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Phylogenetic analysis of the Papaveraceae s.l. (incl. Fumariaceae, Hypecoaceae, and Pteridophyllum) based on morphological characters

By

Joachim W. Kadereit, Frank R. Blattner, Kirstin B. Jork
and Andrea Schwarzbach

With 2 figures and 3 tables in the text

Abstract

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A phylogenetic analysis of the Papaveraceae s.l. (incl. Fumariaceae, Hypecoaceae, and *Pteridophyllum*) based on altogether 39 mainly morphological characters is presented. The 24 most parsimonious cladograms obtained were rooted with *Pteridophyllum* as basal clade. *Pteridophyllum*, Fumariaceae plus Hypecoaceae, Chelidonioideae s.str. (*Bocconia*, *Chelidonium*, *Eomecon*, *Hylomecon*, *Macleaya*, *Sanguinaria*, *Stylophorum*), Eschscholzioidae (*Dendromecon*, *Eschscholzia*, *Hunnemannia*), *Glaucium*/*Dicranostigma*, and Papaveroideae (*Arctomecon*, *Argemone*, *Canbya*, *Meconopsis*, *Papaver*, *Roemeria*, *Romneya*, *Stylomecon*) incl. Platystemonoideae (*Hesperomecon*, *Meconella*, *Platystemon*) were recognized as monophyletic groups in all most parsimonious cladograms. Sister group relationship among these six units followed the order (*Pteridophyllum* (Fumariaceae/Hypecoaceae (Chelidonioideae s.str. (Eschscholzioidae (*Glaucium*/*Dicranostigma* (Papaveroideae incl. Platystemonoideae)))))).

The most important results are 1. the monophyly of Fumariaceae/Hypecoaceae and particularly Papaveraceae s.str., which recently has been suggested to be paraphyletic after the exclusion of Fumariaceae/Hypecoaceae, 2. the position of *Glaucium*/*Dicranostigma* separate from Chelidonioideae s.str., where these two genera have been placed traditionally, and 3. the phylogenetic position of Platystemonoideae as sister group of *Canbya* within Papaveroideae, making the traditional Papaveroideae paraphyletic.

Introduction

The aim of this paper is to summarize and interpret cladistically the current understanding of morphological variation within the Papaveraceae s.l. This family of small size and largely north temperate distribution, containing not only the opium poppy (*Papaver somniferum* L.) as an ancient source of morphine,

but also "plusieurs plantes d'ornement très-élégantes" (SPACH 1839), is an exceptionally well-investigated taxon. Morphological variation within Papaveraceae s.l. has been well documented but remains to be analysed using cladistic methods. This analysis will be limited to the investigation of generic (and partly infrageneric) affinities within the Papaveraceae s.str., and to the relationship among Papaveraceae s.str. and Fumariaceae, Hypecoaceae, and *Pteridophyllum* Sieb. & Zucc. Cladistic analyses of the Fumariaceae and Hypecoaceae have recently been presented by LIDÉN (1986) and DAHL (1989).

The Papaveraceae s.l. consists of Papaveraceae s.str. (c. 23 genera, c. 240 species, Table 1), Fumariaceae (16 genera, c. 500 species), Hypecoaceae (one genus, c. 18 species), and the monotypic *Pteridophyllum*, commonly included in the Hypecoaceae. Recently, the latter three groups have been subject of exhaustive accounts by LIDÉN (1986), DAHL (1989, 1990, 1992), and BRÜCKNER (1985) respectively. Apart from a general account of the morphology of the Papaveraceae s.str. or parts of it by ERNST (1962a, b, 1967), fruit morphology and anatomy (BRÜCKNER 1982), seed morphology and anatomy (BRÜCKNER 1983a, GUNN & SELDIN 1976, GUNN 1980), inflorescence and vegetative morphology (GÜNTHER 1975a, b), pollen morphology (ERDTMANN 1966, LAYKA 1976), and alkaloids (SANTAVY 1970, 1979; PREININGER 1986) have been investigated thoroughly in the last 30 years. Exhaustive karyological information has been provided by, e.g., SUGIURA (1940) and ERNST (1962a).

All these contributions built on the account by PRANTL & KÜNDIG (1889) and the comprehensive treatments by FEDDE (1909, 1936) in "Das Pflanzenreich" and in the second edition of "Die natürlichen Pflanzenfamilien". Recent systematic accounts of Fumariaceae, Hypecoaceae (LIDÉN 1993a as Fumarioideae and Hypecoideae), *Pteridophyllum* (LIDÉN 1993b, Pteridophyllaceae), and Papaveraceae s.str. (KADERLEIT 1993) are available in KUBITZKI (1993).

Sister group relationships of the Papaveraceae s.l.

After the disassembly of the "Rhoadales" (where the Papaveraceae s.l. were combined with some of the families of today's Capparales mainly on the basis of flower and fruit morphology) for chemical (HEGNAUER 1960), serological (JENSEN 1967), and morphological (MERXMÜLLER & LEINS 1967, KARRER 1991) reasons, the Papaveraceae now are included in the herbaceous Magnoliidae (KUBITZKI 1993). An affinity of the "Rhoadales" to the "Polycarpicaceae" had already been discussed long ago, as is recognizable from the historical development of the assignment of families to this order (HARMS 1936). Much of this discussion has been summarized by FEDDE (1909, 1936). The herbaceous Magnoliidae correspond to TAKHTAJAN'S (1987) Ranunculidae. From the woody Magnoliidae the Ranunculidae are distinguished by the possession of tricolpate pollen grains and the lack of oil cells. While it has been suggested that Magnoliidae after the exclusion of Ranunculidae may well be paraphyletic (DONOGHUE &

DOYLE 1989), *rbcL* sequence data imply that Magnoliidae and Ranunculidae may not be closely related (CHASE et al. 1993, QIU et al. 1993) but belong into different major clades of the angiosperms characterized by monosulcate and tricolpate pollen grains respectively.

The Papaveraceae s.l. are united by the possession of secretory idioblasts or laticifers (except *Pteridophyllum*), the presence of two (rarely three) sepals and a syncarpous gynoecium of two or more carpels. Secretory idioblasts or laticifers are absent from all other families of the Ranunculidae, and the gynoecium is monomerous or pseudomonomerous in the Berberidaceae (incl. Nandinaeae), and apocarpous in the remaining families. These are Lardizabalaceae s.l. (incl. Sargentodoxaceae), Menispermaceae, and Ranunculaceae s.l. (incl. Circaeasteraceae and Hydrastidaceae). Nelumbonaceae, which possess articulated laticifers mainly in the vascular bundles, and an apocarpous gynoecium of several carpels sunk into the receptacle, probably also form part of the Ranunculidae (DONOGHUE & DOYLE 1989, HUBER 1991). Epicuticular waxes of *Nelumbo* Adans. appear to closely resemble those of Papaveraceae (BARTILOTT 1994). A cladistic analysis of the Ranunculidae except Papaveraceae (BARTILOTT 1994). A cladistic analysis of the Ranunculidae except Papaveraceae s.l. was presented recently by LOCONTE & ESTES (1989).

The Ranunculidae have sometimes been subdivided into Ranunculales (Lardizabalaceae, Menispermaceae, Berberidaceae and Ranunculaceae) and Papaverales (Papaveraceae s.str., Fumariaceae, Hypecoaceae, *Pteridophyllum*; e.g., STEBBINS 1974, DAHLGREN 1980, CRONQUIST 1981, TAKHTAJAN 1987, THORNE 1992). A close relationship between Papaverales and Berberidaceae, however, was suggested by MARKGRAF (1958) and MERXMÜLLER & LEINS (1967), and indeed an affinity of the "Rhoadales" to Berberidaceae had already been suggested by MURBECK (1912). We agree with this latter opinion and want to offer a more precise statement of relationships.

In a recent cladistic analysis of Magnoliidae by LOCONTE & STEVENSON (1991) the Ranunculaceae were identified as sister group of the Papaveraceae. The characters used for the recognition of this relationship were herbaceous habit, sheathing leaf bases, alternipetalous stamens, spiral stamen arrangement (the compatibility of these latter two character states is not clear), and the presence of 8-oxygenated flavonols. A close relationship between the two families is also supported by similarities in diverse amino acid sequences found by MARTIN & DOWD (1991). With the Berberidaceae, on the other hand, the Papaveraceae s.l. share the presence of protopine alkaloids. Whilst these are very widespread in the Papaveraceae s.l. (HEGNAUER 1969), in the Berberidaceae they have been reported mainly from *Nandina* Thunb. (HEGNAUER 1964) and *Berberis* L. (HEGNAUER 1989). They may constitute a synapomorphy of these two families.

Because herbaceous habit and sheathing leaf bases can also be found in the Berberidaceae, and the stamen arrangement in Papaveraceae is not spiral (MERXMÜLLER & LEINS 1967, KARRER 1991, RONSE DEGRAENE & SMETS 1992a), in contrast to the statement of LOCONTE & STEVENSON (1991), an association of either Ranunculaceae or Berberidaceae with Papaveraceae can be based on the

presence of 8-oxygenated flavonols or the presence of protopine alkaloids. As regards protopines, these sporadically occur in unrelated families like Amaryllidaceae (HEGNAUER 1963), Rutaceae (HEGNAUER 1973), and Rubiaceae (HEGNAUER 1990). Within Magnoliidae, protopines are restricted to Papaveraceae and Berberidaceae, while 8-oxygenated flavonols, according to GIANNASI (1988), are more widespread and also occur in the Sargentodoxaceae (here included in Lardizabalaceae). They do not occur in the Fumariaceae (incl. Hypecoaceae). In view of this distribution of the two classes of compounds we prefer to regard Berberidaceae rather than Ranunculaceae as sister group of Papaveraceae s.l. Similarities in wood anatomy ("vessel restriction", vascentric tracheids, diagonal aggregations of vessels) between woody Papaveraceae and *Nandina* and *Berberis* (CARLQUIST & ZONA 1988) may support this relationship. CARLQUIST & ZONA (1988), however, point out that some of these characters are also found in the Ranunculaceae (*Clematis* L.) and a few unrelated families, and that their phylogenetic rather than functional interpretation in some cases appears questionable. *RbcL* sequence data (CHASE et al. 1993) do not help to decide the above issue. According to these data, Ranunculaceae, Berberidaceae, Lardizabalaceae and Menispermaceae (also Eupteleaceae) as a clade are sister group to Papaveraceae. An affinity of Papaveraceae to Begoniaceae recently was suggested by RONSE DEGRAENE & SMETS (1990). The subdivision of the Ranunculidae into Ranunculales and Berberidales needs to be abandoned when Berberidaceae and Papaveraceae are recognized as sister groups.

The systematic positions of two genera are particularly problematic. This is *Nandina* in the Berberidaceae, sometimes excluded from that family (MEACHAM 1980, HUBER 1991), and *Pteridophyllum* in the Papaveraceae s.l., usually included in Hypecoaceae (as Papaveraceae-Hypecoideae, FEDDE 1909, 1936), but recently suggested to be closer to Papaveraceae s.str. (BRÜCKNER 1985) or treated as an independent family, Pteridophyllaceae (Murbeck) Sugiyura ex Nakai (LIDÉN 1993b). The inclusion of *Nandina* in Berberidaceae, where it occupies a basal position (LOCONTE & ESTES 1989), is justified by the presence in this genus of a monomeric or pseudomonomeric gynoeceum. *Nandina* differs from all other genera by having anthers with longitudinal slits (ENDRESS & HUFFORD 1989), while otherwise anthers are valvate in this family. Its pollen wall structure (NOWICKE & SKVARLA 1981) and floral anatomy (TEREBAYASHI 1985) also are unusual in the family. The two reasons to associate *Pteridophyllum* with Papaveraceae are its two sepals and its bicarpellate gynoeceum. The genus lacks idioblasts or laticifers (FRIEDEL 1938, LIDÉN pers. comm.), which characterize Papaveraceae s.str., Fumariaceae, and Hypecoaceae. Its association with Hypecoaceae by, e.g., FEDDE (1909, 1936) was based mainly on the presence of four unspurred petals and four stamens in these two groups. As regards the stamens, the four stamen primordia arise on diagonal radii alternating with the petals in *Pteridophyllum*, whereas in Hypecoaceae (and Fumariaceae) only two primary stamen primordia arise in a lateral position opposite the outer pair of petals (LEHMINGER 1985). These different patterns, which result in four diagonal

stamens in *Pteridophyllum*, two lateral stamen complexes consisting of one dithecal and two monothechal units in most Fumariaceae, and two lateral and two median complexes in Hypecoaceae, of which the lateral ones are considered dithecal and the median ones to consist of two monothechal units, were interpreted to represent different forms of a basically biseriate androecium with an outer tetramerous and an inner dimerous whorl by RONSE DEGRAENE & SMETS (1992b).

It is most intriguing to find that calcium oxalate crystals in the inner epidermis of the outer integument of the seeds are absent from *Pteridophyllum* (BRÜCKNER 1985) but present in *Nandina* although not in other members of the Berberidaceae (CORNER 1976). Such crystals hitherto were believed to characterize Papaveraceae s.l. (BRÜCKNER 1983a) in spite of the fact that they are found in several unrelated families (CORNER 1976). This character distribution, on the background of the relationships just described (Berberidaceae/*Nandina* — Papaveraceae s.l./*Pteridophyllum*), can be interpreted most parsimoniously as a parallelism.

The subdivision of the Papaveraceae s.l.

The Papaveraceae s.str., Fumariaceae, and Hypecoaceae are unambiguously separated by floral characters. The Papaveraceae have actinomorphic flowers with sepals enclosing the corolla in bud, the inner whorl of petals mostly is somewhat smaller than the outer whorl, and the androecium consists of an unfixed and normally large (> 4) number of stamens (fixed at four to 12 in *Meconella* Nutt. and six to 12 in *Cambya* Parry ex A. Gray; ERNST 1962a, 1967). There are no nectaries. In Fumariaceae and Hypecoaceae the sepals do not enclose the corolla, and this is dissymmetric or zygomorphic and consists of two very dissimilar pairs of petals. There are four stamens in two dissimilar pairs (sometimes interpreted as six; RONSE DEGRAENE & SMETS 1992b), and nectariferous tissue is found at the base of the stamens in all genera except *Adlumia* DC. (NORRIS 1941, LIDÉN 1986). The Hypecoaceae are characterized by green sepals, lack of spurs on the outer petals and deeply 3-cleft inner petals and four free stamens. In contrast, the Fumariaceae have petaloid sepals, usually one or two spurred outer petals (the absence of spurs is most parsimoniously interpreted as derived in this group), and two bundles of stamens each having one dithecal and two monothechal anthers [divided into six separate "stamens" in some species of *Dicentra* Bernh. (LIDÉN 1986)]. For a different interpretation of the androecium see RONSE DEGRAENE & SMETS (1992b). Fumariaceae and Hypecoaceae also differ in inflorescence morphology. Inflorescences (mostly) lack a terminal flower in Fumariaceae, but not in Hypecoaceae and Papaveraceae s.str. (TROLL & WEBERLING 1989).

The most recent treatment (LIDÉN 1993a, as Fumarioideae) subdivides Fumariaceae into tribes Corydalleae and Fumarieae, of which the first, containing five genera, is characterized by a persistent style with a usually large and flattened stigma, and the second, containing 11 genera in three subtribes, by a caducous