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THE GENUS PAPAVER L. IN THE MEDITERRANEAN AREA

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Abstract

In the MED-CHECKLIST area, *Papaver* is represented by 32 species with 51 subspecies. After a brief discussion of the phylogeny of this polyphyletic genus, its morphological, karyological, phytochemical and ecological differentiation is described, and patterns of geographical distribution are analyzed. *Papaver* is distributed very unevenly in the Mediterranean area, and only a minority of taxa are W Mediterranean. The consideration of the phylogeny and general distribution of the genus leads to the conclusion that *Papaver* is best regarded as part of the Turano-Anatolian genetic element of the Mediterranean flora, and up to now has failed to significantly expand to the West.

Introduction

In the countries covered by MED-CHECKLIST (GREUTER & al., 1989), the genus *Papaver* L. is represented by 32 of its altogether c. 70 species (GOLDBLATT, 1974; KADEREIT, 1986a, b, 1987a, 1988a, 1990, 1993a; KADEREIT in press; KADEREIT & al., in press) (see Appendix). These 32 species contain 51 subspecies and belong to nine of the 12 sections recognized in the genus (KADEREIT & al., in press). The three sections not represented occur in California (*P.* sect. *Californicum* Kadereit; KADEREIT 1988b), S Africa (*P.* sect. *Horrida* Elkan; KADEREIT, 1988c), and the Caucasus Mts. (*P.* sect. *Subscaposa* Wendt ined.; WENDT, 1976), and the vast majority of the species not found in the Mediterranean are the arctic representatives of the arctic-alpine sect. *Meconella* Spach.

It is the aim of the present paper to briefly summarize the phylogeny of *Papaver,* to describe its differentiation in terms of morphology, karyology, phytochemistry and ecology, and to describe and analyze its geographical distribution in the Mediterranean area.

The phylogeny of *Papaver* s.l.

Papaver has long been recognized to be part of subf. Papaveroideae (ERNST, 1962; KADEREIT, 1993b; KADEREIT & al., 1994) which in the family is distinguished by the possession of a polycarpellate gynoecium. Within subf. Papaveroideae, *Papaver* together with *Meconopsis* Vig., *Roemeria* Medik. and *Stylomecon* G. Taylor forms a monophyletic group of mostly Old World distribution (JORK & KADEREIT, 1995; SCHWARZBACH & KADEREIT, 1995). The analysis of these genera with various molecular characters has clearly shown that *Papaver* in its present circumscription is not monophyletic but rather polyphyletic (KADEREIT & SYTSMA, 1992; JORK &

KADEREIT, 1995; KADEREIT & al., in press). A monophyletic *Papaver* s.str. must be restricted to the perennial sects. *Pseudopilosa* M. Popov ex Günther and *Macrantha* Elkan, the biennial sect. *Meconidium* Spach, and the annual sects. *Papaver, Carinatae* Fedde and *Rhoeadium* Spach. Sectional limits between the latter three groups are unclear, and they probably need to be combined into one monophyletic group (KADEREIT & SYTSMA, 1992; KADEREIT & al., in press). The phylogenetic affinities of the perennial sect. *Meconella* are unclear, as are those of the perennial sect. *Pilosa* Prantl and the annual sect. *Horrida*. The annual sects. *Argemonidium* Spach and *Californicum* have their closest relatives in *Roemeria* and *Stylomecon*, respectively. Although no molecular data are available for sect. *Subscaposa* WENDT ined., the morphology of this monotypic group suggests that it is not part of *Papaver* s.str. It has been hypothesized that *Papaver* s.l. incl. *Roemeria* and *Stylomecon* arose polyphyletically from a paraphyletic *Meconopsis* as the result of Tertiary climatic aridification (JORK & KADEREIT, 1995; KADEREIT, & al. in press). Whereas the most primitive representatives of *Meconopsis* are distributed in humid forest floor habitats, and this genus of some 50 species shows a disjunction between the Himalayan area and W Europe, *Papaver* (except for the arctic-alpine sect. *Meconella*), *Roemeria* and *Stylomecon* are found in more or less arid places. Irrespective of its polyphyletic nature, I here want to consider *Papaver* in its traditional circumscription.

The diversification of *Papaver* s.l. in the Mediterranean area

Morphological diversification of *Papaver* s.l. in the Mediterranean area is most conspicuous in growth habit. Seven of the 32 species are perennials and represent all perennial sections of the genus (sects. *Meconella, Pilosa, Pseudopilosa, Macrantha*) except for sect. *Subscaposa*, the biennial sect. *Meconidium* is represented by all its four species, and the remaining 21 species are annuals representing four (sects. *Argemonidium, Papaver, Carinatae, Rhoeadium*) of the currently accepted six annual sections (see Appendix).

As regards flower morphology, sect. *Macrantha* is exceptional in having 3-merous instead of 2-merous flowers. Beyond that, flowers vary considerably in size and colour. Flowers can be white, yellow, pink, violet, orange or variously red, and there exists variation in the presence or absence, size, colour and shape of spots at the base of the petals. According to MCNAUGHTON & HARPER (1960) and SNITZER-PASTERNAK & GALIL (1970) the ability of pollinators to distinguish between closely related taxa is very limited, but more distantly related taxa can be discriminated. The stamens mostly have filiform filaments, but clavate filaments can be found in sects. *Macrantha, Argemonidium* and in part of sect. *Papaver.* Filament colouration varies between light and dark (KADEREIT, 1988d). Occasionally the anthers have apical appendages (KADEREIT, 1986b, 1987a) of unknown function but apparently phylogenetic significance (KADEREIT & SYTSMA, 1992). Substantial variation can be found in capsule morphology. Within *Papaver* s.str. this variation is largely limited to capsule size, form and indumentum. There is also some variation in pore size, and *P. macrostomum* Boiss. & Huet ex Boiss. is exceptional in shedding the entire stigmatic disc at capsule maturity (KADEREIT, 1987a). Capsule morphology is very divergent in two of those sections

which are not part of *Papaver* s.str. In sect. *Argemonidium* the stigmatic disc continues into the capsule as a solid plug and is shed entirely late in the season, and in sect. *Meconella* the stigmatic disc is virtually absent and consists largely of the stigmatic rays (MARKGRAF, 1958). In an experimental comparison of different species of sects. *Rhoeadium* and *Argemonidium* it could be shown that capsule morphology and capsule shape strongly influence the pattern of seed dispersal (KADEREIT & LEINS, 1988; BLATTNER & KADEREIT, 1991). *Papaver curviscapum* Nab. of sect. *Meconidium* is most unusual by burying its capsules in crevices or holes of the vertical cliffs where it grows (KADEREIT, 1993a). Seeds in *Papaver* s.l. are uniformly reniform, and limited variation is found in seed size and surface structure (KADEREIT, 1986a; KADEREIT, 1988a).

As far as chromosome numbers are known, karyological variation by and large is limited to the annual sections. The perennial and biennial sects. *Meconella* (KADEREIT, 1990), *Pilosa* (WENDT, 1976; NOVÁK, 1983), *Pseudopilosa* (MAIRE, 1964) and *Meconidium* (FEDEROV, 1969, NOVÁK, 1982) and the monotypic annual sect. *Carinatae* (KADEREIT, 1987a) in the Mediterranean area contain only diploids. Polyploid series comprising diploids, tetraploids and hexaploids are found in sects. *Macrantha* (GOLDBLATT, 1974), *Argemonidium* (KADEREIT, 1986a), *Papaver* (KADEREIT, 1986b) and *Rhoeadium* (KADEREIT, 1988a). Dysploid reduction of the chromosome base number from x = 7 to x = 6 is known from sects. *Pseudopilosa* (MAIRE, 1964), *Meconidium* (FEDEROV, 1969) and *Argemonidium* (KADEREIT, 1986a). *Papaver somniferum* L. has been suggested to be a fertile triploid (KADEREIT, 1986c, 1987b, 1991).

It should be obvious that *Papaver* shows substantial differentiation in terms of alkaloid chemistry (SANTAVY, 1970, 1979).

All species of *Papaver* appear to grow in open and variously disturbed habitats. Accordingly, ecological differentiation most probably is very limited, although *P. alpinum* L. of sect. *Meconella* is unusual in being found exclusively on mobile alpine scree slopes. Edaphic differentiation has been claimed to exist in Israel (SNITZER-PASTERNAK & GALIL, 1970), but the frequent co-occurrence both of species in their natural range and of synanthropic species in Europe (MCNAUGHTON & HARPER, 1960) testifies to their very limited ecological differentiation. There exists, however, a conspicuous altitudinal differentiation between the perennials and biennials on the one hand, and the annuals on the other hand. Whereas the perennials and biennials almost all are mountain taxa which mostly grow above 1000 m altitude, the annuals mostly are lowland taxa.

Patterns of geographical distribution

Within sections, the predominant pattern of geographical distribution of species and subspecies, with the exception of synanthropically widespread taxa, is one of parapatry or allopatry. Such distribution is found in sects. *Meconella, Pilosa, Argemonidium, Pseudopilosa* and *Papaver.* In sect. *Rhoeadium* some overlap occurs between more distantly related species, and overlapping distribution is also found in sects. *Macrantha* and *Meconidium.* The generally found parapatric or allopatric distribution in many cases

perhaps is best interpreted to reflect comparatively young geological age of the taxa involved. The differentiation of, e.g., *P. pilosum* Sibth. & Sm. of sect. *Pilosa* into five subspecies limited to distinct mountain ranges in W Anatolia might be the result of glacial or postglacial habitat fragmentation, and among the annual species parapatric distribution of close relatives may indicate parapatric differentiation of more widely distributed progenitors in the recent past. Examples for this are the subspecies of *P. dubium* L. and *P. argemone* L. or the complex of species related to *P. rhoeas* L.

Overlap between sections is substantial (KADEREIT, 1988d). From this conclusion the annual sects. *Papaver, Carinatae* and *Rhoeadium,* which by and large have allopatric ranges, must be excepted. As already indicated above, sectional limits in this group are unclear, and their distribution may be another indicator of their very close phylogenetic relationship.

Of all sections of *Papaver* s.l. present in the Mediterranean area, only sects. *Meconella* and *Pseudopilosa* show wide geographical disjunctions. In the case of the alpine *P. alpinum* L. of sect. *Meconella* the disjunctions between the various European mountain ranges will be the result of postglacial warming and thus of young age. The distribution of sect. *Pseudopilosa,* however, which is found in NW Africa and S Spain (*P. atlanticum* (Ball) Coss., *P. rupifragum* Boiss. & Reuter) and NE Turkey and the Caucasus Mts. (*P. lateritium* K. Koch; KADEREIT, in press), exemplies a group of Mediterranean/Irano-Turanian disjuncts recognized by DAVIS & HEDGE (1971). According to these authors, such distributional pattern is found mainly in groups centred in the Irano-Turanian area, and is likely to be of Tertiary origin. If this interpretation should be correct, it seems justified to assume that at least part of the sectional differentiation of *Papaver,* which above had been postulated to be of Tertiary origin, also is of Tertiary age.

As a whole, *Papaver* has an obvious centre of diversity in SW Asia and the E Mediterranean. Only very few taxa can be regarded as W Mediterranean. These are *P. atlanticum* and *P. rupifragum* of sect. *Pseudopilosa, P. somniferum* subsp. *setigerum* (DC.) Arcangeli of sect. *Papaver,* and *P. pinnatifidum* Moris of sect. *Rhoeadium.*

Two possible explanations for this pattern can be offered. 1, *Papaver* once was more evenly distributed in the Mediterranean area. The Quaternary climatic changes which affected the W Mediterranean more than the E Mediterranean and SW Asia (ZOHARY, 1973; LANG, 1994) resulted in the unbalanced diversity seen today. 2, *Papaver* basically is an Irano-Turanian genus. The truly Mediterranean representatives, mostly annuals, probably are of recent origin, and up to now have failed to expand to the West.

In order to decide between these two alternatives, it is necessary to take into account both the extant distribution of the genus and its phylogeny as far as known. The presence of *P. atlanticum* and *P. rupifragum* of sect. *Pseudopilosa* in the W Mediterranean, this geographical range above had been interpreted to be of Tertiary age, can be taken to indicate that Quaternary survival was possible in the W Mediterranean. The phylogenetic analysis of *Papaver* s.l. (KADEREIT & al., in press) has clearly shown that within *Papaver* s.str. sect. *Pseudopilosa* occupies a basal position, and that the annual sections (*Papaver, Carinatae, Rhoeadium*) are more closely related to the perennial sect. *Macrantha* and the biennial sect. *Meconidium.* Both these latter sections are exclusively E Mediterranean/SW Asian in distribution. These two

arguments, the distribution of sect. *Pseudopilosa* and the phylogenetic affinities of the annual sections, clearly favour the latter of the above two hypotheses.

In conclusion, *Papaver* in the Mediterranean area must be regarded as part of the Turano-Anatolian genetic element (ZOHARY, 1973) of the Mediterranean flora.

Appendix

Systematic position and geographical distribution of *Papaver* in the MED-CHECKLIST area. Numbers in brackets after sectional names indicate the total number of species/species in the MED-CHECKLIST area.

Papaver s.l.

sect. *Meconella* Spach (c. 30/1)

P. alpinum L.	
subsp. *lapeyrousianum* (Guterm.)Kadereit	France, Spain
subsp. *rhaeticum* (Leresche)Markgraf	France, Italy
subsp. *kerneri* (Hayek)Fedde	Bosnia-Hercegovina, Bulgaria, Slovenia, Yugoslavia (Montenegro)
subsp. *ernesti-mayeri* Markgraf	Italy

sect. *Pilosa* Prantl (1/1)

P. pilosum Sibth. & Sm.	
subsp. *pilosum*	Anatolia
subsp. *strictum* (Boiss. & Balansa) Wendt ex Kadereit	Anatolia
subsp. *spicatum* (Boiss. & Balansa) Wendt ex KADEREIT	Anatolia
subsp. *glabrisepalum* Kadereit	Anatolia
subsp. *sparsipilosum* (BOISS.)KADEREIT	Anatolia

sect. *Argemonidium* Spach (4/3)

P. hybridum L.	widespread
P. apulum TEN.	Bosnia-Hercegovina, Greece, Italy, Sicily
P. argemone L.	
subsp. *argemone*	France, Italy, Portugal, Spain
subsp. *nigrotinctum* (Fedde)Kadereit	Aegean, Anatolia, Greece
subsp. *davisii* Kadereit	Anatolia
subsp. *meiklei* Kadereit	Cyprus
subsp. *belangeri* Taht.	Anatolia, Israel, Jordan, Syria

Papaver s.str.

sect. *Pseudopilosa* M. Popov ex Günther (3/3)

P. lateritium K. Koch	
subsp. *lateritium*	Anatolia
subsp. *monanthum* (Trautv.)Kadereit	Anatolia
P. rupifragum Boiss. & Reuter	Morocco, Spain
P. atlanticum (Ball)Coss.	
subsp. *atlanticum*	Morocco
subsp. *mesatlanticum* (Maire)Kadereit	Morocco

sect. *Macrantha* Elkan (3/2)

P. orientale L.	Anatolia
P. pseudo-orientale (Fedde)Medw.	Anatolia

sect. *Meconidium* SPACH (4/4)

P. armeniacum (L.)DC.	
subsp. *armeniacum*	Anatolia
P. libanoticum Boiss.	
subsp. *libanoticum*	Lebanon
subsp. *polychaetum* (Schott & Kotschy ex Boiss.) KADEREIT	Anatolia
P. persicum Lindl.	
subsp. *persicum*	Anatolia
subsp. *tauricolum* (Boiss.)Kadereit	Anatolia
subsp. *microcarpum* (Boiss.)Kadereit	Anatolia
P. curviscapum Nab.	Anatolia

sect. *Papaver* (4/4)

P. somniferum L.	
subsp. *somniferum*	widespread as crop and ruderal
subsp. *setigerum* (DC.) Arcangeli	Algeria, Balearic Islands, Corsica, Cyprus, France, Greece, Italy, Morocco, Sardinia, Sicily, Spain, Tunisia
P. gracile Boiss.	Aegean, Anatolia, Cyprus
P. glaucum Boiss. & Hausskn.	Anatolia, Syria
P. decaisnei Hochst. & Steudel ex Elkan	Egypt, Sinai

sect. *Carinatae* Fedde (1/1)

P. macrostomum Boiss. & Huet ex Boiss.	Anatolia

sect. *Rhoeadium* Spach (17/13)

P. pinnatifidum Moris	Algeria, Balearic Islands, Corsica, Italy, France, Morocco, Sardinia, Sicily, Spain, Tunisia
P. purpureomarginatum Kadereit	Aegean, Anatolia, Cyprus, Greece
P. dubium L.	
subsp. *dubium*	widespread
subsp. *lecoqii* (Lamotte)Syme	widespread
subsp. *laevigatum* (M. Bieb.)Kadereit	Anatolia, Bulgaria, Krim
P. arachnoideum Kadereit	Anatolia
P. arenarium M. Bieb.	Anatolia
P. commutatum Fischer & C. Meyer	
subsp. *euxinum* Kadereit	Anatolia
P. guerlekense Stapf	Aegean, Anatolia, Cyprus, Greece
P. stylatum Boiss. & Balansa ex Boiss.	Anatolia
P. clavatum Boiss. & Hausskn. ex Boiss.	Anatolia
P. umbonatum Boiss.	Israel, Jordan, Lebanon, Syria
P. carmeli FEINBRUN	Israel
P. humile FEDDE	Egypt, Israel, Jordan, Sinai
P. rhoeas L.	widespread

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