

## Chemo-Dahlgrenogram of the Tribe Papavereae

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### Abstract

The review puts forward and extends the chemo-dahlgrenogram of the genus *Papaver* over *Papavereae*. — Tertiary *Cathcartia* owns watery latex as *Romneya* (*Palaeoaster*'s sister), but is evolved by sole sand-like crystals in seeds' coats. On the other hand, *Cathcartia*, that synthesizes indeno-benzoazepine alkaloids, differs substantially from *Meconopsis*. Therefore *Cathcartia* is an independent entity representing the starting-point for *Papavereae*. — *Meconopsis cambrica* Vig. is missing *Meconopsis* constituents mentioned before, but synthesizes armepavine derivative aporphines, as well as meconic acid and nudicaulin (stated at *Papaver* sections, but being unproved at *Meconopsis* taxa). Therefore the species belongs to *Papaver* genus, and its original name *Papaver cambricum* Linnaeus is effective again. — *Meconopsis* polycarpic (sometimes monocarpic) species of ser. *Simplicifoliae* accumulate retro-protoberberines, but ser. *Grandes* only berberine. Monocarpic species of *Aculeatae* and *Robustae* are characterized by isopavines, oriental line derivative aporphines and harmaline alkaloids. Monocarpic life span of *Meconopsis* taxa is analogous with the biennial *Papaver* sect. *Meconidium*. — Separation of the Californian, annual *Stylomecon heterophylla* with phthalideisoquinoline alkaloid content from the Asian genus *Meconopsis* is also proved, alike to some annual or biennial *Papaver* taxa. — *Roemeria* species with aporphines and protoberberines are joined to *Papaver* section *Argemonidium*. Chemism of *Roemeria refracta* with rhoeadanes, promorphinanes is more similar to *Papaver* genus, in contrast to *R. hybrida* synthesizing spirocyclic-coupled proaporphines, unique at *Papavereae*. — The previous *Papaver* chemo-dahlgrenogram must be changed by detaching sect. *Pseudopilosa* (oxoprotopines, phthalideisoquinoline, aporphines and thebaine derived from oriental line) from the previously defined sect. *Pilosa* (aporphines and promorphinanes derived from reticuline). — The chemo-dahlgrenogram of the tribe *Papavereae* was constructed according to above data.

### INTRODUCTION

Chemo-dahlgrenogram of sections belonging to *Papaver* genus is published (Tétényi, 1993). It is a timely problem to extend the chemo-dahlgrenogram to the related genera at *Papavereae*. Nevertheless, the concept of *Papavereae* is changed, since Loconte et al. (1995) has moved the genus *Canbya* from the tribe to the subfamily *Platystemonoideae* with the same chromosome number ( $x=8$ ), three carpellate gynoecia and annual habit. The genus *Glaucium*, together with *Dicranostigma*, is separated into a new subfamily *Glaucioideae* by Hoot et al. (1997), however this classification is not accepted. The last change for *Papavereae* is the segregation of the genus *Argemone* based on morphological divergences and restriction fragment length polymorphism (RFLP) analysis, excluding it from *Papaver*, *Roemeria*, *Stylomecon*, *Meconopsis* (Kadereit et al., 1997). Chemo-dahlgrenogram of the tribe *Papavereae* must include in all of these facts.

### CHEMOTAXONOMIC CLASSIFICATION OF PAPAVEREAE

#### Origin of *Papavereae* and Classification of the Taxon *Cathcartia*

The supposed origin of *Papavereae* is based on the fact that the area from Eastern

Himalayas, North Burma through Sichuan till West Hubei in Central China was not affected by Quaternary glacial periods. Therefore the distant *Meconopsis* taxa living in this area must be considered the starting point for each member of the tribe (Jork and Kadereit, 1995). However this Asian place could be only a secondary branching for *Papaveroideae*, because the primary source was found in America. Excavations proved that the *Palaeoaster* (*Papaveraceae*) genera flourished at North America during Late Cretaceous. The distant Californian *Romneya* (*Papaveroideae*) is the sister taxon of these poppies, as it is proved by cladistic analysis of Smith (2000, 2001).

Fedde (1909) separates *Papaveroideae* into two tribes: *Romneyae* with colorless-watery and *Papavereae* by variously colored milky juices. *Romneya*'s plants are unique by accumulating big and sand-like calcium-oxalate crystals in the inner epidermis of the seeds' coat, as it is proved by Brückner (1982). This double capacity means divergence within *Papaveroideae*, since genera *Argemone* and *Arctomecon* have only big crystals (alike to the other three subfamilies of *Papaveraceae* s.str.), while ultimately the *Papavereae* genera accumulate sand-like crystals only.

The evolution-step from *Romneya* to *Meconopsis* can be found at *Cathcartia*, this unrelated genus is included in the genus *Meconopsis* (sect. *Eucathcartia*) by Taylor (1936). This classification is criticized by Grey-Wilson (1993), since *Cathcartia* is grown at mesic forest floor habitat and not at alpinic. Moreover, it has different morphological (dimeric flowers, with uniformly yellow stamens and petals, carpels with dorsal traces etc.), and chromosome characters (diploids, with  $n=14, 16$ ). An RFLP analysis proves its separation from other *Meconopsis* taxa as a basal clad (Jork and Kadereit, 1995).

Chemism of *Cathcartia* were compared to *Romneya* and other taxa of *Papavereae* (Table 1). The primary nature of *Cathcartia* can be found in its watery, transparent latex, alike to *Romneya*, (not milky as e.g., of *Meconopsis*). This character suggests a Tertiary origin for *Cathcartia*. On the other hand, three oxoprotopine derivative indenobenzazepines are unique in *Papaveraceae* s.str. (Hegnauer, 1989). Since *Cathcartia* differs from the genus *Meconopsis* by its chemism and its ecological, morphological, chromosomal and RFLP analyses, thus it must be an independent entity. Its reinstatement as a separate genus from *Meconopsis* is well based, thus it must be placed at the central point of the chemo-dahlgrenogram, being the ancestral taxon for *Papavereae*.

### **Taxonomy of *Meconopsis cambrica* Vig. syn. *Papaver cambricum* L.**

The West European endemic Welsh Poppy, of Tertiary origin receives its Latin name by Linnaeus (1753). Viguiet (1814) classifies it as a new genus *Meconopsis cambrica*. The other species of this genus are discovered far in the Himalayan region during 19<sup>th</sup> and 20<sup>th</sup> Centuries.

Morphological features of the Welsh Poppy (pseudodorsal venation of ovary, flowers homogeneously yellow in color) and its blocked growing zone between innovative sprouts, (alike to *P.* sect. *Pilosa*) do not occur at Himalayan *Meconopsis* (Günther 1975). The apparent identity of yellow flower petals and filaments of the Welsh Poppy is caused by nudicaulin pigment (stated at *Papaver* sections, but unproved at *Meconopsis*). Meconic acid is disclosed in its latex, however is not found in Asian species. Diploid chromosome characteristics ( $2n=28$ , once stated 22) of the Welsh Poppy prove the divergence from *Meconopsis*, and a RFLP analysis places the Welsh Poppy next to *P. atlanticum* (sect. *Pseudopilosa*) (Kadereit et al., 1997). Alkaloid biosyntheses of the Welsh Poppy are different from the Asian *Meconopsis* in three terms (Table 2). The flavinantine, palmatine and *N*-methylmecambridine content of the Welsh Poppy is not disclosed at *Meconopsis* taxa (Preininger, 1986; Bentley, 1990-2002). On the other hand, Welsh Poppy is identical to *Papaver* taxa (Tétényi, 2000): roemerines and meconic acid in seven, and promorphinanes can be found at three *Papaver* sections. Retroprotoberberines can be found in the *P. nudicaule* group (*Meconella* sect.), and sects. *Pseudopilosa* (Eastern group) as well as in *Macrantha*.

Since the Welsh Poppy owns a homologous chemism to the *Papaver* genus, but is lacking isopavines, – disregarding Welsh Poppy's style on capsule and absence of dorsal

veins (same at *P. sect. Meconella*) – Linnaeus' classification and the name *Papaver cambricum* are again in force (Tétényi, 2001). This taxon could be placed of the genus *Papaver* among the identical polycarpic, perennial, nudicaulin filamented sects. *Pilosa*, *Meconella* at the chemo-dahlgrenogram.

### Systematics of the Genus *Meconopsis* Vig.

The genus *Meconopsis* had a continuous Tertiary area that was fragmented by the upheaval of the Himalayan Mountains. It contains more than 40 species (Kadereit et al., 1997) characterized by life span differences occurring at the following ranks:

- a/ subsect. *Cumminsia* contains the polycarpic ser. *Bellae* and the monocarpic *Primulinae*;
- b/ ser. *Grandes* consists of the polycarpic *M. sherriffii*, and *M. betonicifolia* (sometimes biennial), as well as the monocarpic *M. integrifolia*;
- c/ *M. simplicifolia* shows infraspecific diversity by a polycarpic purple-blue flowered and another monocarpic light blue varieties. Furthermore monocarpic species of ser. *Aculeatae* (*M. aculeata*, *M. horridula*) flower in their 2<sup>nd</sup>-3<sup>rd</sup> year, while those of the ser. *Superbae* (*M. superba*, *M. regia*) into bloom only in 4<sup>th</sup>-5<sup>th</sup> year of life in cultivation (Grey-Wilson 1993). Table 3 shows lifetime diversities of the genus.

Nine *Meconopsis* species were chemically analyzed in details (Table 4). Five other species contain only protopine, being unsuitable for any valuation (Tétényi, 2000).

Arranging of polycarpic ser. *Simplicifoliae* could be near to the similar genus *Cathcartia* and to *P. cambricum* in the chemo-dahlgrenogram. Ser. *Grandes* must occupy a position not to far from the previous taxon. The monocarpic ser. *Aculeatae* and ser. *Robustae* could be rendered next to the biennial *P. sect. Meconidium* (owning well-separated vegetative/reproductive phases of lifetime), by the analogy of the previously mentioned taxa, in the chemo-dahlgrenogram of the genus *Meconopsis*.

### Classification of *Stylomecon heterophylla* Taylor

The annual *Stylomecon* species has been mentioned as an example for being an Arcto-Tertiary element of Californian flora (Stebbins and Major, 1965). It is described as *Meconopsis heterophylla* Benthham, but then is separated according to its lifetime and ecologic adaptation from the alpine *Meconopsis* as a new genus *Stylomecon* (Taylor, 1934). It has distinct style on its ovary with pseudodorsal veins alike to *P. cambricum*. This venation type characterizes also the annual *P. californicum*, but is not found at any *Meconopsis* taxa (Jork and Kadereit, 1995).

Chemism of *Stylomecon* is characterized by meconic acid in its latex just like at all taxa of the genus *Papaver* (including *P. cambricum* and *P. californicum*), in contrast to the genus *Meconopsis*. *Stylomecon* synthesizes a phtalideisoquinoline alkaloid (stylophylline) being disclosed at some evolved *P. taxa* (annuals *P. somniferum*, *P. decaisnei*, *P. rhoeas* and biennials *P. cylindricum*, *P. armeniacum*), but has not analyzed in *Meconopsis*. *Stylomecon* accumulates chelerythrine occurring only at *P. armeniacum* (*P. fugax*) in *Papaver* genus. Since characteristic *Meconopsis* constituents (isopavines, rhoeadanes and harmane alkaloids) are absent at *Stylomecon*, thus its distinction is also based on chemical proofs. — Overmore, flowers of *Stylomecon* have pleasant fragrance reminiscent to *Convallaria majalis* (Grey-Wilson, 1993). The fragrance of *P. alpinum* (*P. sect. Meconella*) is similar to clove, and of *M. speciosa* (Cobb, 1989) alike to hyacinth in *Papavereae*.

Based on morphological, life span and chemical characteristics as well as an RFLP analysis, *Stylomecon heterophylla* could be placed near to *P. californicum* at the chemo-dahlgrenogram. Both taxa form the fourth line of *Papavereae*, regardless on the dark purplish filaments (*Stylomecon*) and yellow ones at its "close affinity" (Jork and Kadereit, 1995). This relationship as well as the multidimensional scaling proved that *Stylomecon* occupied a place among *Papaver* species (Tétényi and Füstös, 2002).

### Classification of the Genus *Roemeria* Med.

The supposed origin of this annual species is caused by the Tertiary aridifications. Its separation from *Chelidonium* as an independent genus is stated by Medicus (1792). Nevertheless Günther (1975) merged it with *Papaver* as a section (near to the *P.* section *Argemonidium*), but this was not accepted. *Roemeria*'s two species ( $2n=14, 22, 24$ ) inhabit open, arid regions in the Mediterranean area, the Middle East and Central Asia. An RFLP analysis states mixed position among *Roemeria* with *P.* sect. *Argemonidium* (Kadereit and Sytsma, 1992), however multidimensional scaling resulted in separate 3D arrangements for these two species (Tétényi and Füstös, 2002).

*Roemeria* and *Argemonidium* taxa both have dark violet filaments; however, their relationship is also stated chemically. Traces of meconic acids and aporphines of both types are present in the latex (derivatives of orientalinaline as well as of arnepavine, seldom enantiomers). *R. hybrida* synthesizes further a unique type of proaporphines (spirocyclic roehybrine coupled with dimethoxytryptamine). Data on some other alkaloids are presented in Table 5. Protoberberines are analyzed at each taxon, however *P. hybridum* has berberine while *R. hybrida* has isocorypalmine (found at *P. somniferum* and *P. armeniacum* too). Morphinans are present in *R. refracta* and *Argemonidium* (as enantiomers of amurine at some *Papaver* taxa) and flavinantine of *P. cambricum*, but absent at *R. hybrida*. Harmane alkaloids are lacking from *R. refracta*, but *R. hybrida* and *P. pavoninum* contain this type, also occurring at five *Meconopsis* species. *R. refracta* pavines (eschscholtzine, eschscholtzinol) are unique in the tribe *Papavereae*, and roelactamine is the first pavine lactone. Reframoline, being one of the numerous isopavines, was stated at *Meconopsis speciosa*. *R. hybrida* does have neither isopavines nor pavines. Rhoeadanes are lacking at the genus *Roemeria*, while *P.* sect. *Argemonidium* synthesizes various alkaloids of this type, as well as 13-oxoprotopine of *P. hybridum*. Regarding these data, *R. refracta* is chemically closer to *P.* sect. *Argemonidium*, than *R. hybrida*, thus this divergence must be indicated at the chemo-dahlgrenogram.

### A Change in Infrageneric Classification of the Genus *Papaver*

Twelve perennial *Papaver* species are included in the section *Pilosa* (Prantl and Kündig, 1891). Nevertheless the "Flora SSSR" has separated four species from the section on morphological and area differences into a new sect. *Pseudopilosa* (Popov, 1937). This classification remains unaccepted. Böhm and Günther (1972) state presence of the alkaloid amurine at *Pilosa*, but absence at *Pseudopilosa*. Kadereit (1996) divides the twined section taxonomically in view of area and leaf-vernations differences.

Classification of *Pilosa* and *Pseudopilosa* taxa could be determined by chemodiversity: whether they form one section (both have nudicaulin in filaments), or are two independent entities on section level. *Papavereae*'s biosyntheses consist of a main alkaloid course (norcoclaurine→protopines), and ramifications of types (morphinans, rhoeadanes etc.) presenting true possibility to prove the degree among taxa (Tétényi, 1989). For the interest of comparable presentation, a circle diagram by telescoped main course (in center) and radial pathways to alkaloid groups branches was sketched (Fig. 1a). Arrows of presented circle diagrams of both taxa show important divergences in the clockwise (Fig. 1b): rhoeadanes of *Pilosa* are blocked by intermediate papaverrubines (*P. pilosa* ssp. *spicatum*, ssp. *heldreichii*) and rhoeadine (ssp. *pilosum*), while *Pseudopilosa* synthesizes exclusively end-variation molecules: rhoeadine at four taxa, linked with isorhoeadine of two and with oreodine of one species. Oxoprotopines (oreonone, alpinone etc.) are analyzed only at two species of *Pseudopilosa*. Benzophenanthridine (chelirubine), retroprotoberberines (mecambridge, macrantaline, macrantoridine) and phthalideisoquinoline (narcotine) are found only at *Pseudopilosa* taxa. *Pilosa* synthesizes *S*-reticuline originated aporphines: *R*(-)-glaucine, (not *S*(+)-glaucine of *Glaucium* taxa), *N*-methylglaucine (found at *Stephania*, *Menispermaceae*), and laurotetanine (stated in *Eschscholtzia californica*). In contrast to it, *Pseudopilosa* is characterized by *S*-orientalinaline derivatives (isothebaine, oridines, corydines, menisperine). *R*-arnepavine issued aporphines occur at both sections, e.g., the ancestral latericine. *Pilosa* contains a group of mecambrine derivatives (*S*-

roemerine, (+)-roemrefidine, roemeramine) and liriodyne (oxoaporphine), while *Pseudopilosa* has only nuciferine and mecambrine. *Pilosa* produces promorphinanes (amurines, nudaurines, and flavinantine), and an intermediate to true morphinanes (salutaridine in tr.), while *Pseudopilosa* has thebaine, a real morphinane.

All of these chemisms of both taxa are very divergent, thus *Pilosa* and *Pseudopilosa* could be originated in all probability by different areas. Their separation is justified at section level, thus *Papaver*'s chemo-dahlgrenogram (Tétényi, 1993) must be changed.

## CONCLUSION

*Cathcartia* is the starting-point for *Papavereae* s.str. *P. cambricum* belonging to the genus *Papaver*, thus its Linnaean name is again effective. Monocarpic taxa of the genus *Meconopsis* are analogous in lifetime with biennial *P.* sect. *Meconidium*. Chemism of *Stylomecon* justifies its separation from the genus *Meconopsis*. Chemism of *Roemeria refracta* are closer to *P.* sect. *Argemonidium* than *R. hybrida*. The detaching of *P.* sect. *Pseudopilosa* from the sect. *Pilosa* is proved by chemodiversities. — The new construction of the chemo-dahlgrenogram of the tribe *Papavereae* (Fig. 2) became possible in compliance with above proves and arguments.

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## Tables

Table 1. Differences in chemical characteristics of three *Papaveroideae* taxa.

Taxa	Size of calcium oxalate crystals	Latex condition	Indenobenzazepine alkaloids
<i>Romneya</i>	some big crystals encircled by a majority of sand-like ones	watery	<u>absent</u>
<i>Cathcartia</i>	sand-like	watery	ribasines
<i>Papavereae</i>	sand-like	milky	<u>absent</u>

Table 2. Chemical diversity among the Welsh Poppy and nine Asian *Meconopsis* species.

Taxa	Isopavines	Armepavine derivative aporphines	Harmane alkaloids
Asian <i>Meconopsis</i> species	amurensinines 6 species reframoline 1 species	<u>absent</u> 9 species	norharmane 5 species
Welsh Poppy	<u>absent</u>	mecambrine, mecambroline S-roemerine, roemeroline	<u>absent</u>

Table 3. Diversity in life span of *Meconopsis* taxa.

Taxa	Lifetime	Series (number of species)
	strict polycarpic	<i>Bellae</i> (1), <i>Simplicifoliae</i> (2), <i>Grandes</i> (2)
subsect. <i>Cumminsia</i>	polycarpic/ rarely monocarpic	<i>Simplicifoliae</i> (2), <i>Grandes</i> (1)
	monocarpic/ rarely polycarpic	<i>Aculeatae</i> (1)
subsect. <i>Eupolychaetia</i> subgenus <i>Discogyne</i>	bi- triennial perennial	<i>Grandes</i> (1), <i>Aculeatae</i> (3), <i>Aculeatae</i> (8), <i>Primulinae</i> (2), <i>Superbae</i> (3), <i>Robustae</i> (8); (2)

Table 4. Chemical characteristics of *Meconopsis* taxa.

Series (number of taxa)	filament color	Typical alkaloids
<i>Simplicifoliae</i> (2)	pale-violet or whitish	berberine, mecamidines
<i>Grandes</i> (2)	creamy	berberine, amurensinines
<i>Aculeatae</i> (1)	n.d.	reframoline, amurine
(3)	dark blue	amurensinine, norharmane
(1)	dark blue	amurensinine, norharmane, magnoflorine
<i>Robustae</i> (5)	whitish	amurensinines, norharmane, magnoflorine

Table 5. Chemical characteristics of the *P.* sect. *Argemonidium* and *Roemeria* species.

Taxa	Morphinanes	Isopavines and pavines	Harmene alkaloids
<i>Papaver</i> sect. <i>Argemonidium</i>	salutaridine tr.	<u>absent</u>	demethoxy-harmane
<i>Roemeria refracta</i>	<i>S</i> -amurine <i>S</i> -noramurine <i>S</i> (+)flavinantine	reframidine roelactamine eschsoltzinone	<u>absent</u>
<i>Roemeria hybrida</i>	<u>absent</u>	<u>absent</u>	roeharmane roecarbolines

**Figures**

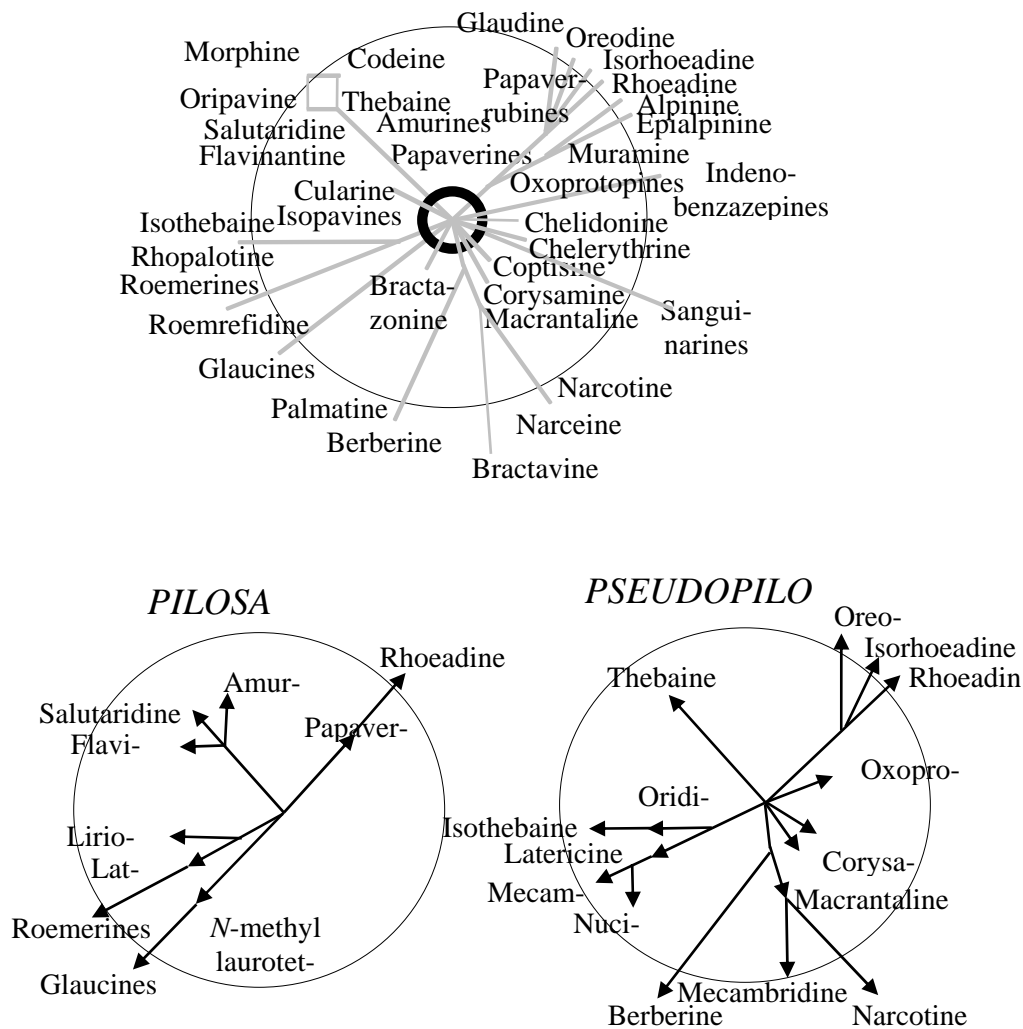


Fig. 1. Circle diagram of alkaloids: a) Biosynthetic constitutional types of the main course (● telescoped) and ramification groups of *Papavereae*. b) Real differences according to the radially diverse pathways (shown by arrows) of two *Papaver* sections.



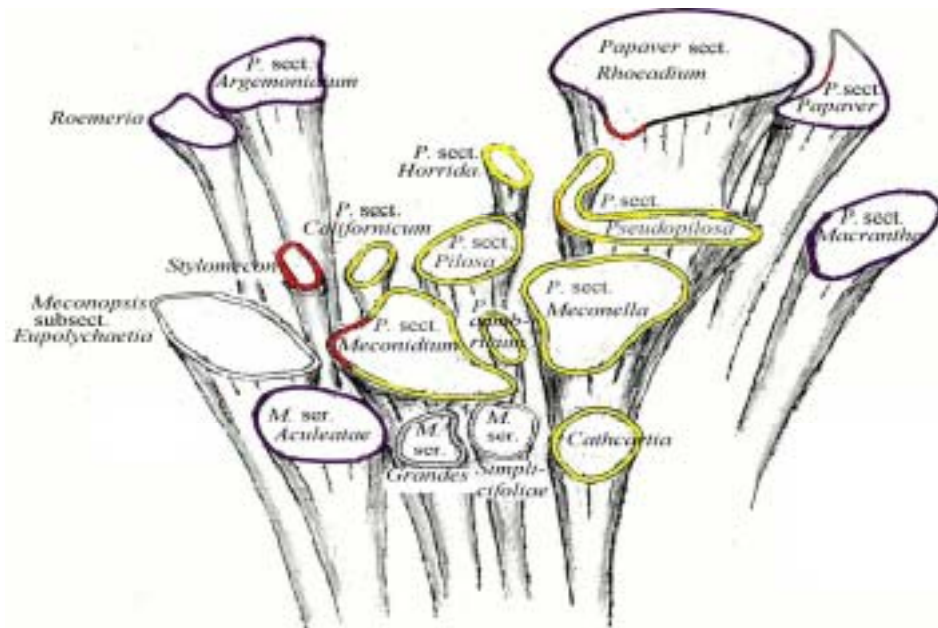


Fig. 2. Chemo-Dahlgrenogram of the tribe *Papavereae*, filaments' colors were shown.