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### **Abstract**

Different taxonomic approaches proved that any classification should be based on chemical features in the family PAPAVERACEAE either. Thus the genus *Papaver* is characterized by the overall presence of meconic acid in the latex and of rheoadanes, as well as - restricted to some sections - of pigments, alkaloids etc. This chemotaxonomic basis emphasized many relationships in the tribe **Papavereae**.

The inherence of biochemical similarities and differences of *Papaver* sections are stressed one after the other: starting with *Meconella*, pointing out a cline type alkaloid variation in *Meconidium*, and after dealing with some other sections finishing by the most developed *Papaver*. Based on all of these data-relations, analogous changes of pigmentation and development of alkaloid biosyntheses at the sections it is suggested a chemotaxonomically plausible, classification of the genus *Papaver*.

### **Introduction**

Since the systematically fundamental disruption of the order Rhoeadales to orders Papaverales and Capparales on biochemical basis [Hegnauer 1961], both Dahlgren [1983] and Gottlieb [1982] verified it by the distribution of benzylisoquinolines in angiosperms, or by the evolution of these alkaloids.

Earlier infrafamilial classifications of the PAPAVERACEAE by Fedde [1909, 1936], Hutchinson [1925] and Ernst [1962] were based mainly on morphological characters. Table 1. shows that these authors systematized differently the genus *Papaver* including it either into a tribe with two other genera [Hutchinson], or in a subfamily with seven others [Ernst].

It was still an important systematization of Fedde to separate the tribe **Romneyeae** from **Papavereae** not only by morphological characteristics, but on the basis that the former taxon is constituted by two genera with water-like, colourless juice of vessels, contrary to the differently coloured, milky latex of other genera forming the last tribe.

### **Chemical characteristics of the genus *Papaver***

It is a general property of the species belonging to the genus *Papaver* that their latex contain meconic acid as well as they have rheoadane type alkaloids. Meconic acid can not be found in *Glaucium*, *Romneya* or *Argemone*, but it is present in traces at both species of *Roemeria* and at 3 of the examined 4 *Meconopsis* species [Fairbairn-Williamsen 1976]. Rheoadanes are present in 7 *Meconopsis* species, but absent from 3, however sole *M. cambrica* possess it together with meconic acid. Rheoadanes have not

been revealed in any other genus of the **Papavereae**, but were found in *Bocconia frutescens* (**Chelidoneae**) [Hegnauer 1989].

Besides these general chemical characteristics there exist some special ones restricted to certain sections of the genus. Nudicaulin, this three-glucosyded yellow pigment of stamens and petals appears in some sections [Harborne 1965], and is present in *M. cambrica* too, but being quite different from the yellow flower-flavonoids at *Glaucium* or *Argemone*. Anthocyanidins give rise to the violet-black, characteristic colour of filaments at all other sections of *Papaver*, and of blotched petals at some species of these sections, as well as colouring petals completely at some *P. dubium* taxa and *P. somniferum* cultivars. This character does not occur elsewhere in the family, than at *Roemeria* filaments and at *R. hybrida* petals only.

Certain sections of the genus *Papaver* might contain special alkaloids. Isopavines were found in two sections, alike as in both species of *Roemeria* and in four species of *Meconopsis* - absent from *M. cambrica* - however nowhere else in **Papavereae**, and only pavines at *Argemone*. Retroprotoberberines are very various in three sections of *Papaver*, however only one of this type, mecambidine was found in *M. cambrica*, while not detected in other **Papavereae** taxa. Morphinoids do not take place besides the genus *Papaver*, while their presence is characteristic for two sections and for certain species belonging to other sections [Tétényi 1989]. Promorphinanes are disclosed in three sections of *Papaver* and in both species of *Roemeria* as well as in *Meconopsis cambrica* [Preininger 1986]. Nevertheless compounds (amurine, flavinantine) of this type occurring in *Papaver* have 9R stereochemistry, differing from the 9S epimers in the two other genera [Goezler et al. 1990].

Brückner [1982 and 1983] publishing results based on fruit and seed morphological-anatomical characters of the tribe considers only one material that of calcium-oxalate crystals' state in the special seed-epidermis layer. Crystals can be present as well developed individual specimens, or like a powder, and she postulates the last state as evolved character - *Papaver* belonging here.

Evaluating these enumerated general and special chemical characteristics the genus *Papaver* seems to be the most variable regarding its biosynthetic routes, therefore it represents the most developed taxon in the **Papavereae** tribe. The genus *Roemeria* and *Meconopsis cambrica* - together with other *Meconopsis* taxa - are its nearest relatives. The American genera *Stylomecon*, *Argemone* and *Canbya* play secondary role, however not so distinct as *Romneya* and *Arctomecon*, agreeing with Fedde's opinion concerning their separation to the **Romneyeae** as with Hutchinson's and Ernst's one that *Glaucium* fits better to **Chelidoneae**.

### **Biochemical similarities and differences of *Papaver* sections**

The *Meconella* section is chemically characterized - besides the presence of meconic acid - by isopavine biosyntheses. These accumulate mostly amurensines alike in *Meconopsis*, but together with refranidine - the same is one of various isopavines found in *Roemeria* - at *P. anomalum* and *P. radicum*. Retroprotoberberines (alborine and orientolidine) are accumulated in the section, except *P. nudicaule* and *P. radicum*. The promorphinanes (amurine and nudaurine) appear at almost all taxa, but morphinoids were not revealed, only the salutaridine level was reached at *P. alpinum* taxa. Aporphines are usually lacking, and when present, then the orientaline derived isothebaine can be found at *P. croceum* and *P. nudicaule* ssp. *amurense*. Rhoeadanes are widespread also, together with alpinigenine at *P. alpinum* taxa - and with its precursor muramine at *P. pseudo-canescens* and *P. anomalum*.

Nudicaulin was generally found in stamens and petals, even in case of white flowers.

Flora Europaea [1964] discriminates white and yellow flowered taxa of *P. alpinum*. The most strange biochemical quality characterizing the *P. alpinum* group is that of the fine pleasant clove scent of flowers.

Yellow filaments, meconic acid and rheoadanes characterize the section *Meconidium* too. Its solitary flowered species are different: *P. polychaetum* with papaverrubines and aporphines, while *P. curviscapum* with alpinigenine and flavinantine. Inflorescences instead of flowers are solitary at *P. urbanianum* (papaverrubines, muramine, norarmepavine) and at *P. trinifolium* (amurine, thebaine, oreodine and papaverrine).

The poly-inflorescence taxa of the *P. armeniacum* group can not be separated correctly to species by morphological means: botanist tried it, but Flora of USSR [1937] noted, that there is a South-North transition only, nothing else. English and Turkish, as Russian and Czech chemist did their best to remove this botanical factor of uncertainty, and to clear up Anatolian and Caucasian plants' chemistry. They found important infraspecific chemical differentiation at their botanical taxa. Nevertheless chemical data arranged in Table 2. show continuous transition - irrespective of their originally chosen taxa - thus it exists a chemical variation of cline type. *P. armeniacum* group's cline includes chemo- syndromes with ancestral characteristics (alpinigenine, amurensinine) and evolved ones (thebaine, narcotine).

*P. cylindricum* belonging to this section has evolved chemical qualities (narcotine, thebaine and oripavine), furthermore morphine was also disclosed - due to the demethylation of oripavine - but small amount of codeine.

The only annual American species of the genus *P. californicum* - qualified to an autonomous section *Californicum* [Kadereit 1988b] - has yellow filaments too and is characterized by muramine and the simple benzylisoquinoline latericine.

The *Pilosa* section is homogenous regarding its meconic acid content and yellow filaments, but is diversified in any other chemical features. It exists in three different area, the smallest one being occupied by the *P. monanthum* group in the Western part of the Caucasus. Retroptoberberines prove its relationship to *Meconella* - where *P. lisae* is classified on morphological basis sometimes. Aporphines are oridine derivatives - ancient character again - as the presence of latericine at *P. monanthum*. *P. oreophilum* however shows developing tendency because it contains various rheoadanes (rheoadine, isorheoadine, oreodine), thebaine and narcotine.

Taxa belonging to *Pilosa* s. str. have their habitat limited to Asia-Minor. They contain dihydronudaurine as promorphinane together with salutaridine at *P. pilosum*, but with flavinantine at *P. spicatum* group. Rheoadanes are present here as papaverrubines, - and muramine precursor at *P. pilosum* - while aporphines as glaucine and dehydrooemerine.

At this point could be included *P. aculeatum*, the only poppy species of the South Hemisphere representing the section *Horrida*, because it has similar morphological characteristics to *Pilosa* s.str. [Kadereit 1988a]. The presence of salutaridine and aculeatine at *P. aculeatum* proves similar promorphinoid steps as well as the blocked rheoadane synthesis at the level of papaverrubines. The pale pink petal however do not occur in *Pilosa*.

Returned to the third *Pilosa* branch, which lives in North West Africa and Southern Spain, we meet taxa of *P. rupifragum* which grow old after three years and are lacking promorphinanes as well as retroptoberberines. The presence of muramine and of isothebaine is like in *Meconella*, and in case of this first alkaloid to *P. pilosum* also.

Contrary to the sections presented so far, the section *Macrantha* belonging taxa have violet-black filaments - albeit nudicaulin was proven in one case. Differences in the pigmentation of flower parts are shown in Table 3.

Meconic acid is present in all taxa of the section, but alkaloid production shows various combinations of the biosynthetic routes leading either to isothebaine, or orientalidine-narcotine, or thebaine-oripavine [Tétényi 1986]. Ontogenetical studies of young plants could prove that all of these alkaloids can occur more or less in any taxa. Pathways of retroprotoberberines and of isothebaine are like in *Meconella* and in *P. monanthum* group, while the presence of alpinine and the sometimes blocked morphinoid biosynthesis at salutaridine are as in *P. alpinum*. Nevertheless morphine was found in small quantities at all samples of examined taxa - but only traces of codeine [Wieczorek et al. 1986].

The *Argemone* section is quite unique within the genus because its taxa contain only traces of meconic acid. Pollen colours are also differing from other poppies: pink at *P. pavoninum*, purple at *P. argemone* and blue at *P. hybridum*. Filaments are violet-black alike to *Macrantha*, but petals of *P. hybridum* have cyanidins only. Alkaloid content is generally low. Rhoeadine is present always, together with isorhoeadine at *P. argemone* and with glaudine at *P. hybridum*. Other alkaloids are of special quality: *P. pavoninum* contains the aporphine roemeridine (*Roemeria*) and a carboline derivative - only a similar compound occurs at *P. rhoeas* and at two *Meconopsis* species. *P. hybridum* has a unique, structurally unknown alkaloid, the pahybrine. Traces of thebaine were found in *P. argemone*.

Taxa belonging to the *Rhoeadium* section (including *P. macrostomum*) have normal level of meconic acid, and their filaments are violet-black. A pigmentation peculiarity occurs sometimes at *P. rhoeas*: filaments with yellow colour. Differentiation of latex colour had been disclosed by Schratz and Egels already in 1958. Feinbrun [1963] distinguished ssp. *humile* with white and ssp. *sharonense* with yellow latex colour at *P. humile* species. Kubat [1980] systematized the whole dubium group on the latex colour basis.

Other classifications based on pigments can be found too: Flora Europaea [1960] e.g. separates *P. dubium* by its violet anthers from *P. laevigatum*, *P. lecoqii*, *P. pinnatifidum* having yellow or brownish-yellow anthers. Kadereit [1988c] distinguished the orange-red from violet flowers in *P. dubium* var *lecoqii*, as well as added *P. malvaeflorum* Doumergue - with violet blotched white or pale violet flowers - to the *P. dubium* group.

Alkaloid similarities and differences of the three acknowledged groups of *Rhoeadium* are presented as Table 4. - rhoeadanes and berberines as present always were not included.

Taxa of the *Papaver* section have meconic acid and their filaments are mostly violet-black, except of light-red ones at *P. gracile* and of pale violet or white ones at some poppy cultivars. *P. glaucum* and *P. somniferum* contain similar pelargonidins and cyanidins. The rhoeadane alkaloid glaucamine is characteristic for *P. glaucum* and was found in *P. somniferum* too. Except this alkaloid the papaverrubine level is characteristic for *P. setigerum* and *P. somniferum* alone. *P. decaisnei* has the same rhoeadanes as the *P. dubium* ssp. *erosum* - this being also true for its coptisine and corytuberine. *P. glaucum* in turn accumulates dehydroroemerine found in the *Dubium* group - and in the *Pilosa* section. The isothebaine precursor orientalinaline was found in *P. somniferum*. Retroprotoberberines are absent in the section, however phtalides are characteristic for *P. setigerum* and *P. somniferum*.

Morphinoids were not found at *P. decaisnei* and *P. glaucum*, they follow still a special demethylation route through codeine to morphine in *P. gracile*, *P. setigerum* and *P. somniferum*. This last taxon has some cultivars which have doubled demethylation ability, thus producing morphine through oripavine too. Papaverine is associated with morphinoids at all of these three taxa, but many poppy cultivars are without this alkaloid.

### Chemotaxonomic and evolutionary evaluation of the genus *Papaver*

Finishing this compressed review on chemical features of the *Papaver* sections it must be evaluated those biosynthetic connections which rule over the whole genus.

A special design of the genus *Papaver* is constructed according to Dahlgren's idea on cross-sectioned branches of the phylogenetic tree (Figure 1.). The number of species belonging to the sections is directly proportional to each other. The outlines of the sections are constructed according to their biochemical affinities. The different colouring of barks at these branches would represent a variability in accordance with the colour of filaments of taxa. Sections with yellow coloured bark form the inner group.

The perennial *Meconella* section is characterized by yellow filaments and by isopavine, retroprotoberberine, promorphinan alkaloids - thus relationships to *Meconopsis* and *Roemeria* genera - therefore it seems to be the most ancestral section of the genus and deserves the central place of a starting-point. It is encircled with other yellow filamented sections which belong to two descendent lines.

The first line is formed by their shortened life cycle characterized biennial *Meconidium* - with infrequent, ancient occurrence of isopavines, alpinigenine and promorphinanes, but replacing these last ones by the morphinoid thebaine as well as retroberberines by the phtalide narcotine - and by the annual, American *Californicum* sections. This last one had been classified - as a species - in the *Rhoeadium* section, but this systematization is unacceptable on chemical basis: the pigmentation and alkaloids of *Californicum* prove the relationship to *Meconella*.

The second line conducts to the disintegrated, perennial *Pilosa* section. Its three survived groups represent different evolutionary tendencies: the *P. monanthum* group (*Pseudopilosa*) - at the secondary gene-center - shows obvious ancient retroprotoberberine links originating from *Meconella* and forwarding to *Macrantha*. Its most evolved taxon, the *P. oreophilum* doubled this berberinate synthesis by producing narcotine, which is alike at *P. pseudo-orientale* (*Macrantha* again) as well as the morphinoid thebaine. In contrast, the *P. pilosum* group (*Pilosa* s.str.) synthesizes ancient and derived promorphinanes - alike the *Meconella* - and seems to be connected with the annual, African *Horrida* by homologous alkaloids, but with pink petals and spread far out of the gene-center. *P. rupifragum* taxa has realised an evolutionary trend by shortened life cycle, but their chemical characteristics show some resemblance to *Meconella*. On the other side it comes nearer to the *Rhoeadium* section by morphological grounds.

*Macrantha*, *Argemonidium*, *Rhoeadium* as well as *Papaver* (partially) sections possess violet-black filaments, and are descendants, thus are placed into outer positions at the dahlgrenic arrangement of the design. These sections raised similar adaptive chemosyndromes - due to more or less analogous events - however this parallellisme squares with their different norms of reactions producing different pigments' compositions for reaching the same - maybe defending - goal.

The perennial *Macrantha* is the most ancient section among them proved by its alpinine and retroprotoberberines as well as by its sometimes large oripavine constituent. Section's abilities to change orientalidine biosynthesis to narcotine and to expand the violet-black colour to blotches of petals are evolutionary characteristics.

The annual *Argemonidium* is surely younger, but because it contains only traces of meconic acid, unique alkaloids and very various anthocyanidins - extended to the pollen colours also - it seems proved, that this section is the odd one out of the genus.

*Rhoeadium* is differentiated in three twigs. The *P. rhoeas* group - due to its huge area - is very variable including perennial and annual taxa with violet-black - rarely yellow - filaments, and has wide differentiation of latex-colour, not cleared by chemical

investigations. Its alkaloids are very various: phtalides, morphinoids, aporphines and rheoadanones as well as other strange structures. The *P. arenarium* group - comprising *P. macrostomum* (thus not as independent *Carinatae* section), - seems to be more reduced in its chemism characterized by the dominance of various simple isoquinolines and aporphines. The third, the *P. dubium* group represents the most developed taxon of the section. Its accommodation ability seems reflected in its alkaloids differing definitely from the two other groups. The pale violet petals at some taxa represent further evolutionary step in the extension of anthocyanidin pigmentation - and a connection to the section *Papaver*. Two taxa of this group have direct alkaloid links - through *P. decaisnei* - to the section *Papaver* also.

The section *Papaver* is quite divergent from the others, because it unifies species joined by supposed hybridization(-s) issued through the autosterility of *P. glaucum*. Taking into account this descent it cannot be accepted any separation of the parent taxa from their offsprings - proposed to an autonomous taxa *Glaucia*. It can be stated the speciality of *P. setigerum* and *P. somniferum* only by their basic chromosome number (11), but anthocyanidins are the same as at *P. glaucum*, and this is true for glaucamine too. The morphinoid biosynthesis route is issued from the *P. gracile* parent, therefore *P. somniferum* and *P. setigerum* use the same demethylation pathways through codeine to morphine. The more ancient oripavine transit-route to morphine seems preserved at some poppy cultivars and is alike in *P. cylindricum*, *P. oreophilum* and in the *Macrantha* section, but developed in its efficiency. The presence of orientaline in *P. somniferum* seems to be a blocked atavisme towards perennial sections.

The domestication, selection and breeding of so various poppy cultivars is surely due to the initially spontaneous, afterwards conscious interference of mankind - which concerns an important task for the historians.

Besides alkaloid, latex and anthocyanidin characters of the genus *Papaver* it can not be forgotten the clove scent at the *P. alpinum* group: a unique chemical feature in the section *Meconella*, in the genus *Papaver* and in the whole *PAPAVERACEAE*, which might be an atavistic connection to the *LAURACEAE*.

Concluding all of the above briefed biochemical data, analogous changes of pigmentation and developments of alkaloid biosyntheses, as well as evaluating their taxonomic significance - according to nowadays' knowledge - I presented this chemotaxonically plausible, evolutionary classification of the genus *Papaver*.

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**Table 1 - Related genera of Papaver in infrfamily PAPAVERACEAE systems**

Fedde 1909, 1936	Hutchinson 1925	Ernst 1962
by degree of relationship		in alphabetic order
<b>Papavereae</b> Glaucium Roemeria Cathcartia Meconopsis Argemone Papaver Canbya	<b>Papavereae</b> Meconopsis Argemone Papaver	<b>Papaveroldeae</b> Arctomecon Argemone Canbya Meconopsis (incl. Cathcartia) Papaver Roemeria Romneya Stylomecon
<b>Romneyeae</b> Romneya Arctomecon	<b>Chelldonleae</b> Glaucium Canbya Arctomecon Cathcartia Roemeria (and others)	<b>Chelldonoldeae</b> Glaucium (and others)
	<b>Platystemoneae</b> Romneya (and others)	



Table 2 - Cline type arrangement of data on polychemisme at the Papaver armeniacum group

Taxon	Rhoeadanes	Proaporphines Aporphines	Promorphinane Morphinane	Phtalids, Berberine	Isopavine; Papaverine
p[5]	alpinigenine rheoadine glaudine				
t[5]	rheoagenine epiglaudine glaudine				
f[5]	oreodine rheoadine glaudine				
c[2]	papaverrubine A,B,C,D,E	glaziovine R(-)nuciferine S(+ )nuciferine			
a[5]	rheoagenine glaudine	lirinidine			
ac[6]	oreodine	unkn.aporphine	salutaridine*		
a[4]	rheoagenine	floripavidine	thebaine		
p[5]	alpinigenine	floripavidine		narcotine	
f[7]	oreodine rheoadine	floripavidine mecambrine	salutaridine	narcotine	
a[7]	oreodine rheoadine	floripavidine mecambrine		narcotine	papaverine
t[5]	oreodine rheoadine			sinactine	amurensinine
f[3]	rheoadine alpinigenine	armepavine	thebaine	narcotine	amurensinine
t[7], fl[1]		floripavidine	salutaridine		
t[5]		mecambrine lirinidine	thebaine		
p[7]		floripavidine mecambrine	salutaridine	narcotine	
t[5]		roemerine pronuciferine		narcotine	
f[9]		mecambrine roemeroline		cheilanthifoline	
f[8]				papaveroxine narcotine	

a=armeniacum ac=acrochaetum c=caucasicum f=fugax fl=floribundum p=persicum t=tauricolum

1 Konovalova et al.1935; 2 Preininger et al. 1971; 3 Phillipson et al.1973;  
4 Phillipson-Sariyar 1978; 5 Phillipson et al.1981; 6 Preininger 1986;\*Wieczorek et al.1986.  
7 Sariyar 1983a, 1983b; 8 Sariyar-Shamma 1986; 9 Czelombitko-Israilov 1988.

**Table 3 - Distribution of pigments in flowers of *Macrantha* species [after Bohm 1986]**

	<i>P. bracteatum</i>	<i>P. pseudo-orientale</i>	<i>P. orientale</i>
<b>Petals</b>	pelargonidin-3 sophoroside (main pigment)		pelargonidin-3 sophoroside
	pelargonidin-3 sophoroside 7 glucoside (by pigment)	pelargonodin-3 sophoroside 7 glucoside	
<b>Blotches</b>	cyanidin-3 sophoroside (main pigment)	cyanidin-3 sophoroside (main pigment)	unspotted, but traces of cyanidin-3 sophoroside
	cyanidin-3 glucoside (traces)	cyanidin-3 glucoside (traces)	
	cyanidin-double-glycosided (traces)		
<b>Stamens</b>	cyanidins (not double-glycosided)	cyanidins (not double-glycosided)	main cyanidin doubleglycosided
	pelargonidins practically absent at all three species		

**Table 4 - Alkaloid connections and differences at the Rhoeadium section**

	P. arenarium group	P. rheas group	P. dubium group
<b>Simple benzyliso- quinoline</b>	papaverine macrostomine sevanine glucomarine	0	oxyhydrastinine
<b>Aporphine</b>	isocorydine roemerine	isocorydine roemerine rhopalotine	isocorydine roemerine roemeroline sinactine
<b>Morphinoide</b>	thebaine(traces)	thebaine	thebaine
<b>Proto- berberine</b>	$\beta$ - stylopine methoxyhydroxide	$\beta$ - stylopine methoxyhydroxide	$\alpha$ - stylopine methoxyhydroxide
<b>Phtalide</b>	0	adlumidiceine narcotine narceine	0
<b>Strange structures</b>	0	coulteropine (Romneya) N-methyl tetra hydronorharmine (Meconopsis)	0

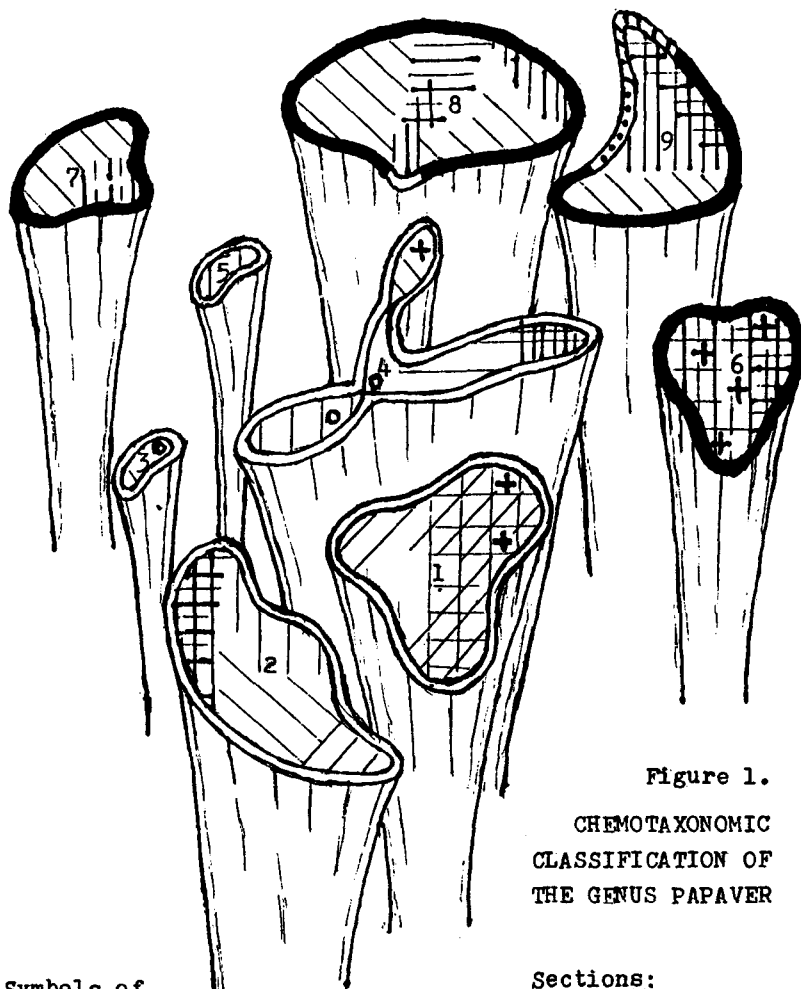


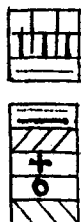
Figure 1.

CHEMOTAXONOMIC  
CLASSIFICATION OF  
THE GENUS PAPAVER

Symbols of  
Alkaloids

/on cross-  
sections/

pro-  
morphinane  
Morphinoid  
retroproto-  
berberine  
phtalide  
isopavine  
isothebaine  
latericine  
others



Filaments'  
colours

/on barks/

yellow



violet-  
black



pale or  
whitish



light

red



Sections:

- 1 Meconella Spach
- 2 Meconidium Spach
- 3 Californicum  
Kadereit
- 4 Pilosa Prantl
- 5 Horrida Elkan
- 6 Macrantha Elkan
- 7 Argemonidium Sp.
- 8 Rhoeadium Spach
- 9 Papaver