can be interpreted in a number of ways for taxonomic conclusions concerning sects. *Californicum* and *Horrida*. Both sections are successively sister to the highly supported (99 BP; Fig. 3) core group of *Papaver* comprising sects. *Carinatae*, *Meconidium*, *Oxytoma*, *Papaver*, *Pilosia*, *Pseudopilosa* and *Rhoeadium*. However, sects. *Californicum* and *Horrida* possess the characteristic 4-bp indel at positions 248–252 in the *trnL–F* region shared with *Asian Meconopsis* and representatives of sect. *Meconella*. The disjunct geographical distributions of sect. *Californicum* (North America) and sect. *Horrida* (South Africa) might indicate a wider distribution of *Papaver* at some point during its evolutionary history, with extinction occurring in North America and Africa leaving these two sections geographically isolated (Randel, 1974; Kadereit et al., 1997), or indicate long-distance dispersal. Taking into account the outlying positions of sects. *Californicum* and *Horrida* in the molecular trees, they seem to derive from a relatively ancient lineage of *Papaver*. The positions of *Californicum* and *Horrida* within the core *Papaver* clade in the analyses here are congruent with previous molecular analyses (Kadereit and Sytsma, 1992; Kadereit et al., 1997).

It is recommended that sects. *Californicum* and *Horrida* be elevated to the rank of subgenera within *Papaver*, i.e. subgen. *Californicum* and subgen. *Horrida*. The separation of *Stylomecon heterophylla* from *Papaver* is rejected. The clear relationship of this species to *P. californicum*, as
indicated by similarities in morphology, geographical distribution, and nucleotide sequences within the ITS and trnL–F gene regions, favours its inclusion in subg. Californicum. Considering these differences in capsule morphology, subg. Californicum should contain two species, Papaver Californicum and P. heterophylla (=Stylomecon heterophylla).

Meconopsis cambrica. The only European species of Meconopsis, M. cambrica, is well separated from the representatives of Asian Meconopsis in the molecular analysis here. Meconopsis cambrica occupies a well-supported (99 BP; Fig. 3) sister-group position to the remaining sections of Papaver (excluding Argemonidium, Californicum, Horrida and Meconella). This supports the view (Kadereit et al. 1997) that two distinct lineages within Meconopsis s.l. exist and that Meconopsis in its current circumscription is neither monophyletic nor distinct from Papaver. Meconopsis cambrica shares diagnostic trnL–F indels with the majority of Papaver (excluding Argemonidium, Californicum, Horrida and Meconella). Meconopsis cambrica could have arisen either in parallel with the Asian representatives of Meconopsis, clade 2, i.e. core Papaver (sects. Carinatae, Papaver, Pilosa, Pseudopilosa, Oxytoma, Meconidium and Rhoeadium), or from within a lineage best recognized as members of an expanded Meconopsis. Both these views were proposed by Kadereit et al. (1997), who favoured the latter view based on geographical, phytochemical and morphological considerations. Topological considerations alone favour parallel evolution as M. cambrica is embedded in clade 2 in our ITS-trnL–F trees.

It is evident from the results of this analysis that incongruence exists with previous taxonomic classifications regarding the positioning of M. cambrica. If M. cambrica is recognized as Meconopsis, Papaver s.s. (i.e. after the exclusion of the groups discussed above) is not monophyletic. It is suggested to include M. cambrica (as Papaver cambrica L.) in Papaver. However, an appropriate treatment of this species is difficult owing to the lack of apparent morphological similarities with extant Papaver species. There is no obvious section or group of species with which to place Papaver cambrica. Although unsatisfactory from a taxonomic perspective it may be necessary to describe a new monotypic section for this species within Papaver. The alternative is to leave it as incertae sedis until further evidence is found regarding its placement.

Section Pseudopilosa (represented in the combined analysis by P. atlanticum and P. rupifragum) forms a well-supported group in the combined analysis (100 BP; Fig. 3) and is sister to the remaining sections of Papaver s.s. Representatives of sect. Pseudopilosa are characterized by having unique 5- and 4-bp indels at positions 75–79 (A, Fig. 1) and 216–219 (B, Fig. 1) of the ITS region, respectively (Table 2). The species of this section are of subscape to scapose habit and are found in south-western Asia, northern Africa and southern Spain.

Section Pilosa comprises a single perennial subscape species with a number of subspecies found predominantly in western Turkey (Kadereit, 1996). The species is characterized by convolute leaf vernation, poricidal capsule dehiscence and pale filiform filaments. The separation of sect. Pilosa from sect. Pseudopilosa based on morphological and phytochemical differences (Popov, 1937; Günther, 1975; Kadereit, 1996) is supported by the results of the combined analysis here (Fig. 3). Papaver pilosum is sister to sects. Oxytoma and Meconidium (86 BP). Section Oxytoma comprises a polyploid series including diploid P. bracteatum (2n = 14), tetraploid P. orientale Fedde (2n = 28) and allo-hexaploid P. pseudo-orientale Fedde (2n = 42) and is found predominantly in the Caucasus Mountains, eastern Turkey and north-western Iran (Goldblatt, 1974). The group is characterized by their perennial habit, poricidal capsule dehiscence, and dark filaments and anthers. Section Meconidium, comprising four biennial species (represented in the analysis here by two subspecies of P. armeniacum), occupies a continuous geographical range in southern and eastern Turkey, the Caucasus Mountains, northern Iraq and north-western Iran and possesses glabrous or bristly capsules, valvate capsule dehiscence, and pale filaments and anthers. Sections Meconidium, Oxytoma and Pilosa are heterogeneous morphologically, and identification of synapomorphies for this group is difficult. The three species of sect. Oxytoma are clearly monophyletic (98 BP; Fig. 3). Genomic and fluorescence in situ hybridization studies (Carolan, 2004) have indicated that the diploid P. bracteatum was a parent of the hexaploid P. pseudo-orientale. The clear inter-relationship between these species has been demonstrated previously using AFLP fingerprinting (Carolan et al., 2002).

The remaining sections of Papaver s.s. are sects. Carinatae, Papaver and Rhoeadium. The results of the molecular analyses question whether these sections are monophyletic. Papaver sect. Rhoeadium consists of 17 predominantly annual species (Günther, 1975; Kadereit, 1989) and is represented in this study by Papaver commutatum, P. dubium and P. rhoeas. The centre of diversity of sect. Rhoeadium is south-western Asia and the Aegean area with some species found in the central or western Mediterranean, the Balkans and the western Himalayas (Kadereit, 1989). Characteristic morphological traits include poricidal capsule and dark (sometimes light) filaments. However, the section is extremely diverse in morphological characteristics. Kadereit (1989) recognized three species groups within sect. Rhoeadium based on geographical and morphological traits. The first group contains species with longer than broader capsules, such as P. dubium, and only tetraploid (2n = 28) and hexaploid (2n = 42) species. The
The single representative of sect. *Carinatae* (*P. macros-tomum*) consistently fell within the *P. rhoes* group and shares its diagnostic *trnL–F* indel (Figs 1 –3; E, Table 2). *Papaver macros-tomum*, distributed in Iran, Iraq and Turkey, possesses all the morphological characteristics of sect. *Rhoeadium* but has been separated into a separate section based on the possession of a deciduous stigmatic disc (Fedde, 1909; Kadereit, 1987). No support for the separation of *P. macros-tomum* from sect. *Rhoeadium* is found in the ITS and *trnL–F* trees.

The four annual representatives of sect. *Papaver* (represented in this study by *P. glaucum* and *P. somniferum*) from the western Mediterranean and south-western Turkey to Cyprus, Iran, Afghanistan and Pakistan do not form a monophyletic group in our analyses of ITS and *trnL–F*. Species of this section are characterized by the possession of more or less strongly auriculate–amplexicaulous leaves, poricidal capsule dehiscence and dark (sometimes pale) filaments. *Papaver glaucum* shows more sequence similarity to sect. *Rhoeadium*. This division within sect. *Papaver* has previously been demonstrated (Kadereit and Sytsma, 1992). The study by these authors also demonstrated that *P. glaucum* and *P. gracile* (members of this section) are more closely related to *P. rhoeas* and *P. dubium* of sect. *Rhoeadium*. Many morphological and geographical similarities exist between the two sections (see Kadereit, 1988a). Phytochemically, *P. glaucum* differs from *P. somniferum* in not accumulating morphinan alkaloids but rather has some alkaloids similar to those found in *P. rhoeas* (Preininger et al., 1981; Preininger, 1986). *Papaver gracile*, *P. glaucum* and *P. decaisnii*, like the majority of *Papaver*, have a base chromosome number of *n* = 7. *Papaver som-niferum* has a base chromosome number of *n* = 11 (Hammer and Fritsch, 1977). These differences in chromosome number and alkaloid spectra led Novak and Preininger (1980) and Preininger et al. (1981) to separate these three species into their new sect. *Glaucu*. Reckin (1973) transferred these species to sect. *Rhoeadium*. The presence in *P. glaucum* of the diagnostic 5-bp indel at positions 186–191 of the *trnL–F* region (E, Table 2), characteristic for the *Papaver rhoes* group, further questions the classification of *P. glaucum* in sect. *Papaver*.

Although our study could demonstrate the non-monophyly of sects. *Papaver* and *Rhoeadium*, limited sampling of species and limited support for some groups do not allow us to reclassify *Papaver s.s.* confidently into sections apart from the inclusion of *M. cambrica* just discussed. However, *Papaver s.s.* should be treated as *Papaver* subg. *Papaver*. It seems likely from the molecular results that subg. *Papaver* will contain sects. *Meconidium*, *Oxytona*, *Papaver* (including *Rhoeadium* and *Carinatae*), *Pirola* and *Pseudopilosa*.

**Evaluation of morphological characters previously viewed as diagnostic for *Papaver***

*Papaver* has been defined primarily by the possession of a capsule with a sessile stigmatic disc. The results of the molecular analyses presented here clearly demonstrate that a number of species with sessile stigmatic discs are close relatives of taxa that possess a style. This is demonstrated by *S. heterophylla* and *P. californicum* and *P. sect. Meconella* and Asian *Meconopsis*. Furthermore, the structure of the stigmatic disc in sect. *Argemonidium* is different from all other stigmatic discs due to the formation of a plug-like structure in the interior of the capsule. This can be regarded as evidence for its independent evolution from other species with a typical stigmatic disc.

*Papaver* has generally been considered to represent the most derived lineage of Papaveroideae, and hence the sessile stigmatic disc was deemed to be an advanced character. The results here are congruent with this view with respect to *Papaver s.s.* only. In light of the groupings generated in our phylogenetic analysis it is not inconceivable that the sessile stigmatic disc has arisen on a number of occasions from ancestors with a style. Independent origins of the stigmatic disc in *Papaver* have been suggested previously (Kadereit and Sytsma, 1992).

Two morphological characters were considered of primary significance for the evaluation of relationships within *Papaver*, particularly at the inter-sectional level. These are the mode of capsule dehiscence and the degree of pigmentation of filaments and anthers. The possession of pale filaments and anthers by the majority of genera of Papaveroideae and of dark filaments in part of *Papaver s.s.* indicates that pale filaments might be ancestral. Dark filaments seem to have evolved more than once, or there have been reversals to pale filaments in some sections (e.g. *Meconidium* and *Pirola*). Molecular and morphological data separate sect. *Argemonidium* from the other sections with dark filaments (*Carinatae, Oxytona, Papaver* and *Rhoeadium*).

Sections *Meconella* and *Californicum* have valvate capsule dehiscence and an outlying position with respect to the
other sections of Papaver. This indicates that valvate capsule dehiscence may be primitive. However, this character is also found in sect. Meconidium, which falls within Papaver s.s. Its presence here suggests that this character is a synapomorphy for the species of sect. Meconidium. Thus, the results of this analysis indicate that valvate capsule dehiscence has evolved independently at least three times within Papaver s.l.

The combination of morphological, biogeographical and molecular characters has made possible a novel interpretation of relationships in Papaver and allies, and allows for more useful taxonomies to be generated. A formal taxonomic revision of Papaver infrageneric groupings is in preparation.

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LITERATURE CITED


