Bot. Jahrb. Syst., Band 108, Heft 1, Stuttgart

ISSN: 0006-8152 [CODEN: BJPPAQ] 108 (1) 1—144 (1986)

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Die Botanischen Jahrbücher erscheinen heftweise. 4 Hefte bilden einen Band. Jedes Heft wird einzeln berechnet. Es ist beabsichtigt, jährlich etwa 4 Hefte herauszugeben.

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Printed in Germany.

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GEIGER DRUCK GmbH, 7240 Horb a. N.

Bot. Jahrb. Syst.	108	1	1—16	Stuttgart, 17. Dezember 1986

KT/1.

A revision of Papaver L. sect. Papaver (Papaveraceae)

DE LIEGE
DÉPARTEMENT DE BOTANIQUE
UNITÉ DE DOCUMENTATION
Echange LEJEUNIA
Cote : P 1680

By

J. W. Kadereit

With 3 figures in the text

Abstract

KADEREIT, J. W.: A revision of *Papaver* L. sect. *Papaver* (Papaveraceae). — Bot. Jahrb. Syst. **108**: 1—16. 1986. — ISSN 0006-8152.

Papaver sect. *Papaver* is recognized to comprise four species. These are *P. somniferum* with ssp. *somniferum* and ssp. *setigerum*, *P. gracile*, *P. glaucum* and *P. decaisnei*. Recent suggestions to exclude *P. gracile*, *P. glaucum* and *P. decaisnei* from the section (RECKIN 1973, NOVAK & PREININGER 1980, PREININGER et al. 1981) are discussed and rejected on the basis mainly of morphological evidence.

Introduction

Ever since FEDDE's (1909) revision of the Papaveraceae, *Papaver* sect. *Papaver* has not been dealt with as a whole. Apart from the accounts of different parts of the section in diverse regional floras, notably Flora of Turkey (CULLEN 1965a), Flora Iranica (CULLEN 1966) and Flora of Iraq (CULLEN 1980), numerous publications relating to individual species or groups of species have been written. DANERT's (1958) revision of *P. somniferum* L., also discussing earlier attempts of a classification of this very variable species, HAMMER & FRITSCH's (1977) discussion of the relationship of *P. somniferum* and *P. setigerum* DC., VENT's (1970) investigation of *P. glaucum* Boiss. & Hausskn. and *P. decaisnei* Hochst. & Steudel ex Elkan and RECKIN's (1973) treatment of *P. gracile* Boiss. are some of the more important contributions which should be mentioned here. On the background of recent suggestions to change the delimitations of section *Papaver* by RECKIN (1973), NOVAK & PREININGER (1980) and PREININGER et al. (1981) it was thought desirable to prepare a new revision of this section. At the same time, a detailed knowledge of the different species was needed as a basis for a separate study of the phylogenetic affinities of *P. somniferum* (KADEREIT 1986).

0006-8152/86/0108-0001 $ 04.00

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History of the section

At the time when the first subdivision of the genus was proposed by BERNHARDI (1833), only *P. somniferum* and *P. setigerum* had been described. He named *P. somniferum* as a representative of his group d. *Mecones*. This name *Mecones* was first assigned sectional rank by ELKAN (1839), who included only *P. somniferum* (including *P. setigerum*) in this section. As a species of dubious status with close similarities to *P. somniferum*, ELKAN (1839) named *P. pilosum* Sibth. & Sm., of which, however, he had seen neither any plant material nor an illustration. In modern accounts (CULLEN 1965b) this latter species is treated as part of *Papaver* sect. *Pilosa* Prantl. *P. decaisnei*, which later has been included in section *Papaver*, was treated as part of an emendated *P. dubium* L. by ELKAN (1839). Also SPACH (1839) included only *P. somniferum* in his section *Meconium*. FEDDE (1909) included the following species in his section 4. *Mecones*: *P. somniferum*, *P. setigerum*, *P. glaucum*, *P. gracile* and *P. decaisnei*. Although without any formal rank, these taxa were grouped together by BOISSIER (1867) as annuals with glabrous capsules, amplexicaulous cauline leaves and either filiform or clavate filaments. Recently, RECKIN (1973) suggested that of FEDDE's (1909) section *Mecones P. glaucum*, *P. gracile* and *P. decaisnei* should be transferred to section *Orthorhoeades* Fedde (= *Rhoeadium* Spach), and that *P. aculeatum* Thunb. should be united with *P. somniferum* and *P. setigerum* in section *Mecones*. This suggestion was based mainly on cytological considerations, but also on chemical and morphological evidence, which will be discussed in detail below. With the same reasoning, NOVAK & PREININGER (1980) and PREININGER et al. (1981) established the new section *Glauca*, including *P. glaucum*, *P. gracile* and *P. decaisnei*, leaving only *P. somniferum* and *P. setigerum* in section *Papaver*. In the present account, section *Papaver* will be treated in FEDDE's (1909) circumscription.

Papaver sect. Papaver

Syn.: *Mecones* Bernh., Linnaea 8: 463. 1833;
P. sect. *Meconium* Spach, Hist. Nat. Veg. Phan. 7: 12. 1839;
P. sect. *Mecones* (Bernh.) Elkan, Tent. Monogr. Gen. Papaver: 30. 1839; incl.: *P.* sect. *Glauca* Novak & Preininger, Preslia 52: 98. 1980. — Lectotype: *P. somniferum* L., Britton & Brown, Ill. Fl. N.U.S. ed. 2, 2: 136. 1913.

Erect unbranched or branched annual herbs; leaves narrowly obovate, elliptical, oblong, ovate or cordiform, pinnatipartite to undivided; lower leaves ± distinctly petiolate, upper leaves sessile and ± strongly amplexicaulous-auriculate; plants with patent or appressed setae on various parts or entirely glabrous, green or ± strongly glaucous. Flower buds ovoid to oblong; sepals with patent setae or glabrous; petals obovate to rotund or broadly reniform, white, pink, light to dark violet or variously red, with or without basal markings; filaments filiform or clavate, anthers oblong; capsule obovoid, elliptical, ovoid, cylindrical or globose, shortly to distinctly stipitate; margin of stigmatic disc without or with non-overlapping or overlapping free lobes; capsule poricidal or remaining closed at maturity; seeds reniform, yellowish to brown to blackish, ± glaucous.

Key to the species

1 Capsule distinctly stipitate, cylindrical, elliptical, broadly ovoid or globose 2
— Capsule not distinctly stipitate, narrowly obovate to elliptical 3
2 Plant glabrous or with appressed setae on pedicel and rarely on sepals; petals dark red, outer ones broadly reniform; anthers with terminal appendage. . . . . 3. *P. glaucum*
— Plant rarely glabrous, mostly with patent setae at least on major veins of lower leaf surface; petals of various colours, mostly light violet, outer ones broadly obovate to rotund; anthers without terminal appendage . . . . . 1. *P. somniferum*
3 Plant with patent setae at least on major veins of lower leaf surface; petals pink . . . . . 2. *P. gracile*
— Plant glabrous; petals red . . . . . 4. *P. decaisnei*

1. P. somniferum L., Sp. Pl. 1: 508. 1753.
"Habitat in Europae australioris ruderatis"

Erect annual herb, 15—150 cm high, unbranched or branching in upper ⅔, never branched from the base. Plant green or more or less strongly glaucous. Leaves 2.0 × 1.0 — 33.0 × 18.0 cm, narrowly obovate, elliptical, oblong, broadly ovate or almost cordiform in outline, deeply divided to incised, coarsely serrate or dentate, obtuse or acute, often apiculate; lobes antrorse, ovate to oblong, coarsely serrate or biserrate, dentate or crenate, obtuse or acute, often apiculate; lower leaves more or less distinctly petiolate, upper leaves increasingly sessile with auriculate-amplexicaulous base; leaves rarely glabrous, sparsely to densely setose. Pedicel 5.0 — 26.0 cm long, glabrous or with patent or appressed setae. Buds 1.0×0.7—3.0×2.0 cm, ovoid to oblong, glabrous or with few to many setae mainly in upper half. Petals broadly obovate to rotund, white or variously violet or red, with or without basal markings of variable size, sometimes eroded or laciniate at apical margin. Stamens many, 0.7 — 2.5 cm long, shorter to longer than ovary; filaments filiform or clavate, whitish or pale violet to dark violet or almost black; anthers 0.7 — 5.0 mm long, oblong, yellow to greenish-brown; ovary obovoid, elliptical, ovoid, cylindrical or globose, 0.6×0.3 — 2.2×0.7 cm, distinctly stipitate; capsule obovoid, elliptical, ovoid, cylindrical or globose, 1.4×0.8 — 9.5×6.5 cm, distinctly stipitate, poricidal or not; stigmatic disc with 5—18(—22) stigmatic rays; free lobes of stigmatic disc

overlapping or not; seeds reniform, 0.6—1.6 mm long, yellowish, brown or blackish, variously glaucous.

Key to the subspecies

1 Sepals glabrous; filaments clavate, mostly whitish or pale violet; leaves mostly without or with only very few setae on upper surface. ssp. *somniferum*
— Sepals with few to many setae; filaments clavate or filiform, dark violet or almost black; leaves mostly setose on upper surface . . . . . ssp. *setigerum*

1a. Papaver somniferum L. ssp. **somniferum**

Syn.: *P. album-et-nigrum* Crantz, Stirp. Austr. 2: 129. 1763.
P. amplexicaule Stokes, Bot. Mat. Med. 3: 181. 1812. — Lectotype: "Calyces glabrous, leaves amplexicaul, incise" (Descr.).
P. somniferum var. *album* DC., Syst. Nat. 2: 82. 1821. — Holotype: Woodv. Med. t. 185 (Ic.).
P. indehiscens Dumort., Fl. Belg. Prodr.: 130. 1827. — Lectotype: "capsulis glaberrimis globosis, per maturitatem indehiscentibus..." (Descr.).
P. somniferum var. *hortense* Hussenot, Chard. Nanc.: 39. 1835. — Lectotype: "Graine noire. capsule déhiscente ovale, non atténuée, mais stipitée..." (Descr.).
P. somniferum var. *stipitatum* Hussenot, Chard. Nanc.: 39. 1935. — Lectotype: "Graine noire. capsule indéhiscente ovée..." (Descr.).
P. somniferum var. *leptocaulotum* Fedde in Engler, Pflanzenr. 40 (IV. 104): 342. 1909. — Type: *Sintenis 836*, 21.6.1889, Keban-Maden (B!).
P. somniferum ssp. *songaricum* Basilevsk., Trudy Prikl. Bot. — 29: 134. 1928. — Lectotype: "Capsula globosa, subglobosa..." (Descr.).
P. somniferum ssp. *indicum* Vesselov., Trudy Prikl. Bot. Suppl. 56: XII. 1933. *P. glaucum* ssp. *indicum* (Vesselov.) Rothm., Ind. Sem. Inst. Gaterslebense 1948: 42. 1949. — Lectotype: "Leaves small and firm, plants of short habit with scanty foliage..." (Descr.).

As a cultivated plant, *P. somniferum* ssp. *somniferum* has been spread very widely by man and often escapes cultivation.

2n = 20 (HRISHI 1960), 22 (HAMMER & FRITSCH 1977, KADEREIT 1986), 44 (HAMMER & FRITSCH 1977)

In the past, various characters like petal colour and petal margin, the presence of "double flowers", opening of the capsules by pores or not, capsule shape, shape of the stigmatic disc, seed colour, leaf shape, habit etc. have been given differing weight in the construction of an infrasubspecific (or infraspecific) classification of ssp. *somniferum*. In the latest attempt, DANERT (1958) established four groups of varieties based on characters of the stigmatic disc and seed colour. Further division into altogether 52 varieties was based on petal colour. As this approach, like all the earlier ones, must be regarded as purely technical without any phylogenetic significance, I want to abstain from presenting an own infrasubspecific classification. I understand ssp. *somniferum* as containing all cultivated material.

For a more detailed discussion of the taxonomic history of ssp. *somniferum* the reader is referred to DANERT (1958).

1b. Papaver somniferum ssp. **setigerum** (DC.) Corb., Nouv. Fl. Normand.: 30. 1893. — Basionym: *P. setigerum* DC., Fl. Franc. 6: 585. 1815. — Type: *M. Requien s. n.* L'île du Levant (G!).

Syn.: *P. setigerum* var. *cylindrocarpum* Fedde in Engler, Pflanzenr. 40 (IV. 104): 342. 1909. — Holotype: *G. V. 26*, 27.5.1855, Les champs de Cabrera (MPU!).

As a weed in vineyards, cornfields, olive groves, under palms, on roadsides or in scrub on sand, volcanic ash, igneous rock or chalk.

Flowering (2—)4—5(—6).

The geographical distribution of *P. somniferum* ssp. *setigerum* is shown in Figs. 1 and 2.

2n = 22 (HAMMER & FRITSCH 1977), 44 (HAMMER & FRITSCH 1977, KADEREIT 1986).

Although most material of *P. somniferum* can be assigned to the two subspecies on the basis of the absence or presence of setae on the sepals and the light or dark colour of the filaments, there are a few specimens without setae on the sepals but with dark filaments. The separation of ssp. *somniferum* and ssp. *setigerum* at specific rank on the basis of only the indumentum of the sepals does not seem to be justified. Although DANERT (1958) used this character together with the presence or absence of apical setae on all teeth of the leaves to key out the two taxa at specific rank, HAMMER & FRITSCH (1977) claim to have seen material with setose sepals otherwise referable to ssp. *somniferum*. All other characters used for the separation of the two taxa, the denser indumentum of ssp. *setigerum*, its more deeply divided leaves, the smaller size of its capsule, which is either elliptical or obovoid in shape, its mostly overlapping free lobes of the stigmatic disc, these lobes are never overlapping in ssp. *somniferum*, the lower number of stigmatic rays and the smaller size of its seeds cannot be used for a clear distinction, as has already been stated very clearly by HAMMER & FRITSCH (1977). Thus, the two taxa seem to be accommodated best at subspecific rank. This conclusion coincides with DEWET's (1981) proposal to assign subspecific rank to wild, weed and cultivated complexes respectively of cultivated species.

Specimens of ssp. *setigerum* with filiform filaments have been seen from Cyprus, the Maltese Islands and Spain.

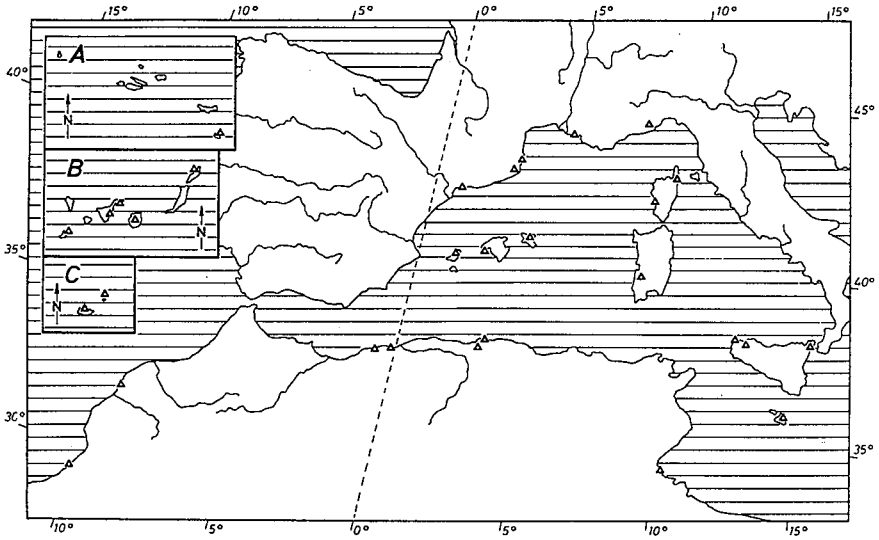


Fig. 1. Distribution of *P. somniferum* ssp. *setigerum* A: Azores, B: Canary Islands, C: Madeira.

The possibility of regarding ssp. *setigerum* as a wild form of ssp. *somniferum*, as originally proposed by DECANDOLLE (1883), has been discussed recently by HAMMER & FRITSCH (1977) and KADEREIT (1986).

2. Papaver gracile Boiss., Ann. Sci. Nat. Bot. Sér. 2, **16**: 372. 1841. — Type: *M. Aucher-Éloy 372*, 1837, Caria (G!).

Erect annual herb, 30—70 cm high, unbranched or branching in upper ⅔, rarely from the base. Plant green or weakly glaucous. Leaves 2.5×1.5—9.0×2.5 cm, narrowly obovate, oblong or ovate, deeply divided to incised, coarsely serrate or crenate, obtuse or acute; lobes antrorse, ovate to narrowly triangular, irregularly incised, crenate or entire, obtuse or acute; lower leaves more or less distinctly petiolate, upper leaves increasingly sessile with auriculate-amplexicaulous base; leaves sparsely to rather densely setose, with setae at least on major ribs of lower leaf surface. Pedicel 15.0—35.0 cm long, glabrous or with few patent or appressed setae. Buds 0.8×0.5—1.2×0.7 cm, ovoid to elliptical, glabrous or with few setae. Petals obovate, uniformly pink in colour. Stamens many, 3.5—7.0(—9.0) mm long, shorter to longer than ovary; filaments filiform, light red; anthers 0.5—1.1 mm long, oblong, light blue; ovary narrowly obovoid, 5.0×2.5—8.0×4.0 mm; capsule narrowly obovoid, 13.0×5.0—18.0×8.0 mm, indistinctly stipitate; stigmatic disc with 4—8 stigmatic rays, margin mostly entire, sometimes sinuate-undulate, without free lobes; capsule poricidal; seeds reniform, 0.5—0.7 mm long, brown, glaucous.

As a ruderal or in open vegetation on calcareous or igneous rocks.

Flowering (3—)4—5(—6).

The geographical distribution of *P. gracile* is shown in Fig. 2.

2n = 14 (KADEREIT 1986), 28 (RECKIN 1973, CAINE 1977).

Recently, GREUTER (1979) described *P. gracile* f. *tenuisectum* from Kastellorizo as a new form with bipinnatisect basal leaves and pinnatisect cauline leaves with linear lobes. This occurred as a single specimen in an otherwise normal population.

My counts of 2n = 14 chromosomes for this species differ from the chromosome number of 2n = 28 reported by RECKIN (1973) and CAINE (1977). As I can confirm the identification of RECKIN's material, it seems that this species is polymorphic for its chromosome number. It certainly would be interesting to find out the distribution of the two cytotypes.

As regards the distribution of the species (Fig. 2), I have not seen one specimen cited by CULLEN (1965a) *(Huber-Morath 10386*, Mut to Kirobasi, 1300 m), which would extend the species' range considerably to the east.

3. Papaver glaucum Boiss. & Hausskn., Fl. Orient. **1**: 116. 1867. — Lectotype: *C. Haussknecht, s.n.* 17.5.1865, Inter segetes pr. Tscharmelik (G-Boiss.!). Isotypes: (B!, W!)

Syn.: *P. rogersii* Exell, J. Bot. **68**: 82. 1930. — Type: *F. A. Rogers 162*, Irak: near Chem che mal (BM!).

P. gaubae Cullen & Rech. f., Fl. Iranica **34**: 16. 1966. — Holotype: *K. H. Rechinger 712a*, 3.6.1937, Montes Elburs centr.: In ditione oppidi Keredj (W!).

Erect annual herb, 10—70 cm high, unbranched or branching in upper ⅔, often branched from the base. Leaves glabrous, strongly glaucous, 2.0×1.0—13.0×4.0 cm, narrowly obovate, elliptical, oblong or ovate, deeply divided to incised, obtuse or acute; lobes strongly antrorse, ovate to narrowly triangular or linear, serrate or entire, obtuse or acute; lower leaves more or less distinctly petiolate, upper leaves increasingly sessile with auriculate-amplexicaulous base. Pedicel 17.0—25.0 cm long, glabrous or sometimes with appressed setae. Buds 1.5×0.9—3.0×2.0 cm, ovoid to elliptical, glabrous or very rarely with few patent setae. Petals broadly reniform to transversely elliptical to broadly obovate or almost rotund, dark red, often at least the inner pair with black basal spots. Stamens many, 8.0—12.0 mm long, shorter to longer than ovary; filaments filiform, dark violet to almost black; anthers 0.8—2.2 mm long, oblong, greenish-brown, with small globose, whitish appendage; ovary broadly elliptical to cylindrical, 8.0×6.0—13.0×7.0 mm, distinctly stipitate; capsule broadly obovoid, elliptical, cylindrical or ovoid, 11.0×7.0—18.0×16.0 mm, distinctly stipitate; stigmatic disc with (5—)7—14 stigmatic rays; free lobes of stigmatic disc mostly overlapping; seeds reniform, 0.6—0.8 mm long, brown, weakly glaucous.

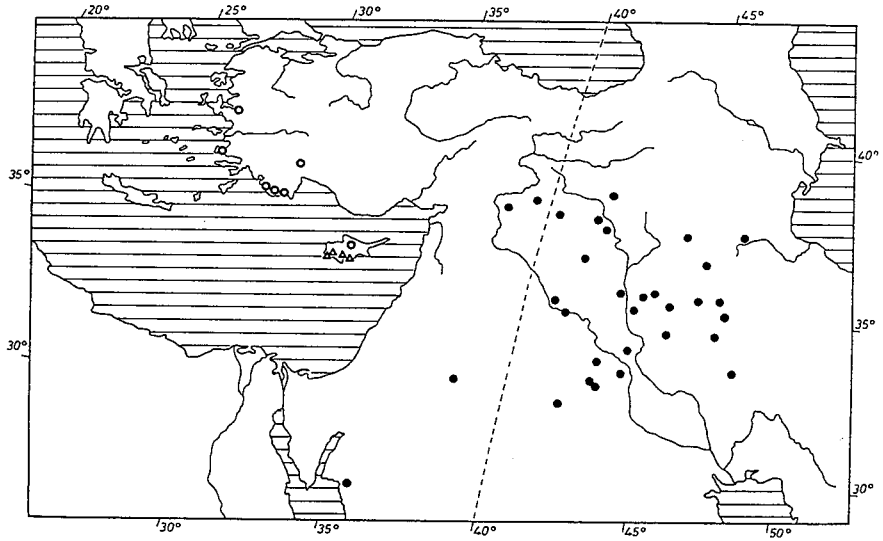


Fig. 2. Distribution of *P. somniferum* ssp. *setigerum* (△), *P. gracile* (○) and *P. glaucum* (●).

As a weed or in open vegetation on scree, rocks, sand, clay, shale, conglomerate rocks, sandstone, limestone, gypsaceous sand.

Flowering 3—6(—7).

2n = 14 (VENT 1970, KADEREIT 1986).

The geographical distribution of *P. glaucum* is shown in Fig. 2.

P. gaubae Cullen & Rech. f., described from only one collection, in my opinion represents only a depauperate form of *P. glaucum*. In habit, leaf shape, indumentum, petal shape and colour as well as the presence of an anther appendage it is identical to this species. The capsule characters used in the diagnosis of *P. gaubae*, namely its turbinate shape and the bidentae free lobes of the stigmatic disc, which are present in only one of the specimens of the type gathering, while another specimen has typically broadening and overlapping lobes with a somewhat irregularly dentate apex, can also be found in other specimens of *P. glaucum* from diverse parts of the species' range. Equally, I can find no differences between *P. rogersii* Exell and *P. glaucum*. What has been referred to as *P. rogersii* also must be regarded as somewhat depauperate material. This opinion is shared by CULLEN (1966, 1980). RECHINGER (1959, 1964) maintains *P. rogersii* as an independent species mainly on the basis of quantitative characters like the height of the plant, the size of the capsule and the number of stigmatic rays. He comments, however, that the distinction between the two species is not clear (RECHINGER 1964). The sheets I have seen of the material RECHINGER identifies as *P. rogersii* clearly are not distinct from *P. glaucum* in more than being somewhat depauperate. The diagnostic character

used by MOUTERDE (1970) for the distinction of the two species, namely the amount of foliage on the main axis above the basal leaves, with only 1 or 2 leaves very near the basal ones in *P. rogersii*, but many leaves well up the axis in *P. glaucum*, seems to me to be dependent on the growth conditions of the plants.

As the presence or absence of appressed setae on the pedicel can differ even within one specimen, and as the distribution of this character shows no regular geographical pattern, I assign no taxonomic value to this character.

4. Papaver decaisnei Hochst. & Steudel ex Elkan, Tent. Monogr. Gen. Papaver: 26. 1839. — Lectotype: *W. Schimper s.n.*, 24.4.1835, Ad montem Sinai (L!). Isotypes: (G!, M!, W!)

Syn.: *P. decaisnei* var. *dielsianum* Fedde in Engler, Pflanzenr. 40 (IV. 104): 344. 1909. — Lectotype: *Aitchinson s.n.*, 12. 1879, Kurrum Valley (B!). Isotype: (K!). Syntype: Griffith 404, Afghanistan (K!).

Erect annual herb, 10—35 cm high, unbranched or branching in upper ⅔, mostly branched from the base. Leaves glabrous, very rarely with apical setae, strongly glaucous, 1.2×0.5—8.0×3.5 cm, narrowly obovate, elliptical, oblong or ovate, deeply divided, obtuse or acute, lobes strongly antrorse, ovate to oblong, distinctly serrate or entire, obtuse or acute; lower leaves more or less distinctly petiolate, upper leaves increasingly sessile with rounded base, rarely auriculate-amplexicaulous. Pedicel 10.0—25.0 cm long, glabrous, very rarely with few patent or appressed setae. Buds 0.7× 0.4—1.2×0.8 cm, ovoid to elliptical, glabrous. Petals obovate, red. Stamens many, 4.5—9.0 mm long, shorter to longer than ovary; filaments filiform, dark violet to almost black; anthers 0.4—0.8 mm long, oblong, brown, sometimes with small apical appendage; ovary narrowly obovoid, elliptical or almost globose, 5.0×4.0—7.0×5.5 mm, indistinctly stipitate; capsule narrowly to broadly obovoid, 8.0×3.5—16.0×8.5 mm, indistinctly stipitate; stigmatic disc with 4—8 stigmatic rays, margin sinuate-undulate or with very short free lobes not exceeding 1.0 mm in length; seeds reniform, 0.6—0.8 mm, brown, glaucous.

As a ruderal or in open vegetation on gravel, granite, shale, sand, calcareous substrate.

Flowering (3—)4—5(—6).

The geographical distribution of *P. decaisnei* is illustrated in Fig. 3.

2n = 56 (VENT 1970).

Of all the taxa in section *Papaver*, *P. decaisnei* is the most critical one in so far as its delimitation both to *P. glaucum* and to *P. dubium* L. of P. sect. *Rhoeadium* Spach is not easy. This has also been observed by CULLEN (1966, 1980).

When *P. decaisnei* is delimited as being entirely glabrous (except for *Kasy 597*, 17.4.1972, S.-Iran: 52 km südl. Sirjan, with patent setae on the pedicel) and having upper cauline leaves with a truncate to rounded or auriculate and somewhat amplexicaulous base and ovate to oblong lobes which are rarely

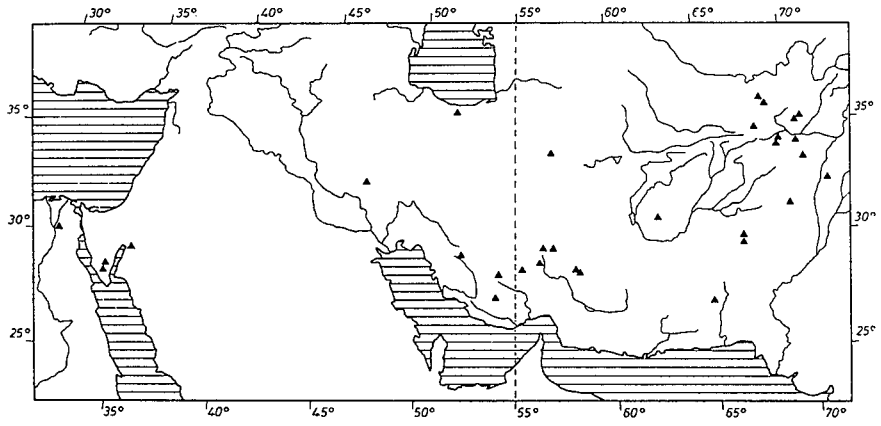


Fig. 3. Distribution of *P. decaisnei.*

more than 3 times as long as broad, the distinction from *P. dubium* with setae on the leaves, axis, pedicel and sepals and upper cauline leaves with a cuneate base and narrowly triangular or linear lobes which often are more than 3 times as long as broad, seems to be possible in most cases. In the Kabul area of Afghanistan the two species can be very similar to each other in capsule shape and habit. Here, the plants often have a somewhat slender habit in that the side branches diverge very little from the main axis. The capsules of such specimens can be equally narrow in both species. From this area, I have seen one specimen (*Volk I/1652*, 6.5.51, Unai) which has upper cauline leaves with auriculate bases but rather narrowly triangular lobes and, above all, hairy leaves, stems and pedicels. This plant must be regarded as intermediate between the two species. One more specimen with scattered appressed hairs on the pedicel and hairs on the leaves from a collection from NE Iran (*Rechinger 50837*, Persia: C: Sharud-Bustam: ad radices montis Peyghambar, S Zamanabad) also is intermediate.

In most of the material, the distinction of *P. decaisnei* and *P. glaucum* presents no difficulty. The distinctly stipitate capsule of *P. glaucum*, which is never more than twice as long as broad makes this species very easy to recognize. In contrast the capsules of *P. decaisnei* have no distinct stalk, are gradually tapering towards their base and mostly are more than twice as long as broad. There are some specimens of *P. decaisnei* from the western part of the species' range in Iran which are similar to *P. glaucum* in capsule proportions. These, however, can be distinguished from *P. glaucum* by the free lobes of their stigmatic disc which, if present, never exceed 1.0 mm in length and are rarely overlapping. These free lobes are much longer in *P. glaucum* and normally are overlapping. Accordingly, the stigmatic disc of the mature capsule exceeds the breadth of the capsule in *P. glaucum*, but not in *P. decaisnei.*

Apparently CULLEN's (1980) concept of *P. decaisnei* is somewhat different from the one presented here, as some of the material he identifies as *P. decaisnei (Rawi 21193, Helbaek 602, 1134)* are referred to *P. glaucum* here. Equally, some of the material listed under *P. decaisnei* by CULLEN (1966) (*Bahai 6675-E, Furse 2359, Haghighi 6552-E, Hedge & Wendelbo 5523, Rechinger 16712, 17893, 18121, 18402, 18668, Regel s.n.* Wazirabad) belong to *P. dubium* on the basis of leaf shape and indumentum in my opinion.

Discussion

The morphological characters used for the subdivision of *P.* sect. *Papaver* proposed by RECKIN (1973) and effected by NOVAK & PREININGER (1980) and PREININGER et al. (1981) are mainly based on wrong observations. This applies to the shape of the capsules, which RECKIN (l.c.) described as "oblong-clavate" for *P. glaucum, P. gracile* and *P. decaisnei.* The capsules of *P. glaucum*, however, are broadly ovoid or obovoid, elliptical or cylindrical and always distinctly stipitate, resembling the capsules mainly of *P. somniferum* ssp. *somniferum.* Equally, I can see no basic differences in the branching of the shoot, which was used as a further argument by RECKIN. Although *P. somniferum* ssp. *somniferum* mostly is unbranched, which is likely to be the result of its cultivation, and although ssp. *setigerum* can be found branching in its upper parts only, there are sufficiently many specimens of *P. glaucum, P. gracile* and *P. decaisnei* branching only in their upper parts. The description of the indumentum of the pedicel (PREININGER et al. 1981) as either absent or of patent hairs in *P. somniferum* ssp. *somniferum* and ssp. *setigerum*, and of appressed hairs in *P. glaucum, P. gracile* and *P. decaisnei* is not correct for *P. somniferum* ssp. *setigerum*, which has either appressed or patent hairs on its pedicel, not for *P. glaucum*, which is either glabrous or has appressed hairs, not for *P. gracile*, in which all three possibilities can be found, and not for *P. decaisnei* with its always glabrous pedicel. As regards the filaments, which have been claimed to be always clavate in *P. somniferum* ssp. *somniferum* and ssp. *setigerum* by PREININGER et al. (1981), filiform filaments can be found in ssp. *setigerum.* Finally, *P. somniferum* ssp. *somniferum* and ssp. *setigerum* cannot be characterized by non-overlapping free lobes of the stigmatic disc as opposed to broad and mostly overlapping lobes in *P. glaucum, P. gracile* and *P. decaisnei*, as done by PREININGER et al. (1981). The free lobes of the stigmatic disc are mostly overlapping in *P. somniferum* ssp. *setigerum* and *P. glaucum*, non overlapping in *P. somniferum* ssp. *somniferum*, absent in *P. gracile* and mostly absent in *P. decaisnei.*

Contrary to the interpretation of section *Papaver* as consisting of two more or less well separated groups, I (KADEREIT 1986) recently put forward the hypothesis that *P. somniferum* ssp. *somniferum* and ssp. *setigerum* are intermediate in their morphology between *P. glaucum* and *P. gracile*, and are to be regarded as the triploid hybrid and its hexaploid derivative respectively be-

tween taxa similar to the diploid *P. glaucum* and tetraploid *P. gracile*. The morphological differences between the two subspecies of *P. somniferum* were interpreted as segregation of parental characters, with ssp. *somniferum* showing more similarity to *P. glaucum*, and ssp. *setigerum* to *P. gracile*. This hypothesis on the origin of *P. somniferum* finds support in the discovery of morphine-type alkaloids in *P. gracile*, and provides an explanation for the different chromosome base numbers found in section *Papaver*, thus removing the last obstacle for the perception of section *Papaver* as a natural group, which is evident from the morphology of the different taxa.

Geographically, section *Papaver* is well diversified. While *P. somniferum* ssp. *setigerum*, except for its presence on Cyprus, is a West-Mediterranean element, *P. gracile* is an East-Mediterranean element. On the other hand, *P. glaucum* can be found in the western part of the Irano-Anatolian province and the eastern part of the Mesopotamian province of the Irano-Turanian region (terminology following ZOHARY 1973), and the closely related *P. decaisnei* occurs mainly along the border of the Irano-Turanian region and the Nubo-Sindian province of the Sudanian region in Iran, Afghanistan and Pakistan and, around Mt. Sinai, in the westernmost part of the Nubo-Sindian province, leaving out the eastern part of the Saharo-Arabian region. ZOHARY (1973) quotes *P. decaisnei* as a representative of the Sudanian element in Iran.

The compatibility system is known in *P. somniferum* ssp. *somniferum* and ssp. *setigerum*, *P. gracile* and *P. glaucum*. The first three of these taxa are self-compatible and strongly self-pollinating in that the anthers already open within the flower bud. At this time, the stigma is already receptive. *P. glaucum*, on the other hand, is perfectly self-incompatible. Although no observations have been made on the pollination ecology of this species, it seems possible that the apical anther appendage plays some part in its pollination.

Probably the occasional presence of such anther appendages in *P. decaisnei* allows to assume a polymorphism of the compatibility system in this species.

Acknowledgements

I should like to express my thanks to Prof. Dr. P. LEINS and Dr. K. H. SENGHAS for critically reading the manuscript, and to Mr. F. RÜCKERT for the preparation of the figures.

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Accepted for publication October 25, 1985.

Address of the author:
Dr. J. W. KADEREIT, Institut für Systematische Botanik und Pflanzengeographie der Universität Heidelberg, Im Neuenheimer Feld 328, D-6900 Heidelberg.

Specimens seen

1a. P. somniferum ssp. somniferum

Ahlberg s.n., 8.1871, Upsalia (BM); *Ali 26003a* (BM); *Almquist s.n.*, 7.1866, Upland (BM, C); *Balfan 66* (BM); *Ballard 1069* (K); *Ballard & Golby 169* (K); *Bjornland & Schumacher 562* (C); *Bonnet s.n.*, 2.6.1873, Neuvon-Cote d'Or (K); *Bonnet s.n.*, 21.7.1879, Val de Sozon (K); *Bourgeau s.n.*, 8.5.1853, Lagos, Algarve (C); *Britton s.n.*, 31.8.1902, Laddesdown, Kent (K); *Brown 669* (C); *Cartedo de Saivo s.n.*, Leisca in Estramadura (K); *Chien s.n.*, 26.4.1936, Chengtu (BM, E, W); *Chung s.n.*, Jukien (K); *Coode & Jones 246* (E); *Copley 3250* (C, W); *Daveae 4817* (BM); *Dubuis 8298* (C); *Edelberg 2124* (C); *Faber 470* (K); *Fernandes, Fernandez & Matos s.n.*, 3.5.1951, entre Alcacez do sal e Grandola (BM, C); *Fries s.n.*, 8.1907, Upsala (BM); *Farrat & Barbey s.n.*, 1879, Lausannes (K); *Gay s.n.*, 30.6.1837, Jardin de Luxembourg (K); *Gelting s.n.*, 21.7.1937, Frederiksø (C); *Gilbert 232* (K); *Gilliat-Smith 1676* (K); *Goncalves 3977* (BM); *Goncalves 4470* (BM); *Gregor s.n.*, 5.8.07, Kent: Aylesford (K); *Graham 486* (BM); *Grøntved s.n.*, 18.7.35, Gørding (C); *Grove s.n.*, 25.6.81, Kopenhagen (C); *Hampshire 556* (BM); *Hampshire 561* (BM); *Hansen s.n.*, 15.10.1961, Copenhagen (C); *Hansen s.n.*, 15.7.1962, Kopenhagen (C); *Hansen s.n.*, 8.7.1964, Bossehage (C); *Hansen s.n.*, 20.4.1967, Insel Santorin (C); *Hansen s.n.*, 9.8.1967, Ronbjerg (C); *Hansen s.n.* 27.5.1969, Porto Santo (C); *Hansen s.n.*, 19.7.1969, Copenhagen (C); *Hansen s.n.*, 26.8.1972, Copenhagen (C); *Hansen s.n.*, 4.8.1984, Rømø (C); *Hansen 6* (C); *Hansen 136* (C); *Ho-Ch'ang Chow 267* (E); *Hosie s.n.*, 1910, China, Kanton or Shensi (K); *Indian Opium Enquiry 29571* (K); *Indian Opium Enquiry 30296* (K) *Jahn s.n.*, 21.8.1905, Eger (W); *Jeronimo 209* (BM); *Johanssen s.n.*, 8.1885, Malmo (BM); *Johanssen s.n.*, 7.1909, Malmo (BM); *Kawan 681* (K); *Keenan, U Tun Aung & U Tha Hla 3855* (E); *Kerr s.n.*, 27.2.1921, Siam (BM); *Køie 1370* (C); *Korb s.n.*, 23.7.1914, Teplitz (W); *Krieger s.n.*, 7.1913, Chemnitz (W); *Lagerwall s.n.* 1914, Stockholm (W); *Lange s.n.*, 3.6.1852, Casa de Campo (C); *Larsen s.n.*, 17.7.1954, Dyrhet (C); *Larsen 1610* (C); *Lindsay 895* (BM , K); *Licent 8569* (BM); *Lowe 192* (BM); *Ludlow & Sherriff 3034* (BM); *Marris 540* (BM); *Martin s.n.*, 12.7.1922, Addiscombe (K); *Maung Po Khant 15248* (K); *Maximowicz s.n.*, 1861, Japonia, Hakodate (BM); *McDonald s.n.*, 1849, Arabia petraea (K); *Meyers & Dinsmore 4973* (E); *Moseley s.n.*, Bermuda (BM); *Newill & Baring-Gould 117* (BM); *Paillot 2407* (BM); *Paulsen 1422* (C); *Petersen s.n.*, 1885, Ved Kristiania (W); *Polunin, Sykes & Williams 1919* (BM, E); *Riddersstolpe s.n.*, 1895, Oland (W); *Rock 1797* (E); *Royle s.n.*, NW India (K); *Sahizu 272* (K); *Schlagintweit s.n.*, 26.—28.7.1856, Tibet: Prov. Nubra: Kardong to Diskit (BM); *Sennen 6794* (BM, W); *Spindler s.n.*, 6.01, Weissenburg (W); *Stainton 2732* (BM); *Steward & Cheo 85* (W); *Taylor s.n.*, 7.1860, Cudham (Kent) (K); *Tharnberg s.n.*, 20.7.1967, Jaegerspris (C); *Thurston s.n.*, 12.7.1913, Cornwall (K); *Tsiang 4803A* (BM, C, W); *Usher s.n.*, 7.1877, Banbury, Oxford (BM); *Vadcourt 4685* (K); *Watt 7208* (K); *Welwitsch 222* (BM); *Wight 55* (K); *Lazar 76* (W); *Zerny s.n.*, 21.8.1919, Ulrichs (W);

1b. P. somniferum ssp. setigerum

Aldridge 1366 (BM); *Autheman 1945* (K); *Bowden & Pasims 1357* (BM); *Bowden & Pasims 1683* (BM); *Bourgeau 680* (BM, K); *Bourgeau s.n.*, 2.5.1883, Gerona (Tremols) & *Champagneux s.n.*, 15.5.42, Les Terres (C); *Cannon 3971* (BM); *Herb. Churchillanum s.n.*, 12.4.69, Mauton (K); *Davis 3469* (BM, W); *Davis 51732* (BM); *Debeaux s.n.*, 6.5.1869 Corse, Bastion Morifom (BM, W); *Edmondson & McClintock 2974* (E); *Faure s.n.*, 21.3.1913, Environs d'Oran (BM); *Faure s.n.*, 9.4.1925, Sidi-Bakti (BM); *Font-Quer 224* (BM); *Herb. Gadèceau s.n.*, (BM); *Garnett G 141/8* (BM); *Gasparini s.n.*, 1839, S. Giuseppe, Sicilia (CGE); *Gussone s.n.*, Palermo (C); *Hansen s.n.*, 15.4.1968, Ibiza, Cala Gracio near San Antonio (C); *Hansen 22* (C); *Hansen 47* (C); *Hansen 229* (C); *Hansen 433* (C); *Huet du Pavillon s.n.*, 21.4.1855, S. Giuliano supra Trapani (K, W); *Hunt s.n.*, 1848, St. Mary's, Azores (K); *Jamin 121* (BM, W); *Joad s.n.*, 4.1869, Menton (K); *Joad s.n.*, 27.4.1880 Alassio, Liguria (K); *Jordan 43* (W); *Kennedy 1172* (K); *Kotschy 856* (W); *Kralik s.n.*, 24.4.1834, Gabes (W); *Lefebvre s.n.*, 24.5.1861, Blidah (BM, W); *Lefebvre s.n.*, d'Alger (W); *Linton s.n.*, Cadagués (BM); *Lowe H 42* (K); *Lowe 130 bis* (BM); *Lowe 153* (BM); *Lowe 193* (BM); *Lowe 910* (BM, K); *Mandon s.n.*, 4.—5.1865—66 (BM, C, W); *Manton s.n.*, 1856—57, Madeira (W); *Maude s.n.*, 3.1932, Puerto Orotava (BM); *Meikle 2868* (C, K); *Miller, Russel & Sutton 584* (BM); *Montago-Pollock 34* (BM); *Murray s.n.*, 23.4.1902, Tacaronte (K); *Reade s.n.*, Maltese Islands (BM); *Requien s.n.*, 5.1848, Ajaccio (W); *Sennen 225* (W); *Sennen 3655* (K, W); *Herb. Swainson s.n.*, 5.1810, 10 miles from Messina (CGE); *Trethewy s.n.*, 1929, Gran Canaria (BM);

2. P. gracile

Bozakman & Fitz 310 (W); *Buttler & Erben 17343* (M); *Davis 3070* (K); *Davis & Polunin 25494* (BM, K); *Davis 40884* (E, K); *Eiselt s.n.*, 10.4.1963, Türkei: Lycia, Dodurga sw. Kestep (W); *Heldreich 644* (B, BM, G); *Kennedy 1736* (K); *Meikle 2719* (C, K); *Schwarz 556* (B); *Schwarz 598* (B); *Sintenis 522* (G, K, M).

3. P. glaucum

Adqa & Sa 1415 (E); *Anders 1223* (W); *Anders 1308* (W); *Archibald 1937* (E); *Barkley 4424* (W); *Barkley 5160* (W); *Barkley & Haddad 7409* (K); *Bowles Scholarship Bot. Exp. 1122* (K); *Bowles etc. 1256* (K); *Bowles etc. 2436* (K); *Bowles etc. 2440* (K); *Baytop 12809* (E); *Davis 42868* (E); *Davis 43238* (E); *Davis & Hedge 28358* (BM); *Dickson 1* (K); *Dickson 1108* (K); *Evin 5864 E* (W); *Evin 5870 E* (W); *Furse 2078* (K); *Gauba 79* (W); Hort. Genèv. 10.5.1869 (G); Hort. Genèv. 27.4.1869 (G); *Handel-Mazzetti 1058* (W); *Handel-Mazzetti 1407* (W); *Haussknecht s.n.*, 17.5.1865, inter segetes pr. Tscharme-

lik (B, W); *Haussknecht s.n.*, 7.1866, Jardin de Naleyres (G); *Haussknecht s.n.*, 5.1867, Djebel Taktayh (B, BM, W); *Helbaek 602* (C, K); *Helbaek 1134* (K); *Helbaek 1138* (K); *Ingham 168* (K); *Fl. of Iraq 4330* (K); National Herbarium Iraq 7046 (K); *NH Iraq 7321* (K); *NH Iraq 13599* (K); *NH Iraq 14671* (K); *NH Iraq 15611* (K); *NH Iraq 21193* (K); *NH Iraq 22146* (K); *NH Iraq 27908* (K); *NH Iraq 30247* (K); *NH Iraq 30532* (K); *NH Iraq 30891* (K); *NH Iraq 30967* (K); *NH Iraq 31942* (K); *NH Iraq 38405* (K); *NH Iraq 40903* (K); *NH Iraq 41724* (K); *NH Iraq 44309* (K); *Jacobs 6672* (W); *Koelz 18611* (W); *Køie 707* (C); *Kotschy 170* (W); *Low 165* (BM); *Maudis 705* (K); *Meade 161* (BM); *Meinertzhagen s.n.*, 26.4.33, Rutbah (BM); *Mouterde 453* (G); *Mouterde 11428* (G); *Pabot s.n.*, 11.5.1955, Col de Kham(ru) (G); *Pabot s.n.*, 11.5.1955, Rives du Tigre (G); *Pabot s.n.*, 17.5.1955, Jebel Abd el Aziz (G); *Rechinger 712a* (W); *Rechinger 10169a* (B, E, G, K, M, W); *Rechinger 12530* (W); *Rechinger 15647* (W); *Rechinger 39364* (W); *Rogers 0150* (BM); *Rogers 0162* (BM); *Sintenis 917* (K); *Sintenis 2710* (W); *Strauss s.n.*, 2.4.1909, In m. Kuh-i-Amtscheck (W); *Thesiger 1090* (BM); *Thesiger 1091* (BM); *Wendelbo, Assadi & Shirdelpur 12130* (W); *Wendelbo & Assadi 16524* (W); *Wheeler s.n.*, 22.5.1955, Jarmo (K); *Wheeler s.n.*, 11.5.1956, Shaqlawah (E); *Wheeler s.n.*, 25.5.1961, Baghdad: Jarriyah (E); *Wheeler s.n.*, 17.5.1957, Serzang (E);

4. P. decaisnei

Aitchinson s.n., 12.1879, Kurrum Valley (B, K); *Biggs 13163* (BM); *Boissier s.n.*, 3.1864, Arabia petraea, convent du Sinai (G); *Bornmüller 6099* (BM); *Bot. Sect. Min. of Agric. Egypt 201295* (K); *Collenette 956* (K); *Cramer s.n.*, 7.5.1891, Sinai, au sud du convent (G); *Crookshant 43* (K); *Davis 9035* (BM); *Davis 9094* (K); *Davis & Bokhari 56247* (E); *Dieterle 225* (M); *Drummond 14816* (K); *Drummond 14817* (E); *Edelberg 254* (C); *Edelberg 528* (C); *Foroughi 15920* (W); *Frauenfeld s.n.*, 1855. Sinai (W); *Gilli 855* (W); *Gilli 856* (W); *Gilli 857* (W); *Gilli 858* (W); *Griffith 404* (K); *Harsukh 20454* (K); *Herb. Hookerianum 781* (K); *Johnston s.n.*, 10.4.1897, Khyber Pass (E); *Kasy 597* (W); *Kerstan F-84* (W); *Koelz 15896* (W); *Kotschy 823* (BM, W); *Lace 3983* (K); *Lamond 1112* (G); *Lindberg 1019* (W); *Meinertzhagen s.n.*, 3.1928, Feiran Oasis (BM); *Mirzayan 229 E* (W); *Mirzayan 230 E* (W); *Moussavi s.n.*, 23.5.75, Fars: Estahbanat, Kuh-e-Barreh (E); *Moussavi s.n.*, 25.5.75, Fars: Neyriz, Moshkan (E); *Muschler s.n.*, 1.1903, Cairo, Nokkahan (K); *Neubauer 88* (W); *Neubauer 424* (W); *Neubauer 425* (W); *Neubauer 4164* (W); *Parris s.n.*, 3.5.1975, Kerman prov., east side of Khabr massif (E); *Podlech 17230* (M); *Podlech 17643* (M); *Podlech 17796* (M); *Podlech 30273* (M); *Podlech 30361* (M); *Rechinger 3063* (W); *Rechinger 3078* (W); *Rechinger 3124* (B, G, K, M, W); *Rechinger 3690* (W); *Rechinger 3786* (G); *Rechinger 16657* (M, W); *Rechinger 28254* (W); *Rechinger 28406* (W); *Rechinger 28447* (W); *Rechinger 29195* (W); *Rechinger 29903* (W); *Rechinger 50837* (W); *Ruttner 104* (W); *Ruttner 452* (W); *Schimper s.n.*, 24.4.1835, ad montem Sinai (G, M, W); *Sharif 232 E* (W); *Stainton 2185* (BM, E).

Bot. Jahrb. Syst.	108	1	17—50	Stuttgart, 17. Dezember 1986

Studies in Annonaceae. VI
A leafanatomical survey of genera of Annonaceae in the Neotropics

By

A. K. van Setten and J. Koek-Noorman

With 26 figures and 2 tables in the text

Abstract

SETTEN, A. K. VAN & KOEK-NOORMAN, J.: Studies in Annonaceae. VI. A leafanatomical survey of genera of Annonaceae in the Neotropics. — Bot. Jahrb. Syst. 108: 17—50. 1986. — ISSN 0006-8152.

Within the scope of the multidisciplinary research project on systematics of Annonaceae, a survey of the leafanatomical features and their distribution in the neotropical Annonaceae is presented. The studied specimens form a rather homogeneous group, as may appear from the family description given here. A detailed study of the leafanatomical features reveals, that differences are mainly found in the indument, the position and contents of the idioblasts, the structure of the primary vein, the type of crystals in the epidermal cells, and the type of sclereids.

Based on character states, phenetic similarities and differences are discussed and compared with the classifications of FRIES (1959) and WALKER (1971).

Introduction

In 1982 a multidisciplinary research project on systematics of Annonaceae was started. For a survey of the scope and planning of this project, see MAAS (1984). One of its objectives is to provide genus-descriptions which are based on as many features as possible. Among other subdisciplines of plant systematics, the leaf anatomy is a valuable source of information.

Although the Annonaceae are represented by many species in all tropical areas, thusfar few studies have been carried out with regard to the occurrence and variation of leafanatomical features and their taxonomic significance in

0006-8152/86/0108-0017 $ 08.25

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