A REVISION OF *PAPAVER* L. SECTS. *PILOSA* PRANTL AND *PSEUDOPILOSA* M. POPOV EX GÜNTHER (PAPAVERACEAE)

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A revision of the perennial *Papaver* L. sects. *Pilosa* Prantl and *Pseudopilosa* M. Popov ex Günther is presented. Sect. *Pilosa* is considered to contain one species with five subspecies: *P. pilosum* Sibth. & Sm. subsp. *pilosum*, subsp. *glabrisepalum* Kadereit *subsp. nov.*, subsp. *strictum* (Boiss. & Balansa) Wendt ex Kadereit *comb. et stat. nov.*, subsp. *spicatum* (Boiss. & Balansa) Wendt ex Kadereit *comb. et stat. nov.* and subsp. *sparsipilosum* (Boiss.) Kadereit *comb. et stat. nov.* The species is distributed in W Turkey. Sect. *Pseudopilosa* contains three species with five subspecies: *P. rupifragum* Boiss. & Reut., *P. atlanticum* (Ball) Coss. subsp. *atlanticum* and subsp. *mesatlanticum* (Maire) Kadereit *comb. et stat. nov.*, *P. lateritium* K. Koch subsp. *lateritium* and subsp. *monanthum* (Trautv.) Kadereit *comb. et stat. nov.* Whereas *P. rupifragum* and *P. atlanticum* are found in S Spain and NW Africa, *P. lateritium* grows in NE Anatolia, Georgia and the Caucasus Mts.

Keywords. Biogeography, *Papaver* sect. *Pilosa*, *Papaver* sect. *Pseudopilosa*, phylogeny.

INTRODUCTION

The perennial *Papaver* sect. *Pilosa* was first established by Prantl in Prantl & Kündig's (1891) treatment of the Papaveraceae for the first edition of Engler & Prantl's *Die natürlichen Pflanzenfamilien*. It was differentiated from the perennial and scapose sect. *Meconella* Spach by having leafy axes, and from the equally perennial sect. *Macrantha* Elkan by having many-flowered inflorescences and less deeply divided leaves. Although Prantl (1891) mentioned red petal and black filament coloration for sect. *Macrantha*, he did not describe these characters for his new sect. *Pilosa*. This group, however, is well distinguished from sect. *Macrantha* by having salmon-coloured to pale orange petals and pale yellow filaments (Kadereit, 1988).

In view of the fact that the first constituent species of sect. *Pilosa*, *P. pilosum* Sibth. & Sm., had already been described in 1806, it is surprising that early monographers of the genus (Viguier, 1814; Bernhardi, 1833; Spach, 1834) apparently had no knowledge of its existence. Only Elkan (1839), although being aware of its perennial habit, lists the species as a 'species dubia' in his annual sect. *Papaver*. In the treatment by Fedde (1909) as the last monographer of the family, sect. *Pilosa* (including sect. *Pseudopilosa*) contained altogether 12 species.

The section was divided by Popov (1937) into sects. *Pilosa* and *Pseudopilosa*, the latter name being later validated by Günther (1975). Whereas sect. *Pilosa* contains taxa with convolute leaf vernation (Günther, 1975) and morphinane and aporphine

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alkaloids (Öztekin et al., 1985), sect. *Pseudopilosa* is characterized by revolute leaf vernation (Günther, 1975) and protopine and rhoeadine alkaloids (Öztekin et al., 1985). In addition, the taxa of sect. *Pilosa* mostly have well-developed leafy axes, whereas both leafy axes and a subscapose or scapose habit can be observed in sect. *Pseudopilosa*. This difference, however, is by no means diagnostic. The justification of the division of sect. *Pilosa* was doubted by Markgraf (1958), and it was not followed by Cullen (1965a, b). Evidence from the analysis of nrDNA-sequences, however, strongly supports the phytochemical and morphological arguments for the recognition of sect. *Pseudopilosa* as distinct from sect. *Pilosa* (Kadereit, unpubl. results; see below).

Comprehensive treatments of the W Turkish sect. *Pilosa* have been presented by Boissier (1867), Fedde (1909), Cullen (1965a, b) and Wendt (1976), and a brief account of the group was given by Novák (1983). Based on various cultivated material, Turrill (1959) critically discussed some taxa of this group.

The number and kind of taxa recognized in these accounts differ widely. Four species with one additional variety were recognized by Boissier (1867) and also, although in different circumscription, by Cullen (1965a, b), six species with seven additional varieties and forms by Fedde (1909), one species with four subspecies by Wendt (1976), and two species by Novák (1983). In the present account sect. *Pilosa* is recognized to contain one species with five subspecies, one of which is newly described.

The widely disjunct (SW Asia–N Africa/S Spain) sect. *Pseudopilosa* was dealt with comprehensively only by Fedde (1909; as part of sect. *Pilosa*) and Wendt (1976). Whereas Fedde (1909) recognized six species, only three species were recognized by Wendt (1976) and will be recognized here.

Detailed analyses of growth form and inflorescence structure of both sects. *Pilosa* and *Pseudopilosa* have been presented by Günther (1975).

Among the 11 sections recognized in the most recent treatment of *Papaver* L. by Kadereit (1988), sects. *Pilosa* and *Pseudopilosa* are two of four perennial sections, one is biennial, and the remaining six are annual. Probably *P.* sect. *Subscaposa* Wendt unpubl. with *P. lisae* N. Busch from the Caucasus Mts as its only species (Wendt, 1976) needs to be added as a fifth perennial section.

Papaver L. sect. **Pilosa** Prantl in Engler & Prantl, Nat. Pflanzenfam. 3, 2: 142 (1891). Type: *P. pilosum* Sibth. & Sm., Fl. Graec. Prodr. 1: 360 (1806).

Perennials with mostly well-developed leafy axes; leaf vernation convolute. Flowers with salmon-coloured to pale orange petals and pale yellow, filiform filaments; capsules glabrous or hairy.

One species in W Turkey.

P. pilosum Sibth. & Sm., Fl. Graec. Prodr. 1: 360 (1806).
Type: In Olympo Bithyno monte. Sibth. & Sm., Fl. Graec. 5: t. 492 (1825; ic.!).

Plants 10–85cm high, erect, unbranched or branched from base; axes more or less densely covered with patent hairs below and increasingly appressed hairs above, very rarely entirely glabrous.

Leaves 0.8–35 × 0.3–6cm, decreasing in size towards the apex, lowermost leaves distinctly petiolate, upper leaves increasingly sessile; leaves sparsely to very densely covered with more or less appressed hairs, very rarely entirely glabrous, indumentum of lower surface mostly denser than on upper surface; leaves narrowly obovate to broadly or narrowly ovate in outline, entire, coarsely crenate to serrate, pinnatipartite or pinnatifid, or rarely pinnate.

Flowers few to many on very short to long pedicels, pedicels with more or less dense appressed or less often patent indumentum, or rarely entirely glabrous. *Buds* 1–1.9 × 0.7–1.3cm, ovoid, ellipsoid to almost globose, with more or less dense patent to half appressed indumentum or glabrous; *petals* salmon-coloured to pale orange, 2–5.5 × 1.5–6cm, rotund to flabellate; *filaments* and *anthers* yellow, *stamens* 0.8–1.1cm long, shorter to longer than ovary.

Capsules 0.9–2.4 × 0.4–1cm, obovoid to obconical to ellipsoid, glabrous or with sparse to dense indumentum of more or less appressed hairs; *stigmatic disc* flat to umbonate to pyramidical, with 5–8 stigmatic rays, distinctly lobed, lobes more or less narrow and rounded to acute at the apex with smooth entire margin or more or less broad with irregular margin.

2n = 14 (Wendt, 1976; Novák, 1983 for *P. pilosum* and *P. strictum*).

KEY TO SUBSPECIES

1a. Lobes of stigmatic disc narrow, margin smooth (Fig. 1); inflorescence many-flowered, almost always a compound raceme with mostly short pedicels (longest pedicel of mature capsule 0.5–10cm). Plants from Lycia, rarely from Lydia (Fig. 2) ——— 2

1b. Lobes of stigmatic disc often broad, margin mostly irregular (Fig. 1); inflorescence mostly few-flowered, often a simple raceme with mostly long pedicels (longest pedicel of mature capsule 5–35cm) except in plants from N Phrygia and Mysia. Plants very rarely from Lycia ——— 3

2a. Plants with very dense indumentum; capsules mostly hairy (Fig. 6) ——— **iv.** subsp. **spicatum**

2b. Plants with less dense indumentum; capsules always glabrous (Fig. 7) ——— **v.** subsp. **sparsipilosum**

3a. Sepals glabrous or with very few hair. Plants from W Taurus (E Pisidia and E Pamphylia; Figs 2, 4) ——— **ii.** subsp. **glabrisepalum**

3b. Sepals more or less densely hairy. Plants not from W Taurus ——— 4

4a. Middle and upper cauline leaves lobed, lobes narrowly triangular, strongly antrorse; basal leaves mostly present at anthesis; pedicels often very short (0.5–11cm). Plants from N Phrygia and Mysia (Figs 2, 5) ——— **iii.** subsp. **strictum**

4b. Middle and upper cauline leaves mostly crenate to serrate; basal leaves

rarely present at anthesis; pedicels never very short (5–35cm). Plants from Ulu Dag, E Bithynia, Paphlagonia and N Pisidia, very rarely from Lycia (Figs 2, 3) ——— **i.** subsp. **pilosum**

i. subsp. **pilosum. Figs 1–3.**

Syn.: *P. heldreichii* Boiss. var. *pumilum* Boiss. ex Fedde, Pflanzenr. 40 (IV, 104): 359 (1909). Type: *Heldreich* 1048, 21 viii 1845, Mt. Anemas, 6000–6500′ (B!, BM!).

P. apokrinomenon Fedde, Pflanzenr. 40 (IV, 104): 358 (1909). Type: *Bornmüller* 4045, 12 vi 1899, Phrygia: Sultandagh, in saxosis et rupestribus ad Akscheher (Wilajet Konia) (B!, E!, JE!).

P. apokrinomenon Fedde var. *pinnatum* Bornm. ex Fedde, Pflanzenr. 40 (IV,

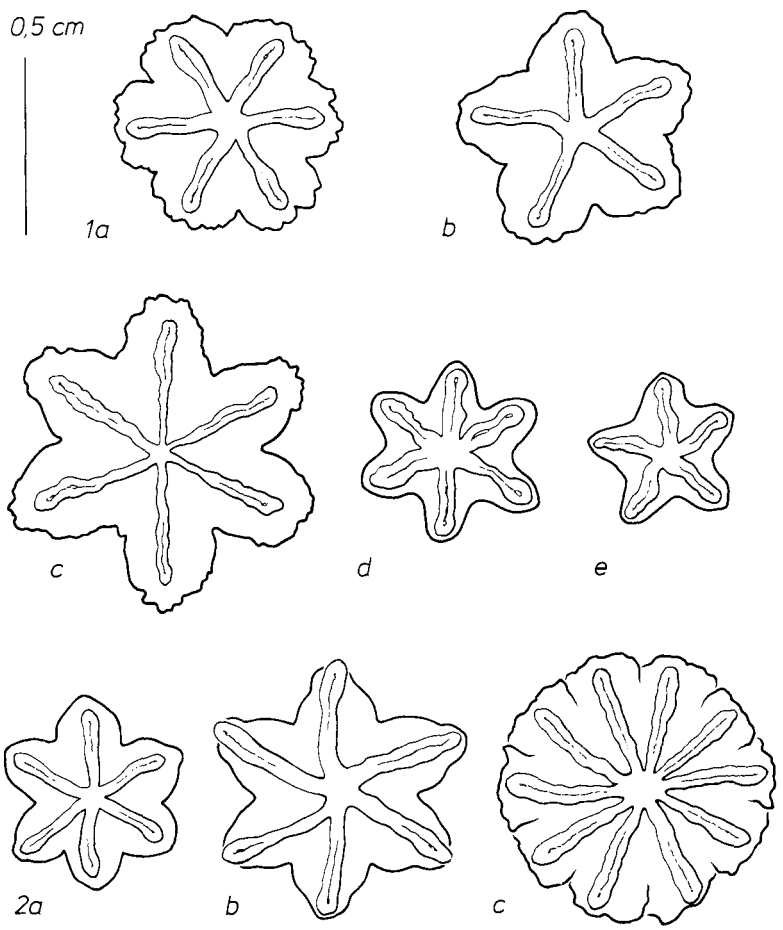


FIG. 1. Stigmatic discs of 1a, *P. pilosum* subsp. *pilosum*; 1b subsp. *glabrisepalum*; 1c subsp. *strictum*; 1d subsp. *spicatum*; 1e subsp. *sparsipilosum*; 2a, b *P. atlanticum* subsp. *atlanticum*; 2c subsp. *mesatlanticum*.



FIG. 2. Geographical distribution of (■) *P. pilosum* subsp. *pilosum*; (◆) subsp. *glabrisepalum*; (▲) subsp. *strictum*; (●) subsp. *spicatum*; (○) subsp. *sparsipilosum*.

104): 358 (1909). Type: *Bornmüller* 4044, 12 vi 1899, Phrygia: Sultandagh, in saxosis et rupestribus ad Akscheher (Wilajet Konia) (B!, E!, JE!, K!).

P. pseudostrictum Fedde, Pflanzenr. 40 (IV, 104): 360 (1909). Type: *Sintenis* 4756, 23 vii 1892, Paphlagonia. Wilajet Kastambuli. Tossia: in herbidis prope pag. Pertschim (B!, BM!, G!, JE!, K!).

P. pannosum Schwarz in Feddes Repert. 53: 76 (1944). Type: *Schwarz* 382, 1938, hab. in rupium calcarearum fissuris montis Caldag Cariae ad confines Lyciae (in septentrione oppidi Fethiye siti), ca. 2300m.s.m. (BM!, K!).

P. feddei Schwarz in Feddes Repert. 53: 76 (1944). Type: *Schwarz* 381, 1938, hab. in rupium calcarearum fissuris lapidibusque montis Teke-Punari-Dag (in septentrione oppidi Fethiye olim Makri siti) Lyciae occidentalis, ca. 1500–2500m.s.m. (BM!, K!).

Clearings in *Pinus* or *Picea* woods, open meadows, and stony places among limestone or igneous rocks, 700–2300m. Flowering May–August. The geographical distribution of subsp. *pilosum* is shown in Fig. 2.

Aucher-Eloy 365, Olymp. Byth. (BM, G); *Boissier* s.n., 1842, Olympus (G); *Bornmüller* 4043, 22 v 1899, Bithynia: in regione subalpina montis Keschisch-dagh (Olympi) (G, JE); *Clementi*, 10 viii 185(?)0, Olympi bith., in petrosis alpin. (BM, E, G, K); *Darrah* 93, 19 vii 1969,

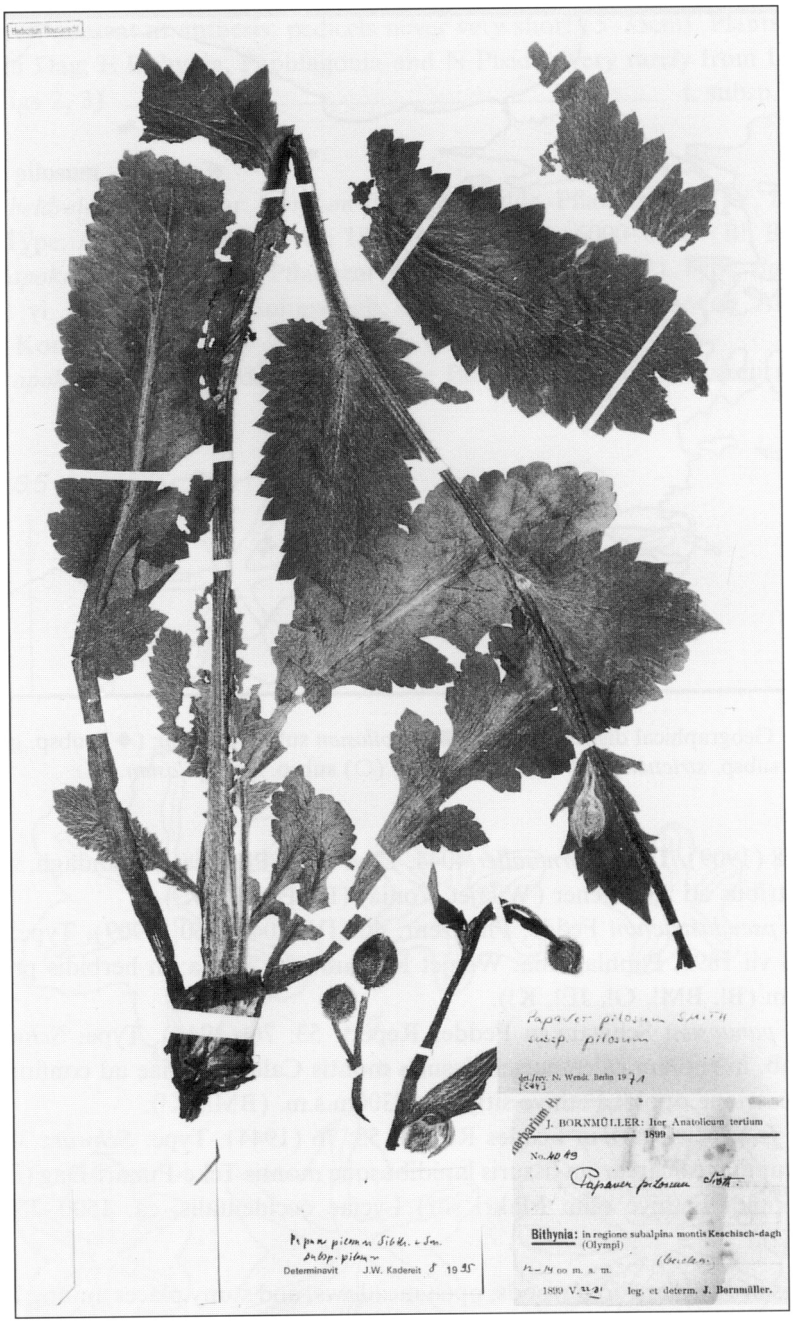


FIG. 3. Representative specimen of *P. pilosum* subsp. *pilosum*.

Kastamonu: Ilgaz Da. *Picea* woods above forestry base. Open meadow, Juniper, 2300m (E); *Davis* 16054, 2 viii 1949, Prov. Isparta, distr. Isaura: Dedegol dag, 2200m (E); *Davis* 37307, 37368 & 37396, 12 vii 1962, Prov. Bolu: Ala dag on Kartal Kaya tepe, rocky igneous slope, 2100–2200m (E); *Davis* 37903, 20 vii 1962, Prov. Zonguldak: Kel tepe above Sorgun yayla, N. limestone cliffs, 1700m (E); *Davis* 38330, Prov. Kastamonu: N. side of Ilgaz Dag, rocky igneous knoll, 1950m (E); *Davis* 38829, 3 viii 1962, Prov. Zonguldak: Keltepe, above Karabük, rocky limestone slopes (southerly), 1800m (E); *Davis* 38897, 3 viii 1962, Prov. Zonguldak: Keltepe, above Karabük, among N. limestone rocks, 1950m (E); *Khan, Prance & Ratcliffe* 719, 17 viii 1960, Prov. Ankara, distr. Kizilcahamam, Isik Dag, steep slopes above tree line (E, K); *Nydegger* 16100, 2 vi 1981, Bursa: Keles–Inegöl, 15km ne Keles, Seitental in Föhrenwald (G); *Pesmen & Güner* 1297, 28 v 1974, Isparta, Egridir, Yaka Köy, Kapiz Deresi, 1400–1500m (E); *Pichler*, vii 1873, Olympi (B, G, JE, K); *Pichler* 7, vi 1874, in declivitate merid. Olympi Bithyn. (G, JE); *Post* s.n., 3 vi 1892, Olympus, 2000 ft. (G); *Raus* 6948, 9 viii 1982, Ankara, Kizilcahamam/Soguksu, Lichtung im *Pinus nigra*-Wald, 1600m (B); *Reuter*, Olympe de Bithynie (G).

The type subspecies of *P. pilosum* is distinguished by the possession of middle and upper cauline leaves with coarsely crenate or serrate margins, often simple racemes with few (3–6) flowers which mostly have long pedicels (up to 35cm), when compound racemes are present the two or three component inflorescences all consist of equally few flowers, by mostly hairy sepals, and by broad stigmatic lobes with an irregular margin. Subspecies *pilosum* occurs in three separate areas (Fig. 2), namely on Ulu Dag, in E Bithynia and Paphlagonia, and in N Pisidia. Very rarely this taxon can also be found in Lycia (see below). Although the Ulu Dag material is more robust than the remainder of the subspecies, and is less often branched from the base, and the N Pisidia material has relatively longer capsules (3–4 vs. 2–3 times as long as broad), the differences in my opinion are not sufficient to justify further subdivision of this subspecies. Dwarf specimens of subsp. *pilosum* (*Heldreich* 1048, *Davis* 16054) have been described as var. *pumilum*, and specimens with pinnate lower leaves (*Bornmüller* 4044) as var. *pinnatum*. On account of their rarity I do not recognize these forms formally. I fail to see any differences between subsp. *pilosum* and Fedde's *P. apokrinomenon*, which was described as having narrower capsules. Equally, I cannot support the distinction between *P. pseudostrictum* Fedde and subsp. *pilosum*, the former of which was described as having narrower and never amplexicaulous leaves. Both these characters, capsule shape and dimensions as well as leaf shape, are far too variable within subsp. *pilosum* to allow formal distinction.

Papaver feddei Schwarz and *P. pannosum* Schwarz cannot be distinguished. Their description as separate species by Schwarz (1944) was based on differences in leaf width, number of flowers, pedicel length, etc. Their inclusion in subsp. *pilosum* as suggested here, although justifiable from a morphological point of view, is somewhat problematical geographically. Their occurrence in Lycia lies clearly outside the main range of subsp. *pilosum* and falls into that of subspp. *spicatum* and *sparsipilosum*. They do not, however, share the characteristic inflorescences or shape of stigmatic lobes with these two subspecies. Turrill (1959), however, regarded *P. feddei* and *P. pannosum* as synonymous with *P. heldreichii*, which I regard as a synonym of subsp. *spicatum*.

ii. subsp. **glabrisepalum** Kadereit, **subsp. nov. Figs. 1, 2, 4.**
Differt a subsp. *piloso* sepalis glabris.
Type: *Davis* 16287, 17 viii 1949, Prov. Mersin distr. Anamur (Cilicia Trachae): between Beskuyu and Carmulu yayla, among rocks, 1900m (holo. K; iso. E, G).

Among rocks, 1700–2100m. Flowering August–September. The geographical distribution of subsp. *glabrisepalum* is shown in Fig. 2.

Davis 14614, 2 ix 1947, Vil. Konya, between Geyik Dagh & Bozkin, 6000 ft. (E); *Davis* 14667, 1 xi 1947, Vil. Antalya/Konya, Kara Dagh (N. of Geyik Dagh), among rocks, 2100m (E); *Davis* 14698, 30 viii 1947, Vil. Antalya (Isauria), (Ilan) Bogaz forest near Geyik Dagh, 5000 ft. (E, K).

Subspecies *glabrisepalum* differs from the above subsp. *pilosum* mainly in its glabrous sepals and glabrous to almost glabrous pedicels. This character can be observed even in specimens with an otherwise very dense indumentum. Glabrous sepals are very rare in subsp. *pilosum* and can, when present, only be found in specimens with either very sparse or totally absent indumentum in all other parts of the plants (*Davis* 37903). In combination with its distinct geographical range the morphology of subsp. *glabrisepalum* justifies its status as subspecies. This new subspecies is heterogeneous for the shape of the stigmatic lobes. One of the few specimens I have seen (*Davis* 14614) shares more or less narrow lobes with a smooth margin with subspp. *spicatum* and *sparsipilosum*.

iii. subsp. **strictum** (Boiss. & Balansa) Wendt ex Kadereit, **comb. et stat. nov. Figs 1, 2, 5.**
Type: *Balansa* s.n., 28 vi 1857, Région montagneux du Mourad-Dagh (Phrygie) (K!).
Syn.: *P. strictum* Boiss. & Balansa, Diagn. Pl. Orient., sér. 2, 6: 8 (1859).

P. strictum var. *psilocalyx* (Boiss. & Balansa) Fedde, Pflanzenr. 40 (IV, 104): 360 (1909). Type: *Sintenis* 610, 20 vii 1883, M. Ida: in marmor. mont. Szu-Su-Dagh (B!, BM!, E!, G!, JE!, K!).

Open rocky places in *Pinus* forest, 1100–1900m. Flowering June–August. The geographical distribution of subsp. *strictum* is shown in Fig. 2.

A., C. & W. 2012, 8 vii 1966, Kutahya, W open scree between pine forest on mountain side (K); *Balansa* s.n., 28 vii 1857, Region montagneuse du Mourad-Dagh (Phrygie) (B, G); *Davis* 36671B, 5 vii 1962, Prov. Kütahya: Murat Dag above Gediz at Hamam, by stream in *Pinus nigra* forest, 1400m (E, K); *Davis* 36704, 5 vii 1962, Prov. Kütahya; Murat Dag (above Gediz) at Kesik Sögüt, *Pinus nigra* forest, 1400m (E, K); *Dudley* 35301, 1 vi 1962, Prov. Burdur, Yesilova–Denizli, 4 miles from Y., by Salda Golu, limestone slopes and scree above Golu, 1100m (E); *M.F.M. in JMW.* 2012, 8 viii 1966, Kutayha; W open scree between pine forest on mountain side, 1900m (K).

This subspecies is well distinguished by the shape of its leaves. Sometimes the lower, but mostly the middle and upper, cauline leaves have entire and narrowly triangular lobes which are very strongly antrorse. Furthermore, the decrease of size between basal and middle cauline leaves in this taxon is more abrupt than in subsp. *pilosum*,



FIG. 4. Holotype of *P. pilosum* subsp. *glabrisepalum*.



FIG. 5. Representative specimen of *P. pilosum* subsp. *strictum*.

and the basal leaves are more commonly still present at the time of anthesis. Some of the material of subsp. *strictum* approaches subspp. *spicatum* and *sparsipilosum* in inflorescence characters. As in these two subspecies the pedicels are often short (*Sintenis* 610, *A., C. & W.* 2012, *Balansa* s.n., 28 vi 1845) but on the whole the inflorescence is far less compact.

iv. subsp. **spicatum** (Boiss. & Balansa) Wendt ex Kadereit, **comb. et stat. nov. Figs 1, 2, 6.**

Type: *Balansa* s.n., vii 1854, collines entourant l'Yaila de Bozdagh, ou il est tres rare (G!).

Syn.: *P. spicatum* Boiss. & Balansa, Diagn. Pl. Orient., sér. 2, 5: 14 (1856).

P. heldreichii Boiss., Fl. Orient. 1: 108 (1867). Type: *Heldreich* s.n., vii 1845, Mons Gheidagh, Tauri Isaurici, 5000′ (K!).

Stony places, 1400–2200m. Flowering July–August. The geographical distribution of subsp. *spicatum* is shown in Fig. 2.

Bourgeau s.n., 4 vii 1860, Lyciae, ad basim montis Ak-Dagh (G); *Davis* 14191, 15 viii 1948, Prov. Antalya (Lycia), Tahtali Dag (above Kemer) below Cukur yayla, stony places, 5000–5300 ft. (E, K); *Davis* 15122, 9 vii 1949, Prov. Antalya, distr. Kemer (Lycia), Taktali dag at Guzleyik yayla, rocky slopes, 1400m (E); *Davis* 15344, 11 vii 1949, Prov. Antalya, distr. Kemer, Taktali dag at Guzleyik yayla, 1500m (E); *Demirdögen* 2513, vii 1964, Antalya, Elmali–Kecova (E); *Forbes* s.n., Lycia, Mamytus (?) Alps (E, K); *Khan, Prance & Ratcliffe* 235, 28 vii 1960, Prov. Antalya: Kas–Elmali road (E); *Khan, Prance & Ratcliffe* 300, 28 vii 1960, Prov. Antalya: distr. Elmali, Bey Dag, screes, 1750m (E); *Schwarz* 181, 25 vii 1938, Prov. Mugla, Distr. Fethiye, Akdag, in rupibus calc. cedreti montis Teke-Punari-Dag (B); *Schwarz* 739, 28 vii 1938, Prov. Mugla, Distr. Fethiye, Akdag, in rupibus Tezli Bel, solo calc., c.2200m (B).

Subspecies *spicatum* is well characterized by its narrow stigmatic lobes with smooth margin, the many-flowered and mostly very dense inflorescence as well as its mostly hairy capsules. Exceptions to the latter character include the type specimen, *Bourgeau* s.n., 4 vii 1860, *Khan, Prance & Ratcliffe* 300, *Schwarz* 739 and *Forbes* s.n. One collection with a laxer and few-flowered inflorescence but hairy capsules is *Demirdögen* 2513. This specimen approaches subsp. *strictum*.

From Fedde's (1909) description of having hairy capsules it seems likely that *P. spicatum* var. *luschanii*, of which I have seen no material, belongs in subsp. *spicatum*.

v. subsp. **sparsipilosum** (Boiss.) Kadereit, **comb. et stat. nov. Figs 1, 2, 7.**

Type: *Bourgeau* 11, 28 vi 1860, in pascuis glareosis montis Elmalu (E!, K!).

Syn.: *P. heldreichii* Boiss. var. *sparsipilosum* Boiss., Fl. Orient. 1: 108 (1867).

Shady rocks, 1700–2000m. Flowering in August. The geographical distribution of subsp. *sparsipilosum* is shown in Fig. 2.

Davis 13876, 3 viii 1947, Vil. Mugla (Lycia): Kara Tepe near Seki yayla, ledge of shady cliffs in Cedar forest, 5200 ft. (E, K); *Davis* 13800, 6 viii 1947, Vil. Mugla (Lycia), Girdev Dagh,



FIG. 6. Representative specimen of *P. pilosum* subsp. *spicatum*.

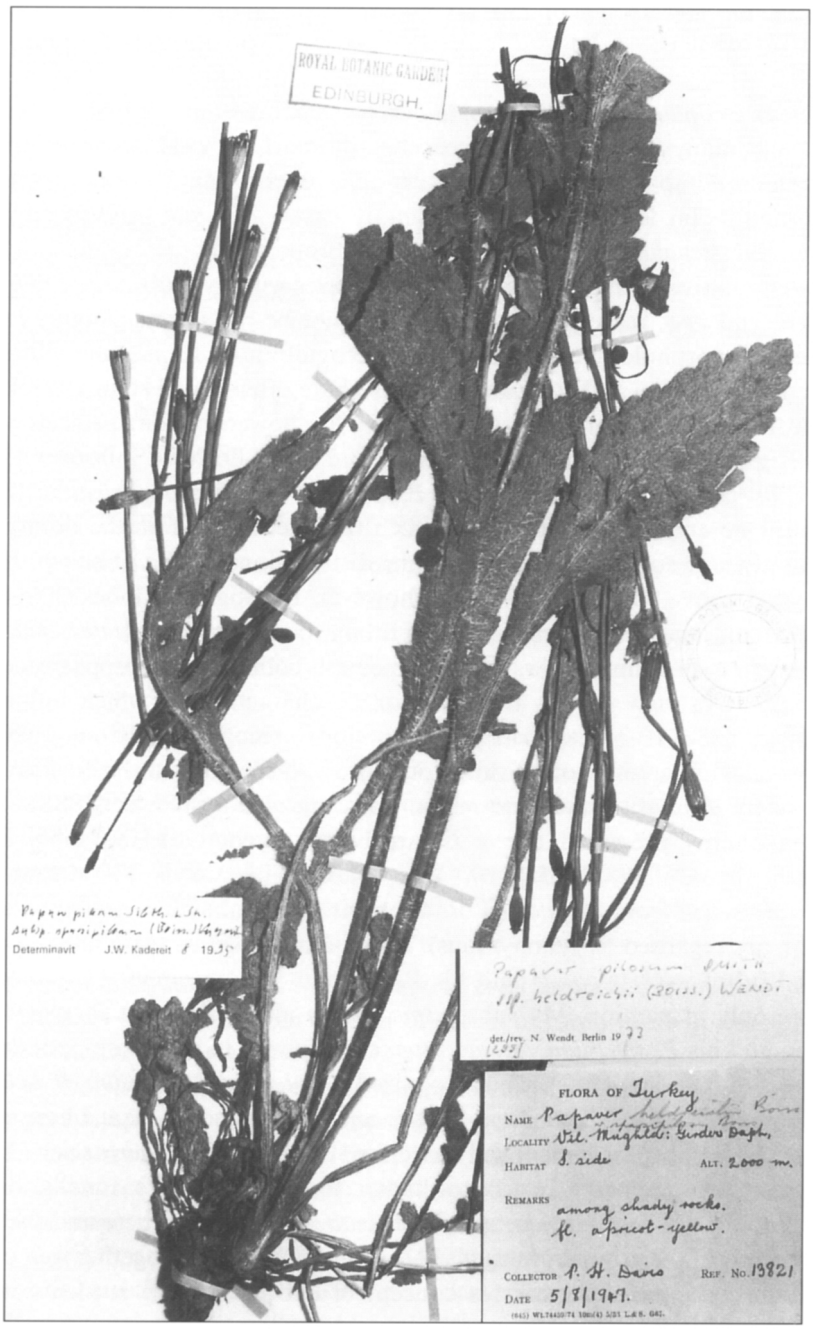


FIG. 7. Representative specimen of *P. pilosum* subsp. *sparsipilosum*.

at Bel Yaila, 1900m (E, K); *Davis* 13821, 5 viii 1947, Vil. Mugla: Girdev dag, S. side, among shady rocks, 2000m (E, G, K).

Subspecies *sparsipilosum* like subsp. *spicatum* has narrow stigmatic lobes with smooth margin, and many-flowered inflorescences with short pedicels, although these are somewhat less compact. It differs from subsp. *spicatum* mainly by its always glabrous capsules and its far less dense indumentum of leaves, axes, etc., and mostly has, as in subsp. *glabrisepalum*, glabrous or almost glabrous sepals.

As an alternative to the recognition of one species with five subspecies, two species with three and two, respectively, subspecies might be recognized. Stigma lobe and inflorescence morphology could justify the recognition of *P. pilosum* with subspp. *pilosum*, *glabrisepalum* and *strictum*, which all share often broad stigmatic lobes with irregular margin and inflorescences with mostly few flowers on long pedicels, whereas narrow stigmatic lobes with smooth margin and many-flowered inflorescences with mostly short pedicels could characterize *P. spicatum* with subspp. *spicatum* and *sparsipilosum*. One argument in support of such treatment would be the occurrence of representatives of subsp. *pilosum* within the distributional range of subsp. *spicatum* as described above. On the other hand, however, the stigmatic lobes characteristic of subspp. *spicatum* and *sparsipilosum* are rarely found in subsp. *glabrisepalum*, and subsp. *strictum* sometimes shows the short pedicels common in subspp. *spicatum* and *sparsipilosum*. In view of this transgression of characters, of which inflorescence morphology is not truly diagnostic, I here prefer to recognize only one species with five subspecies. A subdivision of this group into two species without further subdivision, namely *P. pilosum* and *P. strictum*, was suggested by Novák (1983).

The taxonomy presented above is largely congruent with the subdivision of the group by Cullen (1965a, b). The main difference is his distinction of *P. apokrinomenon* from *P. pilosum* on the basis of indumentum density (these two taxa here are regarded as synonymous), and the inclusion of material of the newly described subsp. *glabrisepalum* into his *P. spicatum* var. *spicatum*. The other differences are only in naming. My subsp. *spicatum* is identical to his *P. spicatum* var. *luschanii*, and his *P. spicatum* var. *spicatum* corresponds to my subsp. *sparsipilosum*. In contrast to Boissier (1867), who recognized *P. spicatum*, *P. pilosum*, *P. heldreichii*, *P. heldreichii* var. *sparsipilosum* and *P. strictum* as independent taxa, I here subsume *P. heldreichii* in subsp. *spicatum*, and recognize subsp. *glabrisepalum* as new. Material of this latter taxon apparently was not known to Boissier (1867). Finally, there is a certain amount of congruence between the treatment presented here and the unpublished account of the group by Wendt (1976) who recognized altogether four subspecies within *P. pilosum*. Whereas his concept of subsp. *strictum* is identical to my perception of this taxon, his subsp. *pilosum* appears to comprise my subspp. *pilosum* and *glabrisepalum*. His subsp. *spicatum* comprises only the Lydian material, and all Lycian material was included in his subsp. *heldreichii*. I perceive subsp. *spicatum* to occur in Lydia and Lycia, and regard some of the Lycian material as subsp. *sparsipilosum*.

The obviously very close affinities among all taxa of sect. *Pilosa* had also been pointed out by Turrill (1959).

Papaver sect. **Pseudopilosa** M. Popov ex Günther in Flora 164: 436 (1975).
Type: *P. rupifragum* Boiss. & Reut., Pugill. pl. Afr. bot. Hispan.: 6 (1852).
Syn.: *Papaver* sect. *Pseudopilosa* M. Popov, Fl. S.S.S.R. 7: 621 (1937, nom. inval.).

Perennials with well-developed leafy axes or of subscapose to scapose habit; leaf vernation revolute. Flowers with salmon-coloured to pale orange petals and pale yellow filiform filaments; capsules always glabrous.

Three species in NW Africa, S Spain and E Turkey, Georgia, Caucasus.

KEY TO THE SPECIES

1a. Stamens as long as or longer than ovary; capsules obovoid. Plants from SW Asia ——— **3. P. lateritium**

1b. Stamens distinctly shorter than ovary; capsules obconical ——— 2

2a. Plants with mostly dense indumentum on green parts. Plants from the Atlas ——— **2. P. atlanticum**

2b. Plants with hairs mainly on middle vein of lower leaf surface. Plants from S Spain and N Morocco (Rif Mts) ——— **1. P. rupifragum**

1. P. rupifragum Boiss. & Reut., Pugill. pl. Afr. bot. Hispan.: 6 (1852). **Fig. 8.**
Type: *Boissier & Reuter* s.n., 1849, Hispania, Serrania de Ronda (K!).
Syn.: *P. rupifragum* Boiss. & Reut. var. *hispanicum* Maire, Flore de l'Afrique du Nord 11: 316 (1964) (homotypic syn.).

P. rupifragum Boiss. & Reut. var. *maroccanum* Font Quer & Pau, Iter Maroccanum 223 (1930). Type: *Font Quer* 223, 22 vii 1930, in saxosis calc. montis Lexhab (Gomara), ad 2050m. alt. (B!, BM!).

Plants 15–45cm high, sometimes almost scapose, erect, branched from base or rarely unbranched; axes with mostly sparse cover of patent or rarely more or less appressed hairs, sometimes entirely glabrous.

Leaves 2–20 × 0.4–2.5cm, decreasing in size towards the apex, lowermost leaves distinctly petiolate, mostly absent at anthesis, upper leaves shortly petiolate or narrowing towards more or less sessile base; leaves with or without setae on middle vein of lower surface and with setae terminating lobes and teeth; leaves oblanceolate to lanceolate, coarsely serrate to pinnatifid or pinnatipartite.

Flowers few to many on long pedicels, pedicels glabrous or with few more or less appressed hairs mostly above. *Buds* 0.8–1.5 × 0.7cm, obovoid, ellipsoid or almost globose, glabrous; *petals* salmon-coloured to pale orange, 1.7–2.8 × 1.7–2.2cm, rotund to obovate; *filaments* and *anthers* yellow, *stamens* 0.5–0.6cm, shorter than ovary.

Capsules 1.7–2.6 × 0.4–0.7cm, obconical, glabrous; *stigmatic disc* more or less flat, with 5–7 stigmatic rays, distinctly lobed, lobes more or less rounded, mostly with entire margin, non-overlapping.

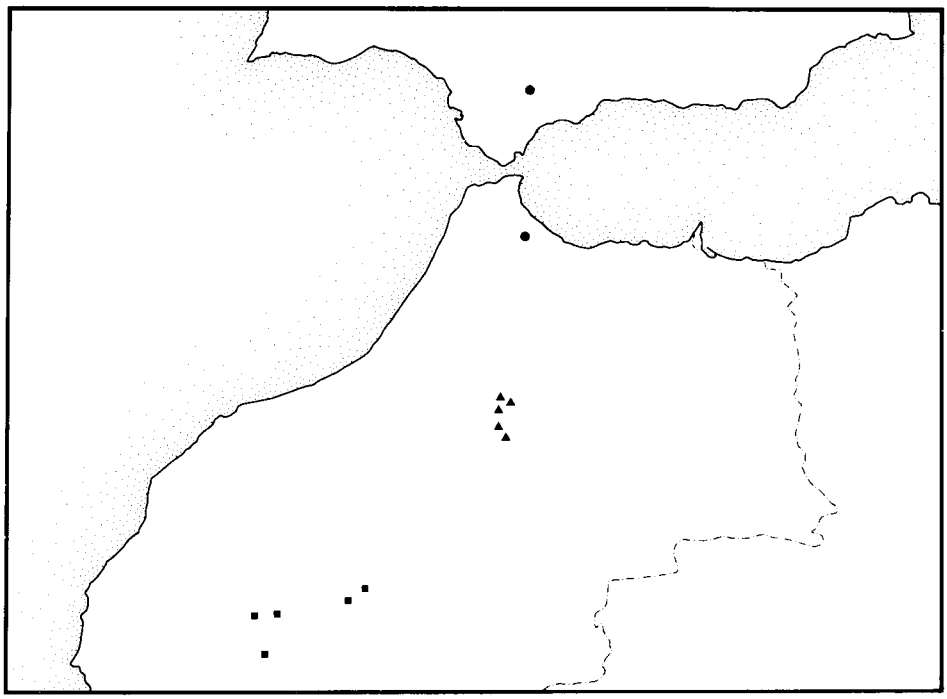


FIG. 8. Geographical distribution of (●) *P. rupifragum*; (■) *P. atlanticum* subsp. *atlanticum*; (▲) subsp. *mesatlanticum*.

2n = 12, 14, 28 (Maire & Quézel, 1964; Castroviejo et al., 1986).

In rocky places, 700–1600m (2050m in Morocco). Flowering May–July. The geographical distribution of *P. rupifragum* is shown in Fig. 8.

SPAIN. *Aparicio* s.n., 30 vi 1983, Villaluenga des Rosario. Sierra del Caillo. Narato Alto. 1200m.s.m. (MA); *Asensi & Guerra* s.n., 15 vi 1979, Sierra del Pinar, Grazalema (MGC); *Borja* s.n., v 1961, Cerro de Sn. Cristobal (MA); *Gors.* s.n., 8 vii 1919, Grazalema (MA); *Goyder* 1135, 8 vii 1983, Sierra del Endrinal, Grazalema (BM); *Haussknecht* s.n., Grazal. Hispan. (JE); *Martinez* 738, 9 vii 1978, Entre Grazalema y Zahara. Vertiente NW de Cerro Prieto Calizas, 700–800m.s.m. (MGC); MGC 26951, 20 vi 1990, Sierra del Pinar (MGC); MGC 27122, 27125, 26 v 1990, Grazalema, Pto de Las Palomas (MGC); MGC 29013, 30 vi 1991, Pto de Las Palomas (MGC); *Reverchon* 531, 14 vi 1890, Pic de Saint Cristobale, sur les rochers (B, BM, E, G, MA).

MOROCCO. *Font Quer* 223, 22 vii 1930, in saxosis calc. montis Lexhab (Gomara), ad 2050m. alt. (B, BM).

On account of its sparse indumentum *P. rupifragum* is an easily recognizable species. It seems questionable whether the Spanish and Moroccan material of *P. rupifragum* should be formally distinguished as done by, for example, Maire & Quézel (1964) and Vent et al. (1968), who refer to the Moroccan population as var. *maroccanum* Font Quer & Pau.

Although the Moroccan plants differ from the Spanish plants in having less deeply divided leaves without hairs on the middle vein of the lower surface, glabrous axes, and, according to Vent et al. (1968), larger seeds, the sample from Morocco is very small and denser sampling might reveal more variability. Both Vent et al. (1968) and myself have seen specimens only from the one collection cited above, and one additional specimen (M. Rif occidental: rocailles calcaires du Mont Krâa, *Font Quer*) was named by Maire & Quézel (1964). If the examination of a larger sample of material from Morocco should prove that this differs consistently from the Spanish material in the leaf, indumentum and seed characters described above, this material would deserve being recognized at subspecific rank. For the reasons given I hesitate to publish this as a new combination.

2. P. atlanticum (Ball) Coss., Ill. Fl. Atlant.: 11 (t. 6) (1882).
Type: *Ball* s.n., 13–15 v 1871, ex regione subalpina Atlantis Majoris in convalle Ait Mesan, supra Arround, alt. 2000–2530 met. (K!).
Syn.: *P. rupifragum* Boiss. & Reut. var. *atlanticum* Ball in J. Bot. 11: 296 (1873).
P. rupifragum subsp. *atlanticum* Maire, Cat. Pl. Maroc 258 (1932).
P. rupifragum subsp. *atlanticum* Maire var. *ballianum* Maire, Flore de l'Afrique du Nord 11: 316 (1964) (homotypic syn.).

Plants 10–65cm high, sometimes almost scapose, erect or slightly ascending, unbranched or branched from base; axes with mostly dense patent indumentum.

Leaves 1.4–15 × 0.4–2.5cm, decreasing in size towards the apex, lowermost leaves distinctly petiolate, upper leaves increasingly sessile; leaves with mostly very dense indumentum of mostly appressed hairs on upper and more or less patent to half-appressed hairs on lower surface; leaves narrowly obovate to lanceolate, coarsely crenate to pinnatifid to pinnatipartite.

Flowers single to few on long pedicels, pedicels mostly with dense indumentum of appressed hairs. *Buds* 1.2–1.4 × 0.5–0.8cm, ellipsoid to obovoid, almost glabrous to densely covered with appressed hairs; petals salmon-coloured to pale orange, 1.7–3.3 × 1.2–2.7cm, obovate to almost round; *filaments* and *anthers* yellow, *stamens* 0.4–0.8cm long, shorter than ovary.

Capsules 1.4–2.7 × 0.5–0.8cm, obconical to narrowly obovoid, glabrous; *stigmatic disc* more or less flat, sometimes curved upwards at margin, with 6–10 stigmatic rays, distinctly lobed, lobes broadening towards tip, overlapping and with more or less irregular margin or narrowing towards tip with mostly smooth margin.

2n = 14 (Maire & Quézel, 1964).

KEY TO SUBSPECIES

1a. Lobes of stigmatic disc narrowing towards tip, margin mostly smooth (Fig. 1); buds with evenly distributed dense cover of appressed hairs. Plants from the Haut Atlas (Fig. 8) ——— **i.** subsp. **atlanticum**

1b. Lobes of stigmatic disc broadening towards tip, mostly overlapping, margin more or less irregular (Fig. 1); buds often glabrous or with very few hairs at base, more densely hairy above. Plants from the Moyen Atlas (Fig. 8) ——— **ii.** subsp. **mesatlanticum**

i. subsp. **atlanticum. Figs 1, 8.**

In rocky places on sandstone, basalt or granite, 1750–3500m. Flowering May–August. The geographical distribution of subsp. *atlanticum* is shown in Fig. 8.

Ait Lafkih et al. 598, 18 vii 1989, 1km below Oukaimeden on road to Vallée de l'Ourika, 2460m, rocky banks above stream (BM, E); *Balls* 2875, 22 vi 1936, Arround, 6.500 ft., scree slopes (BM, E); *Charpin et al.* MAR 395, 31 v 1980, Ouarzazate à proximité du Tizzi Touggoukine (Jab. Siroua), 2400m, rocailles basaltiques (G, MA); *Charpin et al.* MAR 452, vi 1980, à proximité du Tizi n'Tichka (Haut-Atlas) versant Marrakech, 2250–2270m (G); *Charpin et al.* s.n., 31 v 1980, Ouarzazate: pr. Askaoun, Tizi n'Tleta, 2400m, in rupestris (G, MA); *Chaworth-Musters* 7, 18 v 1937, Bou Ourioul (BM); *Chaworth-Musters* 49, 18 v 1937, Djebel Bou Ourioul above Tizi n'Tichka, 2500–3000m (BM); *Davis* 55368, 19 vii 1973, N side of J. Anngour, near Oukaimeden, 2800–3000m, Rocky igneous slopes (BM, E); *Davis* 67582, 16 vii 1981, 3–5km from Oukaimeden to Ait-Lekak, 2500–2600m, rocky sandstone slopes of ravine (E); *Harley* 653, 6 vii 1966, below northern slope of Irhil Ouaougoulzate, south of Oued Bougmez, Province of Peni Mellal, High Atlas. Very dry rocky hillside, rather bare, c. 10,000′ (BM); *Ibrahim* s.n., 16 vii 1882, Djebel Azighza, Province de Demnat (B, G); *Ibrahim* s.n., 19 vii 1882, Djebel Ghat (G, K); *Ibrahim* s.n., 22 vii 1884, Dj. Tabgourt (B, G); *Jury et al.* 8887, 4 vii 1987, 72km S from Marrakech, c. 3km SE of Oukaimeden, near Jebel Angour, 2750m, on SW facing rocky slope (BM, MA); *Lindberg* 3882, 12 vi 1926, Atlas magn., in convalle fl. Aït Messane, in lapidosis, c.1750m (B); *López & Muñoz Garmendia* 9039, 12 vii 1984, Marrakech: Oukaimedene, continución de la pista al teleférico, 2750m, sobre granitos rosados, suelos secos pedregosos y bordes de arroyo (MA); *Newbould* 397, 14 ix 1955, Gebel Toubkal, 11,000′, scree (BM); *Newbould* 498, 16 ix 1955, G. Toubkal nr CAF hut, 11,000′, in shade of large rock, near stream (BM); *Podlech* 48036, 14–16 vii 1989, Hoher Atlas, Umgebung von Oukaimeden und Berge südlich des Ortes, 2600–3000m; Silikat (G); *Spencer* (?) 592, 2 viii 1951, Grand Atlas: scree of Irhil Aori, scree and talus slopes, or boulders (E).

The type subspecies of *P. atlanticum* is well characterized by its often subscapose habit, the presence of an even and dense indumentum of appressed hairs on the sepals, and also by the shape of the stigmatic lobes. It is distributed in the Haut Atlas. I have not seen the specimen from the Antiatlas (Massif du Siroua, Maire & We) cited by Maire & Quézel (1964).

The easternmost specimens of subsp. *atlanticum* from Irhil Aori (*Spencer* (?) 592) and Djebel Ghat (*Ibrahim* s.n.) are transitional to the following subspecies particularly in the shape of the stigmatic lobes. The existence of these intermediate specimens is the reason for treatment of the two taxa at subspecific rank.

Naturalized material of *P. atlanticum* in Great Britain appears to belong to subsp. *atlanticum* although the shape of the stigmatic lobes approaches that of the following subspecies.

ii. subsp. **mesatlanticum** (Maire) Kadereit, **comb. et stat. nov. Figs 1, 8.**
Syn.: *P. rupifragum* Boiss. & Reut. subsp. *atlanticum* (Ball) Maire var. *mesatlanticum* Maire in Bull. Soc. Hist. Nat. Afrique N. 36: 86 (1945).

On calcareous rocks or in sandy places, 1600–2000m. Flowering June–August. The geographical distribution of subsp. *mesatlanticum* is shown in Fig. 8.

Crane 33, 2 viii 1975, Middle Atlas. Mharjdi: 16km West of Timhadit, 1875m, South facing limestone cliff (BM); *Davis* 55077, 11 vii 1973, foot of Jebel Hebri (above Ifrane), 1900m, stony volcanic slope (E); *Davis* 55120, 11 vii 1973, Ifrane, limestone, 1650m, stony banks (BM, E); *Jahandiez* 463, 8 vi 1923, Daïet Achlef, plateaux pierreux, calcaire, 1750m (E, G); *Jahandiez* 525, 2 vi 1924, Bekrit, rocailles herbeuses, 1850m (B, MA); *Jahandiez* 617 bis, 27 vi 1923, Ras el Ma, rocailles calcaire, 1650m (BM); *Lindberg* 4402, 29 vi 1926, Atlas medium, Ras-el-Ma prope pag. Azrou, in Cedreto, c.1600m (K); *Podlech* 47240, 28 vi 1989, Prov. de Meknes: Mittlerer Atlas, Source Vitelle NW Ifrane, 1570m, Trockenflächen (G); *Podlech* 47306, 29 vi 1989, Prov. d'Er-Rachidia: Mittlerer Atlas, Col de Zad an der Strasse von Azrou nach Midelt, 2150m, Felsen, Strassenrand (G, MA); *Podlech* 47595, 4 vii 1989, Prov. de Khenifra. Mittlerer Atlas, Tizi n'Tahout-ou-Fillali an der Strasse von Zaida nach Khenifra, 2070m, Eichenwald, sandige Flächen (G).

The morphological differentiation of *P. atlanticum* in combination with its distributional range had already been recognized by Maire (1945), Maire & Quezel (1964) and Vent et al. (1968). These authors used mainly the indumentum of the sepals, which often are glabrous below and hairy only above in var. *mesatlanticum* from the Moyen Atlas, to differentiate this taxon from var. *atlanticum* from the Haut Atlas. Although Maire (1945) as the author of var. *mesatlanticum* indicates no plant material examined, his description in combination with the geographical range of his new taxon is unambiguous. Because in addition to sepal indumentum the two taxa also differ in the shape of the stigmatic lobes, and in habit subsp. *mesatlanticum* in contrast to the mostly subscapose subsp. *atlanticum* more often has more or less well-developed axes, I believe that treatment at subspecific rank is appropriate.

3. P. lateritium K. Koch, Index seminum: 14 (1853).
Type: In valle fluminis Tschoruck Armeniam a montibus ponticis separante a. 1843 et nunc in horto botanico cultum. *K. Koch* s.n., Tschoruckthal (B!).

Plants 15–55cm high, unbranched to profusely branched from base, scapose or with leafy axes; axes more or less densely covered with patent setae.

Leaves 3–30 × 1.2–4cm, decreasing in size towards the apex, lowermost leaves distinctly petiolate, upper leaves increasingly sessile; leaves with more or less dense appressed indumentum on upper and lower surface, middle vein mostly densely hairy on lower surface; leaves lanceolate to oblanceolate, coarsely serrate to pinnatifid, pinnatipartite or rarely pinnate in lower part of blade.

Flowers single to many on long pedicels, pedicels with mostly dense patent indumentum below and appressed indumentum above.

Buds 1.4–1.7 × 0.8–1.2cm, with mostly dense indumentum of half-appressed setae, ovoid to globose; petals salmon-coloured to pale orange, 3–4.5 × 2.5–4cm, obovate

to rotund; *filaments* and *anthers* yellow, *stamens* 0.8–1.0cm, as long as or longer than ovary.

Capsules 1.3–1.9 × 0.6–0.8cm, obovoid, glabrous; *stigmatic disc* more or less flat, with 4–8 stigmatic rays, shallowly lobed, lobes overlapping or not.

2n = 14 (Novák 1983 for *P. oreophilum* and *P. monanthum*).

KEY TO SUBSPECIES

1a. Plants mostly with leafy axes, from NE Turkey (Anadolu Dag.) or Caucasus (Fig. 9) ——— **i.** subsp. **lateritium**

1b. Plants scapose, from NE Turkey (Yalmizcam Dag.) and adjacent Georgia (Fig. 9) ——— **ii.** subsp. **monanthum**

i. subsp. **lateritium. Fig. 9.**

Syn.: *P. oreophilum* Rupr., Mém. Acad. Imp. Sci. St. Pétersb., sér. 15: 51 (1870). Type: Ossetia: in regione alpina montis Mamisson, in declivitate Ardonensi supra pag. Kalaki, inter 1400 et 1500 hex. parce, 7 Sept. flor. et deflor. legi.

P. lateritium C. Koch β *minus* Boiss., Fl. Orient. Suppl.: 23 (1888).

In pastures, along river banks, in scree, 1700–2400m. Flowering June–August. The geographical distribution of subsp. *lateritium* is shown in Fig. 9.

TURKEY. *Balansa* 1435, 1866, Vallée de Djimil (Lazistan), vers 2000 métres d'altitude (G, JE); *Balls* 1893, 29 vii 1934, Harami Dagh, Haldizan to Anjer, non-lime scree (BM, E, K); *Davis* 21015B, 27 viii 1952, Prov. Rize, distr. Ikizdere: Yetimhoca (Cimil), banks, 2100m (BM, E); *Stainton & Henderson* 6222, 15 vii 1960, Prov. Rize: Ikizdere–Ispir, 5km N of top of pass, in damp alpine meadow, 2000m (E, K); *Watson* 264, 26 vi 1964, Lazic Pontus, road valley from Rize to Ispir, near Ikizdere, sand deposits at river level among boulders and on sandy pastures nearby, 5000′ (K).

CAUCASUS. *Brotherus* s.n., viii 1881, Ossetia: ad mare glaciale Zei ad fl. Ardou (K); *Busch* 29, 2 viii 1928, Région de Koudar, galets de la rivière Koudare-don visàvis du village Tamadjin (G); *Luchwetadse et al.* s.n., 18 vii 1979 (E); *Radde* 184, Tokenio Togati (LE); *Sommier & Levier* 51, 5 viii 1890, Svanetia, in jugo Latpari inter flumina Hippum et Ingur, in glareosis alpinis declivii mer., 2200–2400m (B); *Vasák* s.n., 15 vii 1979, Caucasus occidentalis: distr. Gulripshi, vicinitas pagi Sakeni latior, in declivibus orientalibus montis Guagua (G).

P. lateritium subsp. *lateritium* here includes *P. oreophilum*. Although these two taxa were distinguished or listed at specific rank by Fedde (1909), Cullen (1965a, b) and Popov (1970), Popov (1970) pointed out the close similarity between them, and Cullen (1965a, b) doubted their specific status as well as that of *P. monanthum*. Boissier (1888) included *P. oreophilum* and *P. monanthum* as varieties in *P. lateritium*, and also Wendt (1976) included *P. oreophilum* as a synonym into *P. lateritium*. Irrespective of the geographical gap in the distributional range very little morphological variation can be observed between the Turkish and the Caucasus material. The

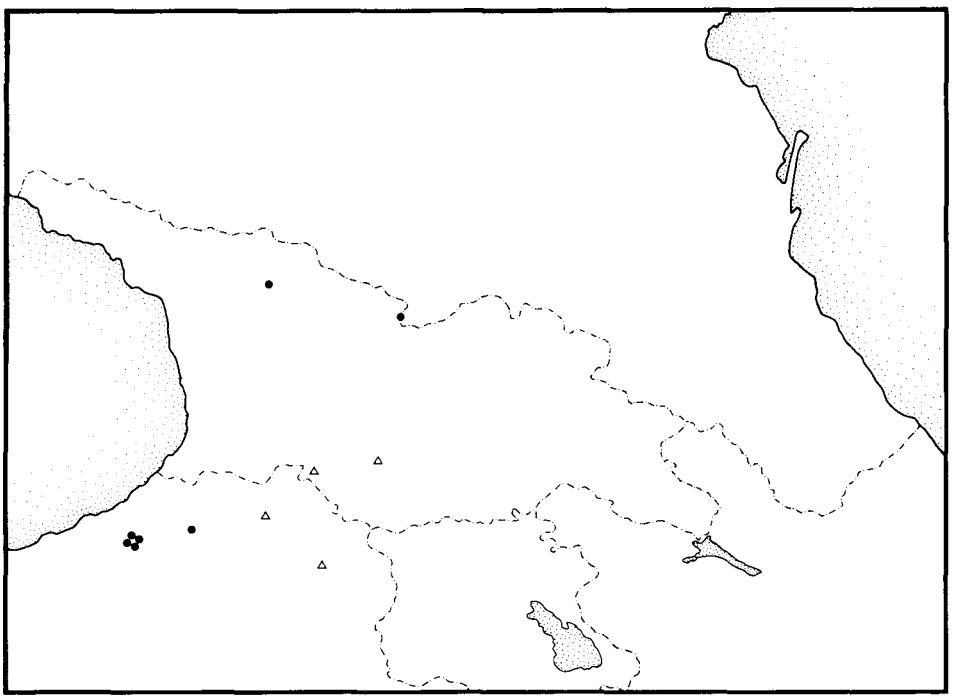


FIG. 9. Geographical distribution of (●) *P. lateritium* subsp. *lateritium*; (△) subsp. *monanthum*.

Caucasus plants perhaps have slightly more divided leaves and relatively broader capsules. A more complete map of the distribution of subsp. *lateritium* in the Caucasus is contained in Wendt (1976).

Although I have not seen any material of *P. monanthum* var. *obtusifolium* (Busch) Fedde, the occurrence of the specimen cited by Fedde (1909: *Akinfiew* 22, 1892) in the Caucasus suggests that it should be included in subsp. *lateritium*.

ii. subsp. **monanthum** (Trautv.) Kadereit, **comb. et stat. nov. Fig. 9.**

Type: *G. Radde* s.n., in montibus Schambobel. G. Radde 5 vii 74, Schambobel (iso. LE!).

Syn.: *P. monanthum* Trautv. in Bull. Acad. Imp. Sci. St. Pétersb. 10: 393 (1866).
P. lateritium K. Koch γ *subacaule* Boiss., Fl. Orient. Suppl.: 23 (1888).
P. oreophilum Rupr. var. *monantha* N. Busch, Fl. Caucasi Crit. 3: 4 (1905).

In meadows, on rocky slopes, 2300–2700m. Flowering June–July. The geographical distribution of subsp. *monanthum* is shown in Fig. 9.

Davis & Hedge 30366, 28 vi 1957, Prov. Coruh (Artvin) distr. Ardanuc: Kordevan dag (Yalnizcam Daglari), 2700m, rocky igneous slopes (BM, E); *Davis & Hedge* 30489, 3 vii 1959, Prov. Kars: SW side of Kisir dag, 2300m, meadows (K); *Schischkin*, 3 vii 1920, Transcaucasia,

Prov. Tiflis, distr. Gori, in pratis alpinis m-tis Savkelos-mta pr. Bakuriani (BM); *Watson* 357, 12 vii 1964, Turkish Armenia, Kisir Dagi group by Lake Cilder, 8000′, SE slopes, sub-alpine & alpine pastures, in flatter areas of deep soil (K).

Subspecies *monanthum* differs from the type subspecies only in its scapose habit with often only a single flower. Otherwise the two taxa are very similar in leaf shape, indumentum, and flower and fruit characters. In view of their geographical separation the assignment of subspecific rank appears justified.

It has been discussed whether *P. monanthum* might be better placed in *P.* sect. *Macrantha*. Whereas Goldblatt (1974) pointed this out as a possibility, Günther (1975) and Wendt (1976) explicitly placed the taxon in this section. The pigmentation of the flowers – the species of *P.* sect. *Macrantha* always have black filaments whereas those of *P.* sect. *Pseudopilosa* are yellow – in addition to the similarities of *P. monanthum* to *P. lateritium* in my opinion is a strong argument against such placement.

Among the species allocated here to sect. *Pseudopilosa*, Fedde (1909) listed *P. ramosissimum* as a new species based on a collection by Sintenis (*Sintenis* 859, 26 v 1888, Kutsche Khan am Karadja-Dagh, K!). As already pointed out by Wendt (1976), this specimen clearly belongs to the annual *P. rhoeas* L.

DISCUSSION

The distribution of *P. pilosum* conforms to general patterns of distribution in Anatolia insofar as its range, in contrast to, for example, *Papaver* sect. *Meconidium* Spach (Kadereit, 1993), lies entirely to the West of Davis' (1971) 'Anatolian Diagonal'. The species can be found in the Irano-Turanian, Mediterranean (West Anatolian and Taurus districts), and Euro-Siberian (Euxine province) regions as delimited by Davis (1971). Its distribution in combination with the close affinities among its component subspecies suggests that the extant range might have formed in postglacial times through the fragmentation of the range of a once more widespread progenitor taxon.

As regards the distribution of the species of sect. *Pseudopilosa* in NW Africa/S Spain and E Anatolia, Georgia and the Caucasus, a number of other taxa of similar distribution have been listed by Davis & Hedge (1971). According to these authors such distributional pattern can be found mainly in groups centred in the Irano-Turanian area. This clearly also applies to *Papaver* and allies. Different from the generalization that whereas the N African members of such disjuncts have penetrated the Mediterranean belt, the SW Asian members are Irano-Turanian in distribution (Davis & Hedge, 1971), *P. lateritium* does not occur in the Irano-Turanian region but rather in the Colchic sector of the Euxine province of the Euro-Siberian region following the delimitations of Davis (1971). Because this region has been claimed to harbour many relict descendants of a Boreal-Tertiary Flora (Davis, 1971), and migration into N Africa (via S Europe) according to Davis & Hedge (1971) was,

apart from Pleistocene interglacials, possible from the end of the Miocene to the beginning of the Pliocene, it seems likely that the disjunction seen in sect. *Pseudopilosa* is of Tertiary origin.

According to the results of Kadereit & Sytsma (1992) and Jork & Kadereit (1995), sect. *Pseudopilosa* occupies a basal position in *Papaver* s.str. (Sects. *Pseudopilosa*, *Meconidium*, *Macrantha*, *Papaver*, *Rhoeadium* Spach, *Carinatae* Fedde). This certainly does not contradict the dating of the disjunct distribution found in this section.

Irrespective of the 'taxonomic origin' of sect. *Pseudopilosa* from sect. *Pilosa* the character distribution described above may indicate that these two sections are not closely related to each other. This was clearly indicated by Wendt (1976) who regards sect. *Pilosa* to be related to sects. *Horrida* Elkan, *Meconidium*, and *Meconella* (and also his unpublished sect. *Subscaposa*), whereas sect. *Pseudopilosa* is postulated to be related to sects. *Rhoeadium*, *Papaver*, *Macrantha*, *Carinatae*, *Argemonidium* Spach and the genus *Roemeria* Medik. The similarities between sects. *Pilosa* and *Pseudopilosa* in habit, filament and petal coloration, and capsule shape were regarded as plesiomorphic or unspecific by Wendt (1976) and Kadereit (1988), although Kadereit (1988) postulated a sister group relationship between sects. *Pilosa* and *Horrida* on the one hand and sect. *Pseudopilosa* on the other hand. Unfortunately no representative of sect. *Pilosa* was included in the DNA analyses by Kadereit & Sytsma (1992) and Jork & Kadereit (1995).

An analysis of ITS-sequences (Kadereit, unpubl. results) now indicates that sect. *Pilosa* indeed is not related to sect. *Pseudopilosa*, and perhaps not even part of *Papaver* s.str. as outlined above.

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