KTH.

Extrait : le reste au canon
sur l'Afrique du Nord

Notes RBG Edinb. 45(2): 225–286 (1988)

A REVISION OF PAPAVER L. SECTION RHOEADIUM SPACH

J. W. KADEREIT*

ABSTRACT. *Papaver* L. sect. *Rhoeadium* Spach (Papaveraceae) is considered to contain sixteen species: *P. pinnatifidum* Moris; *P. purpureomarginatum* Kadereit, *sp.nov.* from the Aegean, adjacent mainland Greece and Turkey and Cyprus; *P. dubium* L. with five subspecies including subsp. *laevigatum* (M.Bieb.)Kadereit, *comb. et stat.nov.*, subsp. *erosum* (Litv.)Kadereit, *comb. et stat.nov.* and subsp. *glabrum* (Royle)Kadereit, *comb. et stat.nov.*; *P. rechingeri* Kadereit, *sp.nov.* from SW Iran and adjacent Iraq; *P. arachnoideum* Kadereit, *sp.nov.* from Turkey; *P. arenarium* M.Bieb.; P. *tenuifolium* Boiss. & Hohen. ex Boiss.; *P. commutatum* Fischer & C. Meyer with two subspecies, including subsp. *euxinum* Kadereit, *subsp.nov.* from N Turkey; *P. chelidoniifolium* Boiss. & Buhse; *P. guerlekense* Stapf; *P. stylatum* Boiss. & Bal. ex Boiss.; *P. clavatum* Boiss. & Hausskn. ex Boiss.; *P. umbonatum* Boiss.; *P. carmeli* Feinbrun; *P. humile* Fedde and *P. rhoeas* L. Distribution maps are provided for all taxa except *P. dubium* subsp. *dubium* and *P. rhoeas* outside SW Asia, and chromosome numbers are given for most taxa. The relationships between the various taxa are discussed and hypotheses are made on the origin of the widespread *P. dubium* subsp. *dubium* and P. *rhoeas*.

INTRODUCTION

Among the annual sections of the genus *Papaver* L., sect. *Rhoeadium* Spach is by far the largest. In the genus only sect. *Meconella* Spach, a group of largely arctic-alpine perennials, contains more species. Apart from the treatment of sect. *Rhoeadium,* or the species known of it, in systematic works of a general nature (e.g. De Candolle, 1821; Spach, 1839) it was dealt with monographically by Viguier (1814) in his *Histoire Naturelles, Médicale et Économique, des Pavots et des Argémones,* by Elkan (1839) in his *Tentamen Monographiae Generis Papaver,* by Kuntze (1887) in *Plantae Orientali-Rossicae* and by Fedde (1909) in *Das Pflanzenreich.* In these works rather different approaches were taken. On the one hand, Elkan (1839) and Kuntze (1887) accommodated all taxa known at their time in two (*P. rhoeas* L. and *P. dubium* L.) or one (*P. rhoeas*) species respectively. On the other hand, a large number of new species were described by Fedde (1909), often from single herbarium specimens only or including obvious monstrosities, and by Timbal-Lagrave (1870, 1892), Jordan (1861, 1864) and Wein (1911 a–c), who worked on a regional scale. Both these attitudes result from the predominance in this section of closely similar and highly variable species. In the present account no taxon is accepted of which only one herbarium specimen has been seen, and a more or less continuous distribution area, except for disjunctions known from many other examples, has been demanded from all species and subspecies recognized. This approach has led to the acceptance of 16 species with nine subspecies and three varieties.

MATERIAL & METHODS

For the SEM-photographs, seeds were stuck on aluminium stubs with double-sided adhesive tape and sputtered with gold in a Balzers Union

*Institut für Systematische Botanik und Pflanzengeographie, Im Neuenheimer Feld 328, 6900 Heidelberg, W Germany.

AG sputter. The photographs were taken on a Leitz AMR 1200 microscope.

For the counting of chromosome numbers, root tips were pretreated in a solution of 0·4% 8-hydroxyquinoline for 2–3 hours, followed by fixation in 3:1 ethanol : acetic acid. After hydrolysis in 1N HCl at 60°C for 6 minutes, they were stained in leucobasic fuchsin for 2–3 hours and squashed in a drop of proprionic orcein.

Origin of material: *P. pinnatifidum*: 30km E of Tiznit on road to Tafraout, Morocco, 12 v 1982, *Davis & King* 68238 (E; seeds and chromosome number); *P. purpureomarginatum*: Ep. Kidhonia: peninsula Akrotiri, Crete, 24 iv 1976, *Greuter & Charpin* 13348 (W; seeds and chromosome number); *P. dubium* subsp. *dubium*: Haan, W Germany, viii 1983, *Kadereit* s.n. (seeds and chromosome number); *P. dubium* subsp. *lecoqii*: Grantchester, England, 11 vii 1983, *Kadereit* s.n. (seeds and chromosome number); *P. dubium* subsp. *laevigatum*: Crimea: distr. Simferopol, 9km S of Simferopol, U.S.S.R., 5 vi 1953, *Davis* 33546 (E; seeds); *P. dubium* subsp. *erosum*: Gorgan: Shahpassand to Bodjnourd, Almeh, Iran, 10 vi 1975, *Herb.Min.Ir. Agric.* 34154 (E; seeds); unknown origin, *Hort.Centr.Cult. Herb. Medic.Brno* no. 100, sub. *P. litwinowii*; Ashkhabad, U.S.S.R. (chromosome number: 2n = 28); Echegradsorsk bei Chatschik, U.S.S.R., 10 vii 1976, *Avetisjan & Manakjan* s.n. (WU; chromosome number: 2n = 42); *P. dubium* subsp. *glabrum*: Bamian: inter Bamian et Bandiamir, Afghanistan, 13 vii 1962, *Rechinger* 18121 (W; seeds); *P. rechingeri*: Distr. Kut Al-Imara: Badra, Iraq, 12–13 iv 1957, *Rechinger* 9203 (W; seeds); *P. arachnoideum*: Sinop A 5, after Kargi, Turkey, 1 vi 1969, *Tobey* 2816 (E; seeds); *P. arenarium*: Megrinsk bei Agarak, U.S.S.R., 27 v 1977, *Avetisjan et al.* s.n. (WU; seeds and chromosome number); *P. tenuifolium*: Schir-Dere in m. Elbrus pr. Derbend, Iran, *Kotschy* 247 (W; seeds); *P. commutatum* subsp. *commutatum*: unknown origin, *Hort.Bot. Hauniensis* s.n. (seeds and chromosome number); *P. chelidoniifolium*: Gilan: 7km W Bandar-E Pahlavi, Iran, 14 v 1971, *Rechinger* 39623 (W; seeds); *P. guerlekense*: Karpathos: in oropedio Katolastos, Greece, 23 v 1963, *Greuter* 5490 (W; seeds); Mugla, 13km S of Fethiye, Turkey, 16–28 v 1976, *Polunin* 13977 (E); Kemer, Turkey, 11 viii 1984, *Kadereit* 84/72; near Termessos, roadside, Turkey, 19 viii 1984, *Kadereit* 84/147 (chromosome number); *P. stylatum*: Prov. Adana: distr. Misis: Nur Dag above Kizildere, Turkey, 17 iv 1957, *Davis & Hedge* 26751 (E; seeds); *P. clavatum*: Mardin: Mardin–Nusaybin, 10–20km from Nusaybin, Turkey, 22 v 1957, *Davis & Hedge* 28425 (BM; seeds); *P. umbonatum*: Jerusalem, Israel, 28 v 1983, *Liston* s.n. (seeds and chromosome number); *P. humile*: Tel Yizhak, Israel, 17 vi 1983, *Liston* s.n. (seeds and chromosome number); *P. rhoeas* var. *rhoeas*: Grantchester, England, vii 1983, *Kadereit* s.n. (seeds and chromosome number).

KEY TO THE SPECIES

1a. Mature capsules twice to more than twice as long as broad 2
1b. Mature capsules less than twice as long as broad 10

2a. Plants with setose and arachnoid hairs 3
2b. Plants with few to many setose hairs only 4
3a. Leaves and axis with arachnoid indumentum; terminal setae on leaf lobes almost always longer than 1·5mm and up to 5mm long. (N and C Turkey W of line Trabzon to Adana) . . . . . **5. P. arachnoideum**
3b. Only axis with mostly few arachnoid hairs; terminal setae on leaf lobes never longer than 1·5mm. (SE Turkey E of Adana towards N Iraq) . . . . . **12. P. clavatum**
4a. Sepals with ± conspicuous subapical processes; leaves often up to 2-pinnatipartite, ultimate segments at least of upper leaves often less than 1mm broad. (Iranian Azerbaijan, Caucasia, Caucasus and E coast of Caspian Sea) . . . . . **6. P. arenarium**
4b. Sepals very rarely with mostly inconspicuous subapical processes; if present, ultimate leaf segments of upper leaves rarely narrower than 1mm 5
5a. Anthers almost always light yellow 6
5b. Anthers never light yellow, but dull yellow-brown, greenish or purplish 8
6a. Setose hairs rather thin-walled and soft, flat in dry material; ultimate leaf segments at least of upper leaves rarely broader than 2mm; pedicel with patent setae. (WC Iran S of Elburz Mts) . . . . . **7. P. tenuifolium**
6b. Setose hairs rather stiff; ultimate leaf segments mostly broader than 2mm; pedicel almost always with appressed setae. (Atlantic Islands, W and C Mediterranean or the Aegean, adjacent mainland Greece and Turkey or Cyprus) 7
7a. Sepal margin almost always dark violet; upper stem leaves often entire or with one basal pair of ± distinctly recurved lobes, rarely with more lobes. (Aegean, adjacent mainland Greece and Turkey or Cyprus) . . . . . **2. P. purpureomarginatum**
7b. Sepal margin never dark violet; upper stem leaves very rarely entire, mostly with many strongly antrorse lobes or teeth. (Atlantic Islands or the W or C Mediterranean) . . . **1. P. pinnatifidum**
8a. Stigmatic disc flat or slightly vaulted at maturity or free lobes of stigmatic disc curved upwards at maturity 9
8b. Stigmatic disc ± distinctly umbonate at maturity 16
9a. Free lobes of stigmatic disc conspicuously curved upwards at maturity; lobes often longer than broad; upper stem leaves with winged petiole mostly clasping axis. (Mt Carmel area in N Israel) . . . . . **14. P. carmeli**
9b. Free lobes of stigmatic disc not or little curved upwards at maturity; lobes mostly about as long as broad or broader 10
10a. Stigmatic disc broader than capsule diameter at maturity 11
10b. Stigmatic disc narrower to as broad as capsule diameter at maturity 13
11a. Capsules gradually narrowing into clavate base; terminal segment of lower leaves mostly less than twice as long as broad; plants almost always with red tinge on leaves, axis or at least some setae. (SW

Turkey E to Cape Anamur, the NW (N Sporades) or SE Aegean or Cyprus) . . . . . **10. P. guerlekense**

11b. Capsules mostly ± strongly contracted at base; if narrowing gradually, terminal segment of lower leaves mostly more than twice as long as broad or upper stem leaves clasping axis with winged petiole 12

12a. Upper stem leaves with winged petiole mostly clasping axis; plants often of ascending habit, mostly with few leaves on primary axis above basal rosette. (Israel, Jordan, Egypt or Libya) . . . . . **15. P. humile**

12b. Upper stem leaves very rarely with winged petiole; if present, very rarely clasping axis; plants mostly of erect habit with mostly many leaves on primary axis above basal rosette. (Widespread weed) . . . . . **16. P. rhoeas**

13a. Ultimate segments of lower leaves very rarely broader than 3mm. (SE Turkey E of Adana towards N Iraq) . . **12. P. clavatum**

13b. Ultimate segments of at least some lower leaves broader than 3mm 14

14a. Capsules often rather strongly contracted below pores; terminal segment of lower leaves mostly less than twice as long as broad; plants almost always with red tinge on leaves, axis or at least some setae. (SW Turkey E to Cape Anamur, the NW (N Sporades) and SE Aegean or Cyprus) . . . . . **10. P. guerlekense**

14b. Capsules ± weakly contracted below pores; plants never with red tinge 15

15a. Pedicel with few patent to half-appressed setae; stigmatic disc always with dark violet marks on margin. (SW Iran or adjacent Iraq) . . . . . **4. P. rechingeri**

15b. Pedicel almost always with ± dense indumentum of appressed setae; stigmatic disc without dark violet marks. (Widespread weed) . . . . . **3. P. dubium**

16a. Plants of ± subscapose habit; capsules below pores 4·5–10mm long, narrowing ± gradually towards base. (SE Turkey around Adana) . . . . . **11. P. stylatum**

16b. Plants ± regularly leafy; if capsules below pores shorter than 10mm, capsules ± strongly contracted at base 17

17a. Ultimate segments of lower leaves very rarely broader than 3mm. (SE Turkey E of Adana towards N Iraq) . . **12. P. clavatum**

17b. Ultimate segments of at least some lower leaves broader than 3mm 18

18a. Terminal segment of lower leaves mostly less than twice as long as broad; basal lobes of uppermost stem leaves often little longer or shorter than basal pair of lobes of terminal segment; umbo mostly distinct. (Syria, Lebanon, Israel or Jordan) . . . . . **13. P. umbonatum**

18b. Terminal segment of lower leaves mostly more than twice as long as broad; basal lobes of uppermost stem leaves mostly distinctly longer than basal pair of lobes of terminal segment; umbo mostly indistinct. (Widespread weed) . . . . . **16. P. rhoeas**

19a. Setose hairs rather thin walled and soft, flat in dry material; ultimate leaf segments at least of upper leaves rarely broader than 2mm. (WC Iran S of Elburz Mts) . . . . **7. P. tenuifolium**

19b. Setose hairs rather stiff; ultimate segments of leaves mostly broader than 2mm 20

20a. Upper leaves trifid with large mostly incised terminal and much smaller lateral almost patent lobes; petals mostly gradually darkening towards their base, rarely with distinct spots; sepals mostly subglabrous; capsules up to 7mm long. (N Iran) . . . . . **9. P. chelidoniifolium**

20b. Petals either uniformly red or with distinct basal or subbasal spots; sepals mostly with ± dense setose indumentum; capsules mostly longer than 7mm 21

21a. Pedicel with mostly very dense indumentum of short (0·4–1·4mm) densely appressed setae; capsules often slightly stipitate. (Caucasia or Iranian Azerbaijan) . . . . . **8. P. commutatum**

21b. Pedicel with patent or with longer appressed setae 22

22a. Free lobes of stigmatic disc conspicuously curved upwards at maturity; lobes often longer than broad. (Mt Carmel area in N Israel) . . . . . **14. P. carmeli**

22b. Free lobes of sitgmatic disc not or little curved upwards at maturity; lobes mostly about as long as broad or broader 23

23a. Upper stem leaves with winged petiole mostly clasping axis; plants often of ascending habit, mostly with few leaves on primary axis above basal rosette. (Israel, Jordan, Egypt or Libya) . . . . . **15. P. humile**

23b. Upper stem leaves very rarely with winged petiole and if present, very rarely clasping axis; plants mostly regularly leafy, mostly of erect habit 24

24a. Terminal segment of lower leaves mostly less than twice as long as broad; capsule base narrowing gradually; plants almost always with red tinge on leaves, axis or at least some setae. (SW Turkey E to Cape Anamur, the NW (N Sporades) and SE Aegean or Cyprus) . . . . . **10. P. guerlekense**

24b. Terminal segment of lower leaves mostly more than twice as long as broad 25

25a. Stigmatic disc as broad as to narrower than capsule diameter, always with dark violet marks on margin; pedicel with few patent to half-appressed setae. (SW Iran and adjacent Iraq) . . . . . **4. P. rechingeri**

25b. Stigmatic disc mostly broader than capsule diameter; if narrower, capsules broadly obovoid, cylindrical or almost globose; pedicel with mostly ± dense indumentum of patent or loosely appressed setae. (Widespread weed) . . . . . **16. P. rhoeas**

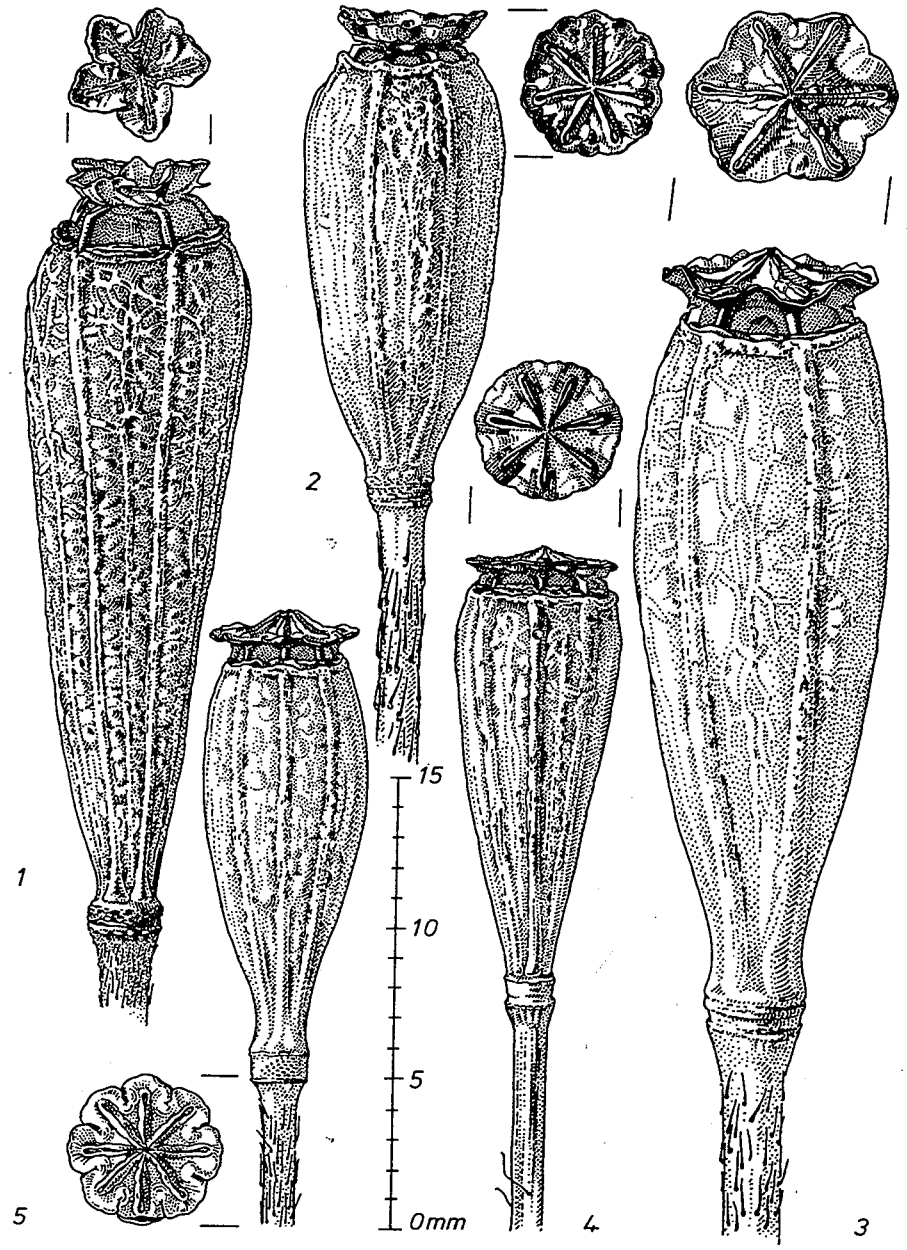


FIG. 1. Capsules of 1, *P. pinnatifidum*; 2, *P. purpureomarginatum*; 3, *P. dubium* subsp. *dubium*; 4, *P. rechingeri*; 5, *P. arachnoideum*.

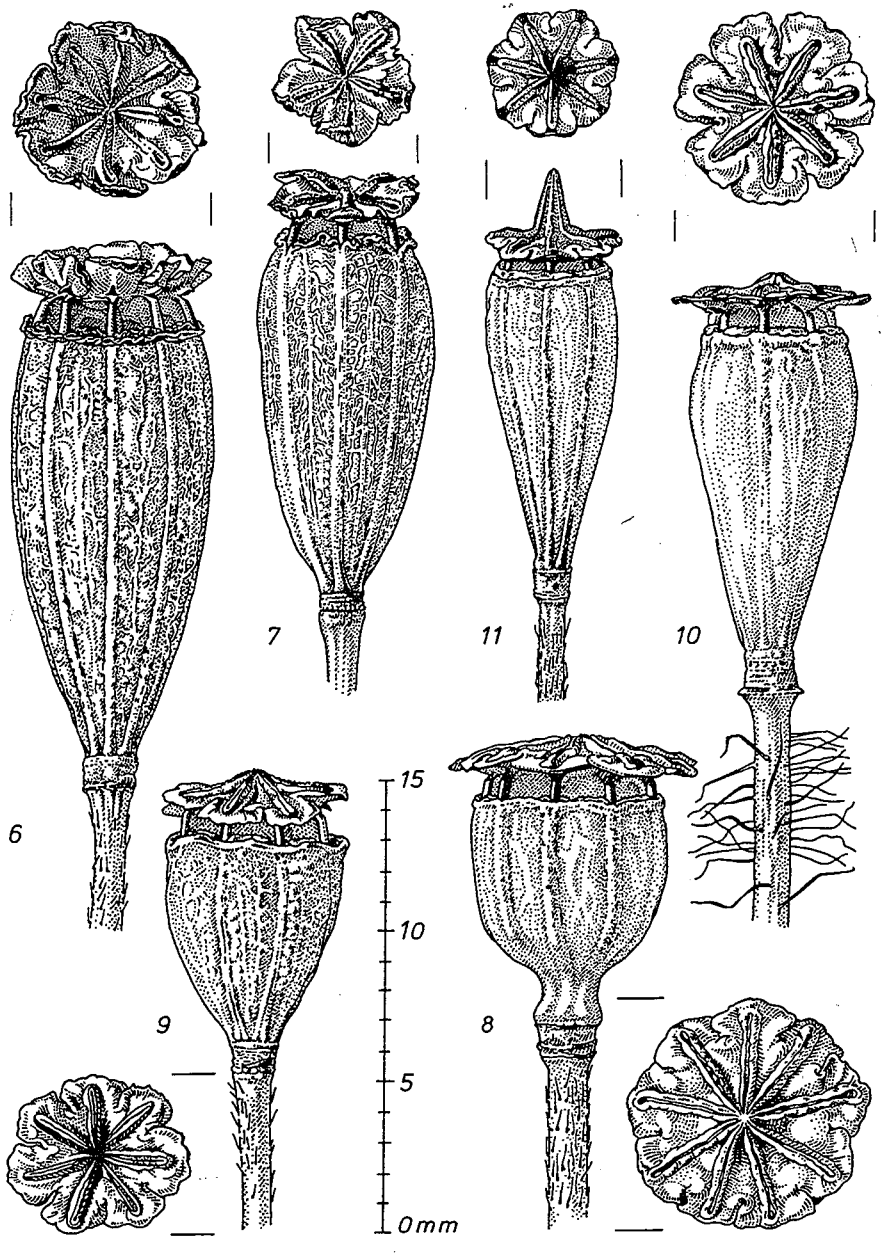


FIG. 2. Capsules of 6, *P. arenarium*; 7, *P. tenuifolium*; 8, *P. commutatum* subsp. *commutatum*; 9, *P. chelidoniifolium*; 10, *P. guerlekense*; 11, *P. stylatum*.

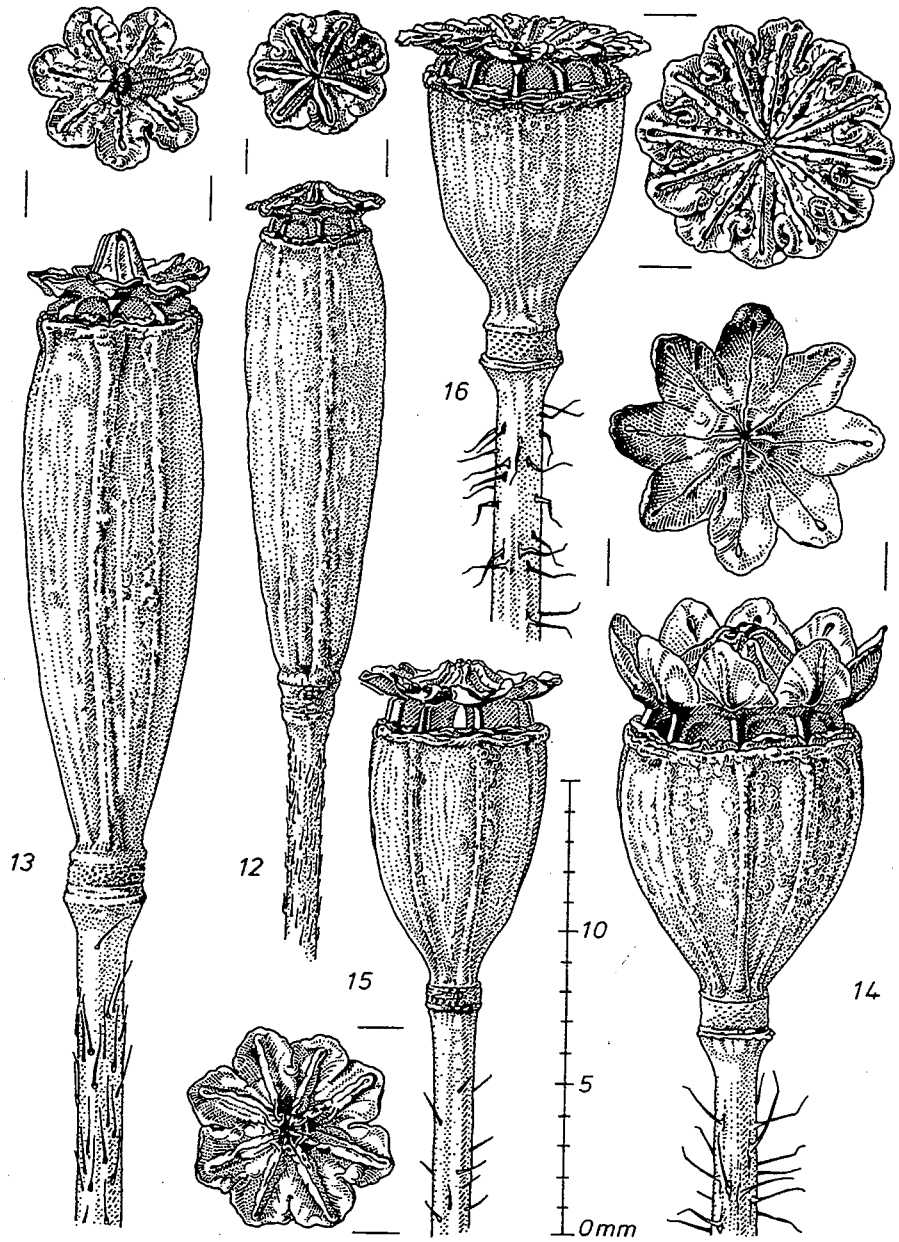


FIG. 3. Capsules of 12, *P. clavatum*; 13, *P. umbonatum*; 14, *P. carmeli*; 15, *P. humile*; 16, *P. rhoeas* var. *rhoeas*.

Papaver Sect. **Rhoeadium** Spach, Hist.nat.vég. phan. 7:16 (1839).
Syn.: *Rhoeades* Bernh., Linnaea 8:463 (1833).
Sect. *Rhoeades* (Bernh.)Elkan, Tent.Monogr.Gen. Papaver: 23 (1839).
Sect. *Orthorhoeades* Fedde in Engler, Pflanzenr. 4, 104:326 (1909).
Type: *P. rhoeas* L., Sp.Pl. 1:507 (1753).

Erect to ascending, very rarely almost decumbent, branched or rarely unbranched annual herbs; leaves variously dissected; lower leaves petiolate; upper leaves shortly petiolate to mostly sessile with narrowly to broadly cuneate to rounded base; plants sometimes glaucous, with few to many patent to appressed setae on all green parts, or sometimes with additional arachnoid hairs; sepals with or mostly without ± conspicuous subapical processes; petals obovate to rotund to flabelliform, variously red, sometimes white or pale violet, with or without black spots of varying size and position; filaments filiform; capsules clavate to cylindrical, obovoid, ellipsoid or almost globose, shortly stipitate or not; stigmatic disc flat, sometimes with distinct central umbo or free lobes of disc curved upwards; seeds reniform.

1. P. pinnatifidum Moris, Fl.Sardoa 1:74 (1837). Figs 1, 4, 13, 17.
Syn.: *P. dubium* L. var. *pinnatifidum* (Moris)Battand. & Trabut, Fl. Algérie 1:21 (1888).
P. dubium L. var. *maroccanum* Ball, J.Bot. 16:311 (1877). Type: Tanger! (G), Casa Blanca! (B).
P. simoni Fouc., Bull.Soc.Sci.Nat. Charente-Inférieure: 164 (1897). Type: Corse: Calvi, lieux vagues, Soc. Roch. 1896 no. 3856 (MPU).
P. teneriffae Fedde, Bull.Herb. Boissier, Sér.5,2:171(1905). Type: Bourgeau Pl.Canar.Exs., 1846, no. 519 (BM, G).
P. tunetanum Fedde in Engler, Pflanzenr. 4, 104:321 (1909). Type: Schweinfurth no. 563, Belvedère bei Tunis (n.v.).
Type: Soleirol! Pl. siccat. e Corsica (n.v.).

Erect annual herb, 10–85cm high, mostly branched from the base. *Leaves* 2–19 × 1–5·5cm, obovate to lanceolate to elliptical or ovate in outline, incised to pinnatifid to pinnatipartite, lower leaves sometimes pinnatisect, upper leaves rarely entire; lower leaves petiolate, petiole 1–8cm long; upper leaves sessile with cuneate to rounded base, with large pair of basal lobes (Fig.13); lobes acute, incised or sometimes entire, strongly antrorse; leaves with ± dense indumentum of ± appressed setae on both surfaces.

Axis with patent setae, pedicel with patent setae below and appressed setae above, very rarely with patent setae throughout. *Flower buds* shortly before anthesis 7–15 × 5–11mm, broadly ovoid to ellipsoid to almost globose; sepals with dense indumentum of mostly appressed, rarely half-appressed setae. *Petals* 1·4–3 × 1·3–3cm, obovate, orange-red, with or without darker base, always without distinct basal spot. *Stamens* many, 5·5–10mm long, shorter to as long as ovary or rarely slightly longer than ovary; filaments filiform, black; anthers 1–1·5mm long, oblong, mostly yellow, rarely purplish. *Capsule* 10–27 × 3·5–8mm, 2·5 to almost 4 times as long as broad, clavate, mostly distinctly contracted below pores

(Fig. 1), very rarely abruptly contracted at base; stigmatic disc with 4–9 stigmatic rays, 3·5–6·5mm broad, narrower than capsule diameter; free lobes of stigmatic disc mostly broadening towards their tips, overlapping; lateral margin of lobes often dark violet to black. *Seeds* 0·5–0·7mm long, brown (Fig. 17).
2n = 28 (mihi).
Flowering 2–6. A weed in fields, by roadsides, or in open vegetation on sandstone or limestone.
The distribution of *P. pinnatifidum* is shown in Fig. 4.

AZORES: Graciosa, 25 vii 1972, *Goncalves* 4347 (BM); Faial, 5 viii 1972, *Goncalves* 4542, 4544 (BM).
MADEIRA: above the Mount, 8 vi 1831, *Lowe* 510 (BM).
CANARY ISLANDS: Gran Canaria: Tafira, 1 iv 1901, *Bornmüller* 2019 (G, W, WU); Lancerotta: in arvis, 1845, *Bourgeau* 325 (BM); Tenerife, near Taganana, 10 iv 1975, *Cannon* 4683 (BM); Gran Canaria, Tejeda, 23 v 1897, *Gelert* s.n. (C); Gran Canaria, San Mateo, 23 iv 1896, *Kuegler* s.n. (B); Gran Canaria, Monte Tafira, 15 ii 1966, *Kunkel* 8550 (B); Gran Canaria, Tafira Alta, 29 i 1967, *Kunkel* 10012 (M); La Graciosa, 7 iv 1970, *Kunkel* 13143 (G); Alegranza, 8 v 1970, *Kunkel* 13465 (G); Tenerife, 6 vi 1894, *Murray* s.n. (BM).
SPAIN: pr. Almeria, 5 iv 1879, Huter, Porta, *Rigo* 846 (E, W); Mallorca, Mirador de R.Roca, 4 iv 1969, *Friis* 1064 (C); Mallorca, Binisalem, 2 iv 1968, *Thornberg* s.n. (C); Mallorca, Terreno, 30 i 1972, *Vollesen & Jacobsen* 2122 (C).
FRANCE: Menton, 1 v 1895, *Bicknell* 3301 (E, G, JE, M, W, WU); Menton, 18 iv 1889 & 22 iv 1891, *Bicknell* s.n. (B, M, W, WU); St Tropez, 13 iv 1861, *Bourgeau* s.n. (G); Corse, Cap Corse, 27 iv 1907, *Briquet* s.n. (G); Menton, 17 iv 1876, *Burnat* s.n. (G, W); Corse, Bonifacio, 16 iv 1909, *Houard* s.n. (G); Corbara, 25 iv 1916, *Kükenthal* 1341 (G); Bastia, 25 v 1907, *Rotgès* s.n. (G); Ajaccio, 25 v 1901, *Roux* s.n. (G); Bastia, 4 ix 1913, *Spencer* s.n. (W); Menton, vi 1877, *Vetter* s.n. (E, G); audessus d'Hyères, iv 1858, ? (G).
ITALY: Bordighera, 30 iv 1911, *Bicknell* 2442 (B, G, WU); Pied de Saline, vi 1862, *Bernet* s.n. (G); Palermo, 1860, *Citarda* s.n. (JE); Bordighera, 25 iv 1893, *Haussknecht* s.n. (JE); Sicilia, *Hb. Jacq.* (W); Sardin, 1839, *Moris* s.n. (G); Marettimo, iv 1905, *Ross* 504 (B, E, G, M, WU); Cagliari, 1835, *Herb. Zuccarinii* s.n. (M).
MOROCCO: 30km E of Tiznit, 12 v 1982, *Davis & King* 68238 (E); Ras Sidi-el-Ahbed, 16 iv 1929, *Font Quer* 161 (BM, G); Chaouia: Boulhaut, 22 iv 1924, *Jahandiez* 199 (BM, G); Tanger, iii 1883, *Kersten* 74 (B, JE); Tangier, 18 iii 1916, *Roffey* s.n. (BM); Gurugu, 16 vi 1931, *Sennen & Mauricio* s.n. (BM); Zeluan, 5 vi 1932. *Sennen & Mauricio* s.n. (BM); Tanger, 29 iii 1910, *Vaucher* 32 (G).
ALGERIA: Tipasi, 29 v 1975, *Davis* 58324b (BM); Prov. d'Oran, Plainejet Coteaux, *Durando* s.n. (W); Oran, 21 iii 1915, *Faure* s.n. (M); Beni-Mansour, 6 iv 1861, *Lefebvre* s.n. (W); Mostaganem, iv 1848, ? (W).
TUNISIA: Gabes, iv 1938, *Boulenger* 38484 (JE); Tunis, v 1916, *Cuénod* s.n. (G).

P. pinnatifidum is a distinct species recognizable in the first instance by the shape of its upper leaves. These are sessile with a mostly rounded and sometimes cuneate base which continues into the basal pair of lobes, which are triangular in outline and acute. Most specimens I have seen of this taxon have light yellow anthers, and the capsules are characteristically clavate. The distribution of *P. pinnatifidum* is virtually identical with that of *P. somniferum* L. subsp. *setigerum* (DC.) Corbière (Kadereit, 1986a), except for the presence of the latter on Cyprus. The presence of *P. pinnatifidum* in Bulgaria, Thrace and Greece had been reported by Hayek (1927), and *P. pinnatifidum* var. *tenuifidum* had been described by Fedde (1909) from Attica. Although the type specimen of the latter has some similarity with *P. pinnatifidum* in its clavate capsules, its leaves are much more finely dissected and the seeds are larger than in

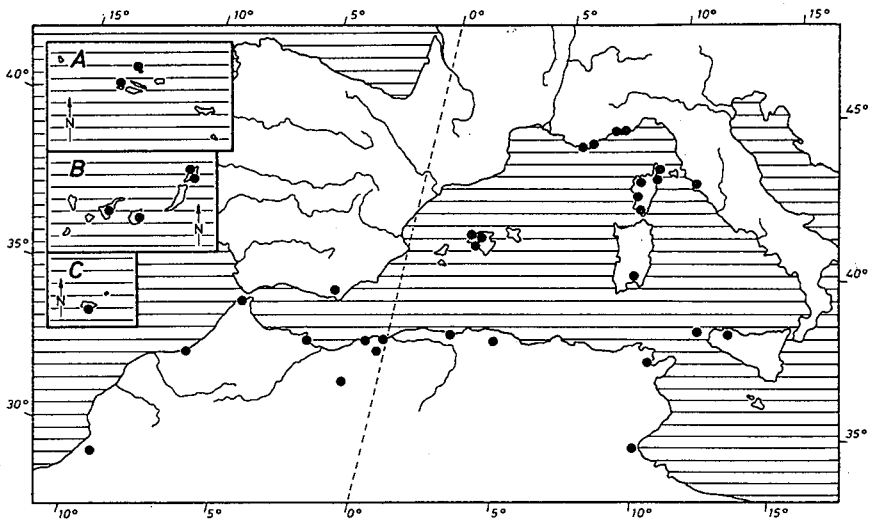


FIG. 4. Geographical distribution of *P. pinnatifidum* (•).

this species. In my opinion it does not belong to *P. pinnatifidum*, but rather to *P. dubium* subsp. *lecoqii* (Lamotte) Syme (q.v.). I have not seen any specimens of *P. pinnatifidum* from east of Sicily. The structure of the seed surface of this species (Fig. 17), in being somewhat porous, perhaps underlines its distinctness.

Although I have not seen the type specimen of *P. pinnatifidum*, I have seen authentic material from TO (*Herb. Moris* no. 46).

2. P. purpureomarginatum Kadereit, **sp.nov.** Figs 1, 5, 7, 13, 17.
Species affinis *P. dubio*, sed plerumque foliis supremis vel integris vel basaliter lobis binatis recurvatis; sepala purpureomarginata; antherae flavae; capsulae maturae ellipsoideae ad obovoideae, discis concavis et marginaliter repandis, purpureonotatis inter lobos.
Type: Türkei: Izmir: Halbinsel von Karaborun, Ildir (N von Cesme), 14 iv 1969, *Fitz & Spitzenberger* 117 (holo. W).

Erect to ascending annual herb, 8–45cm high, unbranched below to mostly branched from base. *Leaves* 2–9 × 0·8–4cm, obovate to ovate or lanceolate in outline, 1–2-pinnatipartite to entire; lower leaves petiolate, petiole up to 5cm long, pinnatipartite to bipinnatipartite (Fig. 13); upper leaves sessile, often entire or with one basal pair of entire recurved lobes (Fig. 13), sometimes with more than one pair of entire more or less recurved lobes; leaves with more or less dense indumentum of ± patent setae on both surfaces, indumentum of lower surface denser than on upper surface.

Axis with patent setae, pedicel with sparse indumentum of appressed setae. *Flower buds* shortly before anthesis 10–16 × 7–10mm, ovoid, sepals mostly with narrow dark violet margin, almost glabrous to moderately covered with patent setae. *Petals* 1·1–2·1 × 0·7–1·9cm, obovate, pale red

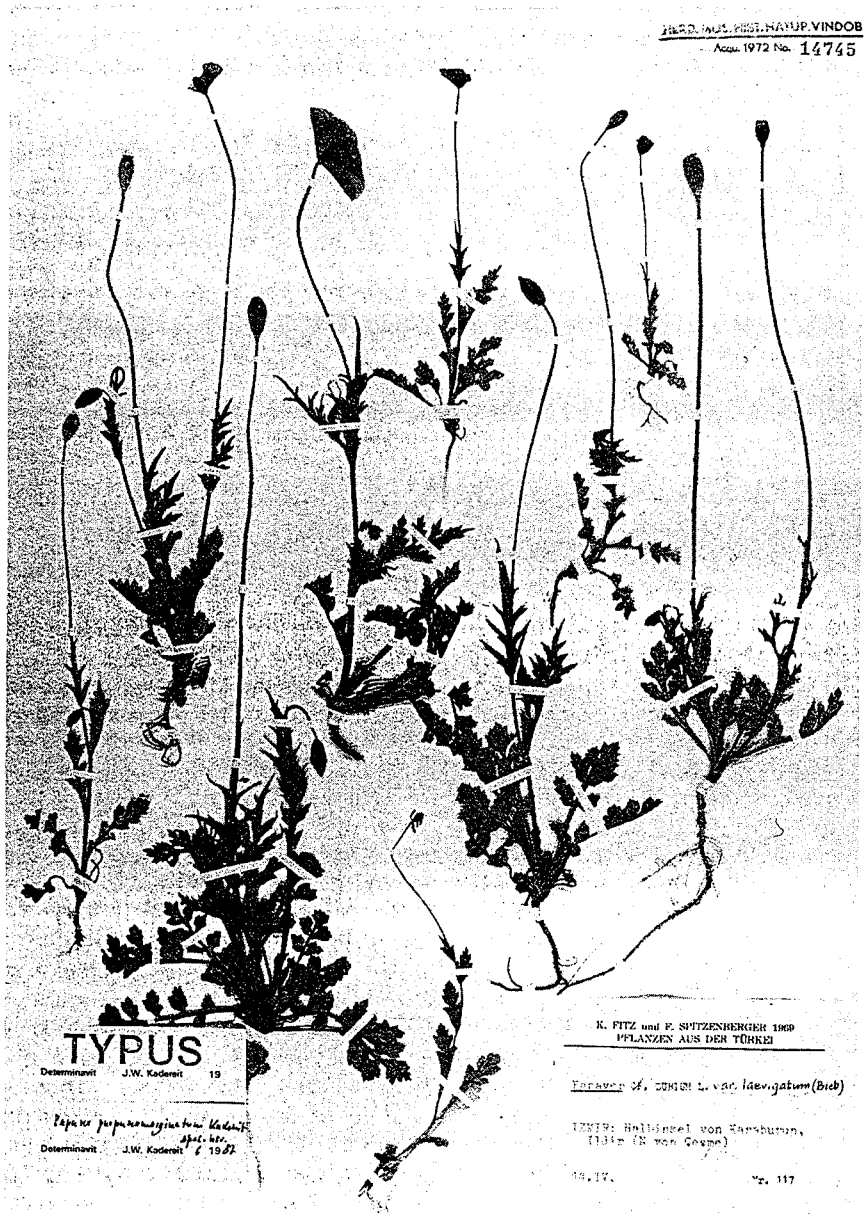


FIG. 5. Holotype of *P. purpureomarginatum* Kadereit, sp.nov.

without basal spots. *Stamens* many, 6–10mm long, shorter than ovary; filaments filiform, black; anthers 0·7–1·6mm long, oblong, mostly light yellow, sometimes brownish. *Capsule* 10–18×4·5–7mm, 2 to 2·5 times as long as broad, ellipsoid to obovoid, distinctly contracted below pores (Fig. 1); stigmatic disc with 4–7 stigmatic rays, 3·5–6mm broad, narrower

than capsule diameter; stigmatic disc mostly shallowly lobed, lobes not overlapping; margin of disc mostly curved upwards at maturity, mostly with dark violet marks between lobes. *Seeds* 0·5–0·7mm long, brown, glaucous (Fig. 17).
2n = 28 (mihi).
Flowering 4–5. A weed by roadsides, or in open vegetation on calcareous substrata, often in somewhat humid habitats.
The distribution of *P. purpureomarginatum* is shown in Fig. 7.
GREECE: Karpathos, 28 v 1886, *Forsyth Major* 199 (G); Kalymnos, 24 iv 1963, *Gathorne-Hardy* 336 (E); Schlucht zwischen Perivolia und Thèrisso, 15 iv 1962, *Greuter* 4157 (G, W); Peninsula Akrotiri, 24 iv 1976, *Greuter & Charpin* 13348 (W); in insula Cea, 21–24 v 1898, *Heldreich* s.n. (WU); Thimena, 25–26 iv 1934, *Rechinger* 4725 (BM, W); Creta, peninsula Korykos, 20 iv 1942, *Rechinger* 12129 (W); Creta, peninsula Titiron, 22 iv 1942, *Rechinger* 12242 (W); Kythera, 4 v 1964, *Rechinger* 24234 (W); Ikaria, 3 v 1976, *Rechinger* 54109 (B, W); Epidauros, iii 1830, *Herb. Zuccarini* s.n. (M).
TURKEY: Mugla: Törgut to Bayir, 15 iv 1965, *Davis* 41135.
CYPRUS: between Kambos and Stavros Tis Psokas, 23 iv 1962, *Meikle* 2644 (C).

Although clearly related to *P. dubium* and vicarious with some of the subspecies of it (Fig. 7), *P. purpureomarginatum* deserves to be given specific rank on account of a number of characters. These are: the upper and, above all, the uppermost stem leaves, which often are entire or have only one pair of narrow, entire and conspicuously recurved basal lobes, though sometimes there is more than one pair of still mostly entire and more or less recurved lobes; the sepals, of which the covering one usually has a narrow dark violet margin; the mostly light yellow anthers; and the often ellipsoid capsule with its concave disc and violet marks between the shallow lobes. In its uppermost leaves and yellow anthers *P. purpureomarginatum* somewhat resembles *P. pinnatifidum*. From *P. pinnatifidum*, apart from the shape of the capsules and the leaves, *P. purpureomarginatum* also differs in the surface structure of its seeds (Fig. 17), in which it resembles more *P. dubium* which, however, cannot be easily distinguished from many other species in the section.

The one specimen of *P. purpureomarginatum* I have seen from Cyprus (*Meikle* 2644), though clearly belonging to this species (on account of the dark violet margin of the covering sepal, the yellow anthers and the coloration of the stigmatic disc), differs from all other specimens in its obtuse flower buds, which are normally distinctly pointed, and in having upper leaves with a greater number of lateral lobes which are more divided. From the proportions of the ovary of this specimen it seems that the capsules are relatively broader. Meikle (1977) included the Cyprus specimen in *P. postii* Fedde, together with *Davis* 3491 and *Syngrassides* 1599. These were cited as *P. postii* also by Burtt (1949), who described them as having yellow anthers. I have not seen the last two specimens, which most likely also belong to *P. purpureomarginatum*. All three specimens were collected in NW Cyprus.

3. P. dubium L., Sp.Pl. Appendix: 1196 (1753).

Erect annual herb, 8–90cm high, unbranched below to mostly branched from base. Green parts of plant glaucous or not. *Leaves* 1–19×0·5–

8·5cm, obovate to ovate in outline, 1–2-pinnatipartite; lower leaves petiolate, petiole up to 7cm long; upper leaves shortly petiolate to sessile with cuneate to rounded base; lobes antrorse to sometimes almost patent, pinnatipartite to incised to distantly serrate or entire; leaves with more or less dense indumentum of ± patent setae to sometimes glabrous on upper surface and with very few setae on major veins of lower surface.

Axis with few to many patent setae, pedicel with few to many appressed setae. *Flower buds* shortly before anthesis 9–18×5–12mm, ovoid to ellipsoid, with sparse to dense indumentum of more or less appressed setae or sometimes glabrous. *Petals* 1–4×0·5–3·6cm, narrowly to broadly obovate, with entire or somewhat laciniate apical margin, white, rarely pink, pale violet or mostly orange-red without or with black spots of variable size and position, rarely petals entirely black. *Stamens* more or less many, 4–10mm long, shorter to longer than ovary; filaments filiform, light violet to black; anthers 0·3–1·9mm long, oblong, brownish to greenish, sometimes with small apical appendage. *Capsule* 8–26×4–11mm, 2 to 4·3 times as long as broad, very rarely just under 2 times as long as broad, narrowly obovoid to sometimes clavate (Fig. 1); stigmatic disc with 4–11 stigmatic rays, 3–8mm broad, narrower to sometimes as broad as capsule diameter; free lobes of stigmatic disc mostly broadening towards their tips, overlapping or not, sometimes disc very shallowly lobed. Latex white, cream, colourless or yellow. *Seeds* 0·5–1mm long, brown, glaucous.

1a. Plants mostly with very sparse indumentum to almost glabrous, mostly strongly glaucous. (Turkey, rarely Greece or Iran, around Black Sea, or Afghanistan) 2
1b. Plants mostly with ± dense indumentum, glaucous or not. (N Africa, Europe, West Turkey, Caucasia, Azerbaijan or Iran, rarely Afghanistan) 3
2a. Lobes of upper leaves often conspicuously wavy; apical margin of petals entire, petals with small to large basal black spot, sometimes spot leaving only narrow red margin or rarely petals entirely black. (Turkey, rarely Greece or Iran, or around Black Sea) . . . . . **iii.** subsp. **laevigatum**
2b. Lobes of upper leaves straight; apical margin of petals entire or eroded to laciniate, petals without or with mostly small black spot removed from base. (Afghanistan to Nepal) . . . . . **v.** subsp. **glabrum**
3a. Lobes of uppermost leaves mostly few, entire; basal pair of lobes mostly broadly triangular, continuing into mostly rounded leaf base; apical margin of petals entire or eroded to laciniate, petals without or with mostly small black spot removed from base. (Caucasia, Azerbaijan or Iran, rarely Afghanistan) . . . . . **iv.** subsp. **erosum**
3b. Lobes of uppermost leaves mostly dissected; basal pair of lobes mostly ovate in outline; apical margin of petals entire, petals without or with black basal spots 4
4a. Latex white or cream, brown to black when dry; petals red, mostly without basal spots; capsules mostly gradually narrowing towards base. (Europe) . . . . . **i.** subsp. **dubium**

4b. Latex yellow or turning yellow, red when dry; if latex colourless, petals white; if latex white (SE Europe or W Turkey) plants with rather dense indumentum and upper leaves dissected into very narrow lobes, lobes rarely more than 1·5mm broad; petals red or white, rarely pink or pale violet without or with (SE Europe or W Turkey) black basal spots; capsules often somewhat abruptly narrowing at base. (Europe or W Turkey) . . . . . **ii.** subsp. **lecoqii**

i. subsp. **dubium.** Figs. 1, 13, 17.

Syn.: *P. obtusifolium* Desf., Fl.Atlant. 1:407 (1798). Type: Habitat in Atlante prope Belide (P).
P. lamottei Boreau, Fl.Centre France (Ed. 3) 2:30 (1857). Type: Base des Monts-Domes.-Creuse.-Allier.-Cher (type material unknown).

'Habitat inter Sueciae, Angliae segetes'.

Upper leaves (Fig. 13) sessile with cuneate base, rarely shortly petiolate. *Petals* orange red, mostly without basal spot. *Capsule* mostly narrowing gradually towards its base. *Latex* white or cream when fresh, brown to black when dry.

2n = 42 (mihi).

Flowering 3–8. Mostly occurring as a ruderal or segetal weed on various substrata.

GREAT BRITAIN: Wolverhampton, vi 1878, *Fraser* s.n. (WU); Yorkshire, near Thirsk, *Baker* s.n. (G).
FRANCE: La Flotte, Ile de Re, 13 vi 1858, *Letourneux* 2610 (G); Savoie: Macot, 20 v 1861, *Perrier* s.n. (G).
SPAIN: Prov. Valencia: Sagunto, 31 iii 1953, *Merxmüller & Wiedmann* 146b/53 (M); Catalogne: Vilajuiga, 24 iv 1908, *Sennen* 527 (W).
PORTUGAL: Coimbra, v 1887, *d'Araujo e Castro* s.n. (W).
BELGIUM: Rometenne—Rochefort, 15 vi 1934, *Stomer-Masseroy* 110 (W).
NETHERLANDS: Overveen, 12 vii 1888, *Raunkjaer* s.n. (C).
SWEDEN: Torö, Braten, 23 viii 1929, *Asplund* 845 (G); Båstad, vii 1864, *Strandmark* s.n. (W).
DENMARK: Ebeltoft, Djursland, 14 vii 1970, *Holm-Nielsen & Pedersen* 643 (G); Zealand: N of Ringsted, 19 vii 1972, *Svendsen* 580 (M).
GERMANY: Oberelchingen, 30 vi 1961, *Doppelbaur* 401 (M); Berlin, 10 vi 1967, *Hertel* 7213 (M).
POLAND: Posen, bei Schlichtlingsheim, vi 1863, ? (W).
SWITZERLAND: Valais: Simplon, 22 vii 1888, *Chenerard* s.n. (G); Tessin: entre Agno et Bioggio, 2 vi 1906, *Braun* s.n. (G).
AUSTRIA: Gmünd-Neustadt, 17 vii 1969, *Forstner* s.n. (W); Nordtirol: Wipptal, 24 vii 1971, *Polatschek* s.n. (W).
CZECHOSLOVAKIA: Brno, 15 vi 1927, *Jirasek* 319 (WU).
ITALY: Prov. Sondrio: Dazio, 6 vi 1965, *Buttler* 6905 (M); Messina, 2 v 1923, *Béguinot* 2677 (WU).
AZORES: Sao Miguel, 14 v 1978, *Rechinger* 57743 (M).
CANARY ISLANDS: Tenerifa, v 1879, *Hillebrand* s.n. (WU); Gran Canaria, 30 iii 1966, *Kunkel* 8996 (G).
MOROCCO: Djebel Afougueur, 3 vii 1876, *Ibrahim* s.n. (G); in convalle fl. Ait Messane, 3 vi 1926, *Lindberg* 3505 (B).
ALGERIA: Cherchell, 18 iii 1962, *Charpin* s.n. (G); half way between Tikjda and Tizi-N'Kouilal, 23 vi 1975, *Davis* 59475 (BM).
TUNISIA: Oued Gabes, 1 v 1854, *Kralik* 26 (G); Djebel Bou Hedma, iv 1968, *Young* 22 (BM).

Apart from the countries listed above, subsp. *dubium* can also be found in SE Europe and Turkey as well as the south western USSR and also Egypt and Libya. In all these countries it seems to be extremely rare. This subspecies has its northern limit in S Scandinavia, and, as far as I have seen, its eastern limit in Poland. As an introduction *P. dubium* subsp. *dubium* is also known from other continents.

ii. subsp. **lecoqii** (Lamotte)Syme, Engl.Bot. (Ed. 3) 1:30 (1863). Figs 6, 13, 17.
Syn.: *P. lecoqii* Lamotte, Ann.Sci.Auvergne 23:429 (1851).
Type: Auvergne, 1853, ex herb. Jordan (neo. BM; Kubat, 1980).

Upper leaves (Fig.13) sessile with cuneate base or often shortly petiolate. *Petals* orange red or white (yellow when dry), rarely pink or pale violet, without or with black basal spots. *Capsule* often abruptly narrowing at base. *Latex* yellow or turning yellow when fresh, red when dry, or sometimes latex colourless when fresh, brown to black when dry.

1a. Petals orange-red, pink or pale violet . . . var. **lecoqii**
1b. Petals white (yellow when dry) . . . var. **albiflorum**

var. **lecoqii**
Syn.: *P. tenue* Ball, J.Bot. 11:296 (1873). Type: in jugo Tagherot, 15 v 1871, *Ball* s.n. (G).
P. dubium L. var. *cassandrinum* Charrel, Österr.Bot.Z. 41:374 (1891). Type: Cassandra, 5 v 1891, *Abd-Ur-Rahman Nadji* s.n. (B).
P. subadpressiusculo-setosum Fedde, Bull.Herb.Boissier, Sér. 5, 2:171 (1905). Type: Algier: champs cultivé de la colline des Hammah-Les-Platanes près Alger, 2 v 1851, *Jamin* 121 (B, G, W).
P. pinnatifidum Moris var. *tenuifidum* Fedde in Engler, Pflanzenr. 4, 104:321 (1909). Type: Pentelikon, 1885, *Haussknecht* s.n. (JE).
P. tumidulum Klokov in Klokov & Wissjul., Fl.RSS Ucr. 5:502 (1953). Type: RSS Ucr., insula Kojuv-Tuk, in declivio ad marum, 16 v 1928, *Prjanischnikov* s.n. (KW).
2n = 28 (mihi).
Flowering 3–9. Mostly occurring as a ruderal weed or in vineyards etc., on various substrata.
GREAT BRITAIN: Charlton, Hitchin, 20 vii 1914, *Little* s.n. (BM); Middleton, *Wilmott* 410624A (BM).
FRANCE: Charance, 31 v 1896, *Faure* 5b (G); Weissenburg i/Elsass, vi 1898, *Spindler* s.n. (B).
SPAIN: El Arenal, 16 vii 1956, *Deverall & Flannigan* 101 (E); Cerdagne, Villeneuve, 25 vi 1926, *Sennen* 5666 (W).
BELGIUM: Rochefort, 15 vi 1934, *Stomer-Masseroy* 111 (W).
GERMANY: Kelheim, 14 vi 1900, *Vollmann* s.n. (M); Mülheim am Rhein, 3 vi 1894, *Wirth* s.n. (W).
SWITZERLAND: Neuchatel, *Godet* s.n. (G); Merishausen, 7 vii 1969, *Greuter* 8578 (G).
AUSTRIA: Wien XVI, 7 vi 1968, *Forstner* s.n. (W); Hainburg, 28 iv 1920, *Zerny* s.n. (W).
ITALY: Sardinia: Sassari, x 1923, *Béguinot* 2677 (G); Ischia, 1857, *Gussone* s.n. (G).
CZECHOSLOVAKIA: Jungbrunzlau, 20 v 1920, *Korb* s.n. (W); Znojmo, 16 v 1948, *Švestka* 1310 (G).

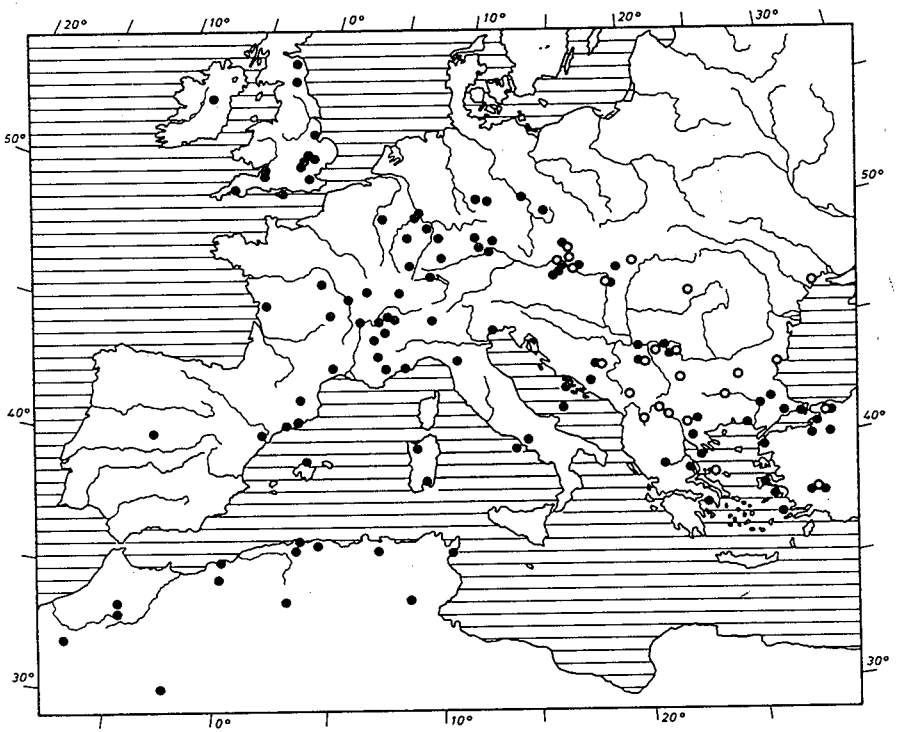


FIG. 6. Geographical distribution of *P. dubium* subsp. *lecoqii* var. *lecoqii* (•) and var. *albiflorum* (○).

HUNGARY: zwischen Drenkova und Svinicza a.d. Donau, 1 vi 1909, *Watzl* s.n. (WU).
YUGOSLAVIA: Mostar, 16 v 1906, *Janchen* s.n. (WU); Avala prope Beograd, 5 v 1967, *Mayer* 61308 (M).
ALBANIA: Plostan, 28 vi 1918, *Dörfler* 814 (WU).
BULGARIA: Distr. Goce Delcev: Paril, 7 vi 1980, *Kuzmanov* 80532 (B).
GREECE: prope Volos, 4 v 1961, *Rechinger* 22649 (B); Kalampaka, 20 v 1896, *Sintenis* 333 (WU).
TURKEY: Edirne, 27 iv 1970, *Rix* 1501 (E); Izmit, 11 iv 1972, *Uotila* 15509 (E).
MOROCCO: Djebel Ghat, 29 vi 1881, *Ibrahim* s.n. (G); Daiet Achlef, 11 vi 1923, *Jahandiez* 518 (G).
ALGERIA: 10km from Guelma to Constantine, 13 v 1971, *Davis* 52301 (E); Chanzy (près Oran), 18 v 1924, *Faure* (W).
TUNISIA: Hammamet, v 1944, *Cuénot* s.n. (G); Gafsa, 4 iv 1938, *Simpson* 38139 (BM).

var. **albiflorum** Besser, Enum.Pl. (Ed. 2):47 (1822)
Syn.: *P. albiflorum* (Besser)Pacz., Acta Horti Bot. Univ. Jurjev 6:147 (1906).
P. dubium L. var. *albiflorum* Boiss., Fl.Orient. 1:115 (1867). Type: in regione media montis Korthiati Macedoniae, *Orphanides* 3605 (G-Boiss.).
P. maculosum Schur, Verh.Naturf.Vereins Brünn 15:67 (1877). Type: Zackelsberg bei Groβscheuren, Heuwiese bei Klausenburg (n.v.).

P. albiflorum (Besser)Pacz. subsp. *austromoravicum* Kubát, Preslia 52:111 (1980). Type: Moravia australis: Pouzdřany, 22 v 1977, *Kubát* s.n. (n.v.).

Type: legit Andrz. in Podoliam austr. (n.v.).

2n = 28 (Koopmans, 1970; Kubát, 1980).

Flowering 4–7. Mostly occurring as a ruderal weed or in vineyards etc., on various substrata.

AUSTRIA: Wien, 9 v 1866, *Dörfler* s.n. (E); Achau, 6 v 1915, *Vetter* (W).
CZECHOSLOVAKIA: Pollauer Berge, 28–29 v 1939, *Neumayer* s.n. (WU); Kl.Karpaten, Ruine Ballenstein, 13 v 1913, *Ronniger* s.n. (W).
HUNGARY: Adlersberg bei Budapest, 12 v 1906, *Janchen* s.n. (W); Theben, 20 v 1909, *Vetter* s.n. (W).
YUGOSLAVIA: Dojran See Gebiet, Nicolic, v 1917, *Burgeff* 1476 (M).
ROMANIA: prope oppid. Cluj, 23 v 1921, *Borza & Peterfi* 782 (W); Insel bei Brzapalanka, 1892, *Lorenz* s.n. (W).
BULGARIA: prope Varna, 25 v 1907, *Schneider* s.n. (W); Ladovo, 24 vi 1898, *Stribrny* s.n. (E).
GREECE: Ins. Alonnisos, 15 v 1965, *Phitos* 2342 (M); Thessalia: Mons Olympos, 26 vii 1970, *Rechinger* 38755 (B).
TURKEY: Constantinople: Touzla, 25 iv 1897, *Nemetz* s.n. (WU); Pascha-Kissla, 25 v 1875, *Sintenis* 556 (B).

To distinguish between subsp. *dubium* and subsp. *lecoqii* is certainly meaningful, but not always very easy. Most important for this is the colour of the latex and the breadth of the lobes of the upper leaves. In subsp. *dubium* the latex is white to cream when fresh and turns light to dark brown or black when dry. In Europe west of Lower Austria subsp. *lecoqii* seems to have either yellow to orange latex, or white to cream latex which turns yellow after some time on exposure to air; when dry the latex is red in both cases. In SE Europe and W Turkey latex of subsp. *lecoqii* can be either yellow (it then turns red when dry), or colourless when fresh and brown to black when dry. In white-flowered material both forms of latex can be found. White-flowered plants with yellow latex cannot be meaningfully separated from red-flowered subsp. *lecoqii* on account of their latex, the shape of the capsules which, as often, but not always, in red-flowered subsp. *lecoqii* are narrowing rather abruptly at their base, and the lobes of the upper leaves, which rarely are more than 2mm broad. In addition, white- and red-flowered material can often be found in mixed populations. Equally, it is meaningless to separate white-flowered material with colourless latex from such with yellow latex, as both are very similar in capsule and leaf shape. In the south east of SE Europe and in W Turkey white-flowered specimens are rather rare, and most specimens have red flowers. These either have yellow latex which turns red when dry, or colourless latex which becomes brown. The separation of the latter group with colourless latex from subsp. *lecoqii* is not justified in my opinion, as this south eastern red-flowered material is very similar to the white-flowered material in having upper leaves with very narrow lobes (these are often only about 1mm broad), which often are entire and have a rather dense indumentum. Like most white-flowered specimens these red-flowered ones mostly have black basal spots on their petals, which is far less common in red-flowered specimens from further north or west.

Thus, apart from latex colour, which is not a straightforward character

in part of the distribution area of subsp. *lecoqii*, the narrow lobes of the upper leaves in plants from the south east are important for their recognition as subsp. *lecoqii*. The distribution of subsp. *lecoqii* thus defined is shown in Fig. 6.

Generally the lobes of the upper leaves of subsp. *lecoqii* tend to be narrower than in subsp. *dubium*, and the leaves tend to be more densely hairy. It is not possible, however, to quantify these differences for the purpose of identification. The same applies to the shape of the capsules, which narrow rather gradually towards their base in subsp. *dubium*, but more abruptly in subsp. *lecoqii*. This difference seems to be related to the quantity of fertilized ovules in the lower part of the ovary (McNaughton & Harper, 1960c). As regards the length of the stamens in relation to the ovary, McNaughton & Harper (1960c) observed that the stamens are shorter than the ovary in subsp. *dubium*, but that some of the stamens are as long as the ovary in subsp. *lecoqii*. Although I can confirm this from my own observations in Great Britain, this character is very difficult to observe in herbarium material. It is often problematical whether in these highly self-fertilizing forms the growth of the ovary after fertilization has already started, in which case the stamens will very quickly be shorter than the ovary in subsp. *lecoqii* also. Accordingly, I am not able to say whether this character works within the entire distribution area of subsp. *lecoqii*. From my knowledge of the herbarium material I cannot confirm another diagnostic character for the two subspecies described by McNaughton & Harper (1960c): they observed glaucous seeds in subsp. *dubium*, but chocolate-brown seeds in subsp. *lecoqii*.

As judged from the crossability of the two subspecies and the pattern of bivalent formation in their hybrid (Koopmans, 1970; Humphreys, 1975a, b) subsp. *dubium* and subsp. *lecoqii* are very similar to each other genomically, as are red- and white-flowered forms of subsp. *lecoqii*, in which regular meiosis was observed by Koopmans (1970). While subsp. *dubium* is very widespread, most certainly through human influence, subsp. *lecoqii* is more limited in distribution (Fig. 6). Its distribution area is perhaps best characterized as submediterranean-subatlantic. More than subsp. *dubium* it seems to prefer calcareous substrata (Clapham et al., 1962; Heß et al., 1970). It is difficult to say to what extent the distribution of subsp. *lecoqii* has been influenced by man, but its presence in the British Isles, at least, seems to be due to synanthropic spread. The eastern limit of its distribution in W Turkey more or less coincides with the western limit of subsp. *laevigatum* (M.Bieb.) Kadereit (Fig. 7). The approach to European *P. dubium* chosen here, namely the recognition of two subspecies, differs from that used by Kubát (1980) for the forms occurring in Czechoslovakia. In what I regard as *P. dubium* subsp. *lecoqii* Kubát distinguished four taxa: *P. lecoqii*, *P. confine* Jordan, *P. albiflorum* subsp. *albiflorum* and *P. albiflorum* subsp. *austromoravicum*. With the exception of *P. albiflorum* subsp. *albiflorum* as far as I can gather from Kubát (1980), the dry latex of all these taxa is red, and is either yellow (*P. lecoqii*, *P. albiflorum* subsp. *austromoravicum*), turns yellow when exposed to air (*P. confine*) after being white to cream, or is colourless (*P. albiflorum* subsp. *albiflorum*) when fresh. All these taxa are tetraploids with 2n = 28 chromosomes. Although I include all these

different forms in subsp. *lecoqii* for the reasons given above, it should be noted that Kubát's (1980) classification corresponds to the one presented here insofar as the distinction between hexaploids and tetraploids is the same. The work of Kubát (1980) also clearly demonstrates the variability of subsp. *lecoqii*.

I have not seen the type material of *P. schweinfurthii* Fedde (in Engler, *Pflanzenr.* 4, 104:307, 1909), described from Tunis, which from its description clearly belongs to *P. dubium*. I am not able to say, however, whether it must be referred to subsp. *dubium* or subsp. *lecoqii*. The same applies to *P. collinum* Bogenh. (in Boreau, *Fl.Centre France* (Ed.3) 2:29, 1857) and probably also to *P. malvaeflorum* Doumergue (Assoc.Franc. Avancem.Sci.Conf. 455, 1896). I have not made an effort to allocate to either subsp. *dubium* or subsp. *lecoqii* the species described and explicitly related to *P. dubium* by Jordan (1852, 1861). These are *P. modestum, P. confine, P. erosulum, P. vagum, P. erroneum, P. luteo-rubrum* and *P. errabundum*.

iii. subsp. **laevigatum** (M.Bieb.)Kadereit, **comb. et stat. nov.** Figs 7, 13, 17.

Syn.: *P. laevigatum* M.Bieb., Fl.Taur.–Caucas. 3:364 (1819).
P. rhodopeum Velen., Sitzungsb.Königl.Boehm.Ges.Wiss. Prag, Math.-Naturwiss.Cl. 37:5 (1893). Type: Infra saxa locis calidis supra Stanimaka (n.v.).
P. lacerum Popov in Komarov, Fl. URSS 7:641, 749 (1937). Type: Paphlagonia Wilayet Kostambuli, 1892, *Sintenis* 3702 (G); Marsifoun, *Manissajian* 451b (LE).
P. maeoticum Klokov in Klokov & Wissjul., Fl. RSS Ucr. 5:503 (1953). Type: Distr. Staliniensis, prope opp. Zhdanov (Mariupol), 2 vii 1925 (KW).

Type: Hab. in collibus circa Odessam, nec non in rupibus circa thermos Constantinomontanus (LE).

Plants mostly with sparse indumentum, glaucous. *Upper leaves* (Fig. 13) sessile with cuneate to rounded base, lobes antrorse, narrow, serrate to entire, often conspicuously wavy, upper surface often glabrous. *Petals* with small to large black basal spot, often leaving only narrow red margin, rarely petals entirely black; anthers sometimes with small apical appendage.

Flowering 4–7. A weed in fields, or in open vegetation on calcareous rocks, serpentine or conglomerate. The distribution of subsp. *laevigatum* is shown in Fig. 7.

GREECE: Distr. Kozani, in monte Vourinon, 5–7 vii 1956, *Rechinger* 17723 (B).
BULGARIA: Veles, *Burgeff & Herzog* 127 (M); Bulgaria, vii 1910, *Stribrny* s.n. (WU); Distr. Varna, Adjeniler, ? (WU).
USSR: Odessa, vi 1874, *Blau* s.n. (B); Distr. Simferopl: 9km S Simferopl, 5 vi 1959, *Davis* 33546 (E); Caucasus, *Fischer* s.n. (E); Odessa, *Frivaldsky* s.n. (WU); Odessam, *Lang & Szovits* 63 (G, M, W).
TURKEY: Angora, 7 v 1933, *Balls* 224 (E); Ak Dagh, Erzingan, 26 vii 1934, *Balls* 1509 (BM); Taşköprü (Kastamonu), *Baytop* 11317 (E); Amasia, 29 iv 1889, *Bornmüller* 145 (W, WU); Galatia: in valle Kawakli-Dere, 31 v 1929, *Bornmüller* 13718 (G, W); Galatia: ad pagum Kajaš, *Bornmüller* 13719 (BM); Paphlagonia: ad oppidum Čankri, 29 v 1929, *Bornmüller* 13721 (BM, G, W); Iskilip, *Coode & Jones* 1816 (E); Baba Dag above Seki, 22 iv 1965, *Davis* 41536 (E); Karacasu, *Davis* 41669 (E); Amassia, 2 v 1891, *Manissadjian* 119 (M); Asia Minor, 22 v 1913, *Papazoghlov* s.n. (BM); Prov. Nigde, Ala Dağ, *Parry* 109 (E); Szanschak Gümüschkhane, 18 vi 1894, *Sintenis* 5902 (G); Vil. Samsun, Hauza, *Tobey* 938 (E); Merzfun–Hacıköy, 11 v 1969, *Tobey* 2514 (E); Ankara, 20 v 1955, *Walter* 1209 (B); Sariyar, 28 iv 1955, *Walter* 1443 (B).
IRAN: pr. Teheran, *Kotschy* s.n. (BM).

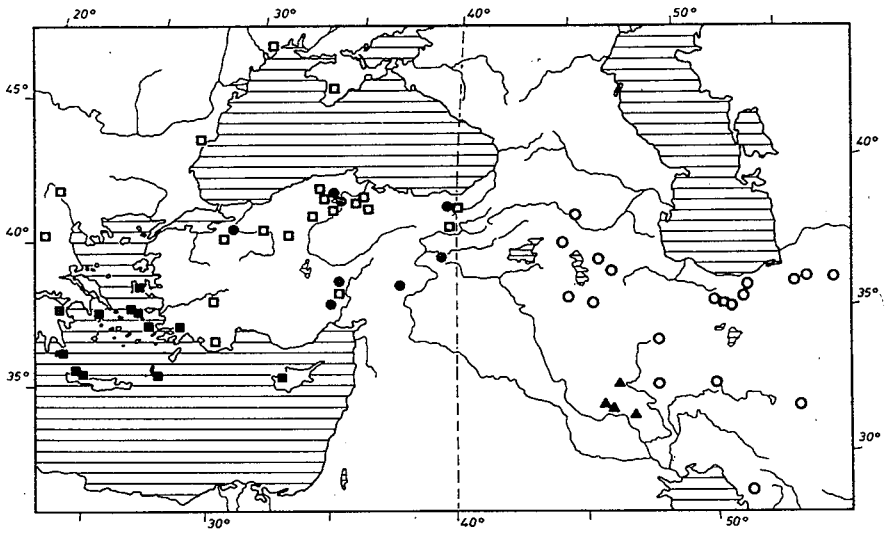


FIG. 7. Geographical distribution of *P. purpureomarginatum* (■), *P. dubium* subsp. *laevigatum* (□), *P. dubium* subsp. *erosum* (○), *P. rechingeri* (▲) and *P. arachnoideum* (●).

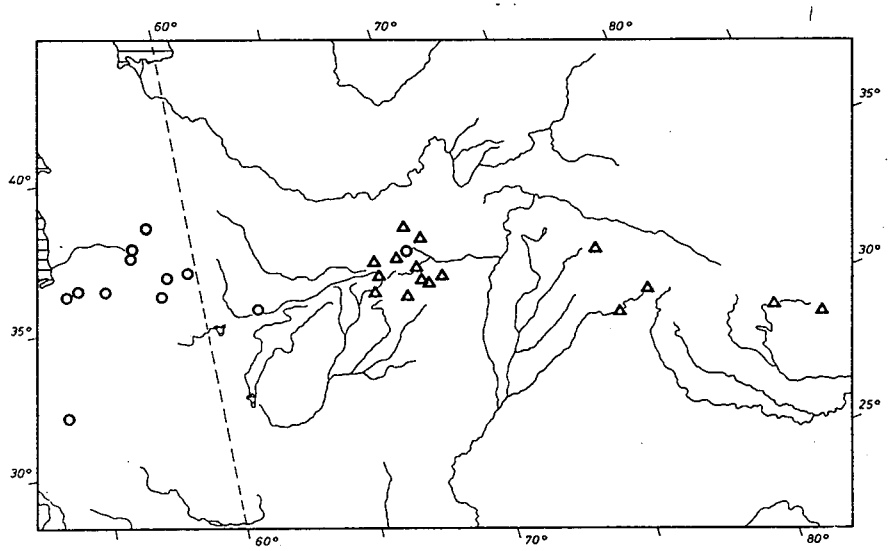


FIG. 8. Geographical distribution of *P. dubium* subsp. *erosum* (○) and subsp. *glabrum* (△).

The distribution of this taxon (mainly in Turkey and around the Black Sea with rare and isolated occurrences in Greece and Iran), in combination with the glaucidity of the plants, their mostly sparse indumentum,

Plants often with red tinge. *Axis* with patent, pedicel with patent or mostly appressed setae. *Flower buds* shortly before anthesis 14–22×7–12mm, ovoid to ellipsoid, with ± dense indumentum of ± patent setae. *Petals* 1·2–3·3×1–4cm, broadly obovate to flabelliform, crimson, mostly with large black basal spots or spot black and apically white. *Stamens* many, 6·5–10mm long, shorter to longer than ovary; filaments filiform, black; anthers 0·8–2·2mm long, oblong, brownish to violet. *Capsule* 7–13×4–8mm, 1·5 to 2·6 times as long as broad, obovoid (Fig. 3); stigmatic disc with 6–10 stigmatic rays, 4–7mm broad, as broad as to narrower or broader than capsule diameter; free lobes of stigmatic disc broadening towards their tip, mostly overlapping. *Seeds* 0·7mm long. brown, glaucous (Fig. 19).

2n = 14 (mihi).

Flowering 2–5. Mostly found as a weed in fields or often in sand dunes.

The distribution of *P. humile* is shown in Fig. 16.

ISRAEL: Palestine: Mars Saba, 6 iv 1880, *Barbey* 28 (G); Ascalon, 31 iii 1911, *Dinsmore* 2598 (E, JE); Tel-Aviv: Nahlat-Izhak, 7 iv 1936, *Eig et al.* s.n. (BM); Negev, Wadi Mshash, 17 iii 1956, *Feinbrun* s.n. (BM, E); Akhziv, 17 iv 1958, *Feinbrun* s.n. (E); Shefela, 28 iii 1963, *Feinbrun* s.n. (E); Turaibeh, 15 iii 1956, *Gruenberg* s.n. (BM); Beersheba, 12 iv 1946, *Lupton* s.n. (BM); Medaba, 24 iv 1911, *Meyers & Dinsmore* M598 (E); Jaffa, 3 iii 1911, *Meyers & Dinsmore* 1548 (E, JE); Jaffa, *Meyers & Dinsmore* B4598 (E).
JORDAN: between Petra and foot of Mt Hor, 17 iv 1945, *Davis* 9082 (E).
EGYPT: Abou Mazrouk, 24 iii 1880, *Barbey* 30 (G); Alexandria, 15 ii–15 iv 1909, *Blumencron* 63 (WU); Abu Sir, 14 iii 1944, *Davis* 6521, 6521B (BM, E); Burg El Arab, 14 iii 1944, *Davis* 6530, 6530B (BM, W); Amria, 15 iii 1944, *Davis* 8365 (BM, E); Alexandriae, *Ehrenberg* 3 (B); Marmaricae, *Gauba* 143 (W); S of Amria, 2 iv 1971, *Ibrahim & Mahdi* s.n. (G); circa Alexandriam, 14 iii 1836, *Kotschy* s.n. (W); ad lacum Mareotim, ii 1855, *Kotschy* 128b (W); Mersa Matruh, i 1928, *Meinertzhagen* s.n. (BM); Burg-El-Arab, 7 v 1949, *Shabetai* s.n. (G); Mariut: Abusir, 23 iii 1961, *Täckholm* s.n. (G); Ras El Hekma, 16 ii 1965, *Täckholm* s.n. (G); Amria, *Wilmott* 390322 (BM).

P. humile is a species with strong similarities to *P. rhoeas*. It can be distinguished from it mainly by the base of its upper leaves. Whilst the upper leaves are mostly sessile in *P. rhoeas*, they are distinctly petiolate in *P. humile* as well as in *P. carmeli*. The petioles are broadly winged in most cases and have a ciliate margin and mostly clasp the axis over their entire length. Different from *P. rhoeas*, in which the basal pair of lobes of the upper leaves is mostly much bigger than the basal pair of lobes of the middle lobe, the basal lobes are only slightly longer or even shorter than the basal lobes of the middle lobe in most material I have seen of *P. humile* and *P. carmeli*. In addition to these differences both *P. humile* and *P. carmeli* mostly have a red tinge on the axis and/or leaves, red setae, and sometimes, particularly in *P. carmeli*, a red-tinged stigmatic disc; such coloration of the plant is less common in *P. rhoeas*. From *P. rhoeas, P. humile* also usually differs in habit: it often is of decumbent to ascending growth, and the main axis often has only one or two leaves above a basal rosette. In the shape of the middle lobe of the upper leaves, which is often lanceolate to elliptical in outline and incised to pinnatipartite with strongly antrorse acutely triangular teeth or lobes, *P. humile* and *P. carmeli* can resemble *P. umbonatum*.

As regards the distinction of two subspecies of *P. humile* by Feinbrun (1963), subsp. *humile* with white latex from sandy and loess-sandy soils from the Negev and southern Shefela in Israel, and subsp. *sharonense* Feinbrun with yellow latex from sandy clay in the Coastal Plain north of Ashgalon, I feel unable to form an opinion on the basis of the herbarium material available to me. In view of the geographical separation of forms with white and yellow latex respectively, which is not, as in *P. dubium*, recognizable in herbarium material, I think that the recognition of two subspecies is justified. In its distribution *P. humile* may extend further west in North Africa than shown in the distribution map (Fig. 16). I have seen one specimen (*Petrovich* 230, WU) from Benghasi which might belong to *P. humile*.

The combination at subspecific rank in *P. rhoeas* of *P. humile* was made by Holmboe (1941) for material from Cyprus. As I have not seen the material available to that author I cannot judge its identity. As I have seen no material of *P. humile* from Cyprus, I suspect that Holmboe (1914) was dealing with impoverished sand forms of *P. rhoeas*. Such forms from Cyprus were described by Chrtek & Slavik (1981) as *P. rhoeas* subsp. *cyprium* (see below), which I do not maintain as a separate taxon.

16. P. rhoeas L., Sp.Pl. 1:507 (1753). Figs 3, 15, 19, 20.

'Habitat in Europae arvis, agris'.

Syn.: *P. integrifolium* Viguier, Hist.Nat.Pavots: 38 (1814). Type: Bocc.Mus. p.77. tab. 65. ic. 1; Barrel. Icon. 1191 (illustrations, n.v.).

P. roubiaei Viguier, Hist.Nat.Pavots: 39 (1814). Type: Sur un terrain sablonneux près de Frontignan, 1813, *Roubieu* s.n. (MPU).

P. trilobum Wallr., Ann.Bot.: 149 (1815). Type: inter Viciam Fabam prope Osterhausen; inter Brassicam Napum ad Heringen (n.v.).

P. polytrichum Boiss. & Kotschy ex Boiss., Diagn. Sér. 2, 5:14 (1856). Type: circa Zebdaine prope Damascum, 2 vi 1855, *Kotschy* 11 (lecto. G-Boiss., Feinbrun, 1963).

P. rumelicum Velen., Sitzungsb.Königl. Boehm.Ges. Wiss. Prag, Math.-Naturwiss.Cl. 1889:29 (1890). Type: Prope Sliven, *Skorpil* s.n. (n.v.).

P. rapiferum Fedde, Bull.Herb.Boissier, Sér. 5, 2:170 (1905). Type: Balkis ad Euphratem, 30 iii 1865, *Haussknecht* s.n. (W).

P. tenuissimum Heldr. ex Fedde, Bull.Herb.Boissier, Sér. 5, 2:446 (1905). Type: Flora Attica in m. Parnethe pr. Dekeleiam, 28 vii 1880, *Heldreich* s.n. (B).

P. humifusum Fedde, Bull.Herb.Boissier, Sér. 5, 2:447 (1905). Type: antiliban près de Damas, 14 v 1856, *Gaillardot* 1516 (JE).

P. postii Fedde, Bull.Herb.Boissier, Sér. 5, 2:447 (1905). Type: Top of southern spur of Nusairy Mts, 4 viii 1890, *Post* 3 (lecto. G, isolecto. B).

P. caespitosum Fedde in Engler, Pflanzenr. 4, 104:302 (1909). Type: Loja, 12 vii 1876, *Winkler* s.n. (holo. B).

P. hirto-dubium Fedde in Engler, Pflanzenr. 4, 104:303 (1909). Type: Courroi, viii 1860, *Tueskievicz* s.n. (MPU).

P. pseudo-haussknechtii Fedde in Engler, Pflanzenr. 4, 104:304 (1909). Type: Attica: Athenae, in Lykabetto, v 1885, *Haussknecht* s.n. (JE).

P. thaumasiosepalum Fedde in Engler, Pflanzenr. 4, 104:307 (1909). Type: Esparsettefelder bei Kissingen, *Schweinfurth* s.n. (JE).

P. ameristophyllum Fedde in Engler, Pflanzenr. 4, 104:308 (1909). Type: inter segetes Mogliano, *Mayer* s.n. (B).

P. robertianella Fedde in Engler, Pflanzenr. 4, 104:323 (1909). Type: in ins. Lero, 23 iv 1877, *Heldreich* s.n. (B).

P. subumbilicatum Fedde in Engler, Pflanzenr. 4, 104:324 (1909). Type: Attica: Athenae, in m. Lykabetto, 1885, *Haussknecht* s.n. (JE).

P. expectatum Fedde in Engler, Pflanzenr. 4, 104:326 (1909). Type: Schleinitz b. Oderfeld, vii 1874, *Haussknecht* s.n. (B).

P. rhoeas L. subsp. *cyprium* Chrtek & B. Slavik, Preslia 53:48 (1981). Type: Cyprus, in arenosis maritimis 2km situ mer.-orient. ab opp. Paphos, 9 iv 1978, *Chrtek & Slavik* s.n. (holo. PR).

Erect to ascending or sometimes almost decumbent annual herb, 10–60cm high, mostly branched from the base. *Leaves* 1–24 × 0·5–6cm, obovate to ovate in outline, pinnatifid to pinnatipartite; lower leaves petiolate, petiole up to 7(–11)cm long, incised to pinnatifid; terminal segment mostly more than twice as long as broad, often much longer; upper leaves mostly sessile, sometimes very shortly petiolate, petiole shorter 0·5cm, broadly winged; uppermost leaves mostly trifid with one large middle lobe and two smaller basal lobes; basal lobes incised to pinnatifid, sometimes serrate, antrorse, mostly distinctly bigger than basal segments of middle lobe; middle lobe incised to pinnatifid or sometimes more or less regularly serrate; leaves with more or less dense indumentum of patent setae on both surfaces (Fig. 15).

Axis with patent, pedicel with patent or appressed setae; setae white, yellow or dark violet to red. *Flower buds* shortly before anthesis 9–28 × 5–18mm, ovoid to ellipsoid or obovoid, sometimes with ± distinct subapical processes, with ± dense indumentum of patent to appressed setae. *Petals* 1·3–5·1 × 0·8–10cm, broadly obovate to distinctly flabelliform, brick red to crimson or rarely white, without or with black spots or black and apically white basal spots; outer pair of petals mostly substantially bigger than inner pair. *Stamens* many, 4–10mm long, shorter to longer than ovary; filaments filiform, light red to black or rarely white to yellow; anthers 0·3–2·6mm long, oblong, brownish or rarely yellow. *Capsule* 5·5–16(–20) × 4·5–14mm, as long as broad to 2·1 times as long as broad or very rarely up to 3 times as long as broad, rarely narrowly to mostly broadly obovoid to cylindrical or almost globose, sometimes shortly stipitate (Fig. 3); stigmatic disc with 6–16 stigmatic rays, 3·5–12mm broad, mostly broader than capsule diameter, mostly flat, sometimes slightly umbonate; free lobes of stigmatic disc mostly broadening towards their tip, overlapping. *Seeds* 0·6–0·9mm long, brown, glaucous (Fig. 19).

2n = 14 (mihi).

Flowering 4–10. Usually a weed in cultivated or waste land.

1a. Pedicel with patent setae . . . . . var. **rhoeas**

1b. Pedicel with appressed setae . . . . . var. **strigosum**

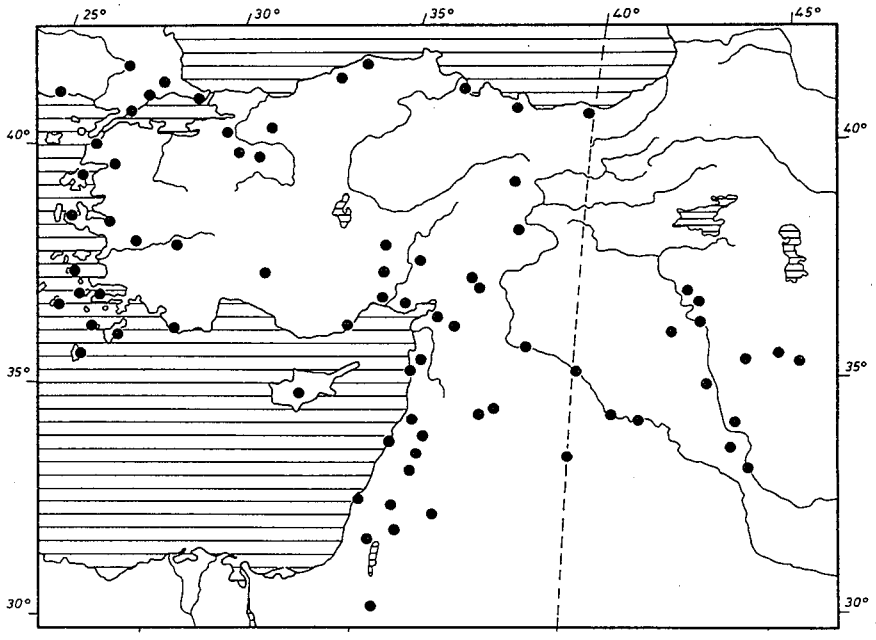


FIG. 20. Geographical distribution of *P. rhoeas* (•) in SW Asia.

var. **rhoeas**

GREAT BRITAIN: Lewes, 22 vi 1960, *Ball* s.n. (M).
FRANCE: Allues, Tarentaise, 11 viii 1978, *Meilleur* 490 (G).
SPAIN: Sierra de Alcaraz, 27 vi 1974, *Leadley & Petty* 116 (C).
PORTUGAL: Coimbra, *D'Araujo E Castro* s.n. (WU).
BELGIUM: Braine l'Alleud, 21 vii 1963, *Lucion* s.n. (G).
SWEDEN: Follinbo, 30 viii 1930, *Fries* s.n. (C).
DENMARK: N of Aarhus, 16 x 1964, *Pedersen* 76 (G).
GERMANY: Weimar, viii 1905, *Bornmüller* s.n. (B).
POLAND: Czernichow prope Krakow, 14 vi 1956, *Zarzycki* s.n. (C).
SWITZERLAND: Martigny, Branson, 12 vi 1967, *Burdet & Greuter* 617 (C).
AUSTRIA: Gösting bei Graz, 11 vii 1948, *Höpflinger* s.n. (C).
CZECHOSLOVAKIA: Ricmanice, 19 vi 1963, *Slavonovsky* s.n. (WU).
ITALY: Paestum, 6 vi 1968, *Albrecht* s.n. (M).
HUNGARY: Budapest, vii 1878, *Ronutiu* s.n. (G).
YUGOSLAVIA: Dalmatien: Murter, 15 vi 1977, *Ern* s.n. (B).
ROMANIA: Oltenia, 31 v 1971, *Cirtu & Teodorescu* s.n. (WU).
ALBANIA: Shkodra, 21 vi 1916, *Janchen* s.n. (WU).
BULGARIA: Tirnowo, 24 v 1894, *Urumoff* 146 (WU).
GREECE: montis Pelion prope Volos, 4 v 1961, *Rechinger* 22648 (W).
TURKEY: Arslanköy, 2 vii 1982, *Tarmann* s.n. (WU).
USSR: Simpheropol, 25 vii 1977, *Vasak* s.n. (W).
SYRIA: Est de Palmyra, 2 iv 1955, *Pabot* s.n. (G).
LEBANON: el Kaa, 17 iv 1957, *Pabot* s.n. (G).
IRAQ: Samarra, 4 v 1957, *Rechinger* 9452 (G).
JORDAN: Buseira, 29 iv 1955, *Hunting Aero Service* 136 (E).
AZORES: Sao Miguel, 30 v 1978, *Rechinger* 58115 (M).
MADEIRA: Garajau, 21 iii 1984, *Press & Short* 225 (BM).
CANARY ISLANDS: Gran Canaria, Las Palmas & Tejeda, 6 iv & 25 v 1897, *Gelert* s.n. (C).
MOROCCO: Fes, 2 vi 1981, *Alyafi* s.n. (G).
ALGERIA: Bersekrane to Ain Temouchent, 26 iv 1971, *Davis* 51577 (E).
TUNISIA: Sousse, 10 v 1896, *Murbeck* s.n. (WU).
LIBYA: Elebier, 24 iii 1970, *Davis* 49877 (E).

P. rhoeas is widely distributed in Europe, North Africa and wide parts of South West Asia. Beyond the countries listed above *P. rhoeas* is comparatively rare. As an introduction *P. rhoeas* is also known from other continents. The distribution of *P. rhoeas* in SW Asia is shown in Fig. 20.

var. **strigosum** Boenn., Prodr.Fl.Monast.Westphal.: 157 (1824).
Type: ad ripes Rheni, nec non prope Münster! Velen! Coesfeld! (types unknown).
Syn.: *P. strigosum* (Boenn.)Schur, Verh.Naturf.Vereins Brünn 15:66 (1877).

P. rhoeas var. *strigosum* is distinguished from the type variety by its indumentum of appressed setae on the pedicel. It mostly occurs together with the type variety and can be found in its entire distribution area.

Among the species treated in the present account, *P. rhoeas* is the most problematical. Due to the variability found in leaf and capsule shape and indumentum of the pedicel its delimitation from some of the preceding species, notably *P. guerlekense*, *P. umbonatum*, *P. carmeli* and *P. humile*, presents some difficulties. By the mostly broadly obovoid shape of its capsules with their mostly flat stigmatic disc which in most cases is broader than the capsule diameter, and the mostly sessile and distinctly trifid uppermost leaves, however, it should be possible to recognize most material of this species. With the occasional presence of rather narrowly obovoid capsules, slightly umbonate stigmatic discs or petiolate upper leaves *P. rhoeas* seems to combine some of the characters of the species named above. This is probably the result of its origin from one or more of these species.

The variability of *P. rhoeas* perhaps is reflected in its very extensive synonymy. Of the 45 binomials accepted by Fedde (1909), 12 are recognized here. Of the remaining 33 names I regard 17 as synonyms of *P. rhoeas*, of these, 12 were newly described by Fedde (1905, 1909). It may be significant for the status of these 12 'species' that all of them were described from just one specimen each. In *P. rhoeas* Fedde (1909) recognized 20 varieties and 6 subvarieties, and in *P. strigosum*, which I here treat as a variety of *P. rhoeas*, 7 more varieties and 1 subvariety were recognized. Earlier authors diligent in the description of new segregate species of *P. rhoeas* were Timbal-Lagrave (1870, 1892), Jordan (1861, 1864) and Wein (1911a–c). The last author alone described 13 species (including one hybrid) from the southern Harz Mountains, claiming that even an anti-Jordanian requires more than 2 binomials (*P. rhoeas*, *P. strigosum*) to accommodate the variation of *P. rhoeas*, and claiming a better foundation for his than for Jordan's species. This reasoning I do not believe or follow. Although it must be admitted that *P. rhoeas* is very variable in size, indumentum, leaf and capsule size and shape, partly due to genetic variability and partly to a high degree of phenotypic plasticity, the abundance of names must surely be connected to the importance and conspicuity of the species as a weed. A historical component in the classification of plants and animals beyond their measurable structure of variability certainly cannot be denied and has been pointed out repeatedly by Walters (1986). A comparison of the variability of different species of *Papaver* with that of *P. rhoeas* would be interesting in this respect. I do not believe that the relation of amount of variability to number of published names is proportionally as high in most other members of such a comparison as it is in *P. rhoeas*.

In the following discussion of the synonymy of *P. rhoeas* I will not consider further the binomials by Jordan (1861, 1864: *P. insignitum*, *P. arvaticum*, *P. erraticum*, *P. agrivagum*, *P. cereale*, *P. cruciatum*, *P. segetale*, *P. rusticum*), which by the author were explicitly connected with *P. rhoeas* and included in that species or *P. strigosum* by Fedde (1909); those by Timbal-Lagrave (1870, 1892: *P. dodonaei*, *P. erraticum* = *P. erucifolium*, *P. fuchsii*, *P. caudatifolium*), which again were connected with *P. rhoeas* by the author and included in it by Fedde (1909); and those by Wein (1911a–c): *P.* x *feddeanum*, *P. osswaldii*, *P. propinquum*, *P. commixtum*, *P. paucisetum*, *P. anisotrichum*, *P. omphalodeum*, *P. intricatum*, *P. cinerascens*, *P. fastidiosum*, *P. interjectum*, *P. balanocarpum*, *P. spurium*), which from the descriptions given all seem to belong to *P. rhoeas*. Instead, I restrict myself to those names recognized at specific rank by Fedde (1909) and relevant names from later publications.

P. rapiferum, although described as a perennial or biennial, without doubt belongs to *P. rhoeas*. Occasionally *P. rhoeas* seems to behave at least as a biennial, as was also stated for *P. rumelicum*, which was given varietal rank by Fedde (1909). *P. roubiaei*, *P. postii*, *P. caespitosum* and *P. pseudo-haussknechtii*, and also *P. rhoeas* subsp. *cyprium*, all represent rather small and somewhat tufted specimens which on account of the shape of the capsules and in most cases of the leaves—only the type specimen of *P. postii* has less than normally dissected leaves—must be referred to *P. rhoeas*. Part of the type collection of *P. roubiaei* and the type of *P. postii* have pedicels with appressed setae. Specimens with very small and somewhat stipitate and turbinate capsules matching the type of *P. postii* can be found in various parts of the range of *P. rhoeas*. As regards the amplified description of *P. postii* given by Burtt (1949), this most likely relates to *P. purpureomarginatum*, as already discussed above under that species. *P. trilobum*, of which I have not seen the type material but authentic specimens annotated by Wallroth (W), with three-lobed leaves and almost glabrous axes, leaves and sepals, and also *P. thaumasiosepalum* with large lacerate sepals both belong to *P. rhoeas* on account of the shape and size of their capsules and, in the case of *P. thaumasiosepalum*, leaf shape. They must be regarded as rare, freak mutants. The same seems to apply to *P. integrifolium* from the description and synonymy given by Viguier (1814). Also *P. ameristophyllum* with entire obovate leaves and a pedicel with appressed setae must be referred to *P. rhoeas*.

Papaver polytrichum, *P. tenuissimum*, *P. humifusum*, *P. hirto-dubium*, *P. robertianella*, *P. subumbilicatum* and *P. expectatum* are all specimens with unusually long capsules which otherwise, however, from indumentum, leaf shape and shape of the stigmatic disc and its free lobes, must be referred to *P. rhoeas*. Of these seven binomials *P. polytrichum* is the one which has been used most frequently. It was described by Boissier as being related to *P. rhoeas*, but differing in its smaller height, denser

indumentum of patent setae, smaller flowers, and by having yellow instead of violet pollen. Its capsules were described as 'turbinato-obconicis' and later (Boissier, 1867) as 'clavata obovata-oblonga', whereas those of *P. rhoeas* were described as 'obovata'. *P. polytrichum* was accepted as a species by Post (1932), Rechinger (1959), Feinbrun (1963), Zohary (1966) and Mouterde (1970), and treated as a subspecies of *P. rhoeas* by Thiébaut (1936). One of the type specimens named by Boissier (1856), 'Antilibani inter Rascheya et Damascum, *Boissier* s.n. G-Boiss.' belongs to *P. rhoeas* in every respect, while the other type collection named by him, 'circa Zebdaine prope Damascum, *Kotschy* 11, G-Boiss.' is distinguished by narrowly obovoid to clavate capsules which are about 3 times as long as broad. Among the numerous duplicates (B, JE, 4x W) of this latter collection, which was chosen as lectotype by Feinbrun (1963), capsule length varies to some extent so that in some specimens (W) the capsules cannot be distinguished from those of *P. rhoeas*. As rather long capsules thus represent only an extreme of a continuous variation, I do not wish to assign formal rank to such forms. It must be admitted, however, that specimens with capsules similar to the lectotype of *P. polytrichum* are quite frequent in the Antilebanon area; examples are *Gaillardot* 1515 (G), *Gaillardot* s.n., Antiliban près de Damas (JE), *Mouterde* 3685 (G), *Pabot* s.n., Rayak (G), *Pabot* s.n., Jebel Qassyoum (G) and *Peyron* 1776 (G). In capsule proportions and the fact that some of the synlectotype collections have slightly umbonate capsules, what has been named *P. polytrichum* also resembles *P. umbonatum*. On account of the shape of the leaves, however, I prefer to accommodate this material in *P. rhoeas*.

P. pasquieri Dubuis & Faurel, *Bull.Soc.Hist.Nat.Afrique N.* 54:102 (1964), described from Iran, of which I have seen no type material, probably belongs to *P. rhoeas*.

As regards specimens with yellow to white filaments and yellow anthers and without black spots on the petals otherwise referable to *P. rhoeas*, these are known in horticulture as Shirley Poppies (Cullen, 1969).

The preceding seven species which, with the exception of the widespread *P. rhoeas*, are distributed more or less vicariously in the East Mediterranean, form a very closely knit group. Particularly with respect to its distribution the situation found here resembles that in *P. dubium* with its five more or less vicarious subspecies and the Aegean *P. purpureomarginatum* as a close allopatric ally. There are, however, differences in the pattern of variation between the two groups which in my opinion justify the different formal treatment chosen. In *P. dubium* the differences between the subspecies are slight and can be found mainly in leaf shape and indumentum and, in some cases, also in petal shape and coloration and latex colour. Despite the fact that the differences thus are slight, most specimens, with the exception of those of *P. dubium* subsp. *dubium* and subsp. *lecoqii*, can be allocated more or less easily, and the number of intermediate specimens is small. In the group around *P. rhoeas* differences between most species are bigger and can be found in capsule and leaf characters. Intermediate specimens or specimens of different species approaching each other in many characters do exist, although again in small number. Thus *P. guerlekense* can be very similar

to *P. rhoeas* in capsule shape and to *P. stylatum* in leaf shape, *P. stylatum* to *P. umbonatum* in capsule shape, *P. umbonatum* to *P. rhoeas* and *P. clavatum* in capsule shape and to *P. carmeli* and *P. humile* in leaf shape, and *P. carmeli* and *P. humile* to *P. rhoeas* in capsule shape. From the similarities observed it might seem justified to regard *P. guerlekense*, *P. umbonatum*, *P. carmeli* and *P. humile* as subspecies of *P. rhoeas*. Such a treatment would exclude *P. stylatum* and *P. clavatum*, which both have some similarity to *P. umbonatum*, from this group, which seems unnatural particularly in the case of *P. stylatum*. If all these taxa were included into *P. rhoeas* at subspecific rank, with the possible exception of *P. clavatum*, often very distinct entities would be united in one species. In this situation, given the pattern of geographical distribution of the group, I have decided to regard the different entities as formally equivalent despite their differential degree of similarity to each other, and to give them, in view of the distinctive morphology of the majority of specimens, specific rank. I am aware that by choosing this treatment for the seven taxa in question I have cut the Gordian knot. The decision made is based primarily on the equivalency of the members of the group, and only secondarily on the differential similarities observed. Subsequent authors may hold a very different view on this.

General Discussion

Among the annual sections of *Papaver*, sect. *Rhoeadium* is most closely related to sects *Papaver* and *Carinatae* Fedde (Kadereit, 1988a). These three groups are characterized by their glabrous capsules with a flat stigmatic disc and the possession of (mostly) black filaments. Of the biennial and perennial sections of the genus sect. *Macrantha* Elkan shows this combination of characters. Sect. *Carinatae* is distinct on account of its rather strongly keeled stigmatic rays and the deciduous stigmatic disc at capsule maturity (Kadereit, 1987). The only character available for the separation of sects *Rhoeadium* and *Papaver* is the rounded to amplexicaulous base of the upper stem leaves in the latter group. Otherwise, as pointed out before (Kadereit, 1986b), the two groups are very similar to each other. Particularly the distinction of *P. decaisnei* of sect. *Papaver* from *P. dubium* subsp. *glabrum* is difficult. By the occasional possession of apical anther appendages *P. decaisnei* clearly shows its affinity to *P. dubium*, in which such appendages can be found in subsp. *laevigatum* and subsp. *erosum*. As in sect. *Papaver P. decaisnei* is obviously related to *P. glaucum* Boiss. & Hausskn., which also has anther appendages, an affinity of this otherwise distinct species and only representative of the genus in the Syrian Desert to *P. dubium* must be assumed. Equally, *P. gracile* Boiss. of sect. *Papaver* from SW Turkey and Cyprus shows similarities to *P. dubium* particularly in capsule characters. As earlier (Kadereit, 1986a) *P. somniferum* L. (incl. *P. setigerum* DC.) was postulated to be of hybrid origin from taxa similar to *P. glaucum* and *P. gracile*, it seems that sect. *Papaver* finds its closest ally in *P. dubium* of sect. *Rhoeadium*.

One species contained in Fedde's (1909) revision of the section, *P. californicum* A. Gray (incl. *P. lemmonii* Greene), has been accommo-

dated in a section on its own, and suggested to be more closely related to the perennial sect. *Meconella* and the biennial sect. *Meconidium* Spach. This was done on account of the yellow filaments, more or less pyramidal stigmatic disc and valvate capsule dehiscense of this species (Kadereit, 1988b).

In sect. *Rhoeadium*, three groups of species can be recognized. These are not easily characterized by one character, but rather by the coherence of the species contained in them. The first group consist of *P. pinnatifidum*, *P. purpureomarginatum*, *P. dubium* and *P. rechingeri*, the second of *P. arachnoideum*, *P. arenarium*, *P. tenuifolium*, *P. commutatum* and *P. chelidoniifolium*, and the third of *P. guerlekense*, *P. stylatum*, *P. clavatum*, *P. umbonatum*, *P. carmeli*, *P. humile* and *P. rhoeas*.

In the first group, which geographically is more or less continuous and stretches from the Atlantic Islands in the west towards Nepal in the east, only tetraploids (2n = 28) and hexaploids (2n = 42) seem to exist. The chromosome number of *P. rechingeri* is not known. From its leaf shape, *P. pinnatifidum* occupies a somewhat separate position, while *P. purpureomarginatum*, *P. dubium* and *P. rechingeri* are very similar to each other. All taxa of the group are distributed more or less allopatrically. In the case of *P. dubium* subsequent authors might decide to allocate specific rank to those taxa recognized as subspecies here. The reasons for this have already been discussed above. The hexaploid *P. dubium* subsp. *dubium*, which certainly is an introduction in most parts of Europe (Godwin, 1975) and probably arose only under human influence, is either related to forms similar to subsp. *erosum*, the only other subspecies in which hexaploid chromosome numbers are known, or, as is more likely from a morphological and geographical standpoint, to forms similar to subsp. *lecoqii*, from which it is difficult to distinguish and with which it hybridizes easily. Interestingly, subsp. *dubium* is virtually absent from the distribution area of the south west Asian subspecies of *P. dubium*.

Except for *P. arachnoideum*, for which no chromosome number is known, and if the literature records for *P. tenuifolium* and *P. chelidoniifolium* can be trusted, the second group of species consist of diploids (2n = 14) only. Relationships within the group are not as close as in the preceding group, but fairly obvious. Thus *P. tenuifolium* can be, except for its indumentum of very soft hairs, very similar to *P. arenarium*, and *P. chelidoniifolium* to *P. commutatum*, which in turn sometimes cannot be easily distinguished from *P. arenarium*. Except for the last two species, which occur sympatrically, the species of this group again are allopatric in distribution. This includes *P. arachnoideum* which is not obviously allied to any of the other four species, but is probably closest to *P. commutatum* on account of petal and capsule characters. In its overall distribution, this second group is more or less continuous.

The remaining group, with the exception of *P. stylatum* and *P. clavatum*, for which no chromosome numbers are known, again comprises diploids only. This group of very closely related species—only *P. clavatum* stands somewhat apart both morphologically and geographically—is distributed more or less allopatrically along the coastal belt of the East Mediterranean from the Aegean towards Egypt. Only *P. rhoeas* is widespread and overlaps with almost all its allies. It is

impossible to point out a natural distribution area of *P. rhoeas* which, like *P. dubium* subsp. *dubium*, probably originated only under human influence. From the pattern of morphological similarities, *P. rhoeas* is most closely related to *P. umbonatum*, *P. carmeli* and *P. humile*, and one might suspect the place of its origin within the distribution area of these three species, i.e., somewhere along the east coast of the Mediterranean. Like the two preceding groups, this third group of species is more or less continuous in its distribution, and most members are distributed allopatrically. As argued above, subsequent authors may prefer to give subspecific rank within *P. rhoeas* to some or all of the species recognized by me.

As regards the relations between these three groups of species, which for convenience can be named the *P. dubium*-, *P. arenarium*- and *P. rhoeas*-groups, I believe that the last two are more closely related to each other than either is to the *P. dubium*-group. These two groups, with the exception of the widespread *P. rhoeas*, are distributed allopatrically and share capsules in which the stigmatic disc is often broader than the capsule diameter at maturity. Also, both seem to contain diploids only. The latter character, as a primitive condition, may be of no great significance, and the diameter of the stigmatic disc in relation to capsule diameter might be argued to be rather unspecific. In contrast to these last two groups, the *P. dubium*-group contains only species in which the diameter of the stigmatic disc is narrower than or as broad as that of the capsule, and contains, as far as is known, tetraploids and hexaploids only. With the exception of *P. purpureomarginatum* and *P. dubium* subsp. *lecoqii* and subsp. *laevigatum* and *P. guerlekense* it is distributed allopatrically with the *P. rhoeas*-group, and also, with the exception of *P. dubium* subsp. *laevigatum*, subsp. *erosum* and *P. arachnoideum*, with the *P. arenarium*-group. The more distant relationship between the *P. dubium*- and *P. rhoeas*-groups may be reflected in the high sterility of hybrids between *P. dubium* and *P. rhoeas* and the low incidence of bivalent formation in their hybrid (Humphreys, 1975b; McNaughton & Harper, 1960b). In contrast, crossability seems to be good within the *P. rhoeas*-group (Snitzer-Pasternak & Galil, 1970), and Philp (1933) encountered no difficulties in crossing *P. commutatum* and *P. rhoeas*. However, in the absence of more experimental information concerning all three groups, and considering the involvement of genome size differences in the above inter-group crosses (hexaploid × diploid), this experimental evidence should not be overinterpreted. Still, experimental evidence from interspecific hybridizations in sect. *Rhoeadium* may be very helpful in illuminating affinities.

Characters of the seed surface (Figs. 17–19) do not seem to be suited for the easy recognition of groups or, in most cases, species.

As regards the mechanisms of reproductive isolation between sympatric species or subspecies in sect. *Rhoeadium*, pollinator behaviour seems to be of significance only where distantly related species are involved. Thus McNaughton & Harper (1960a) could show that honey bees distinguish between *P. dubium* and *P. rhoeas*, but not between *P. dubium* subsp. *dubium* and subsp. *lecoqii*, which they frequently confuse. Equally, honey bees only sometimes distinguish between *P. carmeli*, *P. humile* subsp. *sharonense* and *P. rhoeas*, and mostly pass several times from one species

to another in one flight (Snitzer-Pasternak & Galil, 1970). Moreover, *Papaver* is visited not only by bees, but also by many other insects such as beetles, which show little discriminatory ability. It thus seems that specific integrity, apart from reduced hybrid fertility or hybrid sterility, can be maintained only by allopatric distribution, which indeed is the prominent pattern of distribution in this and other sections of the genus.

According to the observations by Feinbrun (1963) on the Israelian representatives of sect. *Rhoeadium*, allopatric distribution seems to be linked to rather strong edaphic differentiation. This may also contribute to the reproductive isolation between the different species (Snitzer-Pasternak & Galil, 1970). Very little is known about the ecology of other taxa of this group except for the widespread weeds, but perhaps edaphic differentiation is a feature of general importance. Certainly this deserves further study.

Acknowledgements

I should like to express my thanks to the directors of all herbaria cited for the loan of material or photographs of type specimens, to Mr F. Rückert for the preparation of the drawings, to Miss S. Schwitalla for taking the SEM photographs, to Mr U. Wagenfeld for taking photographs of the type specimens and compiling the seed plates, to Mrs H. Emig for typing the manuscript and to Prof. Dr P. Leins for critically reading the manuscript.

References

ARYAVAND, A. (1975). Contribution à l'étude cytotaxonomique de quelques Angiosperms de l'Iran. *Bot.Not.* 128:299–311.

BOISSIER, E. (1856). *Diagnoses Plantarum Novarum*, Sér. 2, 5. Lipsiae.

—— (1867). *Flora Orientalis* 1. Basel.

BURTT, B. L. (1949). In BURTT, B. L. & DAVIS, P. H., On the Flora of the Nearer East: XXIII. Miscellaneous new species and records. *Kew Bull.* 1949:98.

CANDOLLE, A. P. DE (1821). *Regni Vegetabilis Systema Naturale* 2. Paris.

CHRTEK, J. & SLAVIK, B. (1981). Contribution to the Flora of Cyprus. *Preslia* 53:45–65.

CLAPHAM, A. R., TUTIN, T. G. & WARBURG, E. F. (1962). *Flora of the British Isles*. Cambridge.

CULLEN, J. (1965). In DAVIS, P. H. (ed.), *Flora of Turkey* 1:213–248. Edinburgh.

—— (1966). In RECHINGER, K. H. (ed.), *Flora Iranica*. Lfg. 34:1–27. Graz.

—— (1969). The genus Papaver in cultivation. 1. The wild species. *Baileya* 16:73–91.

DAVIS, P. H. (1971). Distribution patterns in Anatolia with particular reference to endemism. In DAVIS, P. H., HARPER, P. C. & HEDGE, I. C. (eds.), *Plant Life of South-West Asia*: 15–27. Edinburgh.

DOSTÁL, J. (1950). *Květena čSR*. Praha.

EKIM, T. & GÜNER, A. (1986). The Anatolian Diagonal: fact or fiction. In HEDGE, I. C. (ed.), Plant Life of South-West Asia. *Proc.Roy.Soc. Edinburgh* B, 89:69–77.

ELKAN, L. (1839). *Tentamen Monographiae Generis Papaver*. Berlin.

FEDDE, F. (1905). Papaveraceae novae vel notabiles. *Bull. Herb. Boissier*, Sér. 5, 2:165–171 & 438–448.

—— (1909). In ENGLER, A. (ed.), *Das Pflanzenreich* 4, 104:1–430. Leipzig.

FEINBRUN, N. (1963). Taxonomic studies on Papaver sect. Orthorhoeades of Palestine and of some other Mediterranean countries. *Israel J.Bot.* 12:74–96.

GILIBERT, J. E. (1781). *Flora lituanica inchoata*. Grodno.

GODWIN, H. (1975). *The history of the British Flora* (ed. 2). Cambridge.

GOLDBLATT, P. (1974). In Chromosome numbers of Phanerogams. 5. *Ann. Missouri Bot.Gard.* 61:902.

HAYEK, A. (1927). *Prodromus Florae peninsulae Balcanicae* 1. Berlin.

HEß, H. E., LANDOLT, E. & HIRZEL, R. (1970). *Flora der Schweiz* 2. Basel & Stuttgart.

HOLMBOE, J. (1914). *Studies on the vegetation of Cyprus*. Bergen.

HUMPHREYS, M. O. (1975a). The evolutionary relationships of British species of Papaver in section Orthorhoeades as shown by observations on interspecific hybrids. *New Phytol.* 74:485–493.

—— (1975b). Some observations on F2 and backcross plants derived from hybrids between Papaver dubium L. and P. lecoqii Lam. *New Phytol.* 74:495–499.

JACKSON, B. D. (1895). *Index Kewensis* 2. Oxford.

JORDAN, A. (1852). *Pugillus Plantarum Novarum*. Paris.

—— (1861). Diagnoses d'espèces Nouvelles ou Méconnues. *Ann.Soc. Linn. Lyon* 7:456–468.

—— (1864). *Diagnoses d'espèces Nouvelles ou Méconnues* 1. Paris.

KADEREIT, J. W. (1986a). Papaver somniferum L. (Papaveraceae): A triploid hybrid? *Bot.Jahrb.Syst.* 106:221–244.

—— (1986b). A revision of Papaver L. Section Papaver (Papaveraceae). *Bot.Jahrb.Syst.* 108:1–16.

—— (1986c). A revision of Papaver Section Argemonidium. *Notes RBG Edin.* 44:24–43.

—— (1987). A revision of Papaver L. sect. Carinatae Fedde (Papaveraceae). *Nord.J.Bot.* 7:501–504.

—— (1988a). Sectional affinities and geographical distribution in the genus Papaver L. (Papaveraceae). *Beitr.Biol. Pflanzen*. 63:139–156.

—— (1988b). Papaver L. sect. Californicum Kadereit, a new section of the genus Papaver. *Rhodora* 90:7–13.

KOMAROV, V. L. (1937). *Flora URSS* 7. Mosqua & Leningrad.

KOOPMANS, A. (1970). Species differentiation in Papaver dubium. *New Phytol.* 69:1121–1130.

KUBÁT, K. (1980). Bemerkungen zu einigen tschechoslowakischen Arten der Gattung Papaver. *Preslia* 52:103–115.

KUNTZE, O. (1887). Plantae Orientali-Rossicae. *Acta Horti Petrop.* 10:137–262.

MCNAUGHTON, I. H. & HARPER, J. L. (1960a). The comparative biology of closely related species living in the same area. 1. External breeding-barriers between Papaver species. *New Phytol.* 59:15–26.

—— (1960b). 2. Aberrant morphology and a virus-like syndrome in