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A REVISION OF PAPAVER SECTION ARGEMONIDIUM

J. W. KADEREIT*

ABSTRACT. *Papaver* L. sect. *Argemonidium* Spach (Papaveraceae) is considered to contain four species: *P. pavoninum* Fischer & C. A. Meyer, *P. hybridum* L., *P. apulum* Ten. and *P. argemone* L. *P. pavoninum* contains two subspecies, including subsp. *ocellatum* (Woron) Kadereit, *comb. et stat. nov. P. argemone* contains five subspecies including subsp. *davisii* Kadereit, *subsp. nov.* from SW Turkey, subsp. *meiklii* Kadereit, *subsp. nov.* from Cyprus, subsp. *minus* (Boiv.) Kadereit *comb. et stat. nov.* and subsp. *nigrotinctum* (Fedde) Kadereit *comb. et stat. nov.* New chromosome numbers are given for *P. argemone* subsp. *minus*, subsp. *nigrotinctum* and subsp. *meiklii*. The relationships between the various taxa are discussed.

INTRODUCTION

After Fedde's (1909) revision of the Papaveraceae, no revisional work has been done on the three major annual sections of the genus *Papaver*, i.e. sect. *Papaver*, sect. *Rhoeadium* Spach and sect. *Argemonidium* Spach. Among these, sect. *Argemonidium* is well characterized by its bristly capsules. Apart from the treatment of differing parts of the section in various Floras (Boissier, 1867; Mowat & Walters, 1964; Cullen, 1965, 1966, 1980; Meikle, 1977), some of its species have been used in experimental hybridizations (McNaughton, 1960), or have been examined for their floral pigments (Acheson et al., 1962) or alkaloid contents (Vent, 1972). As part of a project dealing with the annual species of the genus *Papaver* (Kadereit, 1986a, 1986b), and in view of the rather uncertain status of some of the taxa ascribed to sect. *Argemonidium*, e.g. *P. nigrotinctum* Fedde (Mowat & Walters, 1964) and *P. minus* (Boiv.) Meikle (Cullen, 1965; Meikle, 1977), a revision of sect. *Argemonidium* based on the examination of representative herbarium material supplemented by information from other sources was thought desirable and is presented here.

MATERIAL & METHODS

For the SEM-photographs, seeds were stuck on aluminium stubs with double-sided sticky tape and sputtered with gold in a Balzers Union 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 experimental material: *P. pavoninum* subsp. *pavoninum*: unknown origin, Royal Botanic Garden Kew no. 21-03 (chromosome

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number); unknown origin, *Hort. Centr. Cult. Herb. Medic. Brno* no. 106 (chromosome number and seeds); *P. hybridum*: Kücüktoy to Altinova, margin of saline, 5 viii 1984, *Kadereit* 84/28 (seeds); *P. apulum*: Igoumenitsa, roadside, 26 viii 1984, *Kadereit* 84/251 (chromosome number and seeds); *P. argemone* subsp. *argemone*: unknown origin, *Hort. Centr. Cult. Herb. Medic. Brno* no. 87 (chromosome number); Haan, building site, viii 1983, *Kadereit* s.n. (seeds); *P. argemone* subsp. *nigrotinctum*: Isle of Pserimos (between Kos and Kalymnos), 6 v 1977, *Hansen* 85 (C) (chromosome number and seeds); *P. argemone* subsp. *minus*: Denizli to Burdur, 37 km behind Denizli, field margin, 21 viii 1984, *Kadereit* 84/178 (chromosome number and seeds, 2n = 14); Diner to Afyon, margin of irrigated field, 21 viii 1984, *Kadereit* 84/191 (chromosome number and seeds, 2n = 28); Afyon to Kütahya, *P. somniferum* field, 21 viii 1984, *Kadereit* 84/200 (chromosome number, 2n = 14); *P. argemone* subsp. *meiklii*: Cyprus, Kato Platres, Royal Botanic Garden Kew no. 56–19 (chromosome number and seeds).

Key to the species

1a. Mature capsule at least twice as long as broad, often without bristles in lower part; sepals with short subapical processes .... **4. P. argemone**

1b. Mature capsule at the most twice as long as broad, mostly with bristles throughout its total length; sepals without or with conspicuous subapical processes 2

2a. Sepals with conspicuous subapical processes; pores of mature capsule ± subdivided by teeth; mature stigmatic disc rather strongly vaulted **1. P. pavoninum**

2b. Sepals without subapical processes; pores of mature capsule not subdivided by teeth 3

3a. Lower part of capsule with ± appressed bristles; mature stigmatic disc strongly vaulted between stigmatic rays; petals without black basal marking..... **3. P. apulum**

3b. Bristles patent in all parts of the capsule; stigmatic disc not vaulted between stigmatic rays; petals with small black basal marking. **2. P. hybridum**

Sect. **Argemonidium** Spach, Hist. nat. veg. phan. 7:19 (1839).
Syn.: Sect. *Argemonorhoeades* Fedde in Engler, Pflanzer. 4,104:326 (1909).
Type: *P. argemone* L.

Erect, ascending or decumbent branched or unbranched annual herbs; leaves variously dissected; lower leaves petiolate, upper leaves sessile, trifid; plants with patent or appressed setae on all green parts, sometimes villose below. Sepals with or without ± conspicuous subapical processes; petals obovate to rotund, with or without various black basal markings; filaments filiform or clavate; capsule clavate to cylindrical, elliptical, obovoid or almost globose, mostly with patent to appressed bristles, rarely without bristles; stigmatic disc not lobed, at the most sinuate; seeds reniform.

1. P. pavoninum Fischer & C. A. Meyer, Ind. Sem. Hort. Petrop. 9:82 (1843).

Mostly erect, sometimes ascending annual herb, 5–55 cm high, unbranched, branching above, or branched from the base. *Axis* with patent setae, sometimes with appressed setae below uppermost leaves, rarely glabrescent below. *Leaves* 20 × 9 to 0·6 × 0·4 cm, decreasing in size towards the apex; lower leaves distinctly petiolate, petiole 1–8 cm long; blade of lower leaves triangular to ovate to elliptical in outline, pinnatisect in lower part, pinnatipartite to pinnatifid in upper part; segments ovate to elliptical to oblong in outline, patent to antrorse, pinnatipartite to pinnatifid; secondary segments antrorse, incised, coarsely serrate or entire; upper leaves increasingly sessile, trifid with long middle segment and somewhat shorter lateral segments; degree of incision as in lower leaves, but decreasing towards the apex; middle and lateral segments of uppermost leaves mostly regularly serrate, sometimes entire; leaves with ± patent setae on both surfaces, teeth ending in long bristle.

Pedicel 2–14 cm long, mostly with appressed (rarely patent) setae. *Flower buds* shortly before opening 6·5 × 5 to 15 × 11 mm, ellipsoid to ovoid; sepals with subapical processes, processes 0·5–5 mm long; buds with ± patent setae. *Petals* obovate, 4 × 3·5 to 1·4 × 1·2 mm, orange-red with dark spot at base or dark markings of 4 petals forming a ring. *Filaments* filiform or clavate, dark violet to black, 2·5–6 mm long, as long or longer than ovary; anthers 0·7–1·5 mm, light blue. *Ovary* 2·5 × 1·5 to 6 × 2 mm, oblong to ellipsoid. *Capsule* (Fig. 1) 7·5 × 4 to 14 × 7 mm, ellipsoid to subglobose, with few to many patent bristles of varying length; stigmatic disc almost semiglobose, with 4–6 stigmatic rays, 3–4·5 mm broad. *Seeds* 0·7 mm long, narrowly reniform (Fig. 2).

2n = 12 (Sugiura, 1936; Kawatani & Ohno, 1965; Caine, 1977; mihi)

2n = 14 (Podlech & Dieterle, 1969)

Flowering 4–6. As a weed in cornfields or by roadsides, in open grassland, on sand, conglomerate rocks, loess, calcareous rocks.

1a. Filaments filiform ..... **i.** subsp. **pavoninum**

1b. Filaments clavate ..... **ii.** subsp. **ocellatum**

i. subsp. **pavoninum**

Syn.: *P. cornigerum* Stocks in Hooker's J. Bot. Kew Gard. Misc. 4:142 (1852).

Type: 'Semina lecta ad lacum Alakul' (LE).

The distribution of subsp. *pavoninum* is shown in Fig. 3.

IRAN: Zabanabad, 30 iv 1975, *Rechinger* 50839 (G); S of Hottan, 12 v 1976, *Hewer* 3691 (K).
TURKMENIYA: Aschabad, 4 iv 1900, *Sintenis* 400 (B, BM, K); ad flumen Tedschen pr. Karry-Bent, 19 iv 1898, *Litwinow* s.n., (E, G); Turkomania, *Antonow* s.n. (K).
KAZAKHSTAN: prope St. Tschinaz, 12 v 1923, *Kaschkarov* s.n. (G); Alma Ata, 10 vi 1937, *Wewodonski* s.n. (B); Songoriae ad flumen Lepsa, 1841, *Karelin & Kiriloff* s.n. (BM, G, W); Montes Karatau et Talas Aiatau, 31 v & 22 vi 1931, *Pavlov* 48 & 298 (B); Mogol-Tan-Turkestan, *Seweizow* s.n. (K); Talkuly, *Krassnow* s.n. & Chiwa, *Kurolkow & Krause* s.n. (K).
UZBEKISTAN: Karatepe, 21 v 1974, *Vasak* s.n. (G); Aryk, 22 v 1974, *Vasak* s.n. (B).
TADZHIKISTAN: Chorbet, 23 v 1974, *Vasak* s.n. (B); Kirgiziya: pr. Gulcza, 21 vi 1900, *Litwinow* s.n. (B, C, K, W); Bajandai pr. Kuldscha, *Regel* s.n. (BM, K); Tian-Shan, 29 v 1974, *Vasak* s.n. (B).

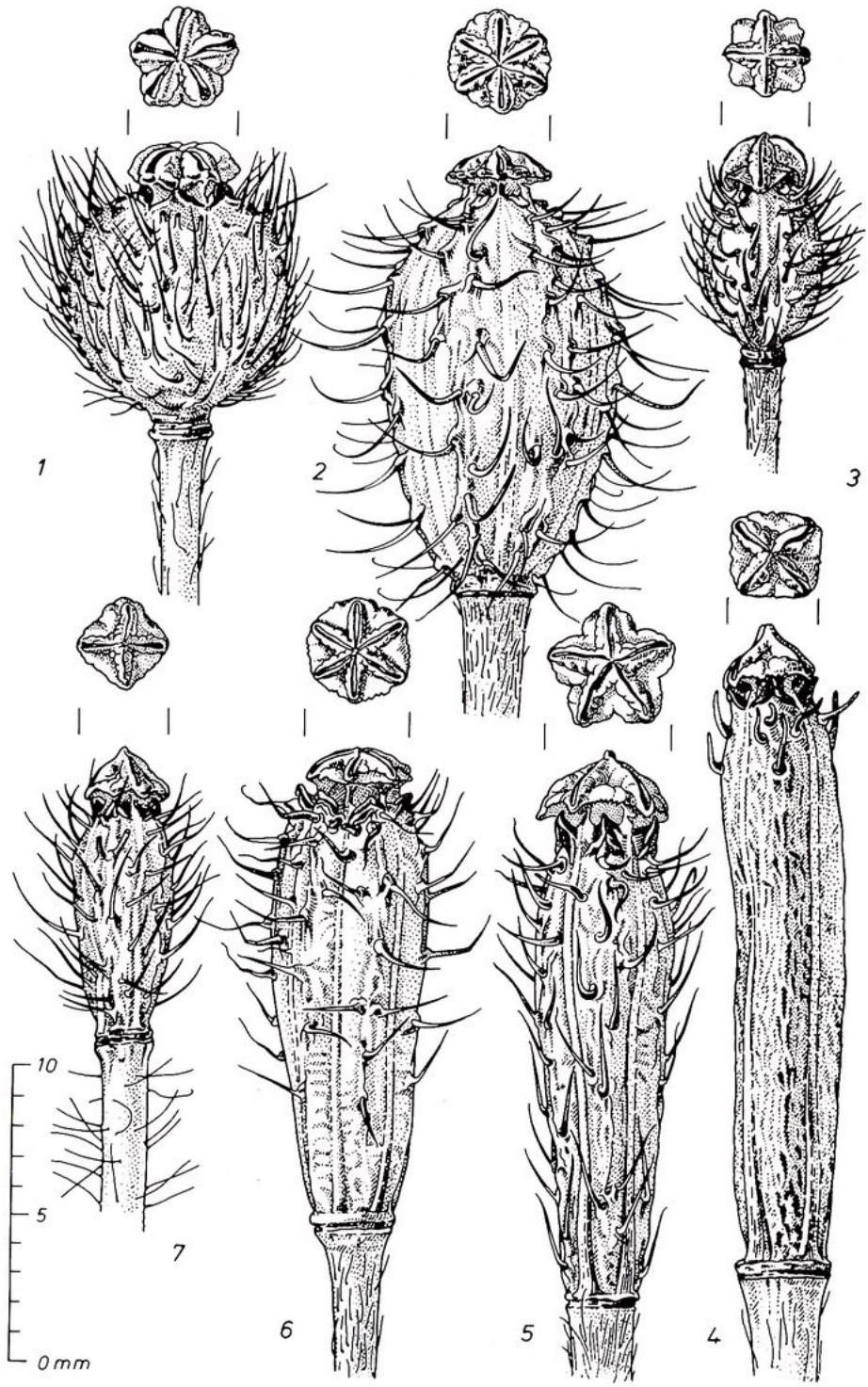

FIG. 1. Capsules of 1, *P. pavoninum* subsp. *pavoninum*; 2, *P. hybridum*; 3, *P. apulum*; 4, *P. argemone* subsp. *meiklii*; 5, *P. argemone* subsp. *minus*; 6, *P. argemone* subsp. *argemone* and 7, *P. argemone* subsp. *nigrotinctum*.

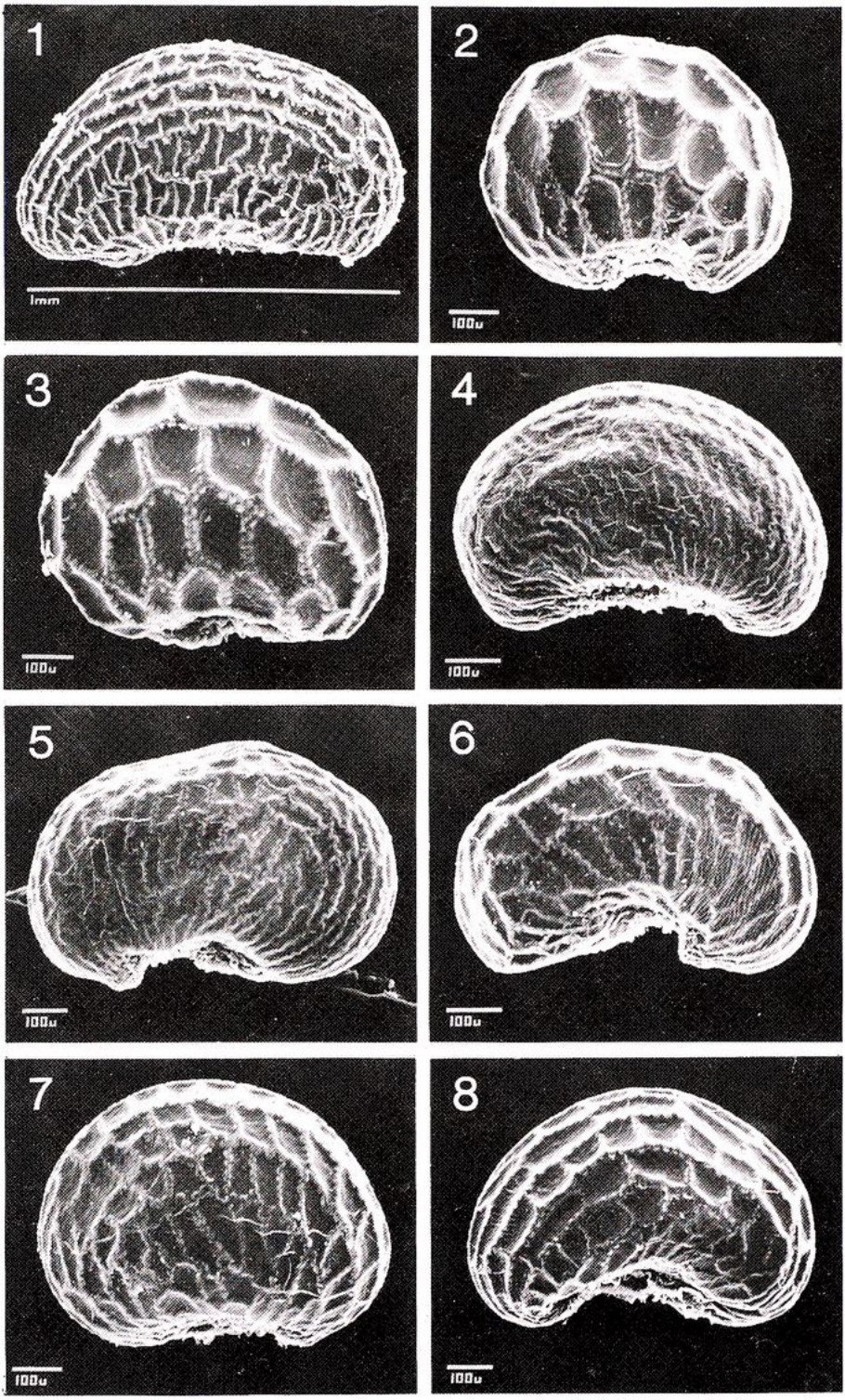

FIG. 2. Seeds of 1, *P. pavoninum* subsp. *pavoninum*; 2, *P. hybridum*; 3, *P. apulum*; 4, *P. argemone* subsp. *meiklii*; 5, *P. argemone* subsp. *minus* (2n = 28); 6, *P. argemone* subsp. *minus* (2n = 14); 7, *P. argemone* subsp. *argemone* and 8, *P. argemone* subsp. *nigrotinctum*.

AFGHANISTAN: Jija, 10 iv 1949, *Koie* 4346 (C); Herat, 29 iv 1949, *Koie* 4345 (C); between Meshed & Herat, 17 iv 1964, *Furse* 5312 (K); 30 m S of Herat, 21 iv 1964, *Furse* 5437 (K); Cheshmeh Obeh, 12 v 1969, *Hedge, Wendelbo & Ekberg* 7934 (E); Daulatabad to Sherber Ghan, 27 v 1969, *Hedge, Wendelbo & Ekberg* 8427 (E); Darrah Siakar, 21 v 1962, *Hedge & Wendelbo* 3397 (E); Khenjan, 13 v 1972, *Kukkonen* 6068 (E); Khenjan to Pule-Khumpri, 13 v 1972, *Kukkonen* 6161 (E); Balahissar, 26 v 1962, *Rechinger* 16063 (G); Doshi, 4 v 1938, *Meinertzhagen* s.n. (BM); Aliabad, 17 v 1964, *Furse* 6040 (K); Kabul, 9 vi 1950, *Volk* 426 (B); Tang-i-Gharu, 8 v 1964, *Neubauer & Podlech* (B); Tang-i-Gharu bei Mahipar, 3 iv 1970, *Podlech* 17306 (G); Eingang zur Tang-i-Gharu, 18 v 1977, *Podlech* 30288 (G); Kunar Tal, 4 vi 1964, *Neubauer & Podlech* 4597 (B); Darrah-i-Khor, 6 iv 1971, *Podlech* 20266 (G); between Barikot & Kamdesh, 25 v 1969, *Carter* 284 (K); Khulm Ghaznigak, 18 iv 1969, *Carter* 64 (K); 10 m N of Gulestan, 21 iv 1971, *Grey-Wilson & Hewer* 569 (K); 20 m S of Khulm, 16 v 1969, *Hewer* 1134 (E, K); Gusalak, 30 iv 1948, *Edelberg* 1549 & 1581 (C); Asasaid, 6 vii 1948, *Edelberg* 2176 (C); Afghanistan, *Herb. East India Comp.* 137 (B, W); Hindukush-Exp., 1935, Herb. *Baschant* s.n. (B); N Hindukush, v 1952, *Frumkin* 153 (G); Afghanistan, 1884–85, *Aitchison* 269 (BM, C); Begram, 1 vi 1940, *Codrington* 5 (BM).

W PAKISTAN: Env. de Quetta, 28–29 iv 1953, *Schmid* 100 & 103 (G); 30 km S of Quetta, 22 iv 1965, *Rechinger* 28394 (G); Quetta to Chaman, 8 v 1965, *Lamond* 969 (C, G); versus Pishin, 8 v 1965, *Rechinger* 28907 (G); Torkham, 30 iv 1969, *Hedge, Wendelbo & Ekberg* 7454 (E); near Kyber, iv–v 1914–15, *Prescott-Decie* s.n. (BM); Tor Khama, 29 v 1965, *Rechinger* 30345 (G); Mingora, 11 viii 1954, *Ali* 25986 (BM, W); Rawalpindi, 7 iv 1940, *Pinfold* 41 (BM, E); Abdal, iv 1926, *Stewart* 12801 (G); Topi Park, Rawalpindi, 7 iv 1940, *Pinfold* 41 (BM, E); lower Swat, 4–8 iv 1956, *Stewart* 27473 (BM); Hazara, 20 iii 1887, *Drummond* 6295 (W); Abbottabad, iii 1934, *Stewart* 13733 (W); Khanai, Baluchistan, *Duthie* s.n. (K); Beluchistan, Villa Abdulla, 12 iv 1888, *Duthie* 8564 (BM, G, K); Drosh, 22 iv 1958, *Stainton* 2268 (BM, E).

ii. subsp. **ocellatum** (Woron) Kadereit, **comb. et stat. nov.**
Syn.: *P. ocellatum* Woron in Bull. Musée Caucas. 11:276 (1918).
Type: Goris-Tskhali (TBI).

IRAN: Haraz valley: near Emarat, 30 iv 1959, *Wendelbo* 475 (E); entre Gach-i-Sar et Chalus, 18 v 1956, *Schmid* 5750 (E, G); Chalus, v 1934, *Trutt* 206 (K); near Arab Ghanli Haji, 27 v 1976, *Hewer* 3880 (K); 5 km W of Moraveh Tappeh, 19 v 1976, *Hewer* 3785 (K).
UZBEKISTAN: Karakala, iv 1931, *Popov* s.n. (C, W).

Apart from the clavate filaments, subsp. *ocellatum* differs from the type subspecies mainly in the length of the sepal processes, which are rather short in all the material I have seen. Although this character is subject to some variability in subsp. *pavoninum*, these processes are usually very conspicuous. Leaf shape and capsule shape are very similar in both subspecies. The vicarious distribution (Fig. 3) in addition to the morphological differences just described justify the subspecific rank used here for the two taxa.

Except for my own chromosome counts, which were made on material of subsp. *pavoninum*, it is not known to which of the two taxa the counts reported in the literature refer.

2. P. hybridum L., Sp. Pl. 1:506 (1753).
Syn.: *P. hispidum* Lam., Fl. Franc. 3:174 (1779).
P. siculum Guss., Fl. Sic. Syn. 2:6 (1844).
'Habitat in Europa australiore'.

Erect or ascending, sometimes almost decumbent annual herb, 5–60 cm high, unbranched, branching above, or branched from the base. *Axis* somewhat villose and glabrescent below, with appressed setae above. *Leaves* 26 × 10 to 1·5 × 1 cm, decreasing in size towards the apex; lower leaves distinctly petiolate, petiole 2–17 cm long; blade of lower leaves ovate in outline, pinnatisect; segments ovate to elliptical to obovate in outline,

antrorse, 1–2-pinnatipartite; secondary segments antrorse, pinnatipartite to entire; upper leaves increasingly sessile, trifid, segments pinnatipartite with strongly antrorse lobes in 1–4 rather distant pairs, or segments entire; lower leaves somewhat villose, upper leaves with ± patent setae on both surfaces, teeth often ending in long bristle.

Pedicel 2–18 cm long, with appressed or sometimes with ± patent setae. *Buds* 11 × 10 to 8 × 5 mm, ellipsoid, broadly ovoid to subglobose; sepals with ± patent setae. *Petals* rotund to obovate, 1·8 × 1·1 to 2·5 × 2·3 cm, bluish red to pink with distinct black basal spots. *Filaments* clavate, dark violet to black, 4·5–8·5 mm long, as long or longer than ovary; anthers light blue, 0·4–0·9 mm long. *Ovary* 4 × 2·5 to 5·5 × 3·5 mm, oblong to ellipsoid. *Capsule* (Fig. 1) obovoid to ellipsoid to subglobose, 7 × 5 to 17 × 11 mm, with patent bristles; stigmatic disc slightly vaulted, with 5–10 stigmatic rays, 2·5–4·5 mm broad. *Seeds* 0·6–0·8 mm long, reniform (Fig. 2).

2n = 14 (McNaughton, 1960; Kawatani & Ohno, 1965; Löve & Kjillquist, 1974; Caine, 1977; Koktay, 1978).

Flowering (1–)3–7(–9). As a weed in fields or by roadsides, in open vegetation on calcareous rocks, loess, loam, sandy soil, terra rossa, schist.

P. hybridum can be found all over Europe west of Poland and outside Scandinavia, where it is very rare, in the Canary Islands, across N Africa, in SW Asia, across the southern USSR, and in the Near and Middle East as far as Pakistan.

GREAT BRITAIN: Guildford, 18 vii 1956, *Hubbard* s.n. (K); Great Casterton, Rutland, 12 vi 1960, *Chandler* s.n. (K).

FRANCE: Aecker bei Molsheim, 25 v 1896, *Schneider* s.n. (B); Angoulins (Ch. Inf.), 30 iv 1893, *Simon* s.n. (B).

SPAIN: Ronda, 7 v 1924, *Ellman & Hubbard* 181 (K); zwischen Antequera und Campillos, 28 iv 1967, *Scholz & Hiepko* 679 (B); Mallorca, 5 km S of Campos, 7 iv 1971, *Cannon* 3755 (BM).

PORTUGAL: inter Portimao ed Monchique, 4 v 1951, *Fernandes, Fernandes & Matos* 3616 (BM); Sines, iv 1926, *Barros* s.n. (B).

GERMANY: Quedlinburg am Harz, vii 1847, *Garcke* s.n. (B); Erfurt, 2 vii 1888, *Rudolph* s.n. (B).

SWITZERLAND: Sitten, Valesia, v 1893, *Wolf* s.n. (BM); Sion, Valais, v 1902, *Wolf* s.n. (W).

ITALY: Lucera, v 1912, *Villani* 1844 (BM); Palermo, iv, *Todaro* 1070 (K).

HUNGARY: inter Bekescsaba et Ujkigyos, 13 v 1923, *Boros* s.n. (BM); Obecse, Bacs-Bodrog, 7 vi 1915, *Kovacs* 742 (K).

YUGOSLAVIA: Stobrich near Split, 23 iv 1935, *Simpson* 35232 (BM); Lesina, Dalmatia, 1843, *Alexander* s.n. (K).

GREECE: Platakia, 10 iv 1972, *Haritomidou* 5 (K); Kaya Bounar, 25 iv 1938, *Tedd* 2137 (K).

BULGARIA: In campis ad?, 12 vii 1898, *Stribrny* s.n. (G).

CYPRUS: Mile 3, Nicosia–F'gusta Rd., 12 iv 1950, *Chapman* 393 (K); near Polis, 21 iii 1962, *Meikle* 2314 (K).

CANARY ISLANDS: Gran Canaria, Monte, 1929, *Trethewy* s.n. (BM); Fuerteventura, Puerto de Cabras, 22 ii 1905, *Pitard* 23 (G); Lanzarote, Mirador del Rio, 4 ii 1973, *Aldridge* 724 (BM).

MOROCCO: 35 km from Marrakech to Chichaoua, 16 iii 1969, *Davis* 48206 (E); Ait Majin, 29 iii 1958, *Whiting & Richmond* 171 (K).

ALGERIA: Misserghin to Bou Tlelis, 27 iv 1971, *Davis* 51697 (BM); Bedeau, 31 v 1925, *Faure* s.n. (K).

TUNISIA: Djebel Bou Hedma, iv 1968, *Young* 14 (BM); 6 km SW Hammamet, 13 iv 1968, *Wagenitz* 1166 (B).

LIBYA: around El Abiar, 24 iii 1970, *Davis* 49934 (E); Attag, Fueihat, 25 ii 1959, *Keith* 747 (K).

EGYPT: near Alexandria, iv 1871, *Hurst* s.n. (K); el Mandarah, 6 iii 1880, *Barbey* s.n. (G).

TURKEY: Bilecik, 24 iv 1966, *Davis* 42125 (K); Ankara to Polatli, 12 vi 1965, *Coode & Jones* 2221 (E).

SYRIA: Damascus, iv 1945, *Norris* s.n. (BM); Tall-Tamar, 17 iv 1939, *Dinsmore* 10443 (K).

LEBANON: infra Araya, 2 iv 1880, *Peyron* 802 (G); El Kaa, 17 iv 1957, *Pabot* s.n. (G).

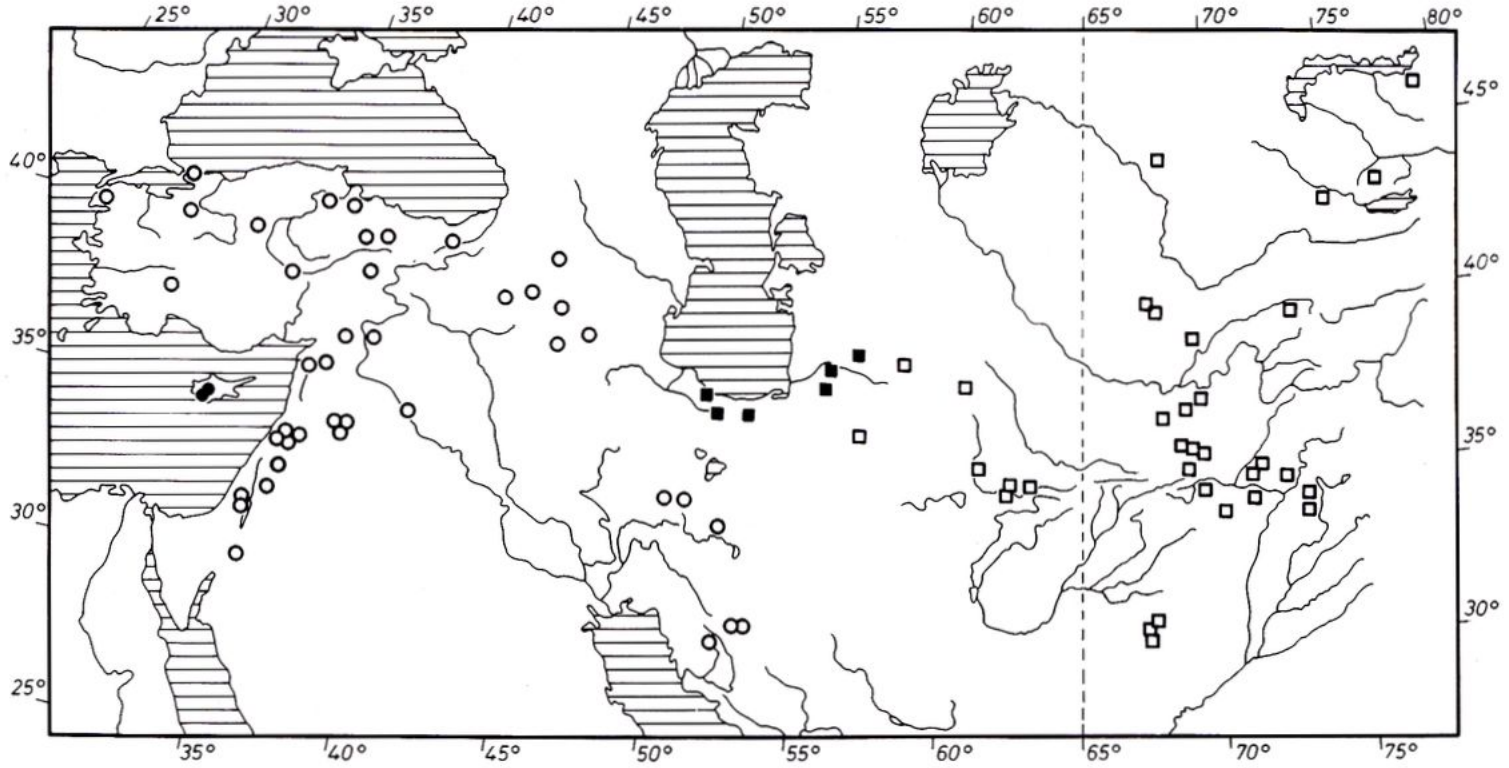

FIG. 3. Geographical distribution of *P. argemone* subsp. *minus* (○) and subsp. *meiklii* (●) and *P. pavoninum* subsp. *pavoninum* (□) and subsp. *ocellatum* (■).

ISRAEL: bank of Jabbok river, 2 v 1911, *Meyers & Dinsmore* G443 (E); Jerusalem, Mt Scopus, 21 iv 1933, *Feinbrun & Bumstein* 238 (K).
IRAQ: 19 km S of Durbendikan, 9 iv 1964, *Barkley & Haddad* 7407 (K); 12 km W of Rawa, 4 iv 1976, Omar, Al-Kaisi, *Hamad & Hamid* 44463 (K).
IRAN: between Masdjed-Soleiman and Lali, 16 iii 1972, *Iranshar & Termé* 34143 (E); prope pagum Gere inter Abuschir et Schira, 20 iii 1842, *Kotschy* 70 (BM).
CRIMEA: distr. Yalta, Nikita, 3 v 1959, *Davis* 33117 (E).
TURKMENIYA: Turcomania. In deserto pr. Ak-Tepe, 13 iv 1898, *Litwinow* 463 (G); Kara-kala, 25 iv 1931, *Popov* 567 (C).
W PAKISTAN: near Maira, Kotli Dist., 23 iv 1954, *Stewart* 27341 (W).

As regards the indumentum of the pedicel in *P. hybridum*, plants with ± patent instead of appressed setae are quite frequent. As these two forms seem to grow in mixed populations in most cases, I do not assign any formal rank to them. The material with patent setae has been described as *P. siculum* by Gussone (1844), a name which often (e.g. Fedde, 1909) has been used at varietal rank (*P. hybridum* var. *siculum* (Guss.) Arc.). It is interesting to observe that the occurrence of this form (S Portugal, Menorca, Sardinia, S Italy, Sicily, S Greece, Aegean Islands, Turkey, Cyprus, Morocco, Algeria, Tunisia, Libya, Israel, Syria, Iraq, Iran) is limited to the southern and eastern part of the species range which might be considered to be its natural distributional area.

3. P. apulum Ten., Fl. Neap. Prodr. App. 5:16 (1826).
Syn.: *P. argemonoides* Cesati, Bibl. Ital. 91:346 (1838).
P. micranthum Bor., Fl. Centr. France 2 (ed. 3):29 (1857).
Type: In Apuliae arvis (? NAP-n.v.).

Erect or ascending annual herb, 10–55 cm high, unbranched, branching above or branched from the base. *Axis* with ± patent setae in lowermost part, with appressed setae above, mostly glabrescent below. *Leaves* 15 × 2·5 to 1·5 × 0·8 cm, decreasing in size towards the apex; lower leaves distinctly petiolate, petiole 1–7 cm long; blade of lower leaves elliptical to obovate in outline, pinnatisect; segments broadly ovate in outline, patent to antrorse, 1–2-pinnatipartite; secondary segments antrorse, pinnatipartite; upper leaves increasingly sessile, trifid with entire linear segments or segments pinnatipartite with strongly antrorse linear lobes; leaves with ± patent setae on both surfaces, teeth often ending in bristle.

Pedicel 5–18 cm long, with appressed setae. *Buds* 6·5 × 4·5 to 13·5 × 11 mm, ellipsoid, broadiy ovoid or subglobose; sepals with few to many ± patent setae. *Petals* obovate, 1·6 × 1·4 to 3·5 × 3·5 cm, pale orange-red to bluish red, without black markings but somewhat darker at base. *Filaments* clavate, dark violet to black, 3·5–7 mm long, as long as to longer than ovary; anthers violet, 0·5–1·2 mm long. *Ovary* 4·5 × 1·5 to 6 × 2 mm, oblong. *Capsule* (Fig. 1) 5·5 × 4 to 12·5 × 6·5 mm, ellipsoid to subglobose, with ± appressed bristles in lower half, patent bristles above; stigmatic disc with 4–6 stigmatic rays, 2·5–4 mm broad; disc between rays distinctly vaulted. *Seeds* reniform, 0·6–0·9 mm long (Fig.2).
2n = 12 (Sugiura, 1936: McNaughton, 1960; Caine, 1977; mihi)
2n = 14 (Kawatani & Ohno, 1965)
Flowering 4–7. As a weed in fields or by roadsides, in open vegetation on calcareous rocks, granite, gneissose granite.
The distribution of *P. apulum* is shown in Fig. 4.

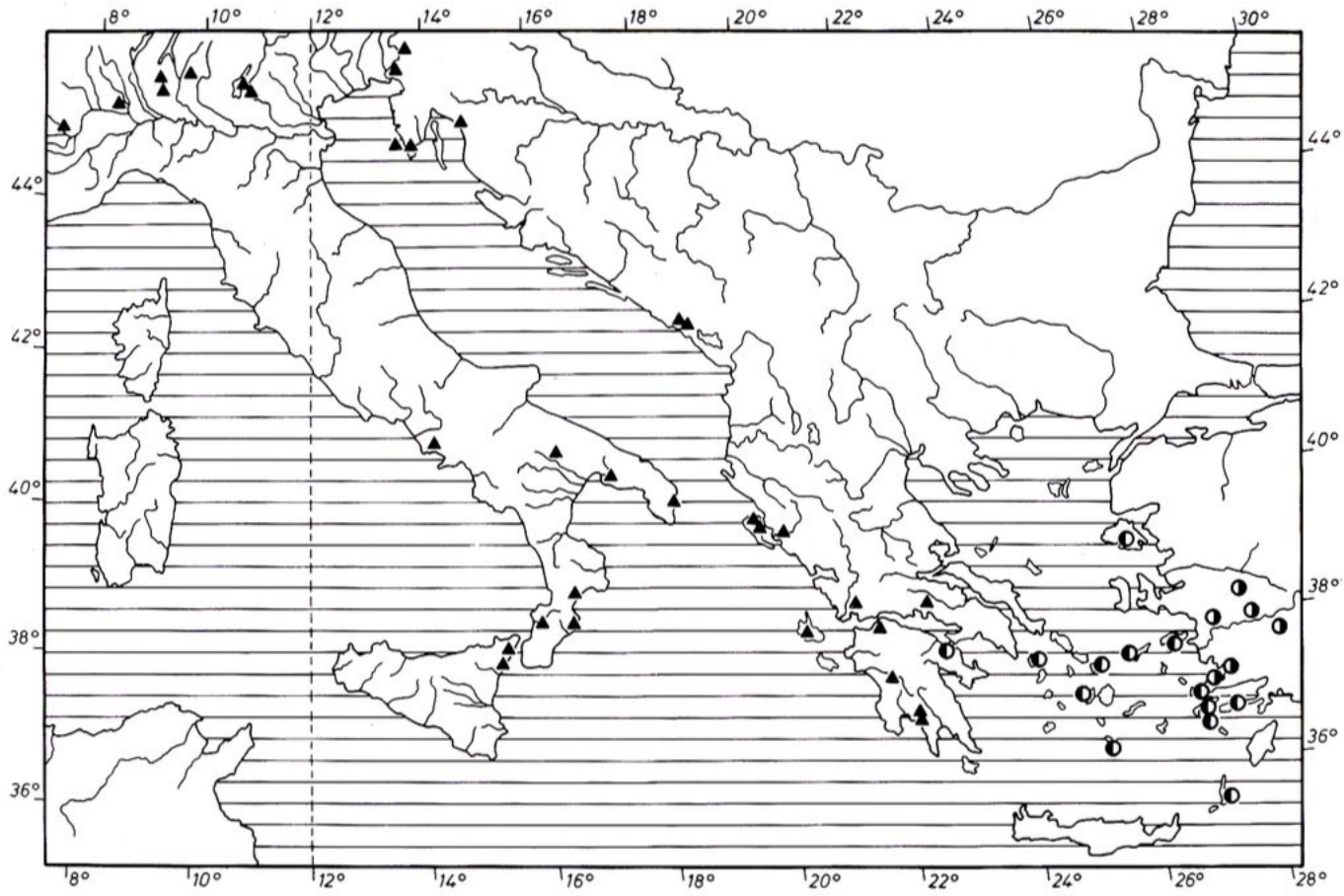

FIG. 4. Geographical distribution of *P. apulum* (▲) and *P. argemone* subsp. *nigrotinctum* (◐) and subsp. *davisii* (◑).

ENGLAND: England, *Prior* s.n. (K).
SWEDEN: Göteborg, 12 vii 1942, *Blom* s.n. (W).
FRANCE: Saint Christophe, Charente Inf., 4 vi, *Girardet* s.n. (BM); St. Léger sous Beuvray, 28 vii 1959, *Charpin* s.n. (G).
GERMANY: Sobernheim a.d. Nahe, 24 vi 1865, *Schlickum* s.n. (B); In Gärten aus früher ausgestreutem Samen verwildert, v–vi 1869, *Schlickum* s.n. (B, CGE); zwischen Frankenthal und Grünstadt, vii 1959, Herb. *Auerwald* s.n. (BM); Leipzig, Großmarkthalle, 3 & 17 vii 1937, *Fiedler* s.n. (B).
CZECHOSLOVAKIA: Olmütz, vi 1936, *Levecek* s.n. (B).
ITALY: environs de Pignerol, *Rostan* s.n. (B, BM, C, E, G, K, W); in alp. Valdensium, v 1879, *Rostan* s.n. (BM, W); Rivoli, 9 vi 1889, *Rigo* s.n. (B, K, W); Rivoli, 8 v 1901, *Rigo* s.n. (G); Rivoli, 15 v 1904, *Rigo* s.n. (BM); environs de Vercelli, *Cesati* s.n. (G); prope Vercellas, *Cesati & Carnel* s.n. (K); inter Mediolanum et Como, *Gorski* s.n. (W); in agro Mediolanensi, Herb. *M.tii a Rainer* s.n. (W); Valtresses, pres Bergamo, *Chenevard* s.n. (G); Torri del Benaco, 1904, *Rigo* s.n. (G); ad Messes in vall. Cluson, v 1892, *Rostan* s.n. (W); Pazzano presso Stilo, 30 v 1921, *Lacaita* 23713 (BM); Monfalcone, 24 v 1904, ? (W); Postici (Napoli), v 1901, *Gaaragno* s.n. (BM); Messina, v 1909, *Ross* s.n. (E, G); Messina, *Otto* s.n. (B); Taormina, 11 v 1927, *Ronninger* s.n. (W); Bosco di Rosarno, 18 v 1907, *Lacaita* 9448 (BM); Catanzaro, 15 v 1877, *Huter, Porta & Rigo* 215 (G, K); Leucaspide nr Taranto, iv 1881, *Lacaita* s.n. (K); Leucaspide nr Taranto, 19 iv 1880 & 8 v 1881, *Lacaita* 5392 & 5393 (BM); Taranto, Gravina in Accettullo, 18 iv 1920, *Lacaita* 21998, 21999, 26558, 831 (BM, G, K); San Basilio (Otranto), 20 iv 1920, *Lacaita* 22000 (BM); Galzignano, 29 iv 1906, *Béguinot, Cobau & Bazzi* s.n. (BM); Florentine ad Ferules, v 1864, *Willmott* s.n. (K); Francavilla, iv 1811, *Swainson* s.n. (CGE); Lancelotta supra Novi, 27 v 1855, ? (W); Insula Veglise, *Sadler* s.n. (W); Treviso, *Mayer* s.n. (W); Monte Pastello, vi 1902, ? (G); Italia, inter segetes, *Cesati* s.n. (W).
YUGOSLAVIA: Tolmein, 25 v 1908, ? (W); Briono Islands, 16 vi 1837, *Bentham* s.n. (K); Brioni Maggiore, 13 vi 1909, *Korb* s.n. (W); Pola/Brioni, v 1901, *Makowsky* s.n. (W); Pola, in agris, 12 v 1867, *Huter* s.n. (BM, K); Pola, 12 vi 1880, *Witting* s.n. (W); Pola, Prato Vincurione, 10 vi 1901, *Untchj* s.n. (B); Pola, Prato Grande, 24 v 1903, *Untchj* s.n. (W); Pola, v, *Schultz* s.n. (CGE, BM); Cattaro to Cettinge, 28 v 1905, *Crawford* s.n. (W); Cattaro, 15 v 1905, Herb. *Schneider* s.n. (G); Cattaro, *Pichler* s.n. (G); in Feldern bei Kameno, 15 v 1928, *Korb* s.n. (W);
ALBANIA: Çajup, Mali Lunxheries, 12 vi 1933, *Alston & Sandwith* 1598 (BM, K); Ljok, Koncikas, 12 vi 1896, *Baldacci* 54 (BM, K).
GREECE: Korfu, Mt Pantokrates, 29 v 1979, *Hansen* 714 (C); Korfu above Strinilas, 31 v 1980, *Hansen* 1002 (C); Corfu, 14 iv 1929, ? (BM); insula Kephalonia, 5 ix 1926, *Bornmüller* 36 (W); prope Argostoli Cephalonia, ? (W); Patras, vi 1893, *Grimburg* 249 (GB); prope pagum Vrusina, 15 v 1961, *Rechinger* 23383 (B); inter Mesolongion et Agrinion, 22 v 1964, *Rechinger* 25379 (B); 20 km W Andritsalna, 20 v 1964, *Rechinger* 25273 (B); in jugo Langada, 12 vi 1958, *Rechinger* 20297 (B); Peloponnesus-Mistras, 30 iv 1961, *Pinatzi* 17788 (G); Attica, Mt Parnes, *Guiol* s.n. (BM); in m. Parnethe pr Dekeleiam, v 1878, *Heldreich* s.n. (W); pr Castros, 3 v 1929, *Guiol* 463 (BM); pr Masclina, 3 v 1929, *Guiol* 503 (BM); between Antartikon and lake Mala Prespa, 4 vi 1932, *Alston & Sandwith* 644 (BM, K).

The occasional occurrence of *P. apulum* in England, France, Sweden, Germany and Czechoslovakia is likely to be the result of human activity.

In view of the rather large number of chromosome counts of 2n = 12 for *P. apulum* there is a certain likelihood that the report of 2n = 14 by Kawatani & Ohno (1965) is based on a misidentification. Indeed, much of the herbarium material I have seen of this species had been identified as *P. hybridum*, which has been consistently reported to have 2n = 14.

4. P. argemone L., Sp. Pl. 1:506 (1753).
'Habitat in Europae campis arenosis'.

Decumbent, ascending or erect annual herb, 5–75 cm high, unbranched, branching above or branched from the base. *Axis* with patent setae to somewhat villose below, with appressed setae above; glabrescent below. *Leaves* 15 × 3·5 to 1 × 0·5 cm, decreasing in size towards the apex; lower leaves distinctly petiolate, petiole 1·5–10 cm long; blade of lower leaves

ovate to elliptical in outline, pinnatisect; segments ovate to elliptical in outline, antrorse, 1–2-pinnatipartite; secondary segments antrorse, incised to entire; upper leaves increasingly sessile, trifid, segments pinnatipartite with strongly antrorse linear lobes; leaves with ± patent setae on both surfaces, teeth often ending in long bristle.

Pedicel 2·5–17 cm long, mostly with appressed, sometimes with patent setae. *Buds* 15 × 12 to 7 × 3·5 mm, broadly to narrowly ovoid to almost oblong; sepals with small subapical processes; buds with ± patent setae to almost glabrous. *Petals* broadly to narrowly obovate, 4 × 4·4 to 0·8 × 0·5 cm, orange red to crimson, with distinct black spots at base, rarely also on apical margin. *Filaments* clavate, dark violet to black, 4–9·5 mm long, as long or longer than ovary; anthers 0·5–1 mm long, light blue, greenish or yellow. *Ovary* 9 × 2·5 to 5·5 × 2 mm, oblong. *Capsule* (Fig. 1) 25 × 5·5 to 8·5 × 3 mm, narrowly obovoid to cylindrical to ellipsoid, with patent to half-appressed bristles mainly in upper part, sometimes with few bristles near apex only or without bristles; stigmatic disc slightly vaulted to distinctly pointed, with 4–6 stigmatic rays, 2·5–4 mm broad. *Seeds* 0·8–0·9 mm long, reniform (Fig. 2).

1a. Stigmatic disc of mature capsule slightly vaulted, about as broad as capsule below pores; lower margin of pores rarely forming a distinct tooth; tooth, if present, never subdividing pores; mostly tall erect plants from Europe west of Greece ..... **i.** subsp. **argemone**

1b. Stigmatic disc of mature capsule strongly vaulted, distinctly pointed, mostly broader than capsule below pores; lower margin of pores forming a distinct tooth; tooth subdividing pores; decumbent, ascending or erect plants from Greece or east of Greece 2

2a. Mature buds less than twice as long as broad, mostly broader than 6 mm; capsules rarely more than four times as long as broad; plants from S Greece, Aegean Islands or SW Turkey 3

2b. Mature buds twice as long as broad or more than twice as long as broad, rarely broader than 6 mm; capsules mostly more than four times as long as broad; plants from Cyprus, Turkey, the Near and Middle East .. 4

3a. Petals crimson, mostly exceeding 3 cm in length; plants mostly taller than 25 cm; plants from SW Turkey ..... **iii.** subsp. **davisii**

3b. Petals orange-red, rarely exceeding 2·5 cm in length; plants mostly shorter than 25 cm; plants from the Aegean Islands and adjacent S Greece and SW Turkey ..... **ii.** subsp. **nigrotinctum**

4a. Capsules with only few bristles near apex; plants mostly taller than 15 cm; plants from Cyprus ..... **iv.** subsp. **meiklii**

4b. Capsules with bristles at least in upper half, rarely with few bristles near apex only; plants rarely taller than 15 cm; plants from Turkey, the Near and Middle East ..... **v.** subsp. **minus**

i. subsp. **argemone**

2n = 40 (Koopmans, 1954; Caine, 1977; mihi)

2n = 42 (McNaughton, 1960; Kawatani & Ohno, 1965; Majovsky et al., 1970)

Flowering 4–8. As a weed or ruderal on varying substrate. Subsp. *argemone* can be found all over Europe except for Scandinavia north of S Sweden and

SE Europe, but is virtually absent from N Africa, from where I have seen only one specimen.

GREAT BRITAIN: E of Nairn, 1 vii 1960, *McCallum Webster* 5607 (K); Wittering, 3 vii 1960, *Horwood* s.n. (G).
FRANCE: 15 km S of Montargis, 26 v 1962, *Brummitt, Gibbs & Ratter* 20 (BM); bei Loivre, vi 1915, *Beger* s.n. (B).
SPAIN: Cerdagne: Montlouis, 12 vii 1916, *Sennen* 2527 (BM); Mirandra de Ebro, 17 v 1909, *Elias* s.n. (BM).
PORTUGAL: Porto, v 1907, *Sennen* 1887 (BM).
NETHERLANDS: between Wageningen and Bennekom, 16 v 1948, *Maas Geesteranus* 4113 (C).
SWEDEN: Etebols, Gotland, 21 vi 1929, *Fries* s.n. (C).
DENMARK: Sattrup Mose, 10 km N of Horsens, 15 vi 1971, *Holm-Nielsen, Jeppesen, Lojtnant & Pedersen* 679 (C); Olde, 15 vii 1943, *Gröntved* 301 (C).
GERMANY: Angermünde, 12 v 1894, *Schulz* s.n. (B); bei Quedlinburg, 16 v 1952, *Dähnn* s.n. (B).
SWITZERLAND: Charrat (Valais), 7 vi 1880, *Chenevard* s.n. (G); Siders, Hügel Géronde, 2 v 1980, *Becherer* s.n. (G).
AUSTRIA: Atzgersdorf bei Wien, 24 v 1877, *Wiesbaur* s.n. (G).
ITALY: Torri des Benaco, 20 v & 3 vi 1905, *Rigo* s.n. (E); Pisa, 15 vi 1886, *Loretti* s.n. (E).
POLAND: Schönlanke, vi 1904, *Bothe* s.n. (B); Rudno (ad pagum Tenczynek), 31 v 1973, *Palkowa & Sztyler* 550 (G).
LATVIA: Doblen in Curland, *Bienert* s.n. (BM).
CZECHOSLOVAKIA: Pisecna role nad Brankon, 14 v 1882, *Zavrel* s.n. (B); prope pagum Havraniky, 14 v 1950, *Svestka* 1309 (C).
HUNGARY: Nyitra, vi 1914, *Ginzey* s.n. (K).

Subsp. *argemone* is well characterized by: the shape of the stigmatic disc of its capsules (Fig. 1), which is not pointed but only slightly vaulted; by the lower margin of the capsule pores, which rarely forms a distinct tooth; and the orange-red colour of its petals, as well as its tall habit. Some of the material I have seen of subsp. *argemone* has entirely glabrous capsules, which mostly is correlated with a rather sparse indumentum also on the green parts. As these plants do not show any regular geographical distribution, I refrain from assigning formal rank to them.

ii. subsp. **nigrotinctum** (Fedde) Kadereit, **comb. et stat. nov.**
Syn.: *P. nigrotinctum* Fedde in Engler, Pflanzenr. 4, 104:330 (1909).
Type: Achaia: in collibus siccis prope Neo-Corinthum, nec non ad radices Acrocorinthi, 26 iv 1885, *Heldreich* 816 (lecto. B; isolecto. BM, E, G, GB, W).
2n = 14 (mihi)
Flowering 3–5. As a weed or ruderal or in open vegetation on sand or calcareous rocks. The distribution of subsp. *nigrotinctum* is shown in Fig. 4.

GREECE: Paros, 5 iv 1967, *Hansen* s.n. (C); Mykonos, 30 iii 1965, *Davis* 40566 (E); Thera, 14 iv 1911, *Hayek* s.n. (GB); Santorin, 21 iv 1967, *Hansen* s.n. (C); Keos, 30 iv 1961, *Gathorne-Hardy* 19/1961 (E); Ikaria, 3 v 1976, *Rechinger* 54111 (B); Samos, 17 vi 1886, *Forsyth Major* 399 (G); Scarpanto, 10 v 1883, *Barbey* 26 (G); Kos, 30 iv 1974, *Hansen* 326A (C); Kos, 4 v 1976, *Hansen* 1084 (C); Pserimos, 6 v 1977, *Hansen* 85 (C); Nisiros, 3 v 1974, *Hansen* 111 (C); Nisiros, 7 v 1974, *Hansen* 195 (C); Mikra Dhili, 15 iv 1911, *Hayek* s.n. (GB).
TURKEY: E of Datca port, 18 iv 1965, *Davis* 41325 (K).

By the proportion of its buds, which are less than twice as long as broad, its orange-red petals which are mostly shorter than 2·5 cm, and, above all, its short and mostly ellipsoid capsules (Fig. 1), which rarely exceed 1·5 cm in length and are never more than 4 times as long as broad, subsp. *nigrotinctum* is rather well distinguished from the other subspecies. Its distinct status is supported by its chromosome number of 2n = 14.

Although originally described as the hybrid between *P. argemone* and *P. apulum* by Fedde (1909), which may have been inspired by the comparatively short capsules, the construction of the stigmatic disc and the capsule pores as well as the black petal markings and its seed coat make this taxon part of *P. argemone*.

iii. subsp. **davisii** Kadereit, **subsp. nov.**
Differt a subsp. *argemone* alabastris latioribus (7–12 versus 4–7 mm) et petalis longioribus (2·6–4 versus 1·3–2·8 cm) coccineis.
Type: Turkey. C 1 Mugla: d. Bodrum, Musgebi to Karatoprak, 50–100 m. Sandy igneous slopes, or edge of fields, *Davis* 40979 (holo. E, iso. K).
Flowering 4–5. As a weed or ruderal or in open vegetation on sand, granite, igneous or calcareous substrata. The distribution of subsp. *davisii* is shown in Fig. 4.

TURKEY: Güllük, 11 iv 1965, *Davis* 40935 (E, K); Ödemis, 20 v 1969, *Barclay* 1540 (K); Sultanhisar, 3 iv 1956, *Davis* 25606 (E, K); Karacasu, 23 iv 1965, *Davis* 41770 (K); Baba Dag above Seki, 22 iv 1965, *Davis* 41537 (E, K); Gökbel, 20 iv 1965, *Davis* 41489 (E, K); Camlibel, 25 iv 1965, *Davis* 41755 (E).

The mostly rather tall (15–37 cm) plants of this new subspecies are rather distinct by the proportion of the buds, which are less than twice as long as broad and broader than 7 mm, and the conspicuously large petals of deep crimson colour. Although some of the specimens seen from near the margin of the subspecies' range (*Davis* 41537, 41770) approach subsp. *minus* in height and bud proportions, they can still be assigned to subsp. *davisii* without much hesitation on the basis of the size and colour of the petals. The capsules of the new subspecies are most similar to those of subsp. *minus*. No living material was available for the determination of the chromosome number of this taxon.

iv. subsp. **meiklii** Kadereit, **subsp. nov.**
Differt a subsp. *argemone* discis stigmaticis acutis et capsulis non nisi sub apice setosis (Fig. 1).
Type: Mandria, 4000 ft, in cultivated plot by roadside, *Meikle* 2836 (holo. K, iso. C).
2n = 28 (mihi)
Flowering 4–5. As a weed or ruderal or in open vegetation on sandy soil or igneous rocks. The distribution of subsp. *meiklii* is shown in Fig. 3.

CYPRUS: Platres, 15 v 1938, *Kennedy* 1173 (K); Platres, Mt Iroodos, 4 v 1955, *Kennedy* 1820 (K); Platres, 10 iv 1941, *Davis* 3180 (BM, E, K); Kato Platres, 5 v 1962, *Meikle* 2863 (C, K); Cyprus, 21 iv 1955, *Merton* 2197 (K).

Although I have seen some specimens of subsp. *minus* with bristles only in the apical portion of the capsule which, morphologically, cannot be distinguished from the Cyprus plants, I think that the evaluation of this material as a subspecies on its own is justified in view of the exclusive occurrence of plants with this type of capsule on Cyprus. Similarly subsp. *argemone* sometimes has capsules with only a few apical bristles, but this subspecies never has the typically pointed stigmatic disc. The structure of the seed coat (Fig. 2) and its chromosome number of 2n = 28 lend support to the subspecific rank assigned to it here. The petals of subsp. *meiklii* are crimson in colour, but are distinctly smaller than those of subsp. *davisii*.

v. subsp. **minus** (Boiv.) Kadereit, **comb. et stat. nov.**

Syn.: *Closterandra minor* Boiv. in Bélanger, Voy. aux Indes-Orient., Botanique, 4e Livraison, unnumbered plate, fig. B (1834–1836).
P. belangeri Boiss., Fl. Or. 1:117 (1867).
P. desertorum Grossh. in Grossh. & Schischk., Sched. herb. plant. orient. exsicc. 1:23 (1924).

Type: Iran (? P–n.v.).

2n = 14 (mihi)

2n = 28 (Kliphuis & Barkoudah, 1977; mihi)

Flowering 3–5. As a weed or ruderal or in open vegetation on gravel, sandy soil, limestone, stony clay, coarse loam or igneous rocks. The distribution of subsp. *minus* is shown in Fig. 3.

TURKEY: Assos, 27 iv 1879, *Virchow* s.n. (B); Thymbra, in collibus, Assos, 7 v & 7 vi 1883, *Sintenis* 37 (B, G, E); Troja, ad colles, 15 iv 1903, *Muschler* s.n. (B); Fener Bagteh, 30 v 1928, *Aznavour* s.n. (G); zwischen Denizli und Tavaz, 6 vi 1955, *Walter* 159 (B); Küplü, 17 v 1978, *Baytop* 39373 (K); Bozüyük, 20 v 1978, *Baytop* 39435 (K); Burdur to Antalya, 11 vi 1962, *Dudley* 35685 (E); Ankara, 6 v 1955, *Walter* 1257 & 1264 (B); Nevsehir, 10 v 1970, *Roper* 64 (E); Osmancik to Kargi, 1 vi 1969, *Tobey* 2516B (E); Samsun Ladik, Akdag, 19 v 1965, *Tobey* 1001 (E); Senkoy, 25 iv 1966, *Watson* 834 (K); Sivas, Yildiz Dag, 14 viii 1967, *Tobey* 2317 (E); Gaziantep, 19 iv 1934, *Balls & Gourly* 806 (BM, K); Gaziantep, 17 iv 1935, *Balls* 2145 (BM, E); Gaziantep, Karah Tash, 19 iv 1935, *Balls* 2145 (K); Sivas: Kangal, 29 v 1960, *Stainton* 8473 (E, K); Biredjik, 24 iv 1888, *Sintenis* 457 (K); Genütschair, 28 v 1889, *Sintenis* 477 (K); Susheri, 17 v 1933, *Balls* 256 (E, K); Ahlat to Adilcevaz, 21 v 1966, *Davis* 43363 (E); 20 km W of Ercis, 31 v 1966, *Albury, Cheese & Watson* 1373 (K); Cilic Taurus, *Siehe* 383 (BM, E); Keglar Poussare, 15 v 1908, Herb. *Aznavour* 429 (G); Szanschak Gümüschkhane, 18 vi 1894, *Sintenis* 5808 (BM, G, K).

ARMENIA SSR: in mont. Darry-Dagh, 20 v 1923, *Grossheim & Schischkin* s.n. (B).

SYRIA: Sanameine, 4 iv 1954, *Pabot* s.n. (G); Barze (Damascus), iii 1945, *Norris* s.n. (BM); Planitiei, 26 iv 1880, *Qaldun* 1105 (BM); Yabroud, 1 v 1951, *Pabot* s.n. (G); Madaya, 6 vi 1951, *Pabot* s.n. (G); Ain Khadra, 18 iv 1954, *Pabot* s.n. (G); Aleppo, 20 iii 1867, *Haussknecht* s.n. (BM); Singarae, 1867, *Haussknecht* s.n. (BM); Alep, 28 iii 1937, *Mouterde* 5755 (G); Palmyre, 16 iii 1956, *Pabot* s.n. (G); Soukrie, v 1956, *Pabot* s.n. (G); Jebel Bichri, 27 iv 1956, *Pabot* s.n. (G); Wadi el Gam, 1 v 1932, *Mouterde* 1080 (G); Syria, 4 iii 1945, *Norris* s.n. (BM); Syria, v 1884, *Post* s.n. (BM).

LEBANON: Bikfaia, 7 iv 1933, *Mouterde* 1863 (G); Ain Zehalta, 4 v 1957, *Pabot* s.n. (G); Rayak, 24 v 1957, *Pabot* s.n. (G); supra Ba'albek, 18–20 v 1910, *Bornmüller* 11349 (G); entre Chlifa et Yammouné, 27 iv 1957, *Pabot* s.n. (G); Antilibans, 27 v 1880, *Peyron* s.n. (G); W of Keniseh, 2 viii 1899, *Post* s.n. (G); range opposite Niha, 21 viii 1899, *Post* s.n. (G); Gebel Keneisse, 2 vi 1879, *Peyron* 621 (G); Zachle, 8 iv 1933 & Messaloun, 8 v 1933, *Meinertzhagen* s.n. (BM); Beilan, 1 iv 1937, *Mouterde* 5850 (G); Dein el Beida, 15 v 1943, *Davis* 6048 (E); Col du Baidar, 20 iv 1951, *Pabot* s.n. (G); Zebedam ad Antilibanum, *Kotschy* s.n. (G).

ISRAEL: Jerusalem, iv 1846, *Boissier* s.n. (G, K); Jerusalem, 1857, *Roth* 505 (B); Jerusalem, 24 iv 1883, *Cramer* s.n. (G); Jerusalem, 12 v 1918, *Meyers* B1142 (G, K); Vallee du Cedron, 6 iv 1880, *Barbey* s.n. (G); Ain Hesban, 27 iv 1911, *Meyers & Dinsmore* M412 (E, G, K).

JORDAN: Wadi Musa to Bir Wabaghat, 19 iv 1945, *Davis* 8749 (E); Jerash, 1928, *Crowfoot* 5 (BM); Balila area, 9 iv 1973, *Al-Eisawi* 1267 (BM).

IRAN: between Bezurgan and Khoi, 22 v 1960, *Furse & Synge* 86 (K); W shore, L. Urmia, 7 v 1963, *Bowles Scholarship Bot. Exp.* 1402 (K); near Tabriz, 1927, *Gilliat-Smith* 2055 (K); S of Dilijair, 19 iv 1929, *Cowan & Darlington* 627 (K); N of Tabriz, 10 v 1929, *Cowan & Darlington* 2016 (K); Kuh-i-Sefid, Arak, 21 v 1963, *Bowles Scholarship Bot. Exp.* 1755 (K); NE of Kazerun, 26 iii 1974, *Davis & Bokhari* D 55880 (E); Persepolis, 18 iv 1842, *Kotschy* s.n. (B, G, W); Surak, 22 v 1896, *Callier* 440 (G); W of Kazoui, 4 v 1929, *Cowan & Darlington* 893 (K); Sultanabad nr Kastin, v 1935, *Lindsay* 201 & 212 (BM); entre Dilijan et Ispahan, 24 iv 1956, *Schmid* 5194 (G).

Subsp. *minus* is recognizable by: the proportions of its buds, which are never less than twice as long as broad and mostly of oblong shape; its small petals, which rarely exceed 2·0 cm in length and can be of either orange-red to scarlet or crimson colour; and its habit and height. Much of the material

I have seen of this taxon has a decumbent or ascending habit, and among the erect specimens there are few which are taller than 15 cm. The capsule of subsp. *minus* is illustrated in Fig. 1. Because of its decumbent or ascending habit, the size of its capsules as well as the size of its petals, I here include what has been called *P. virchowii* Asch. & Sint. ex Boiss. This material, which has been collected only three times in and around Troy, is conspicuous in having additional black marks at the petal margin. In the size of its petals and the proportion of its buds it somewhat approaches subsp. *davisii*. If at all, this material should be recognized at no more than varietal rank within subsp. *minus*. No detailed knowledge is available on the two cytotypes found in subsp. *minus*.

Discussion

Although the four species of *Papaver* sect. *Argemonidium* recognized here are well differentiated in the size, colour and marking of their petals, this, due to the short persistence of the corolla, is a far less conspicuous character than the differentiation of the capsules. This, both the shape of the capsules and the construction of their pores, most likely is related to seed dispersal. The bristles on the surface of the capsules suggest that they are shaken not only by wind, but also by passing animals. Without experimental evidence, it is very difficult to say in what way capsule shape and pore structure affect seed dispersal, but probably both the distance over which seeds are thrown out and the time until the capsules are emptied after opening are influenced. Obviously, the latter parameter also depends on the number of seeds present in a given capsule. It seems safe to assume that seed dispersal is little inhibited in *P. hybridum* and *P. argemone* subsp. *argemone*, the two most successful ruderals in the group, in which the pores are little obscured (Fig. 1). In view of the high ploidy level of *P. argemone* subsp. *argemone* as compared to the other subspecies of *P. argemone*, which testifies its derived status, one could speculate that the reduction of the teeth subdividing the pores in subsp. *argemone*, these being more or less distinctly developed in the remaining subspecies, is an adaptation to its ruderal life. The understanding of the differentiation of capsule characters in the different taxa of sect. *Argemonidium* requires and certainly deserves an experimental investigation.

If the chromosome counts for the different species reported in the literature should be correct, three out of the four species, namely *P. apulum*, *P. argemone* subsp. *argemone* and *P. pavoninum*, would show a dysploid reduction of the haploid chromosome base number from 7 to 6, 7 being the most common and probably the base number in the genus *Papaver*. This has taken place on the diploid level ($2n = 14$ to $2n = 12$) in *P. apulum* and *P. pavoninum*, but on the hexaploid level ($2n = 42$ to $2n = 40$) in *P. argemone* subsp. *argemone*. This interesting case of karyological parallelism is likely to have its basis in a chromosome-morphological disposition for chromosome fusion. This suggestion was put forward already by Sugiura (1940) when discussing the counts of $2n = 12$ for *P. apulum* and *P. pavoninum*, and taken up again by Podlech & Dieterle (1969) comparing their count of $2n = 14$ for *P. pavoninum* with that of $2n = 12$ by earlier authors.

As regards the affinities of the different species of sect. *Argemonidium* to each other, there is an obvious relationship between *P. argemone* and *P. pavoninum*. Although capsule shape is conspicuously different in these two species, they both have subapical processes on their sepals, which, however, are much shorter in *P. argemone* than in *P. pavoninum* subsp. *pavoninum*, though similar to those found in *P. pavoninum* subsp. *ocellatum*. Also, both species show the characteristic subdivision of the capsule pores (Fig. 1), and show, at least when compared with *P. apulum* and *P. hybridum*, some similarity to each other in the number and shape of the cells of the seed coat (Fig. 2). As regards the floral pigments (Acheson et al., 1962), *P. pavoninum* possesses only one of the two cyanidin derivatives and equally only one of the two pelargonidin derivatives found in *P. argemone*.

P. hybridum is quite distinct from *P. pavoninum* and *P. argemone* in its morphology, i.e. the absence of subapical processes on the sepals, the construction of the capsule pores and the characters of the seed coat, in its floral pigments by not containing any pelargonidin derivatives, by having one cyanidin derivative which is absent from both *P. argemone* and *P. pavoninum*, and the absence of a pigment fraction not transported in the method used by Acheson et al. (1962). In *P. hybridum* Vent (1972) found only 4 out of 17 alkaloids found in *P. argemone*. Finally, McNaughton (1960) was not able to produce hybrids between *P. hybridum* and *P. argemone*. Thus the rather distant relationship of *P. hybridum* to *P. argemone* and *P. pavoninum* is well illustrated with evidence from various sources.

The evidence related to *P. apulum* is not entirely straightforward. Morphologically, by the absence of subapical processes on the sepals and the structure of the seed coat, *P. apulum* shows more similarity to *P. hybridum* than to *P. argemone* or *P. pavoninum*. The chemical and experimental evidence, however, point in the opposite direction. Except for the presence of one additional pelargonidin derivative, the floral pigments of *P. apulum* are identical to those found in *P. argemone*, although the cyanidin derivatives are limited to the stamens in *P. apulum* while being present in stamens and petals in *P. argemone* (Acheson et al., 1962). In its alkaloids, possessing 13 of the 17 compounds found in *P. argemone*, *P. apulum* stands closer to this species than to *P. hybridum* (Vent, 1972). McNaughton (1960) encountered no difficulty in producing rather fertile hybrids between *P. apulum* and *P. argemone*, while no hybrids could be produced between *P. apulum* and *P. hybridum*. In view of this evidence, I tend to regard *P. apulum* as a western segregate of *P. argemone* which, in case *P. argemone* subsp. *argemone* is accepted to have reached Europe synanthropically, is vicarious in its distribution. Interestingly, when comparing capsule proportions, *P. apulum* is most similar to *P. argemone* subsp. *nigrotinctum*, the westernmost subspecies of *P. argemone*.

It is interesting to find that while *P. hybridum* can be found frequently in N Africa, *P. argemone* is absent from there. N Africa is likely to be part of the former species' natural range. If the presence of *P. hybridum* in N Africa were the result of synanthropical spread, one might also expect that *P. argemone* subsp. *argemone* had reached this area. Although there is some overlap of distribution between *P. argemone* and *P. hybridum* in SW Asia and the Near and Middle East, one might look at sect. *Argemonidium* as consisting of a 'northern' branch, with *P. pavoninum*, *P. argemone* and *P. apulum*, and a 'southern' branch, formed by *P. hybridum* only.

The distribution of *P. argemone* subsp. *nigrotinctum* may give a hint to the minimum age of the group. Its range rather resembles that of *Tordylium hirtocarpum* Candargy shown by Greuter (1979, based on Runemark, 1968), which is shown to illustrate a distribution pattern transgressing isolation barriers (between the C and S Aegean Islands) roughly 5 million years old. The same age must be demanded for the presence of *P. argemone* on Cyprus, as the last contact between the continent and this island was broken at that time.

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