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The phylogeny of *Papaver* s. l. (*Papaveraceae*): polyphyly or monophyly?

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Key words: *Papaveraceae, Papaver, Meconopsis, Roemeria, Stylomecon.* – cpDNA, phylogeny, polyphyly, extinction.

Abstract: An RFLP analysis of the chloroplast gene *trn*K of 32 species of the genera *Papaver, Roemeria, Stylomecon*, and *Meconopsis* leads to the following conclusions: (1) Asian *Meconopsis* consists of two distinct clades and is paraphyletic in relation to *Papaver, Roemeria, Stylomecon,* and the W European *Meconopsis cambrica.* (2) Sister group relationships of *Roemeria* to *Papaver* sect. *Argemonidium* and of *Stylomecon* to *Papaver californicum* are well-supported. (3) *Meconopsis cambrica* is nested within *Papaver* (incl. *Roemeria* and *Stylomecon*). The consideration of morphology, geographical distribution and ecology leads to the conclusion that *M. cambrica* is best regarded as a member of *Meconopsis*, and that *Papaver* arose polyphyletically from within a paraphyletic *Meconopsis* in response to Tertiary climatic aridification. – The removal of *M. cambrica* from the taxon matrix is discussed. It is concluded that this experiment illuminates the importance of critical taxon sampling, and shows that at least potentially the assessment of taxa as mono-, para-, or polyphyletic may characterize their present status only and need not reflect their phylogenetic history.

Based on the analysis of both morphological (Kadereit & al. 1994) and molecular (Jork & Kadereit 1995, Schwarzbach & Kadereit 1995) characters the genera *Papaver* L., *Meconopsis* Vig., *Stylomecon* G. Taylor, and *Roemeria* Medik. form a monophyletic clade of mostly Old World distribution within *Papaveraceae* s. str. subfam. *Papaveroideae*.

The geographical distribution of *Papaver, Meconopsis, Roemeria,* and *Stylomecon* is characterized by several wide disjunctions. Thus *Stylomecon* occurs in Western N America, *Papaver* is centred in SW Asia but has representatives of wide arctic-alpine distribution, in Western N America and in S Africa, and the mainly Himalayan *Meconopsis* is represented by one species in W Europe. Because the above patterns of disjunction are also found in several other taxa (Meusel 1969, Burtt 1971), they are not likely to be caused by long distance dispersal. Accordingly, these disjunctions imply that far-reaching extinction must have played a major role in the phylogeny of the group.

Although the lack of fossils belonging to the above four genera does not allow us to investigate the role of extinction in their phylogeny directly, the geographi-

cally aberrant members of *Papaver* and *Meconopsis* as well as *Stylomecon* are suitable candidates for experimental extinction, i.e., omission from the taxon matrix, and the investigation of its effects on the interpretation of the phylogeny of the group.

Besides presenting a phylogenetic analysis of *Papaver* and allies as the primary aim of our study, we will examine briefly the effect of experimental extinction on phylogeny reconstruction.

A restriction site analysis of chloroplast DNA by KADEREIT & SYTSMA (1992) led to the result that *Roemeria* and *Stylomecon* are nested within *Papaver* in its traditional circumscription. Unless the generic concept of *Papaver* is broadened, this genus is not monophyletic, but either paraphyletic or polyphyletic. Several critical taxa, however, were not included in that study. These are *Meconopsis*, which on the basis of the systematic distribution of morphological and phytochemical characters appears to be highly relevant for the complete understanding of the phylogeny of *Papaver*, as well as *P. californicum* A. GRAY (sect. *Californicum* KADEREIT) from California and *P. aculeatum* THUNB. (sect. *Horrida* ELKAN) from S Africa as geographically aberrant species.

Because the phylogeny of *Papaver* apparently cannot be understood without the consideration of *Meconopsis, Roemeria* and *Stylomecon*, a short description of all these genera is appropriate.

Among the above four genera, *Papaver* traditionally has been characterized by the structure of its stigmata. The stigmatic tissue is arranged in sessile radial rays over the placentae, and the stigmatic rays are interconnected and form a more or less strongly lobed conical or flat stigmatic disc. At maturity the capsules in most cases open by pores or valves below this disc. From the study of KADEREIT & SYTSMA (1992) it has become evident that the stigmatic discs in various subgroups of *Papaver* are not likely to be structurally homologous.

Papaver is the largest genus in the entire *Papaveraceae* s. str. by comprising c. 70 species. In the latest survey of the genus available (KADEREIT 1988a), 11 sections had been recognized. Their size and geographical distribution are summarized in Table 1 and will be discussed in detail below. There exists one perennial species of dubious affinities, *P. lisae* N. BUSCH from the Caucasus Mts, which had been assigned sectional status (*P.* sect. *Subscaposa* N. WENDT unpubl.) by WENDT (1976). This taxon (Table 1) will not be considered in detail in the present analysis.

Meconopsis today is considered to contain c. 50 species (TAYLOR 1934, JORK & KADEREIT 1995) distributed primarily in the Himalayan area with one species, *M. cambrica* (L.) VIG., in Western Europe. These are perennial monocarpic or polycarpic herbs with only basal or basal and cauline leaves which grow in forest floor and various alpine habitats. When the genus was founded by VIGUIER (1814) by the combination of *Papaver cambricum* L., it was thought to differ from *Papaver* by having ovaries with a distinct style. In the genus, however, as will be discussed in more detail below, species without style exist (Fig. 5). In the last monograph available of *Meconopsis* (TAYLOR 1934) the genus was divided into two subgenera, three sections, two subsections and ten series.

Roemeria comprises three annual species (BAYTOP 1983, 1989; KADEREIT 1987a). In contrast to *Papaver* it has long linear capsules with sessile stigmata but

Table 1. Latest revision, number of species, geographical distribution and sample species used in this study of the major taxa discussed. For details see text

Taxon	References	No. of spp.	Geographical distribution	Sample species
Meconopsis I	Taylor 1934	2–4	Nepal-Bhutan/NE Burma-NW Yunnan/C China	*M. chelidonifolia, M. villosa*
Meconopsis II	Taylor 1934	ca. 45	SC temperate Asia	*M. betonicifolia, M. grandis, M. simplicifolia M. integrifolia, M. punicea, M. discigera M. dhwojii, M. superba, M. paniculata, M. delavayi, M. horridula, M. aculeata*
Meconopsis cambrica	Taylor 1934	1	W Europe	*M. cambrica*
Stylomecon	Taylor 1930	1	California	*S. heterophylla*
Roemeria	Baytop 1983, 1989 Kadereit 1987a	3	SW to C Asia	*R. hybrida* *R. refracta*
Papaver sect.				
Meconella	Rändel 1974a, 1975, 1977a, b	30	panarctic-alpine	*P. alpinum, P. croceum, P. miyabeanum*
Subscaposa (unpubl.)	Wendt 1976	1	Caucasus	–
Pilosa	Kadereit 1996	1	W Turkey	–
Pseudopilosa	Kadereit 1996	3	SW Asia/NW Africa/Spain	*P. atlanticum*
Meconidium	Kadereit 1993	4	SW Asia	*P. persicum*
Macrantha	Goldblatt 1974	3	SW Asia	*P. orientale*
Horrida	Kadereit 1988b	1	S Africa	*P. aculeatum*
Californicum	Kadereit 1988c	1	California	*P. californicum*
Argemonidium	Kadereit 1986a	4	Medit./SW to C Asia	*P. argemone*
Rhoeadium	Kadereit 1989, Kadereit & Lobin 1990	17	SW Asia/Medit./Europe	*P. rhoeas, P. dubium*
Papaver	Kadereit 1986b	4	SW to C Asia	*P. somniferum*
Carinatae	Kadereit 1986b	1	SW Asia	*P. macrostomum*

without a stigmatic disc (Fig. 5). The genus is distributed in the Mediterranean area and SW to C Asia and can be found in mostly open and somewhat disturbed habitats.

Stylomecon heterophylla (BENTH.) G. TAYLOR, the only species of the genus, is an annual of grassy areas and openings in chaparrals in California and Baja California (CLARK 1993). Because of the presence of a distinct style (Fig. 5) the species originally had been described as *Meconopsis heterophylla* BENTH. but transferred into a new genus by TAYLOR (1930) on account of its annual habit, flower colour, and geographical distribution.

We here want to present the results of an RFLP analysis of a PCR amplified region of the chloroplast genome of altogether 32 species of the Old World clade of subfam. *Papaveroideae*, including 15 species of *Meconopsis* and *Papaver aculeatum* and *P. californicum* as relevant species not included in KADEREIT & SYTSMA's (1992) analysis. The taxa analysed represent all four genera involved, and all sections of *Papaver* except the perennial sects. *Pilosa* PRANTL and *Subscaposa*, and all subgroups of *Meconopsis* recognized by TAYLOR (1934) except ser. *Primulinae* PRAIN.

The results of the present analysis will be discussed on the background of the morphological variation and geographical distribution of all taxa involved.

Material and methods

Thirty-two taxa representing the genera *Papaver, Roemeria, Stylomecon,* and *Meconopsis* were included in our analysis. *Argemone mexicana* L., *Eschscholzia californica* CHAM. and *Pteridophyllum racemosum* SIEBOLD & ZUCC. were chosen as outgroups based on the results of an RFLP analysis of the entire family (unpublished results). The origin of leaf material is listed below in alphabetical order. Voucher specimens, if not stated otherwise, are deposited at the place of cultivation of the species.

Argemone mexicana L.: wild origin unknown, cultivated Botanischer Garten (BG) Univ. Mainz (KJ 91/9); *Eschscholzia californica* CHAM.: wild origin unknown, cultivated BG Univ. Mainz (MJG 141); *Meconopsis aculeata* ROYLE: Kashmir, cultivated J. COBB (no voucher); *M. betonicifolia* FRANCH.: wild origin unknown, cultivated J. COBB (no voucher); *M. cambrica* (L.) VIG.: wild origin unknown, cultivated BG Univ. Mainz (KJ 91/46); *M. chelidonifolia* BUR. & FRANCH.: Blooms Nurseries, cultivated RBG Edinburgh no. 19510280, (KJ 92/4); *M. delavayi* (FRANCH.) FRANCH. ex PRAIN: Sino-British Lijiang Exp. 573, Yunnan, China, cultivated RBG Edinburgh no. 19871597; *M. discigera* PRAIN: MCBEATH, R 2524, Nepal, cultivated RBG Edinburgh no. 19912814; *M. dhwojii* G. TAYLOR ex HAY: wild origin unknown, cultivated RBG Edinburgh no. 19695307 (KJ 92/3); *M. grandis* PRAIN: MCBEATH, KEKE 490, Kambachen, Nepal, cultivated RBG Edinburgh no. 19892241; *M. horridula* HOOK.f. & THOMSON: EFHM, SICH 161, Sichuan, China, cultivated RBG Kew no. 1988-4713; *M. integrifolia* (MAXIM.) FRANCH.: Chengdu Edinburgh Exp. 553, China, cultivated RBG Edinburgh no. 19913425; *M. paniculata* (D. DON) PRAIN: wild origin unknown, cultivated J. COBB (no voucher); *M. punicea* MAXIM.: COX, HUTCHISON & MACDONALD 2587 (1987), Jiuzhaigou-Songpan, Kangali Pass, Sichuan, China, (J. COBB, no voucher); *M. simplicifolia* (D. DON) WALP.: wild origin unknown, cultivated RBG Edinburgh no. 19841866; *M. superba* KING ex PRAIN: wild origin unknown, cultivated RBG Edinburgh no. 19820948; *M. villosa* (HOOK.f.) G. TAYLOR: SINCLAIR & LONG 5574, E of Dochong La, Bhutan, cultivated RBG Edinburgh no. 19841951 (KJ 92/2); *Papaver aculeatum* THUNB.: Australia, cultivated BG Univ. Mainz (AS 95/22); *P. aculeatum* THUNB.: South Africa, cultivated BG Univ. Mainz (AS 95/21); *P. alpinum* L.: wild origin unknown,

cultivated Oregon State Univ., Corvallis (AS 93/91); *P. argemone* L.: wild origin unknown, cultivated BG Univ. Mainz (AS 94/117); *P. atlanticum* (Ball) Coss.: wild origin unknown, cultivated BG Univ. Mainz (KJ 93/7); *P. californicum* A. Gray: wild origin unknown, cultivated BG Univ. Mainz (KJ 92/1); *P. croceum* Ledeb.: wild origin unknown, cultivated BG Univ. Mainz (AS 95/23); *P. dubium* L.: ruderal BG Univ. Mainz (KJ 93/10); *P. macrostomum* Boiss. & Huet ex Boiss.: wild origin unknown, cultivated BG Univ. Mainz (AS 95/20); *P.* cf. *miyabeanum* Tatew.: wild origin unknown, cultivated BG Univ. Mainz (KJ 94/7); *P. orientale* Ledeb.: wild origin unknown, cultivated BG Univ. Mainz (KJ 91/39); *P. persicum* Lindl. subsp. *tauricolum* (Boiss.) Kadereit: wild origin unknown, cultivated BG Univ. Mainz (AS 95/24); *P. rhoeas* L.: wayside Gonsenheim/Mainz, Germany (KJ 93/7); *P. somniferum* L. subsp. *setigerum* (DC.) Corb.: wild origin unknown, cultivated BG Univ. Mainz (AS (94/89); *Pteridophyllum racemosum* Siebold & Zucc.: wild origin unknown, cultivated BG Nikko, Japan (MJG 158); *Roemeria hybrida* (L.) DC.: wild origin unknown, cultivated BG Univ. Mainz (AS 94/87); *R. refracta* DC.: wild origin unknown, cultivated BG Univ. Mainz (AS 94/88); *Stylomecon heterophylla*: (Benth.) G. Taylor: E of Glennville, California, USA (AS 93/8).

Methods of DNA isolation and amplification followed those given in Schwarzbach & Kadereit (1995). Molecular characters were obtained from RFLPs of a PCR amplified chloroplast fragment. A ca. 2500 bp region of the large single copy region encompassing *trn*K and *mat*K was used. The structure of the amplified fragment and the position of the primers are shown in Fig. 1.

The amplification products were digested with 23 restriction enzymes: *Alu*I, *Bsa*JI, *Bst*UI, *Cfo*I, *Dde*I, *Hae*III, *Rsa*I, *Msp*I, *Sau* 96I, *Scr*FI (4 bp recognition sites); *Ase*I, *Bam*HI, *Bcl*I, *Bgl*II, *Bsa*BI, *Bst*BI, *Dra*I, *Eco*RI, *Eco*RV, *Ssp*I, *Xba*I, *Xho*I, *Xmn*I (6-bp recognition sites). DNA fragments were electrophoresed in 1.4% agarose gels and stained with ethidium bromide. Restriction sites were mapped by performing double digests.

The cladistic analysis was carried out with PAUP 3.1.1. (Swofford 1993). Unweighted Fitch parsimony as well as weighted parsimony analyses were conducted. Based on the different probability of restriction site gains and losses site gains were weighted 1.3 times over site losses (Albert & al. 1992).

The heuristic search algorithm, with the MULPARS option and TBR branch swapping, and 50 RANDOM data addition sequences in order to detect potential islands of trees (Maddison 1991) were performed. The strict and majority rule consensus trees from all most parsimonious cladograms and the consistency index (CI) and retention index (RI) were calculated. In order to assess relative support for the different clades, a bootstrap analysis was conducted using 50 replicates of heuristic searches, each replicate consisted of 200 random addition sequences without branch swapping. After the exclusion of *Meconopsis cambrica* from the data matrix the analyses were repeated.

Alternative cladogram topologies were examined with the computer program MacClade 3.0 (Maddison & Maddison 1992).

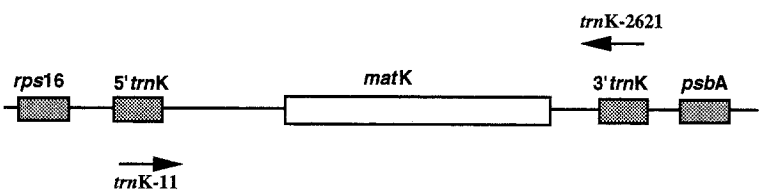


Fig. 1. Map of the *trn*K-gene including the *mat*K intron (2500 bp). Boxed areas represent coding regions. Arrows indicate the position and direction of the primers used in this study

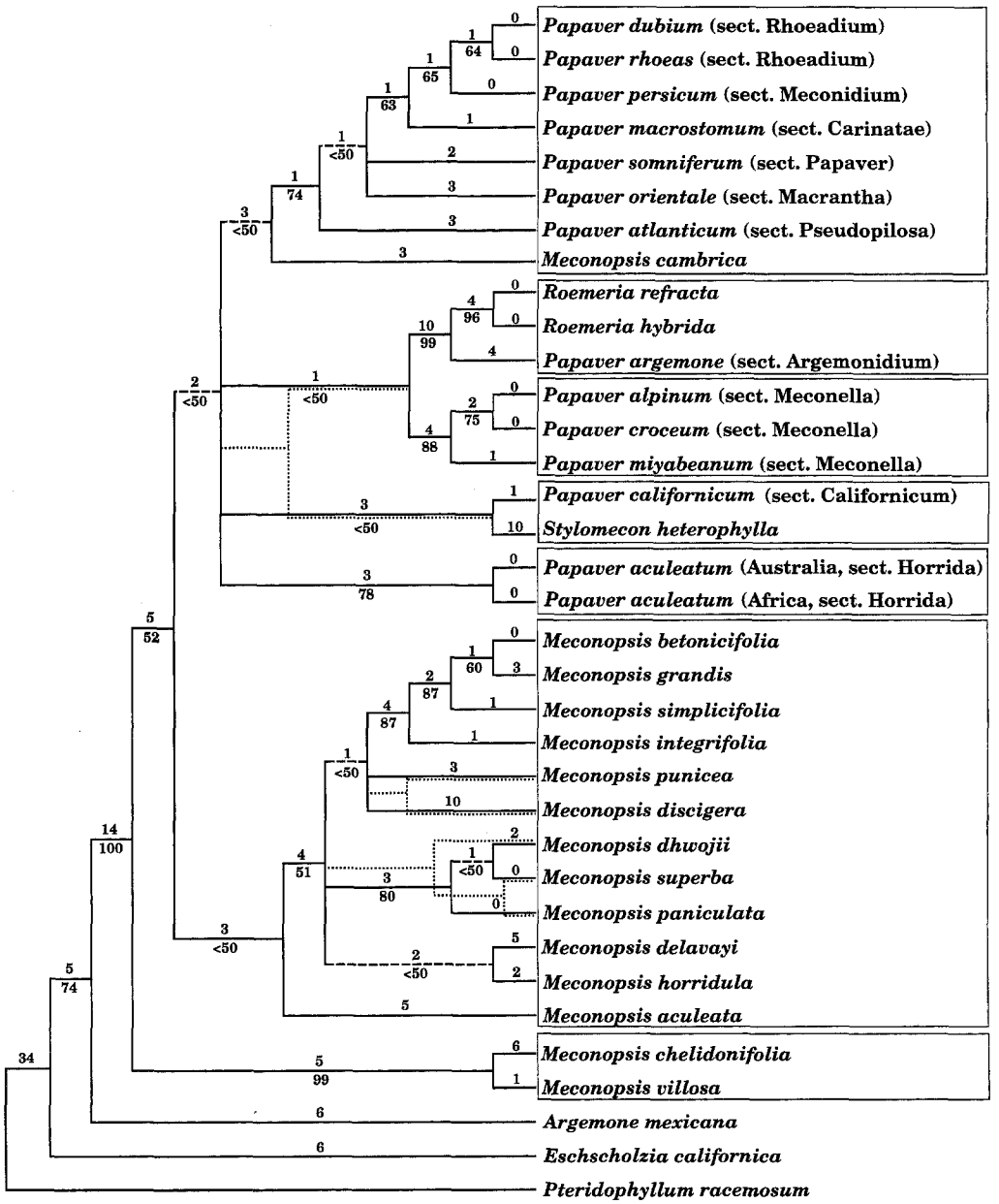


Fig. 2. Majority rule consensus tree of 160 most parsimonious cladograms of 144 steps length obtained from the analysis of the complete taxon matrix. Dashed lines indicate branches which collapse in the strict consensus cladogram, dotted lines indicate branches obtained in the weighted analysis. Figures above branches indicate the number of unambiguous characters supporting that branch, figures below branches indicate bootstrap support

Results

The RFLP analysis yielded 267 characters of which 73 were potentially informative. The Fitch parsimony analysis resulted in 160 most parsimonious cladograms 144 steps long with a consistency index (CI) of 0.507 (excluding non-informative

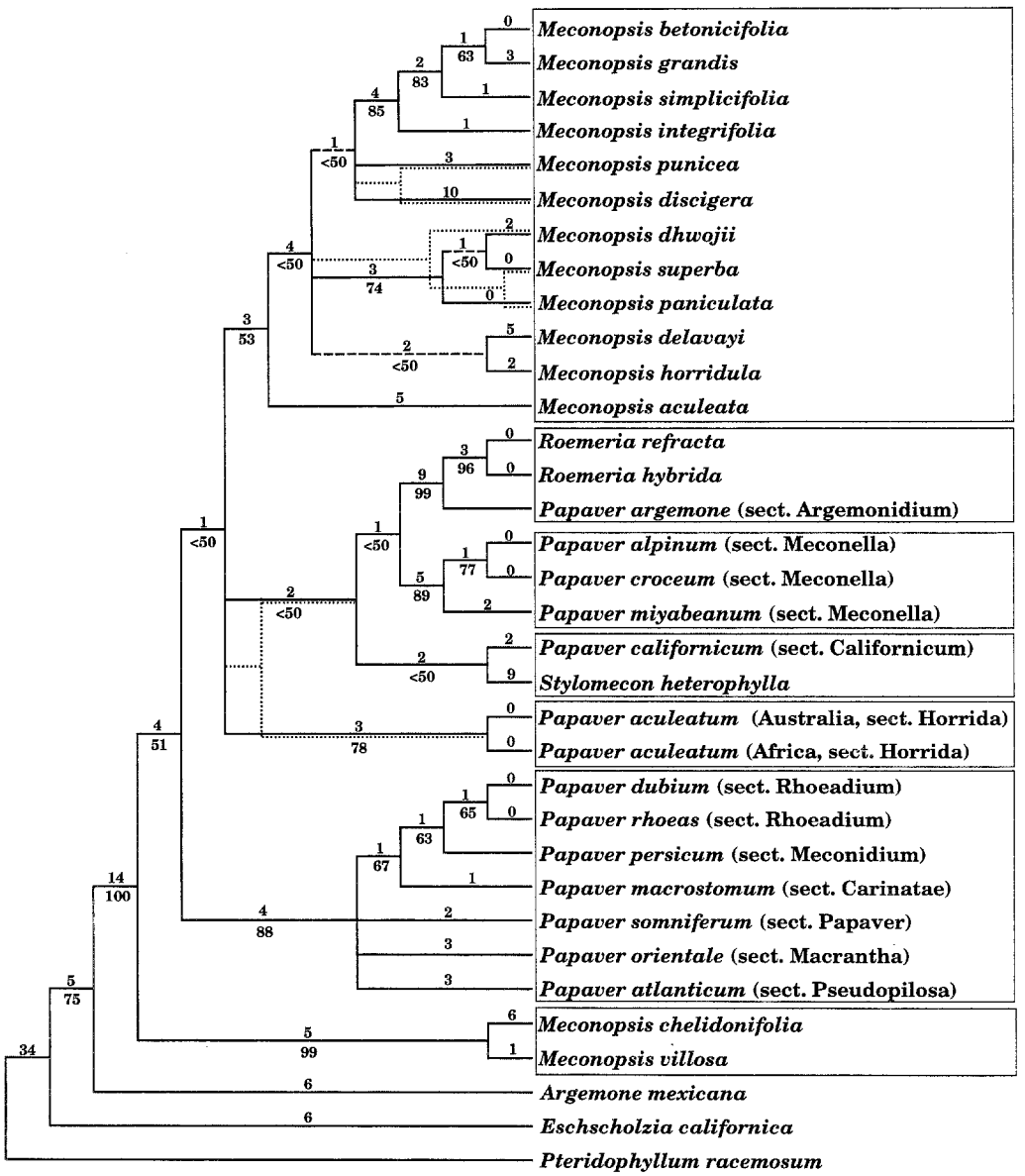


Fig. 3. Majority rule consensus tree of 40 most parsimonious cladograms of 139 steps length obtained from the analysis of the taxon matrix after the exclusion of *Meconopsis cambrica*. Dashed lines indicate branches which collapse in the strict consensus cladogram, dotted lines indicate branches obtained in the weighted analysis. Figures above branches indicate the number of unambiguous characters supporting that branch, figures below branches indicate bootstrap support

characters) and a retention index (RI) of 0.757. The weighted parsimony analysis resulted in a single cladogram 144 steps long after resetting of weights. This cladogram is identical to one of the 160 most parsimonious cladograms of the unweighted analysis. The strict and majority rule consensus trees resulting from the unweighted and weighted analysis are combined in Fig. 2.

After the exclusion of *Meconopsis cambrica* only 40 most parsimonious cladograms with a length of 139 steps, CI of 0.518 and RI of 0.765 were found. After weighting of restriction site gains again a single most parsimonious cladogram was obtained. This is 139 steps long after resetting of weights and identical to one of the 40 most parsimonious cladograms of the unweighted analysis. The strict and majority rule consensus trees resulting from the unweighted and weighted analysis are combined in Fig. 3.

Discussion

Is *Papaver* mono- or polyphyletic? The topology of the consensus tree shown in Fig. 2 allows the following conclusions:

1. Asian *Meconopsis* is not a monophyletic group but paraphyletic in relation to *Papaver* s. l. including *M. cambrica, Stylomecon,* and *Roemeria.*

2. Both *Roemeria* and *Stylomecon* are nested within *Papaver* s. l. *Roemeria* is well-supported sister group to *Papaver* sect. *Argemonidium*, and there is evidence for a sister group relationship of *Stylomecon* to *P. californicum.* The close relationship of *Roemeria* to *P.* sect. *Argemonidium* had been conclusively demonstrated before by KADEREIT & SYTSMA (1992). Both sister group relationships are well-supported by morphological characters (see below).

3. The position of *M. cambrica* within *Papaver* s. l. (incl. *Stylomecon* and *Roemeria*) allows three interpretations. Either (a) *M. cambrica* has arisen from within *Papaver* s. l. (incl. *Stylomecon* and *Roemeria*) in parallel to Asian *Meconopsis* – in this case *Papaver* s. l. (incl. *M. cambrica, Stylomecon,* and *Roemeria*) would be monophyletic – or (b) *M. cambrica* can be regarded as a genuine although disjunct *Meconopsis*. In this second interpretation, which had been adopted already by ENGLER (1879) who also regarded *Stylomecon* as part of this genus, the entire genus *Meconopsis*, and not only its Asian representatives would be paraphyletic in relation to *Papaver* s. l. (incl. *Stylomecon* and *Roemeria*), and *Papaver* s. l. would be polyphyletic. The third alternative is that (c) both *Meconopsis* and *Papaver* s. l. (incl. *Stylomecon* and *Roemeria*) are polyphyletic.

Experimental transfer of *M. cambrica* to the base of *Papaver* s. l. (incl. *Stylomecon* and *Roemeria*), creating a monophyletic *Papaver* s. l. (incl. *Stylomecon* and *Roemeria*) requires three extra steps in the single most parsimonious cladogram obtained in the weighted analysis. Transfers of *M. cambrica* into a sister group relationship to either the basal or the second clade of Asian *Meconopsis* are even longer and require eight and four steps, respectively.

Although bootstrap support of many clades is low (Fig. 2), the paraphyletic status of Asian *Meconopsis* in relation to *Papaver* s. l. (incl. *M. cambrica, Stylomecon,* and *Roemeria*), the sister group relationship of *Roemeria* to *P.* sect. *Argemonidium* and of *Stylomecon* to *P. californicum*, and the position of *M. cambrica* within *Papaver* s. l. (incl. *Stylomecon* and *Roemeria*) are also supported by ITS-nrDNA sequence data (KADEREIT & al., unpubl. results).

(a) Arguments in favour of an interpretation of *Papaver* s. l. (incl. *Stylomecon* and *Roemeria*) as paraphyletic in relation to *M. cambrica*, i.e. in favour of an origin of this species from within *Papaver* s. l. (incl. *Stylomecon* and *Roemeria*) in parallel to Asian *Meconopsis*, are the presence of pseudodorsal veins in the ovary

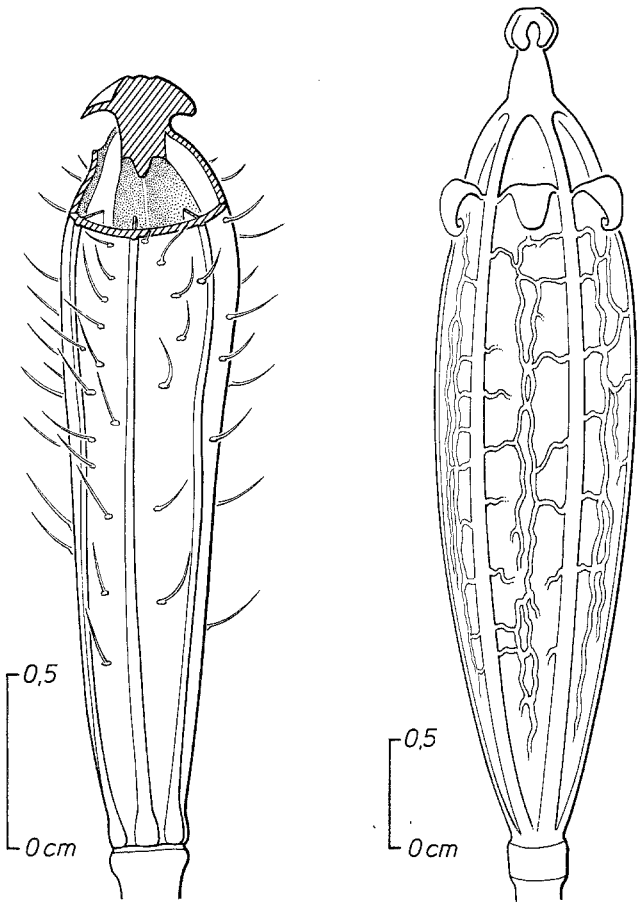


Fig. 4. Schematic drawings of mature capsules of *Papaver argemone* (left) and *Meconopsis cambrica* (right) illustrating the morphology of the stigmatic disc and pseudodorsal capsule venation. For further explanation see text

and capsule (Ernst 1962), and of meconic acid in the latex (Fairbairn & Williamson 1978) in all taxa except Asian *Meconopsis*. *Papaver* sect. *Meconella* contains meconic acid but has no pseudodorsal veins. These two characters might characterize *Papaver* s. l. (incl. *Stylomecon* and *Roemeria*) plus *M. cambrica* as a monophyletic group. A more critical examination of the two characters, however, reveals a far less clear-cut situation.

As regards the presence of meconic acid, only four species of *Meconopsis* were investigated by Fairbairn & Williamson (1978). Although among these meconic acid was clearly present only in *M. cambrica, M. horridula* Hook.f. & Thoms. and *M. regia* G. Taylor contained (unconfirmed) traces, and meconic acid was clearly absent only from *M. napaulensis* DC. In addition, only traces of meconic acid were also found in *P.* sect. *Argemonidium/Roemeria*. This illustrates that the presence of meconic acid in *Meconopsis* might be more widespread than hitherto assumed.

The presence or absence of pseudodorsal veins is a highly complex character. The term pseudodorsal veins has been applied to capsules where the median vein

Table 2. Relevant morphological and other characters of the major taxa discussed. For details see text

Taxon	Meconic acid	Habit	Position of sepal margin lobe	Perianth	Petal colour	Filament shape
Meconopsis I	absent	perennial	left	dimerous	yellow	filiform
Meconopsis II	absent or unknown	perennial and probably partly biennial	left	dimerous/trimerous; partly variable within species	yellow, red, white, violet, blue	filiform or laterally flattened
Meconopsis cambrica	present	perennial	left	dimerous	yellow	filiform
Stylomecon heterophylla	present	annual	left	dimerous	orange	filiform
Roemeria	present	annual	right	dimerous	red, violet	filiform or clavate
Papaver sect.						
Meconella	present	perennial	left	dimerous	yellow, white	filiform
Subscaposa	unknown	perennial	left	dimerous	salmon-coloured	filiform
Pilosa	present	perennial	left	dimerous	salmon-coloured	filiform
Pseudopilosa	present	perennial	left	dimerous	salmon-coloured	filiform
Meconidium	present	biennial	left	dimerous	salmon-coloured	filiform
Macrantha	present	perennial	left	trimerous	red	clavate
Horrida	present	annual	left	dimerous	salmon-coloured	filiform
Californicum	present	annual	left	dimerous	orange	filiform
Argemonidium	present	annual	right	dimerous	red	filiform or clavate
Rhoeadium	present	annual	left	dimerous	red, white	filiform
Papaver	present	annual	left	dimerous	red, pink, white, violet	filiform or clavate
Carinatae	present	annual	left	dimerous	red	filiform

Table 2 (continued)

	Filament colour	Pollen	Pseudodorsal veins (see discussion and Fig. 4)	Capsule indumentum	Stigmatic disc (see discussion and Figs. 4 and 5)
Meconopsis I	pale	tricolpate	absent	absent or present	absent
Meconopsis II	pale or dark	tricolpate, polyporate or inaperturate	absent	absent or present	absent
Meconopsis cambrica	pale	tricolpate	present	absent	absent
Stylomecon heterophylla	dark	tricolpate	present	absent	absent
Roemeria	dark	polyporate	present	absent or present	absent
Papaver sect.					
Meconella	pale	tricolpate or rarely polyporate	absent	present	type 1
Subscaposa	pale	tricolpate	unknown	absent	type 3
Pilosa	pale	tricolpate	present	absent or present	type 3
Pseudopilosa	pale	tricolpate	present	absent	type 3
Meconidium	pale	tricolpate	present	absent or present	type 3
Macrantha	dark	tricolpate	present	absent	type 3
Horrida	pale	tricolpate	present	absent or present	type 3
Californicum	pale	tricolpate	present	absent	type 3
Argemonidium	dark	polyporate	present	present	type 2
Rhoeadium	dark	tricolpate	present	absent	type 3
Papaver	dark or rarely pale	tricolpate	present	absent	type 3
Carinatae	dark	tricolpate	present	absent or present	type 3

of the carpel back does not originate from the carpel base – such veins have been called true dorsal veins – but through the fusion in the carpel median of veins originating from the placental traces (Fig. 4). In the present context it is particularly relevant that although in *Meconopsis* distinct pseudodorsal veins can be found only in *M. cambrica*, which in addition has rudiments of true dorsal veins (BRÜCKNER 1982), the alternative character state, absence of pseudodorsal veins, is polymorphic. Other species of *Meconopsis* may have true dorsal veins or no dorsal veins. In the latter case the carpel backs can be supplied by lateral veins of the main placental traces which, however, do not fuse into compact pseudodorsal veins as in *M. cambrica* (ERNST 1962). This is the situation also found in *P.* sect. *Meconella*. It is conceivable that species with pseudodorsal veins have originated repeatedly from ancestors without dorsal veins but with a network of veins originating from the placental traces.

In summary, both the very insufficient knowledge of the systematic distribution of meconic acid and the structural complexity of carpel venation question the reliability of presence of meconic acid and presence of pseudodorsal veins as phylogenetic markers supporting *Papaver* s. l. (incl. *Stylomecon* and *Roemeria*) plus *M. cambrica* as a monophyletic group, and no other support for such group is known.

(b) Arguments in favour of the interpretation of *M. cambrica* as a true *Meconopsis* are the presence of ovaries and capsules with a distinct style (this character, however, is variable in Asian *Meconopsis*), its perennial polycarpic habit, and similarities particularly to *M. villosa* (HOOK.f.) G. TAYLOR and *M. chelidonifolia* BUR. & FRANCH. as the basalmost clade of Old World *Papaveroideae* in having dimerous flowers, in being diploid, and, above all, in growing in mesic forest floor habitats. *Meconopsis cambrica* and the basalmost clade of *Meconopsis* also share uniformly yellow flowers, but these are caused by different pigments (JORK, unpubl. results).

Because *Stylomecon* has ovaries and capsules with a style, perenniality is widespread in *Papaver*, uniformly yellow flowers with pigments identical to those of *M. cambrica* are found in *P.* sect. *Meconella*, and all sections of *Papaver* s. l. (incl. *Stylomecon* and *Roemeria*) include diploid members, none of the above characters shared between *M. cambrica* and the basal clade of Asian *Meconopsis* can be regarded as apomorphic. Only their similarity in ecology might be a reasonably unambiguous character indicating a close phylogenetic relationship.

On the background of the general trend of climatic aridification during the Tertiary it appears unlikely to us that *Papaver* s. l. (incl. *Stylomecon* and *Roemeria*) which as a genus of always open and mostly arid habitats originated from the mesic *Meconopsis*, secondarily gave rise to *M. cambrica* as an inhabitant again of mesic forest floors. On the basis of these considerations we prefer, as JORK & KADEREIT (1995) did before, to regard *Meconopsis* as a paraphyletic base group of Old World Papaveroideae which gave rise to a polyphyletic *Papaver* s. l. (incl. *Stylomecon* and *Roemeria*). If this interpretation should be correct, the above failure to identify synapomorphies for *Meconopsis* in its present circumscription is inevitable.

It needs to be stressed that our choice between the above two interpretations of the phylogenetic affinities of *M. cambrica* cannot rely on any truly cogent arguments.

(c) All arguments listed above render the interpretation of both *Papaver* and *Meconopsis* as polyphyletic the least parsimonious of all three interpretations.

As further support and elaboration of the above hypothesis of a polyphyletic origin of *Papaver* s. l. (incl. *Stylomecon* and *Roemeria*) we want to characterize its various lineages in detail and try to point at their possible affinities to either certain species or groups of species within *Meconopsis* or to each other.

The relevant morphological characters of all sections of *Papaver, M. cambrica, Roemeria, Stylomecon* and the two major clades of Asian *Meconopsis* are summarized in Table 2. Capsules of the major groups of taxa and such referred to in the following discussion are illustrated in Fig. 5. The characters summarized in Table 2 were not subjected to a formal phylogenetic analysis.

The morphological heterogeneity of *Papaver* s. l. (incl. *Stylomecon* and *Roemeria*). *Papaver* sect. *Meconella*. The perennial *Papaver* sect. *Meconella* is well characterized by its scapose habit, its mostly bristly capsules, and the very deep incision of the stigmatic disc between the stigmatic rays (Fig. 5; type 1 in Table 2), which caused MARKGRAF (1958) to describe the section as essentially lacking a stigmatic disc. Outside the main distributional range in Central, Inner and East Asia, Yakutskaya and Kamchatka, the Beringia area, North Siberia, Scandinavia and Iceland, Greenland, the Canadian Archipelago and North Canada (HANELT 1969, KADEREIT 1988a, RÄNDEL 1974a), representatives of this group also occur in the high mountains of non-arctic Europe (KADEREIT 1990) and in the Rocky Mountains of North America (RÄNDEL 1974b, 1975).

An affinity of *P.* sect. *Meconella* to *Meconopsis* is suggested particularly by one shared character, namely the presence of nudicaulin, a chemically unidentified floral pigment (PRICE & al. 1939, HARBORNE 1967) of *M. cambrica* on the one hand, and of many yellow- and orange-flowering species of *P.* sect. *Meconella* on the other hand. So far no other species of *Meconopsis* with nudicaulin has been found, and the pigment has not been recorded from any other member of the family (JORK, unpubl. results). Also, porate instead of colpate pollen grains can occasionally be found in *P.* sect. *Meconella* (WENDT 1976), and Asian *Meconopsis* (HENDERSON 1965).

The consideration of morphological variation, species diversity, and ploidy level led TOLMACEV (1960), HANELT (1969) and RÄNDEL (1974a) to postulate an Inner Asian origin of the section. The diploid representatives of this group in Asia, *P. croceum* LEDEB. and *P. rubro-aurantiacum* (FISCH. ex DC.) LUNDSTR. (HANELT 1969), are found in North and Central Mongolia, the Altai, and Transbaikalia where they grow on scree slopes, in rock fissures, along streams, in steppe habitats and partly in open larch forests at altitudes between 1800–2300 m. The southernmost representative of this group is the tetraploid *P. croceum* subsp. *chinense* (RGL.) RÄNDEL of Shaanxi and Hubei province in China (RÄNDEL 1974a).

This pattern of geographical distribution probably suggests an affinity of *P.* sect. *Meconella* to *Meconopsis*. Among the species examined of *Meconopsis, M. chelidonifolia* and *M. villosa* can be identified as basal members of the genus (JORK & KADEREIT 1995; Figs. 2 and 3). *Meconopsis chelidonifolia* and its hypothesized close ally *M. oliverana* FRANCH. & PRAIN ex PRAIN (TAYLOR 1934) occupy the easternmost portion of the distributional range of the genus by occurring in

West Sichuan (*M. chelidonifolia*) and East Sichuan and West Hubei (*M. oliverana*), where they grow as scrambling herbs in thickets. Whereas the capsules of *M. chelidonifolia* have a distinct style, this is absent in *M. oliverana* (TAYLOR 1934).

The more or less immediate geographical vicinity of the most primitive members of both *Meconopsis* and *P.* sect. *Meconella* may indeed, in addition to the absence of a style in at least some of the most primitive species of *Meconopsis* (*M. villosa, M. oliverana*), be a further indication of their origin from a common ancestor, or, as interpreted here, the origin of *P.* sect. *Meconella* from within *Meconopsis*. It is not possible, however, to identify a sister group of *P.* sect. *Meconella* within *Meconopsis*. The majority of species of *Meconopsis* on the one hand and *P.* sect. *Meconella* on the other hand could be regarded as alpine/arctic vicariants which might have originated from an ancestor of neither arctic nor alpine distribution during the Pliocene/Pleistocene climatic deterioration. This has been proposed for *P.* sect. *Meconella* and other genera by TOLMACEV (1960).

The experimental transfer of *P.* sect. *Meconella* into a sister group relationship to the basal clade of Asian *Meconopsis* requires seven extra steps in the one most parsimonious cladogram obtained in the weighted analysis. This clearly illustrates that irrespective of the above morphological and geographical considerations such relationship is not supported by the molecular data reported here.

A possible affinity of *P.* sect. *Meconella* to *P.* sect. *Argemonidium/Roemeria* as suggested by Figs. 2 and 3 will be discussed below.

Papaver sect. *Argemonidium/Roemeria*. The four species of the annual *P.* sect. *Argemonidium* are distributed in the Mediterranean area and SW to C Asia and grow in open arid habitats (KADEREIT 1986a, 1988a). Their capsules are bristly, and the stigmatic disc is peculiar in the genus by extending into the capsule as a solid plug (MARKGRAF 1958; Fig. 4; type 2 in Table 2). The disc detaches from the capsules in the course of seed dispersal (BLATTNER & KADEREIT 1991). Except for *P. pavoninum* FISCH. & C. A. MEY. subsp. *pavoninum* the filaments in this group are clavate (KADEREIT 1986a), which is rare in *Papaver*. Different from the above *P.* sect. *Meconella*, and similar to some sections of *Papaver* s. str. (see below), the filaments are of black rather than yellow colour.

The section differs from the remainder of the genus by having the flap-like lobes characteristic of the sepal margin of almost all members of the family on their upper lefthand instead of righthand (dorsal view) margin (ERNST 1962), and by having polyporate instead of 3-colpate pollen grains (ERNST 1962). These two characters also occur in *Roemeria*, of which *R. hybrida* (L.) DC. also shares a peculiar growth form with *P.* sect. *Argemonidium*. After the formation of a basal rosette of leaves these taxa form one very long internode followed by much shorter internodes resulting in a sometimes almost umbellate inflorescence (GÜNTHER 1975). In addition, *R. refracta* DC. like *P.* sect. *Argemonidium* has clavate filaments. These similarities between *P.* sect. *Argemonidium* and *Roemeria* had been noticed by several authors in the past, and have caused GÜNTHER (1975) to combine *Roemeria* at sectional rank into *Papaver*, and MORALES TORRES & al. (1988) to combine species of *P.* sect. *Argemonidium* into *Roemeria*. The obvious relationship between these two groups was confirmed by KADEREIT & SYTSMA (1992) with chloroplast DNA evidence, and fully congruent results were obtained in the present

analysis (Figs. 2 and 3). KADEREIT & SYTSMA (1992) could show that the two species of *Roemeria* included in their study form a clade with the easternmost representative of the group, *P. pavoninum*, which on account of its partly filiform filaments also might be the most primitive species of the section.

As regards the relationship of *P.* sect. *Argemonidium/Roemeria* to *Meconopsis*, this is even less obvious than in the case of the above *P.* sect. *Meconella*. An indication of a relationship between *P.* sect. *Argemonidium/Roemeria* and *Meconopsis* might be a general similarity in capsule morphology particularly between *R. hybrida* and those species of *Meconopsis* without style (Fig. 5; *M. villosa, M. oliverana*), which above had been shown to be basal in *Meconopsis*. The capsules of these two species, however, have no bristles. MARKGRAF (1958) suggested that structures similar to the plug of the stigmatic disc of *P.* sect. *Argemonidium* also occur in *Meconopsis*, but we cannot confirm this observation in the material available to us. Dark filament colouration can be observed in several species of *Meconopsis*.

In the cladograms shown in Figs. 2 and 3 *P.* sect. *Argemonidium/Roemeria* is sister group to *P.* sect. *Meconella*. These three groups share bristly capsules (not *R. refracta* DC.) with deeply sunk stomata (BRÜCKNER 1982), and finely divided leaves in *P.* sect. *Argemonidium, Roemeria* and those representatives of *P.* sect. *Meconella* considered primitive by HANELT (1969) and KADEREIT (1990). Finely divided leaves in combination with a scapose habit as found in *P.* sect. *Meconella* also characterize *M. bella* PRAIN. Finally, porate pollen grains characterize *P.* sect. *Argemonidium/Roemeria*, and can sometimes be found in *P.* sect. *Meconella* (WENDT 1976).

None of the characters shared between *P.* sect. *Argemonidium/Roemeria* and *Meconopsis* or *P.* sect. *Meconella*, respectively, can be regarded as synapomorphies supporting an unambiguous sister group relationship. The sum of morphological evidence, however, on the background of the tree topology discussed, suggests that *P.* sect. *Argemonidium/Roemeria* might well have originated from within *Meconopsis* from an ancestor related to that of *P.* sect. *Meconella*.

Papaver sect. *Californicum/Stylomecon*. The one species of *P.* sect. *Californicum, P. californicum*, is one of two annuals in the genus with yellow filaments. It is distributed in California where it grows in burns, disturbed ground or open woodland (KADEREIT 1988c, CLARK 1993). The capsules of this species have a more or less conical disc (type 3 in Table 2) and open with valves for up to half of their length (Fig. 5). Although *Stylomecon heterophylla* differs from *P. californicum* by having capsules with a distinct style on top of a flat ovary apex (Fig. 5), and by having dark instead of yellow filaments, the sister group relationship between these two W North American taxa found here was not entirely unsuspected. ERNST (1962) pointed out that the two species are virtually identical in leaf shape and other vegetative characters, and indeed *S. heterophylla*, before its transfer into a new genus by TAYLOR (1930), often had been classified as *Papaver lemmonii* GREENE (GREENE 1888).

The relationship of *P. californicum/S. heterophylla* to *Meconopsis* might be indicated by the capsular structure of *S. heterophylla*. Capsules with a style on top of a flat ovary apex as found in this species also occur in, e.g., *M. discigera* PRAIN

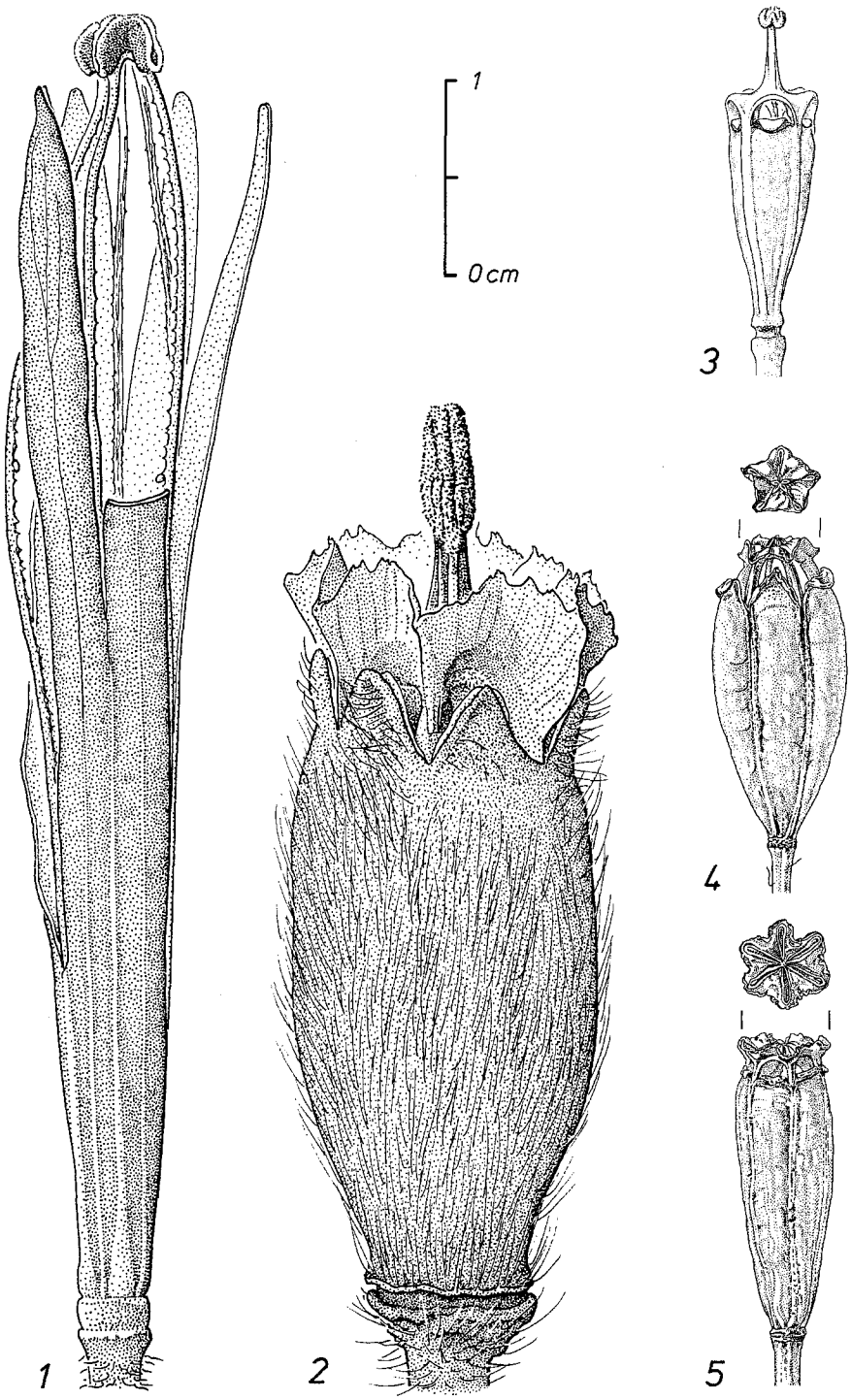
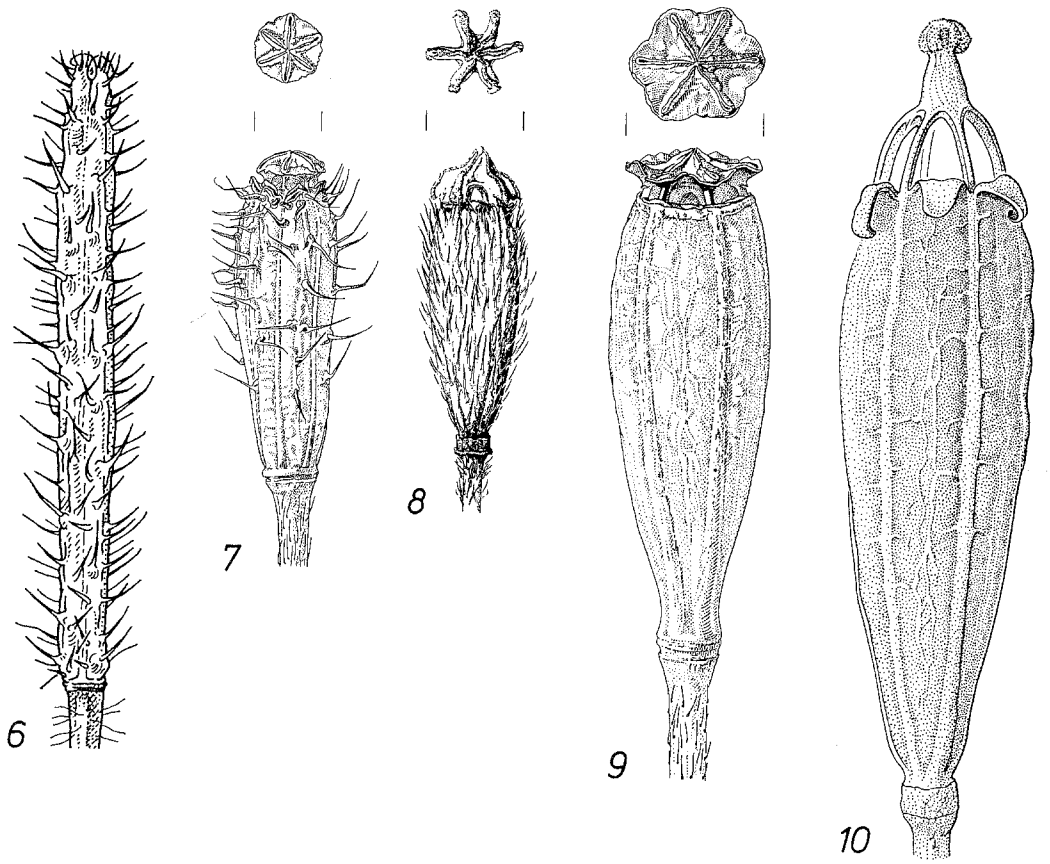


Fig. 5. Mature capsules of *1 Meconopsis villosa, 2 M. discigera, 3 Stylomecon heterophylla, 4 Papaver californicum, 5 P. aculeatum, 6 Roemeria hybrida, 7 Papaver argemone, 8 P. alpinum, 9 P. dubium,* and *10 Meconopsis cambrica*



(TAYLOR 1930; Fig. 5). Although this character, excluding parallelism, is best regarded as a plesiomorphy retained in *S. heterophylla*, it could be interpreted as a reminescence of the origin of *P. californicum/S. heterophylla* from within *Meconopsis*. No morphological or other argument can be found in support of the sister group relationship between *P. californicum/S. heterophylla* and *P.* sect. *Meconella/P.* sect. *Argemonidium/Roemeria* resulting from the weighted analysis (Fig. 2).

Papaver sect. *Horrida*. The only species of *P.* sect. *Horrida*, the annual *P. aculeatum*, is characterized by its indumentum of partly very long (up to 5 mm) and prickly bristles, its yellow filaments, and its long poricidal capsules with a flat stigmatic disc (Fig. 5; type 3 in Table 2). The species is found mainly in disturbed habitats but also on river banks in Eastern S Africa, and in all temperate parts of Australia (KADEREIT 1988b). The identical cpDNA haplotype of S African and Australian material found here certainly provides support for the hypothesis that the Australian material of *P. aculeatum* is of synanthropic origin (KADEREIT 1988b).

Like in the other groups discussed above it is not possible to identify a sister taxon to *P. aculeatum* among extant representatives of *Meconopsis*. Similarities to *P. aculeatum* in indumentum characters can be found, e.g., in *M. horridula* HOOK. f. & THOMSON. This, however, certainly is not an apomorphic character state but either a plesiomorphy or a parallelism. Although not suggested by the molecular

evidence discussed here, the morphology and distribution of *P. aculeatum* and *Papaver* s. str. may indicate their sister group relationship.

More specifically, a relationship of *P. aculeatum* to *P.* sect. *Pilosa* had been suggested by KADEREIT (1988b). This hypothesis, however, finds no clear support in preliminary evidence from ITS-nrDNA sequences (KADEREIT & al., unpubl. results). *Papaver aculeatum* and *Papaver* s. str. have a well-developed stigmatic disc without plug, and their geographical distribution in S Africa and the Mediterranean to C Asian region, respectively, repeats a distributional pattern known from, e.g., *Fumariaceae* tribe *Fumarieae* (LIDÉN 1986, KADEREIT & al. 1995) and several other taxa (BURTT 1971). Such distribution pattern is believed to reflect the existence of a once widespread Tertiary arid flora in Western Eurasia and Africa (MEUSEL 1969, BURTT 1971). This pattern of geographical distribution, however, does not exclude the possibility of an independent origin of *P. aculeatum* and *Papaver* s. str. from within *Meconopsis*. When in the one most parsimonious cladogram obtained from the weighted analysis *P. aculeatum* is transferred to the base of *Papaver* s. str., the resulting topology is three steps longer.

Papaver s. str. The results obtained in the present study and those of KADEREIT & SYTSMA (1992) suggest that *Papaver* s. str. comprises sectt. *Pseudopilosa, Macrantha, Meconidium, Rhoeadium, Papaver,* and *Carinatae*.

Sect. *Pseudopilosa* comprises subscapose perennial herbs with yellow filaments and narrow glabrous capsules with a flat disc, and is distributed in NE Turkey, the Caucasus Mts, and in NW Africa and S Spain where it grows in open arid habitats. Sect. *Pilosa* differs from sect. *Pseudopilosa* by having leafy axes, convolute rather than involute leaf vernation (GÜNTHER 1975), capsules which occasionally are bristly, and in its alkaloid contents (ÖZTEKIN & al. 1985). It is distributed in W Turkey. Preliminary evidence from ITS-nrDNA sequences (KADEREIT & al., unpubl. results) suggests that sect. *Pilosa* may not even form part of *Papaver* s. str., although this is strongly suggested by its morphology. The perennial sect. *Macrantha* has black filaments of clavate shape and rather large and broad glabrous capsules and is distributed in the Caucasus Mts and south of these in E Turkey and NW Iran (GOLDBLATT 1974). Sect. *Meconidium* comprises biennial herbs with either glabrous or bristly capsules with a strongly conical disc opening by valves. The section is distributed in S and E Turkey, the Caucasus Mts, N Iraq and NW Iran, and the Lebanon and Antilebanon Mts (KADEREIT 1993). The remaining three sections comprise annuals (except for one species, see below) with mostly black filaments. The 17 species of sect. *Rhoeadium* have a mostly flat stigmatic disc (Fig. 5) and upper leaves which are sessile but not amplexicaulous. Perenniality in this group is found in *P. gorgoneum* COUT. from the Cape Verde Islands (KADEREIT & LOBIN 1990). The centre of diversity of the section is SW Asia and the Aegean area, and only few species can be found in the C or W Mediterranean area or on the Balkan or further East in the W Himalaya (KADEREIT 1989). Particularly *P. rhoeas* L. and *P. dubium* L. have become widespread through human activity (KADEREIT 1990). The only species of sect. *Carinatae, P. macrostomum* BOISS. & HUET ex BOISS. (KADEREIT 1987b) is distinguished by shedding the stigmatic disc at capsule maturity. The capsules of *P. macrostomum* sometimes are bristly. It can be found in W Iran, NE Iraq, Turkey, and the Caucasus Mts. Finally, sect. *Papaver*,

containing the opium poppy *P. somniferum* L., is characterized by amplexicaulous upper stem leaves. Filaments in this group are not always black. The section is distributed in the W to C Mediterranean area, SW Turkey and Cyprus, the Syrian desert, Sinai, W and S Iran, W Pakistan, and Afghanistan. According to the results of KADEREIT & SYTSMA (1992) sect. *Papaver* may not be monophyletic. It seems possible that sect. *Papaver* needs to be reduced to its type species, *P. somniferum* L. (RECKIN 1973, NOVAK & PREININGER 1980, PREININGER & al. 1981), and that the remaining three species, *P. glaucum* BOISS. & HAUSSKN., *P. decaisnei* HOCHST. & STEUD. ex ELKAN, and *P. gracile* BOISS. group with sect. *Carinatae* or sect. *Rhoeadium*.

It is not possible to find a morphological synapomorphy for *Papaver* s. str. Although this group of sections can clearly be differentiated from the above sectt. *Meconella* and *Argemonidium* on account of the structure of the capsular disc (Fig. 5; type 3 in Table 2), which is not deeply incised (sect. *Meconella*) and has no plug (sect. *Argemonidium*), the discs found in *P. californicum* and *P. aculeatum* are identical to those of *Papaver* s. str. Whereas all annuals of *Papaver* s. str. have mostly black filaments, *P. californicum* and *P. aculeatum*, which also are annual, have yellow filaments. As discussed above, *P.* sect. *Horrida* might well be sister group to *Papaver* s. str. Although the stigmatic disc of *P. californicum* by itself cannot be distinguished structurally from that of *Papaver* s. str. and *P. aculeatum*, the capsules of *P. californicum* are distinctly valvate, whereas those of *Papaver* s. str. and *P. aculeatum* are porate. Only *P.* sect. *Meconidium* has clearly valvate capsules. In conjunction with the sister group relationship of *P. californicum* to *Stylomecon* this may suggest that the capsular structure of *P. californicum* arose in parallel to that of *Papaver* s. str./*P. aculeatum*. When in the one most parsimonious cladogram obtained from the weighted analysis *P. californicum*/*S. heterophylla* are transferred to the base of *Papaver* s. str. plus *P. aculeatum*, the resulting cladogram is three steps longer than the unmanipulated cladogram, and no steps are added in comparison to the transfer of *P. aculeatum* alone (see above). Such a topology would implicate that the type of stigmatic disc found in *P.* s. str., *P. aculeatum* and *P. californicum* would have arisen only once.

The small sample of species of *Papaver* s. str. included in the present analysis allows only a very limited discussion of sectional affinities in this group. The topologies of Figs. 2 and 3, however, do not support the conclusion reached by KADEREIT & SYTSMA (1992) that the perennial and biennial sections (sects. *Pseudopilosa, Macrantha, Meconidium*) on the one hand, and the annual sections (sectt. *Rhoeadium, Papaver, Carinatae*) on the other hand form two monophyletic groups. Apart from the basal position of the perennial sect. *Pseudopilosa* [*P. atlanticum* (BALL) COSS.], the perennial sect. *Macrantha* (*P. orientale* L.) and the biennial sect. *Meconidium* [*P. persicum* LINDL. subsp. *tauricolum* (BOISS.) KADEREIT] are scattered among the annual sections (Figs. 2 and 3).

If *Papaver* s. str. should have originated from within *Meconopsis*, it is not possible to identify a sister taxon within that genus. Although in Fig. 2 *M. cambrica* is sister group to *Papaver* s. str., nothing in its morphology suggests a close relationship. Provided that the perennial and yellow-filamented sect. *Pseudopilosa* is basal in *Papaver* s. str., as found here (Fig. 2), the morphological gap between *Papaver* s. str. and *Meconopsis* would consist mainly in capsule characters. The

yellow filament colouration found in basal members of both groups is a plesiomorphic character state (KADEREIT & al. 1994).

The morphological diversity of *Papaver* s. l. (incl. *Stylomecon* and *Roemeria*) in our opinion supports the hypothesis based on molecular characters that this genus in its traditional circumscription is not a monophyletic but rather a polyphyletic group. Because no single sister group relationship among *P.* sect. *Meconella, P.* sect. *Argemonidium/Roemeria, P. californicum/Stylomecon, P.* sect. *Horrida* and *Papaver* s. str. can be adequately resolved (some support exists for the sister group relationship between sect. *Meconella* and sect. *Argemonidium/Roemeria*), *Papaver* s. l. (incl. *Roemeria/Stylomecon*) may well consist of up to five independent lineages. If, as discussed in detail above, a sister group relationship between *P.* sect. *Meconella* and *P.* sect. *Argemonidium/Roemeria* on the one hand, and between *Papaver* s. str., *P.* sect. *Horrida* and *P. californicum/S. heterophylla* on the other hand is accepted, two independent lineages need to be recognized. All this leaves sectt. *Pilosa* and *Subscaposa* unconsidered.

These two possibilities represent extreme interpretations. Any combination of the five major groups into three or four lineages is also conceivable.

Our failure to identify obvious sister taxa of the various lineages of *Papaver* s. l. (incl. *Stylomecon* and *Roemeria*) within *Meconopsis*, which we interpret as a paraphyletic base group, becomes understandable on the background of the evolutionary scenario postulated by JORK & KADEREIT (1995). If indeed *Papaver* s. l. (incl. *Stylomecon* and *Roemeria*) should have originated from within a once widespread *Meconopsis* during the Tertiary aridification of the Laurasian climate, one cannot expect to find the sister taxa of these various lineages among extant *Meconopsis*. In view of the occurrence of *Meconopsis* in W Europe and the Himalayan area, and the distribution of much of *Papaver* s. l./*Roemeria* in this gap (not *P.* sect. *Meconella, P. californicum/Stylomecon*) it seems reasonable to assume that the taxa linking extant *Meconopsis* with extant *Papaver* s. l. (incl. *Stylomecon* and *Roemeria*) will have become extinct. Accordingly, phylogenetic reconstruction in the Old World *Papaveroideae* is hampered mainly by far-reaching extinction.

It is obvious both from the molecular data presented here and from a structural point of view that the stigmatic disc as the one character defining *Papaver* in its traditional circumscription has arisen repeatedly. It seems possible that the stigmatic disc can be interpreted in relation to the breeding system of the plants. Whereas in *Papaver* s. l. the anthers are positioned above the stigmatic disc in the majority of species, facilitating autogamy, the presence of a distinct style does not allow self-pollination. When combined with the absence of self-incompatibility, many species of *Papaver* are highly efficient self-fertilizers. This ability might have been important in the evolution of both those lines of *Papaver* which colonize open ground in arid climates (at least the annual sections of *Papaver* s. str., *P. aculeatum, P.* sect. *Argemonidium, P. californicum*), and in the largely arctic-alpine *P.* sect. *Meconella* which may suffer from scarcity of pollinators. As far as investigated, self-compatibility and self-pollination are widespread in all sections of *Papaver*.

If *Meconopsis cambrica* were extinct. Whereas it is a mere hypothesis that our ability to reconstruct the phylogeny of *Papaver* is severely hampered by far-reach-

ing extinction, it is possible to experimentally examine the effect of extinction by removing *M. cambrica* from the taxon set. As has become evident above, the interpretation of the phylogenetic affinities of this species creates most problems for the understanding of *Papaver*. Because the distribution of *M. cambrica* in W Europe is very scattered and the species as a rare inhabitant of mesic forest floor habitats will only have just survived the climatic cycles of the Quaternary, it is not an unlikely scenario to let *M. cambrica* go extinct experimentally.

When applying Fitch or weighted parsimony to a taxon matrix without *M. cambrica*, instead of obtaining a monophyletic *Papaver* s. l. (incl. *Stylomecon* and *Roemeria*) as might have been expected from the topology of Fig. 2, *Papaver* is polyphyletic when Asian *Meconopsis* is regarded as paraphyletic (Fig. 3). In addition, sister group relationships within *Papaver* s. l. (incl. *Stylomecon* and *Roemeria*) are somewhat different (Fig. 3).

This simple experiment demonstrates an important point. The effect of the removal of a given taxon need not simply be a gap in an otherwise unchanged topology but may have more complex and unpredictable consequences. This also highlights the importance of critical taxon sampling.

If *Papaver* s. l. (incl. *Stylomecon* and *Roemeria*) had been resolved as monophyletic after the experimental extinction of *M. cambrica*, we would have to conclude that our concepts of monophyly, paraphyly and polyphyly are primarily atemporal because in this case a taxon of probably polyphyletic origin would have appeared to be monophyletic.

The observation of an altered topology after the exclusion of one taxon (with the reservation that the original topology has weak bootstrap support in many parts) is in full accordance with the findings of GAUTHIER & al. (1988) and DONOGHUE & al. (1989) in their discussions of the importance of the incorporation of fossils in phylogeny reconstruction, with those of WHEELER (1992) and LAMBOY (1994) who observed a dramatic effect of taxon sampling on cladogram accuracy in a simulation study, and also with those of LECOINTRE & al. (1993) who examined the effect of species exclusion on phylogenetic inference in Gnathostomes.

When examining the distribution of morphological characters, *M. cambrica* might qualify as a "plesiomorphic sister group". GAUTHIER & al. (1988) and DONOGUE & al. (1989) pointed out that the most profound topological changes in a cladogram might be caused by such plesiomorphic sister groups, "where the added taxon is united with one of the terminal taxa (...) by the derived state of a new character, but possesses the ancestral condition of every other character in the data set". Morphologically, *M. cambrica* meets this definition by sharing pseudodorsal veins and meconic acid with much of *Papaver* s. l. (incl. *Stylomecon* and *Roemeria*), but shares most other characters with the basal Asian *Meconopsis* (nine of 11 characters; see Table 2).

It seems worthwhile to explore further why in some instances but not in others the exclusion of taxa from a data set results in topological changes. This will require the examination of both the properties of the excluded taxa and the overall structure of the entire data set.

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