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# Taxonomic revision, phylogenetics and transcontinental distribution of *Anemone* section *Anemone* (Ranunculaceae)

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The monophyletic *Anemone* section *Anemone* (Ranunculaceae) includes predominantly diploid and outbreeding geophytic perennials. A revised taxonomy of the section with 16 species (and some infraspecific taxa) is proposed on the basis of a critical morphological analysis of living populations and extensive herbarium material, together with karyological, cytogenetical and DNA-analytical data. A key, descriptions, figures illustrating some type specimens and differential characters, examples of seedling development and pollen grain micromorphology (scanning electron microscopy) and distribution maps are presented. The position of *A.* section *Anemone* within the family is illustrated by a plastid DNA phylogram from sequences of the *atpB-rbcL* intergenic region. A penalized likelihood approach permitted the approximate dating of the origin and major differentiation phases of the section. The analysis of 20 morphological characters from all species of *A.* section *Anemone* with *A. blanda* (*A.* section *Tuberosa*) as an outgroup resulted in a morphology-based phylogram which supports the recognition of four subsections, i.e. *Somalienses* (one species, northern Somalia), *Anemone* (three species, Mediterranean area), *Biflorae* (five species, South-West and Central Asia) and *Carolinianae* (seven species, North and South America). These data allow a discussion of the phylogenetic diversification and stepwise expansion of the section since the late Miocene (*c.* 9 Mya). Partly by long distance dispersion, section *Anemone* has developed from a palaeo-Mediterranean ancestor to its present transcontinental distribution. © 2009 The Linnean Society of London, *Botanical Journal of the Linnean Society*, 2009, **160**, 312–354.

ADDITIONAL KEYWORDS: cladistics – geological dates – morphometrics – phylogeography – plastid DNA: atpB-rbcL tree – systematics – transcontinental relationships.

## INTRODUCTION AND HISTORICAL SURVEY

Because of their considerable species diversity and worldwide distribution, *Anemone* L. and the subtribe Anemoninae Spach (Tamura, 1991, 1995; Hoot, Reznicek & Palmer, 1994; Ehrendorfer, 1995; Hoot, 1995b) form one of the most interesting clades of Ranunculaceae. In this paper, we present the results of multidisciplinary studies and a taxonomic survey of *A.* section *Anemone*. This monophyletic group consists of geophytic perennial herbs which are predominantly

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outbreeding and mostly diploid with $2n = 16$. Within the section, we recognize 16 species which have a widely disjunct distribution and occur from the whole Mediterranean region and North-East Africa to South-West and Central Asia and from North to South America.

In a previous paper, we analysed part of *A.* section *Anemone*, i.e. the South-West and Central Asiatic complex of *A. biflora* L., which is treated here as *A.* section *Anemone* subsection *Biflorae* P.Popov (Ziman *et al.*, 1998). That study was based on the examination of 19 natural populations and ample herbarium material and included pictures of pollen grains and achenes. Therefore, in the present multidisciplinary survey, we consider only those data from subsection *Biflorae* which are essential for the survey of the whole section. Furthermore, our team has already reported in detail on a rare and endangered West Mediterranean member of subsection *Anemone*, i.e. *A. palmata* L. (Médail *et al.*, 2002).

The concept of *A.* section *Anemone* as understood here has developed gradually over more than 200 years. Linnaeus (1753) knew four species with tuberous rhizomes in the genus *Anemone*: *A. coronaria* L., *A. hortensis* L., *A. palmata* L. and *A. apennina* L. (all distributed in Southern Europe). In 1764, *A. decapetala* Ard. (from South America) was added. De Candolle (1817, 1824) was the first to recognize infrageneric groups within *Anemone*. Among them, section *Anemonanthea* DC. was characterized by ovoid, pubescent or lanate achenes with short styles, 1–2-flowered stems and petiolate or sessile involucral leaves. Under this section he included three unnamed groups, the first and second with tuberous ovoid rhizomes, the third with elongate–cylindrical (non-tuberous) rhizomes. The first consisted of nine species: *A. coronaria*, *A. palmata*, *A. pavonina* Lam. and *A. stellata* Lam., the new *A. biflora* DC. and *A. pusilla* DC.distributed in Europe and Central Asia and the North and South American *A. caroliniana* Walter, *A. decapetala* and *A. triternata* Vahl; the second group included only *A. apennina*; and the third *A. nemorosa* L., *A. trifolia* L. and several other species.

Since Linnaeus and De Candolle, more than 20 additional tuberous species of *Anemone* have been described. However, only Pritzel (1841) followed De Candolle in recognizing all these tuberous species within *A.* section *Anemonanthea*, despite the fact that he himself was aware of the lanate achenes and cylindrical receptacles in the first group (*A. coronaria* and others) and the only shortly pubescent achenes and hemispherical receptacles in the second group (*A. apennina* and others). Subsequently, most authors placed *A. coronaria* and allied species in one section (or subgenus), whereas *A. apennina* and related species were accommodated in another section. Thus, Hooker & Thomson (1855) initially used *A.* section *Eriocephalus* Hook.f. & Thomson for tuberous species with achenes embedded in dense wool (*A. biflora* and others), but retained those with pubescent achenes in *A.* section *Anemonanthea*. Boissier (1867) followed Hooker & Thomson (1855) by maintaining *A. biflora* and *A. coronaria* in *A.* section *Eriocephalus*.

In revising *Anemone*, Ulbrich (1905/1906) circumscribed *A.* section *Eriocephalus* in a broad sense and included not only tuberous Mediterranean and Asiatic taxa, such as *A. biflora*, *A. coronaria*, etc. (in *A.* subsection *Longistylae* Ulbr. series *Oriba* Adans.), but also American taxa including *A. caroliniana* and others (in *A.* subsection *Brevistylae* Ulbr. series *Multifida* Ulbr. subseries *Tuberosa* Ulbr.). Nevertheless, he also listed non-tuberous species in both of these subsections, including *A. baldensis* L., *A. multifida* Poir., *A. sylvestris* L., etc. In contrast, Ulbrich retained the tuberous *A. apennina* and *A. blanda* Schott & Kotschy in *A.* section *Anemonanthea* (as subsection *Tuberosa* Ulbr.).

Within *A.* section *Eriocephalus*, Popov (1913) described subsections *Coronarioides* P.Popov and *Biflorae* P.Popov on the basis of different shapes of the ultimate lobules of basal leaves: long–acute in *A. coronaria* and allied taxa and short–obtuse in *A. biflora*. Considering the different distribution of the above subsections, the former in the Mediterranean area, the latter throughout Central Asia, Juzepchuk (1937) placed both in *A.* subgenus *Eriocephalus* (Hook.f. & Thomson) Juz., but moved *A.* section *Tuberosa* (Ulbr.) Juz. to *A.* subgenus *Anemonanthea* (DC.) Juz.

In his multidisciplinary treatment of subtribe Anemoninae, Starodubtsev (1991) adopted a narrow generic concept and placed the *A. apennina* complex as *A.* section *Tuberosa* (Ulbr.) Starod., together with the *A. nemorosa* group, in the genus *Anemonoides* mill., whereas the other tuberous species were left in *Anemone* section *Anemone*. Those from the Mediterranean region he placed in the two subsections *Anemone* (*A. coronaria* and *A. hortensis*) and *Oriba* (Adans.) Starod. (*A. palmata*), those from Central Asia (*A. biflora*, etc.) were referred to *A.* subsection *Biflorae* (P.Popov) Starod., and those from North and South America (*A. caroliniana* and others) to *A.* subsection *Carolinianae* Starod.

The taxonomic survey of *Anemone* by Tamura (1967, 1991, 1995) mainly followed Ulbrich (1905/1906) and Juzepchuk (1937). Within the subgenus *Anemone*, Tamura (1995) recognized in his section *Anemone* the Old World subsection *Anemone* (with *A. biflora*, *A. coronaria* and *A. palmata*) and the New World subsection *Carolinianae*, but moved the *A. apennina* group (including *A. blanda* and *A. caucasica*

Willd. ex Rupr.) to *A.* section *Tuberosa* of subgenus *Anemonanthea*. Within *A.* section *Anemone* he recognized subsections *Anemone s.l.* and *Carolinianae* as proposed by Starodubtsev (1991). In *Flora Iranica*, Rechinger & Riedl (1992) also classified *A. coronaria* and *A. caucasica* in different sections, but erroneously listed the latter under *A.* section *Omalocarpus*. Most recently, Sinno-Saoud, Knio & Jury (2007) presented a phenetic analysis of *A. coronaria* and of species in the *A. biflora* complex.

Meanwhile, a number of cytotaxonomic and cytogenetic studies were carried out on Anemoninae by Heimburger (1959), Rothfels *et al.* (1966), Baumberger (1970) and Marks & Schweizer (1974) and on taxa of *A.* section *Anemone* in the New World by Joseph & Heimburger (1966) and in the Old World by Madahar (1967) and Maïa & Venard (1976). The results have contributed much to our understanding of chromosomal differentiation, crossing relationships and reproductive isolation of this clade. Further methodological progress was made possible by the consideration of palynological features by Huyn (1970).

Finally, DNA-analytical approaches were applied successfully to problems of phylogenetics and taxonomy in Anemoninae. On the basis of DNA restriction analyses and morphological data, Hoot *et al.* (1994) combined the genera *Hepatica* Miller, *Pulsatilla* Miller, *Knowltonia* Salisbury and others under *Anemone s.l.* Furthermore, they placed all the Mediterranean, Central Asiatic and American tuberous *Anemone* spp. in the informal '*Coronaria* group' of a much widened *A.* section *Anemone.* This group was characterized by a chromosome base number of $x = 8$, tuberous rhizomes, heteromorphic trilobed to ternately compound leaves, bract-like involucral leaves (different from basal leaves), numerous 'sepals' (= tepals or petaloids), winged achenes often covered with long hairs, etc. In this comprehensive '*Coronaria* group' Hoot *et al.* (1994) included not only *A. coronaria* with allied Old and New World taxa, but also the *A. apennina* group with *A. blanda*. Later, Hoot (1995b: 299) noted that *A. blanda* 'is weakly associated with this *Coronaria* clade, but geographical distribution (Mediterranean), the presence of tubers, and floral morphology (numerous linear sepals) are important characters supporting its inclusion in this tuberous clade'. On the basis of new plastid DNA sequence data, Ehrendorfer & Samuel (2001) showed that *A. blanda* is phylogenetically closer to the *A. nemorosa* group (*A.* section *Anemonanthea*) than to *A.* section *Anemone* and the *A. coronaria* group. As a consequence, Ziman *et al.* (2004) again placed *A. blanda* and the other members of section *Tuberosa* in subgenus *Anemonanthea*.

In the light of all this evidence (see also Ziman & Bulakh, 2004) and additional new evidence presented and discussed here, we follow Starodubtsev (1991) and Tamura (1995) in separating the two sections *Anemone* and *Tuberosa*, despite their obvious relationships. In our opinion, plants of *A.* section *Anemone* are characterized by several basal leaves forming a rosette, (sub)sessile involucral leaves and densely lanate achenes. In contrast, plants of *A.* section *Tuberosa* have solitary basal leaves, petiolate involucral leaves and puberulent achenes, characters they share with *A.* section *Anemonanthea.*

In the present multidisciplinary study of members of *A.* section *Anemone* and some related taxa we try to synthesize available information and to add new data relevant for the differentiation, taxononomy, phylogenetics and eco-geographical radiation of the clade. DNA sequences should help in reconstructing the phylogenetic relationships and dating important phylogenetic phases within tribe Anemoneae and Ranunculaceae. A broad analysis of developmental, morphological and palynological characters of *A.* section *Anemone* should allow the interpretation of character changes and support taxonomic arrangements with a morphology-based phylogram. Available karyological and cytogenetic data are used to illustrate genomic aspects of evolutionary differentiation. Distribution patterns and migration events are documented by detailed new maps.

## MATERIAL AND METHODS

Our treatment is based on living and herbarium material. The latter included about 4000 specimens from 22 major herbaria (AA, BCC, BKL, BM, E, GH, K, KW, KRAM, LE, LW, MARSSJ, NY, PAC, PRG, SAV, TAD, TASH, US, VAB, W, WU). From these, and from field collections, we studied 300 samples in detail for flower and fruit analyses. Standard techniques were employed, including light and scanning electron microscopy (Ziman *et al.*, 1998), the latter particularly for the study of pollen grains.

During field work in Southern Europe and Central Asia (mainly in 1992–1997), we examined 40 populations from 11 taxa with *c*. 800 adult plants. A list of the populations studied in Central Asia is presented in Ziman *et al.* (1998) and a similar list for the populations from Southern Europe in Médail *et al.* (2002). Generally, from each population 20–25 flowering or fruiting plants were randomly chosen. Life history and plant development were studied in 22 populations from seven species and results have been partly published by Ziman *et al.* (1998). Selected specimens from herbarium and field studies are cited for all taxa.

The main results of the character analyses of all species of *Anemone* section *Anemone*, and *A. blanda* as outgroup, are shown in Table 2. They formed the basis for a cladistic analysis using PAUP 4.0b10 (Swofford, 2003). Character states were treated as unordered, i.e. states were not classified into plesio- or apomorphic, and characters were not weighted. Coding of characters is described in the sections on character analysis and differentiation. Maximum parsimony and bootstrap analyses (1000 replicates) were carried out using a heuristic search with tree bisection–reconstruction (TBR) branch swapping. A strict consensus trees was computed from all equally most parsimonious trees. Results are presented in a morphology-based phylogram (Fig. 9).

The plant material used for the DNA sequence analysis of the plastid intergenic spacer *atpB-rbcL* is listed in Table 1. For the relevant methods used, the reader is referred to Ehrendorfer & Samuel (2001) and Schuettpelz *et al.* (2002). For the tree construction (Fig. 8), maximum parsimony and bootstrap analyses were performed as for the morphological data (see above). Important nodes in the resulting DNA phylogram (Fig. 8) were dated by using the



**Table 1.** Taxa of Ranunculaceae, particularly from tribe Anemoneae, used for the plastid *atpB-rbcL* phylogenetic analysis (Fig. 8): names, taxonomic positions, provenances, references and GenBank numbers

| Species | Tribal or sectional affinity | Provenance | Reference | GenBank number |
|---|---|---|---|---|
| *Caltha palustris* L. | Caltheae or Helleboreae | France | Schuettpelz & Hoot, 2004 | AY365401 |
| *Callianthemum coriandrifolium* Rchb. | Adonideae | France | Schuettpelz & Hoot, 2004 | AY365401 |
| *Ficaria verna* Hudson (= *Ranunculus ficaria* L.) | Ranuculeae | Austria | Ehrendorfer & Samuel, 2001 | AF386100 |
| *Clematis vitalba* L. | Anemoneae | Belgium | Miikeda *et al.*, 2006 | AB115457 |
| *C. hexapetala* Pall. | Anemoneae | Cultivated | Schuettpelz *et al.*, 2002 | AY055406 |
| *Anemonastrum narcissiflorum* (L.) Holub (= *Anemone narcissiflora* L.) | Anemoneae | Alaska | Schuettpelz *et al.*, 2002 | AY055414 |
| *Pulsatilla occidentalis* (S.Watson) Freyn (= *Anemone occidentalis* S.Watson) | Anemoneae | Canada | Schuettpelz *et al.*, 2002 | AY055426 |
| *P. grandis* Wender. | Anemoneae | Austria | Ehrendorfer & Samuel, 2001 | AF386094 |
| *Hepatica nobilis* Schreber (= *Anemone hepatica* L.) | Anemoneae | Austria | Ehrendorfer & Samuel, 2001 | AF386099 |
| *Knowltonia vesicatoria* (L.f.) Sims (= *Anemone vesicatoria* (L.f.) Prantl | Anemoneae | Cultivated | Schuettpelz *et al.*, 2002: erroneously cited as *Anemone knowltonia* Burtt-Davy | AY055421 |
| *Anemone rivularis* Buch.-Ham.ex DC.: a | *Rivularidium* | Cultivated | Schuettpelz *et al.*, 2002 | AY055417 |
| *A. rivularis* Buch.-Ham.ex DC.: b | *Rivularidium* | Cultivated | Ehrendorfer & Samuel, 2001 | AF386098 |
| *A. blanda* Schott & Kotschy: a | *Tuberosa* | Cultivated | Schuettpelz *et al.*, 2002 | AY055422 |
| *A. blanda* Schott & Kotschy: b | *Tuberosa* | Rhodes | Ehrendorfer & Samuel, 2001 | AF386093 |
| *A. nemorosa* L. | *Anemonanthea* | Austria | Ehrendorfer & Samuel, 2001 | AF386091 |
| *A. ranunculoides* L. | *Anemonanthea* | Austria | Ehrendorfer & Samuel, 2001 | AF386085 |
| *A. drummondii* S.Watson | *Eriocephalus* | Alaska | Schuettpelz *et al.*, 2002 | AY055424 |
| *A. multifida Poir.*: a | *Eriocephalus* | Argentina | Schuettpelz *et al.*, 2002 | AY055425 |
| *A. multifida Poir.*: b | *Eriocephalus* | USA, Colorado | Ehrendorfer & Samuel, 2001 | AF386083 |
| *A. virginiana* L. | *Eriocephalus* | USA, Minnesota | Ehrendorfer & Samuel, 2001 | AF386088 |
| *A. sylvestris* L. | *Eriocephalus* | Austria | Ehrendorfer & Samuel, 2001 | AF386090 |
| *A. coronaria* L. | *Anemone* | France | Ehrendorfer & Samuel, 2001 | AF386086 |
| *A. hortensis* L. | *Anemone* | France | Ehrendorfer & Samuel, 2001 | AF386096 |
| *A. hortensis* L.: *A. pavonina* Lam. | *Anemone* | Greece | Ehrendorfer & Samuel, 2001 | AF386092 |
| *A. palmata* L., 2*x* | *Anemone* | France | Ehrendorfer & Samuel, 2001 | AF386087 |
| *A. caroliniana Walter* | *Anemone* | USA, Louisiana | Schuettpelz *et al.*, 2002 | AY055423 |

fossil-based calibration established for the closely related genus *Pulsatilla* by Zetzsche (2004). The penalized likelihood approach developed by Sanderson (2002) and the r8s program, version 1.70 (Sanderson, 2004) with the truncated Newton optimization method were used. The optimum smoothing level of 14 was calculated by cross-validation.

## TAXONOMIC TREATMENT OF *ANEMONE* SECTION *ANEMONE*

*Anemone* section *Anemone* includes perennial geophytic herbs. Flowers are perfect and actinomorphic, tepals ('sepals' or petaloids) numerous to five, ± densely pubescent abaxially and glabrous adaxially; stamens are numerous, free and with mainly filiform filaments; carpels mature into numerous ovoid or subglobose, somewhat compressed, densely lanate (villous) achenes with hairs 2–6 mm long; receptacles are cylindrical or shortened and form dense, ± elongate to globose heads in fruit. In detail, aerial shoots are simple or branched scapes with one to few pedicellate flowers in cymes, subtended by an involucre of three subsessile to sessile leaves. The long–petiolate basal leaves are once or twice ternately dissected and mainly form rosettes. Underground organs are tubers which develop from the hypocotyl and the uppermost part of the primary root. Germination is epi- or hypogeal; the seedlings have two cotyledons. All species studied have the basic chromosome number $x = 8$, nearly all are diploid, but occasional tetraploidy occurs. Outcrossing and allogamy apparently dominate, but to what an extent autogamy also occurs needs to be ascertained.

The most essential characters for the taxonomy of section *Anemone* and distinguishing the taxa, in our opinion, are the shape of tubers and rhizomes, the shape of basal leaf petiole bases and blades, the differentiation of involucral leaves, the number of flowers, tepals, tepal basal veins and their anastomoses, the shape of fruiting heads, the size of achenes, styles, their hairs and marginal ribs and the types of pollen grains. Relevant characters are illustrated in Figures 2–7. Table 2 summarizes all important differential characters with mean values and ranges as basis for the morphology-based phylogram (Fig. 9). The distribution of all four subsections of section *Anemone* is shown on a world map (Fig. 10) and that of all accepted species on regional maps (Figs 11–14).

## CONSPECTUS

*ANEMONE* L., *SP. PL.*, **1:** 538. 1753, NOM. CONS.

*Conserved type species: A. coronaria* L., Jarvis, *Taxon* **41:** 557. 1992.

### *ANEMONE* SECTION *ANEMONE*, TAMURA, *ACTA PHYTOTAX. GEOBOT.* **42:** 180. 1991

= *Oriba* Adans. p.p., *Fam. Pl.* **2:** 459, 1763.
≡ *A.* section *Oriba* (Adans.) Spach, *Hist. Nat. Veg.* **7:** 250. 1839.
= *A.* section *Anemonanthea* DC. p.p., *Syst.* **1:** 196. 1817.
= *A.* section *Eriocephalus* Hook.f. & Thomson p.p., *Fl. Ind.* **1:** 20. 1855.

### I. *ANEMONE* SUBSECTION *SOMALIENSES* ZIMAN, BULAKH & KADOTA, *J. JAP. BOT.* **81:** 195. 2006

*Description:* Basal leaves palmately 3-parted, petiole base without stipule-like appendages; involucral leaves similar to basal leaves, basally free; tepals persistent, elliptic–lanceolate, 10–15 mm long, basal tepal veins 3–5, with 1–2 anastomoses; fruiting heads elongate; achenes ovoid, styles 1.2–2.0 mm long, marginal ribs *c.* 0.2 mm wide; pollen 3-colpate.

*Type species: A. somaliensis* Hepper.
1. *A. somaliensis* Hepper

### II. *ANEMONE* SUBSECTION *ANEMONE*

= *A.* subsection *Coronarioides* P.Popov, *Tr. Tiflis. Bot. Sada* **12:** 4. 1913.

*Description:* Basal leaves 3-lobed to 3-sected, petiole base with ± stipule-like appendages; involucral leaves dissimilar to basal leaves, basally connate; tepals 6–18, deciduous, obovate or elliptic–lanceolate, basal tepal veins 3–9 with 1–17 anastomoses; fruiting heads elongate; achenes ovoid, styles 1.5–3.5 mm long, marginal ribs 0.1–0.4 mm wide; pollen pantocolpate, pantoporate or spiroaperturate. Germination hypogeal (always?).

*Type species: A. coronaria* L.
2. *A. coronaria* L.
3. *A. hortensis* L.
4. *A. palmata* L.

### III. *ANEMONE* SUBSECTION *BIFLORAE* P.POPOV, *TR. TIFLIS. BOT. SADA* **12:** 4. 1913

*Description:* Basal leaves 3-parted to 3-sected, petiole base without stipule-like appendages; involucral leaves similar to basal leaves, basally free; tepals lanceolate, persistent, basal tepal veins 5–13 with 0–30 anastomoses; fruiting heads globose; achenes ovoid, styles 1–3 mm long, marginal ribs 0.1–0.2 mm wide; pollen pantoporate.

*Type species: A. biflora* DC.

5. *A. biflora* DC. with var. *biflora*, var. *petiolulosa* (Juz.) Ziman, var. *eranthioides* (Regel) Ziman, var. *gortschakowii* (Kar. & Kir.) Sinno and var. *flexuosissima* (Rech.f.) Ehrend. & Ziman.
6. *A. bucharica* (Regel) Finet & Gagnep.
7. *A. baissunensis* Juz.
8. *A. tschernjaewii* Regel
9. *A. serawschanica* Kom.

## IV. *ANEMONE* SUBSECTION *CAROLINIANAE* STAROD., *BOT. ZHURN.* **74:** 1345. 1989

*Description:* Basal leaf blades 1–2-ternate, petiole base without or with stipule-like appendages; involucral leaves similar or dissimilar to basal leaves; tepals linear–oblong to lanceolate, mostly deciduous, typically with five basal veins, but mostly without anastomoses; fruiting heads elongate; achenes mainly subglobose and somewhat compressed, styles 0.4–1.2(–1.7) mm long, hairs 2–5.7 mm long, marginal ribs mainly (0.2–) 0.5–1 mm wide; pollen 3-colpate to pantocolpate. Germination epigeal.

*Lectotype species: A. caroliniana* Walter

10. *A. caroliniana* Walter
11. *A. tuberosa* Rydb.
12. *A. okennonii* Keener & B.E.Dutton
13. *A. berlandieri* Pritz.
14. *A. edwardsiana* Tharp
15. *A. decapetala* Ard.
16. *A. triternata* Vahl

## I. *ANEMONE* SUBSECTION *SOMALIENSES* ZIMAN, BULAKH & KADOTA

### 1. *ANEMONE SOMALIENSIS* HEPPER, *KEW BULL.* **26:** 57. 1971

*Type:* North Africa. 'Somalia, south of Al Hillas, stony ground in shade, 3000 ft, 10–11.1929; *C. Barrington* in herb. Collenette 413.' (Holotype: K!).

*Description:* Rhizomes tuberous, stout and irregular, *c*. 15 × 12 mm, non-branching. Basal leaves 1–2; petioles 5–9 cm long, without stipule-like appendages at the base, scarcely pubescent or subglabrous; blades monomorphic, palmately 3-parted, 2–4 × 3–6 cm, with sessile primary segments and 30–40 obtuse ultimate lobules, glabrous. Scapes 7–18 cm long, appressed-pubescent above, 1–2-flowered (lateral flower frequently undeveloped). Involucral leaves 3 (4), sessile, partially united at base, resembling the basal leaves, blades 2–3-parted or lobed, with 10–15 obtuse ultimate lobules or teeth, 1.5–2.5 cm long, nearly glabrous. Pedicels 1–4 cm long, pubescent. Tepals 10–18, persistent, elliptic–lanceolate, with wide bases and obtuse dentate apices, monomorphic, blue or mauve, 10–15 × 3–5 mm, with 3–5 basal veins and few anastomoses, glabrous. Stamens 3–4 mm long, with filiform filaments, narrow connectives and ellipsoid anthers. Pollen tricolpate (Fig. 7D). Carpels ovoid, not compressed, *c*. 1 mm long, densely covered with hairs *c*. 1 mm long, styles erect and straight, *c*. 2 mm long. Fruiting heads elongate. Achenes ovoid, 1.6–2.0 × 1–1.2 mm, lanate; hairs 3.2–3.5 mm long; styles straight, 1.2–2 mm long; marginal ribs 0.2 mm wide (Fig. 6D). Chromosome number unknown.

*Notes:* The collector of the type specimen, Barrington Brown, believed this plant to be *A. blanda*, but Hepper (1971) recognized and described it as a new species, *A. somaliensis*, taxonomically close to *A. hortensis*, but differing by its much larger involucral leaves (similar to the basal leaves) and smaller perianth. Thulin (1993) enlarged this description of *A. somaliensis* for the *Flora of Somalia* and further comments were added by Ziman *et al.* (2006). In addition to similarities with the taxa of subsection *Anemone*, one has to consider characters shared with members of subsection *Biflorae* (e.g. *A. tschernjaewii* and *A. serawshanica*): tuber shape, lack of stipule-like appendages at the base of the leaf petioles, involucral leaves not fused at base and much fewer anastomoses between the tepal veins. Most important is the plesiomorphic feature of tricolpate pollen, otherwise found only in members of subsection *Carolinianae* of section *Anemone*. All this justifies its separation as a monotypic subsection.

*Distribution and habitat:* East Africa, Somalia, narrow endemic of Al Hills (Fig. 10). In open limestone habitats in evergreen bush land, 920–1200 m.

*Specimens examined:* Somalia: In mist belt of north-facing limestone escarpment with considerable winter rainfall from North-East Monsoon. Evergreen bushland with *Acokanthera, Buxus*, *Dodonaea, Olea africana*. North of Galgallo, 11°01′N, 49°02′E, 1300 m, 7.12.1969, *Lavranos* 7300 (K); Bari: escarpment South of Bunder Murraya, Buraha Dhasi, 11°38′–39′N, 50°29′–32′E, 1050 m, 16–17.xi.1986, *Thulin & Warfa* (Ups-K).

## II. *ANEMONE* SUBSECTION *ANEMONE*

### 2. *ANEMONE CORONARIA* L., *SP. PL.* **1:** 539. 1753

*Type:* 'Habitat in Oriente, Constantinopoli allata'. (Conserved type: LINN n.710.9.! Suggested by Qaiser in Ali & El Gadi, Fl. Libya **108:** 7. 1984. Proposed by

KEY TO SPECIES

1a. Tepals elliptic–obovate, length/breadth mostly below 2.5, with 3–13 basal veins and at least some anastomoses; achenes ovoid and not compressed; achene styles 1.5–2.5 mm long; marginal ribs mainly 0.1–0.3 mm wide; Mediterranean, South-West and Central Asia, Somalia ........ 2
1b. Tepals linear–oblong, length/breadth ratio mostly > 2.5, typically with five basal veins and without anastomoses; achenes mainly subglobose and compressed; achene styles 0.4–1.2 mm long, marginal ribs (0.2–)0.5–1 mm wide; North and South America ........ 10
2a. Tepals 8–18, mostly deciduous, 18–55 mm long, with 3–9 basal veins and 1–17 anastomoses; achene styles 1.5–2.5 mm long; leaf petiole basis often with stipule-like appendages; Mediterranean, South-West Asia and Somalia ........ 3
2b. Tepals 5–6, persistent, 7–30 mm long, with 5–13 basal veins and up to 30 anastomoses; achene styles 0.5–3 mm long; leaf petiole basis without stipule-like appendages; Central and South-West Asia ........ 6
3a. Stolon-like rhizomes present; basal and involucral leaves much divided; tepals 6–13, with 5–9 basal veins and 15 or more anastomoses, predominately red; achenes with marginal ribs 0.3–0.4 mm wide ....... 2. *A. coronaria*
3b. Stolons absent; basal and involucral leaves little divided; tepals 10–18, with 3–5 basal veins and 1–3 anastomoses, usually not red; achenes with marginal ribs *c.* 0.2 mm wide ........ 4
4a. Basal leaves dimorphic, 3-sected, slightly pubescent; flowers solitary, tepals mostly pink or lilac; achene bodies with hairs 3.5–5 mm long ........ 3. *A. hortensis*
4b. Basal leaves monomorphic, 3-lobed to 3-parted, glabrous; flowers usually not solitary, tepals mostly with other colours; achenes with hairs 3–3.5 mm long ........ 5
5a. Tepals 8–12, deciduous, yellow or reddish outside, dimorphic,15–20 mm long; style of achenes 2–2.5 mm long; leaf petiole base with stipule-like appendages ........ 4. *A. palmata*
5b. Tepals 10–18, persistent, mauve or blue, monomorphic, 10–15 mm long; style of achenes 1.2–2 mm long; leaf petiole base without stipule-like appendages ........ 1. *A. somaliensis*
6a. Tuberous rhizomes irregular; basal leaves more than two, much dissected; involucral leaves with petiole-like bases ........ 7
6b. Tuberous rhizomes subspherical; basal leaves 1–2, little divided; involucral leaves sessile ........ 9
7a. Tepals 10–15 mm long, with 5–9 basal veins and 1–3 anastomoses ........ 5. *A. biflora*
7b. Tepals 15–30 mm long, with 5–13 basal veins and 7–30 anastomoses ........
8a. Tepals red; achenes 2.5–3.0 mm long with hairs 2.5–3.5 mm long and pubescent styles ........ 6. *A. bucharica*
8b. Tepals yellow inside and yellow to reddish outside; achenes 3.5–4.5 mm long, with hairs 4.5–5.5 mm long and glabrous styles ........ 7. *A. baissunensis*
9a. Tepals 8–22 mm long, pilose outside, white or bluish; achenes 3.0–3.5 mm long, with hairs 5.0–6.0 mm long and styles 1.7–2.5 mm long ........ 8. *A. tschernjaewii*
9b. Tepals 7–8 mm long, glabrous, yellowish–green; achenes 1.6–2.2 mm long, with hairs 1.7–2.3 mm long and styles 0.5–1.2 mm long ........ 9. *A. serawschanica*
10a. Tubers subglobose; stolon-like rhizomes present; flowers solitary; achenes with marginal ribs 0.2 mm wide ........ 10. *A. caroliniana*
10b. Tubers elongate; stolons absent; flowers solitary or 2–3; achenes with marginal ribs normally 0.4–0.9 mm wide. ........ 11
11a. Basal leaves 1–2-ternate, petiole base with stipule-like appendages; tepals scarcely pubescent ........ 12
11b. Basal leaves mainly 2-ternate, petiole base without stipule-like appendages; tepals densely pubescent ........ 13
12a. Basal leaves slightly pubescent; involucral leaves basally connate; flowers solitary; tepals white to reddish; achenes 2.7–3.5 mm long ........ 13. *A. berlandieri*
12b. Basal leaves glabrous; involucral leaves not basally connate; flowers two or three; tepals white to bluish; achenes 1.3–2.2 mm long ........ 14. *A. edwardsiana*
13a. Tepals six to 10 (13); achene hairs 2.0–3.5 mm long; North America ........ 14
13b. Tepals > 10; achene hairs 4.0–6.0 mm long; South America ........ 15
14a. Basal leaves glabrous; basal and involucral leaves similar; tepals 10–20 mm long, pink or white ........ 11. *A. tuberosa*
14b. Basal leaves pubescent; basal and involucral leaves dissimilar; tepals 6–12 mm long, greenish–white ........ 12. *A. okennonii*
15a. Involucral and basal leaves dissimilar, basal leaves dimorphic; inflorescences few-flowered; tepals deciduous, 15–20 × 5–8 mm, with five to nine basal veins and one or two anastomoses ........ 15. *A. decapetala*
15b. Involucral leaves similar to basal leaves, basal leaves monomorphic; flowers solitary; tepals persistent, 10–15 × 2–3 mm, with three basal veins and without anastomoses ........ 16. *A. triternata*

Jarvis in Taxon **41:** 557. 1992 and approved in the Vienna Code 2006: 293. See also Taxon **55:** 795–796. 2006 and Javis, 2007).
= *A. pusilla* DC., *Syst.* **1:** 197. 1818.
= *A. cyanea* Risso, *Fl. Nice* 6. 1844.
≡ *A. coronaria* var. *cyanea* (Risso) Ardoino, *Fl. Alp. Marit.* 12. 1867.
= *A. regina* Risso, *l.c.* 1844.
= *A. stellata* Lam. *sensu* Risso, *l.c.* 1844.
= *A. coronarioides* Segond in Doublier, Panescorce, Jaubin, Segond & Maurin, *Prodr. Hist. Nat. Var* 143, 1853. Hanry ex Ardoino, *Fl. Alp. Marit.* 14. 1867.
= *A. rissoana* Segond in Doublier *et al. Prodr. Hist. Nat. Var* 143. 1853. Jord., *Diagn*. 1 : 58 and *Ann. Soc. Linn. Lyon*, sér.2, **7:** 426, in obs. 1861.
≡ *A. coronaria* var. *rissoana* (Segond) Ardoino, *Fl. Alp. Marit.* 12. 1867.
= *A. ventreana* Segond in Doublier *et al. Prodr. Hist. Nat. Var* 143. 1853. Hanry ex Ardoino, *Fl. Alp. Marit.* 14. 1867.
≡ *A. coronaria* var. *ventreana* (Segond) Ardoino, *Fl. Alp. Marit.* 12. 1867.
= *A. mouansii* Segond in Doublier *et al. Prodr. Hist. Nat. Var* 143. 1853. Hanry ex Ardoino, *Fl. Alp. Marit.*12. 1867.
≡ *A. coronaria* var. *mouansii* (Segond) Ardoino., *Fl. Alp. Marit.* 12. 1867.
= *A. rosea* Segond in Doublier *et al. Prodr. Hist. Nat. Var* 143. 1853.
≡ *A. coronaria* ‘forma’ *rosea* (Segond) Foucaud in Rouy & Foucaud, *Fl. Fr.* **1:** 46. 1893.
= *A. coccinea* Jord., *Ann. Soc. LINN. Lyon, sér.* 2, **7:** 425. 1861.
= *A. grassensis* Goaty & Pons, *Bull. Soc. Bot. France* **30**, sess. extraord. 78. 1884.
= *A. alba* Goaty & Pons, *l.c.* 79. 1884.
≡ *A. coronaria* var. *alba* (Goaty & Pons) Burnat, *Fl. Alp. Marit.* 18. 1892.
= *A. coronaria* ‘forma’ *albiflora* Foucaud in Rouy & Foucaud, *Fl. Fr.* **1:** 46. 1893.
≡ *A. coronaria* var. *albiflora* (Foucaud) Sinno, *Bot. J. Linn. Soc*. 15**3:** 435. 2007.
= *A. kusnetsowii* Woron. ex Grossh., *Fl. Cauc*. **2:** 105. 1930.
= *A. coronaria* f. *parviflora* Boiss., *Fl. Orient.* **1:** 11. 1867.
= *A. coronaria* var. *incisa* Boiss., *Fl. Orient.* **1:** 11. 1867.
= *A. coronaria* var. *coerulea* Hort., *Herb. Fl. Fr.* 1. 1867.
= *A. coronaria* var. *plena* Hort., *l.c.* 1867.
= *A. coronaria* var. *phoenicea* Ardoino, *Fl. Alp. Marit*. 12. 1867.
= *A. coronaria* var. *purpurea* ArdAoino, *Fl. Alp. Marit*. 12. 1867.
= *A. coronaria* var. *depauperata* Freyn, *Flora von Lycien, Karien und Mesopotamien* **1:** 13. 1885
= *A. coronaria* var. *chrysanthemifolia* Hort., *Rev. Hort.* 232. 1893.

*Description* (Fig. 1A): Rhizomes tuberous, of irregular shape, but mainly elongate, 20–30 × 10–20 mm, branching and producing thin adventitious roots. In early spring, stolon-like rhizomes may develop. Basal leaves 3–8 in adult plants, monomorphic, petioles 3–15 (20) cm long, scarcely pubescent, their basal parts with stipule-like appendages (Fig. 4A), blades twice-triternate, 1.5–6.0 × 3–8 cm, glabrous, primary segments with petiolules 5–30 mm long, deeply divided, with 70–150 acute ultimate lobules. Scapes 10–13 cm long, scarcely pubescent, 1-flowered. Involucral leaves 3 (4), sessile, basally connate, blades pinnately partite or lobed, with 10–30 acute ultimate lobules, dissimilar to basal leaves. Pedicels 10–25 (30) cm long, densely pubescent. Tepals 6–13, deciduous, elliptical or obovate, basally narrowed, predominately red, but occasionally pink, blue, etc., 20–55 × 14–28 mm, mostly densely pubescent, number of veins at the base 5–9 with 15–17 (or more) vein anastomoses (Fig. 5A). The stamens 10–15 mm long, filaments filiform, anthers ellipsoid, connectives wide. Pollen pantoporate (Fig. 7A). Carpels ovoid, not compressed, *c.* 1 mm long, densely covered with hairs 0.2–0.3 mm long; styles straight, subconic, 1.5–2 mm long, stigmas linear (Fig. 5A). Fruiting heads slightly elongate, 1.5–1.7 × 1.0–1.2 cm. Achenes ovoid, 1.7–2.5 × 1.0–1.2 mm, densely covered with hairs 3.5–4.5 mm long, tipped by nearly straight pubescent styles 1.5–2.5 mm long, marginal ribs up to 0.4 mm wide (Fig. 6A). Chromosome number $2n = 16$ (Heimburger, 1959; Madahar, 1967; Baumberger, 1970; Horovitz, Galil & Zohary, 1975; Maïa & Venard, 1976, etc.).

*Notes:* Linnaeus (1753: 539) originally described *A. coronaria* as ‘*Pulsatilla foliis decompositis pinnatis. . .* ’ in his Hortus Cliffortianus (1738). Under that species he also included in 1753 from Caspar Bauhin’s Pinax ‘β *Anemone tenuifolia multiplex rubra*’. From the six specimens of *A. coronaria* in LINN, n.710.9 was selected in 1984 as the conserved type (see Jarvis, 2007). In our Figure 1A n.710.8, another representative specimen from LINN is illustrated.

As differential features of *A. coronaria*, multi-segmented basal and involucral leaves with linear ultimate lobules and variously coloured flowers were noted by De Candolle (1817, 1824). Other authors (e.g. Boissier, 1867; Hayek, 1927; Maire, 1964; Chater, 1993; Pignatti, 1982, etc.) added the solitary non-yellow flowers with 5–8 tepals, the 3-leaved involucre and the petiolulate primary segments of the basal leaves.


**Figure 1.** Representative specimens of *Anemone coronaria* (A) and *A. hortensis* (B) from the herbarium of the Linnean Society of London (LINN).

De Candolle (1824) described *A. pusilla* and separated it by its elongate tepals. Afterwards, several species close to *A. coronaria* were described on the basis of floral size and sepal colour (e.g. large or small flowers, red, yellow or pink tepals, etc.): *A. cyanea*, *A. rissoana*, *A. grassensis*, etc. Most of these variants were later considered as varieties or simply lumped under *A. coronaria*.

*Anemone kusnetsowii* Woron. ex Grossh. (Grossheim, 1930; not mentioned by Sinno-Saoud *et al.* 2007) was described from the Caucasus (South Karabakh in Azerbajan), without fruits, but with the flowers and leaves resembling those of *A. coronaria*. We follow Juzepchuk *et al.* (1937) and regard *A. kusnetsowii* as one of the numerous forms of *A. coronaria*. The type specimens at K and LE have stolon-like rhizomes, a character diagnostic for *A. coronaria s.s.* and unique within subsection *Anemone*.

Within subsection *Anemone, A. coronaria* has the same chromosome number as *A. hortensis*, but their karyotypes differ considerably (Baumberger, 1970). The $F_1$ hybrids exhibit meiotic asyndesis and are completely sterile (Maïa & Venard, 1976). Thus, in spite of widely overlapping distributions (Fig. 11), there is complete separation of the two species. The somewhat isolated position of *A. coronaria* is also supported by its considerable genetic isolation within section *Anemone* as shown by restriction site analyses and *atpB-rbcL* sequences (Fig. 8).

On the basis of an extensive review of herbarium material, Sinno-Saoud *et al.* (2007) made a phenetic analysis which also showed that *A. coronaria* is clearly separated from *A. hortensis* and from taxa treated here as *A.* subsection *Biflorae*. Considering the great variation in leaf segmentation, flower size and particularly tepal colours within *A. coronaria*, they proposed six infraspecific taxa: (1) var. *coronaria*, (2) var. *albiflora*, (3) var. *cyanea*, (4) var. *parviflora*, (5) var. *ventreana* and (6) var. *rissoana.* Varieties 1–3 have wide and mostly overlapping distributions, 4 is limited to the East Mediterranean area and 5 and 6 are apparently endemic to South-East France and adjacent Italy.

The biology and population genetics of *A. coronaria* has been studied intensively in Israel (Horovitz *et al.*, 1975; Yonash *et al.*, 2004). Seedlings have two cotyledons with petioles free or fused to a long cotyledonary sheath. Cotyledons and primary leaves emerge above ground, but the plumule remains in the soil, i.e. it shows intermediate hypogeal germination (Förster, 1999). Vegetative reproduction is possible by subterranean stolons emerging from the tubers. Stomata occur on the upper and lower side of the leaves (Madahar, 1967). The plants are protogynous, insect pollinated and predominantly outbreeding (allogamous). The remarkable variability in flower colours is ± correlated with ecotypic differentiation on the diverse soil types of Israel. This has been substantiated by DNA fingerprinting (AFLP; Yonash *et al.*, 2004), a method which also allows the documentation of the remarkable diversity of cultivars of *A. coronaria*. These cultivars have apparently been selected from wild populations in the Near East for hundreds of years.

*Distribution and habitat:* Most parts of Southern Europe (Portugal, Spain, Balearic Islands, France, Corsica, Sardinia, Italy, Sicily, Malta, Albania, Macedonia, Bulgaria, Greece, Crete) and Turkey, Cyprus, Syria, Lebanon, Israel, Jordan, Iraq, Iran, Azerbajan, Egypt, Libya, Algeria and Morocco (Fig. 11). There is no evidence for an occurrence in Turkmenistan (suggested by Sinno-Saoud *et al.*, 2007). In herbaceous, mostly Mediterranean communities, olive groves and abandoned fields, 100–700 m.

*Specimens examined:* SPAIN: Zamora, Alcañices, 23.ii.1919, *Font Quer* (Bc); Malaga: Valle de Abdalagis, iii.1971, *Sanchez* (Bc); Malaga, Antequera, Hacia Alora, 6.iii.1980, *Mesa* (Bc).
FRANCE: Lot-et-Garonne: Poudenas, 15.iv.1915, *Coste* (MARSSJ); Herault: Montpellier, 1823, *Nicolas* (KW); Var: La Seyne-sur-Mer, iii.1886, *Robin* (MARSSJ); Var: Maures Mts, Pierrefeu, Mollo-Trocado, 9.ii.1997, *Médail* (MARSSJ); Mollo-Trocado, 30.iii.1997, *Ziman & Médail* (KW); Var: Sollies-Ville au Matheron, 30.iii.1997, *Ziman & Médail* (KW); Alpes Maritimes: Mougins, 15.ii.1916, *Coste* (MARSSJ); Antibes, La Brague, 28.3.1997, *Ziman & Médail* (KW).
ITALY: Sicily: Palermo, 10.iii.1905, *Ross* (GH); Rome, 1919, *Berger* (KW).
GREECE: Athens, 13.iii.1850, *Orphanides* (KW).
CYPRUS: Nicosia, Kykko Camp, 13.ii.1973, *Laukkonen* (BM).
TURKEY: Smyrna, ii.1827, *Schultz* (KW); SMyana, 23.iv.1854, 5.iii.1854, *Balansa* (KW, BM); Izmir, 16.ii.1969, *Fitz* (WU); Managvat, 12.1i1936, *Tengwall* (K); Mugla: Fetiye, Kemer-Kestep, 19.iii.1956, *Davis & Polunin 467* (K); Antalya: Kiremithaner, Karadag, 7.iv.1959, *Hennipman* (K); Seyhan: Tarsus, 16.iii.1965, *Rechinger* (WU); Hatay, Iskenderum, 23.iii.1966, *Cheese* (K); Senkoy, 3.iii.1985, *Sorger* (WU).
IRAN: Kurdistan, 19.iii.1841, *Hohenacker* (KW); Kermanshah: Kazand, 16.iv.1951, *Sharif* (WU); Kurdistan: Erbil, 25.iv.1957, *Riedl* (KW); Kermanshah, Paytagh Pass, 6.iii.1962, *Furse 1021* (BM); Susa midway to Dukan, 18.iii.1975, *Omar 42628* (K).
IRAQ: Abu Ghraib, road between Tel-Kotchek highway and Tel-Afar, Mosul Liwa, 7.iii.1965, *Abbas Al-Ani 9364* (K).
SYRIA: Aleppo, 18.iii.1891, *Kotschy* (KW).
LEBANON: Beirut, i.1863, *Osborn* (K); Tripoli, 29.ii.1966, *Archibald 1013* (K).
ISRAEL: Tel-Aviv, 27.i.1928, *Eig* (KRAM); Capurnaum, 18.iii.1967, *Hepper 3215* (BM).
EGYPT: Kingi-Mariut, 22.i.1928, *Täckholm* (BM).
ALGERIA: Moissons: Khummel, Constantine, 18.iii.1876, *Munby* (K).

### 3. *ANEMONE HORTENSIS* L., *SP. PL.* **1:** 540. 1753

*Type:* 'Habitat in Rhenum & in Italia'. (Lectotype herb. Clifford 334, *Pulsatilla* 4, sheet A, designated by Strid in Jarvis *et al.* Taxon **54:** 469. 2005. See also Jarvis, 2007).
= *A. pavonina* Lam., *Encycl.* **2:** 166. 1783;
≡ *A. hortensis* var. *pavonina* (Lam.) Gren. & Godr., *Fl. France* **1:** 47. 1848.
= *A. stellata* Lam., *l.c.*, 1783.
≡ *A. hortensis* var. *stellata* (Lam.) Gren. & Godr., *l.c.* 1848.
= A. *versicolor* Salisb., *Prodr*. 371. 1796, nom. superfl.
= *A. fulgens* J.Gay, *Prodr.* **1:** 18. 1824.
≡ *A. hortensis* var. *fulgens* (J.Gay) Gren. & Godr., *Fl. Fr.* **1:** 47. 1848.
= *A. latifolia* Bellardi ex Re, *Mem. Acad. Sci. Torin* **33:** 233. 1829.
= *A. hortensis* var. *acutifolia* Spach, *Hist. Nat. Veg.* **7:** 250. 1839.
= *A. hortensis* var. *heldreichii* Boiss., *Fl. Orient.* **1:** 12. 1867.
≡ *A. hortensis* ssp. *heldreichii* (Boiss.) Rech.f., *Denkschr. Akad. Wiss., Math.-Nat. Kl.* **105:** 743. 1943.
≡ *A. heldreichiana* Gand., *Fl. Cret.* **4:** 18. 1916.

*Description* (Figs 1B, 2C): Rhizomes tuberous, irregular, 2–6 × 1–2 cm, branching, without stolons, 3–5, up to 1 cm deep in the soil, producing thin roots. Basal leaves 4–7 in adult plants (Fig. 2C), petioles 5–12 cm long, with widened, stipule-like base (Fig. 4B), slightly pubescent, blades dimorphic, coriaceous, 2–3 × 3–6 cm, glabrous or slightly pubescent (mainly

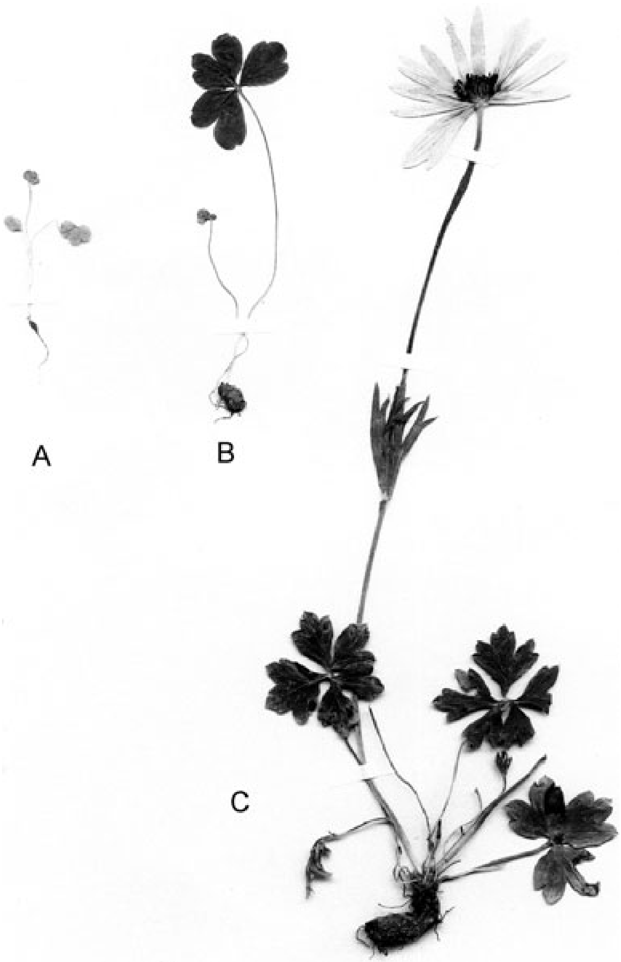


**Figure 2.** Main developmental stages of *Anemone hortensis*: A, seedling. B, juvenile plants. C, adult and reproductive plant [France, Var: Maures Mts, Gonfaron; 30.iii.1997, *Ziman & Médail* (KW)].

along veins); outer basal leaves (which develop in early spring) with trisected blades, petiolules 1–2 mm long or absent, blades little divided or with lobed primary segments only, the ultimate lobules 20–25, obtuse; inner basal leaves (which develop later and live longer) with much divided blades, petiolules 5–15 mm long, ultimate lobules 40–50, acute. Scapes 1–3, 1-flowered, slightly pubescent, 10–2 cm long. Involucral leaves 3, sessile, basally connate, not resembling basal leaves; blades with 2–3 lobes, but sometimes undivided, broadly lanceolate, acute. Pedicels 10–2 cm long, scarcely pubescent. Tepals 10–18, deciduous, obovate to lanceolate, basally narrowed and apically acuminate, purplish–pink (white, bluish or violet), $15–30 \times 6–11$ mm, with 3–5 basal veins and 1–3 anastomoses, scarcely pubescent (Fig. 5B). Stamens *c.* 10 mm long, with filiform filaments and ellipsoid anthers. Pollen spiroaperturate (Fig. 7B). Carpels ovoid, 0.5–1 mm long, densely covered with hairs 0.5–0.7 mm long, with straight styles 1–2 mm long (Fig. 5B). Fruiting heads slightly elongate, *c.* $1.5 \times 1$ cm. Achenes ovoid, $2.9–3.2 \times 1.1–1.7$ mm, villous, hairs 3.5–5.2 mm long; styles 2–2.6 mm long, basally pubescent; marginal ribs *c.* 0.2 mm wide (Fig. 6B). Chromosome number $2n = 16$, rarely also $2n = 32$ (also for *A. fulgens* and/or *A. pavonina*: Heimburger, 1959; Madahar, 1967; Baumberger, 1970; Maïa & Venard, 1976; Tzanoudakis, 1986; Signorini & Mori, 1994: $2n = 16 + 1B$; Mlinarec, Papeš & Besendorfer, 2006, etc.).

*Notes: Anemone hortensis* was already recognized by Linnaeus (1753) in his Hortus Cliffortianus (1738) and described on the basis of its broadly palmatifid leaves and reddish flowers, including a number of earlier synonyms. For its lectotypification, see also Jarvis (2007). As an example of an early collection n.710.15 from LINN is shown in Figure 1B. Several later described species, are now treated as synonyms of the variable *A. hortensis*: *A. pavonina* Lam. (accepted by Ulbrich, 1905/1906; Chater, 1993; Monserrat, 1986 and Pignatti, 1982), *A. stellata* Lam., *A. fulgens* J.Gay (accepted by Pritzel, 1841; Boissier, 1867), etc.

During our examination of available herbarium material, we noted several features of *A. hortensis*, not yet documented. Dimorphic basal leaves and broadened, stipule-like bases of petioles were seen on both the type specimen and the specimen collected in Southern France close to Marseille (Figs 1B, 2C). The outer and inner circle of tepals often differ: the outer tepals are larger, pubescent throughout, have 3–5 basal veins and 1–3 anastomoses, whereas the inner tepals are frequently smaller, glabrous or with hairs along the central vein only, with 3 basal veins and without anastomoses (Fig. 5B). Connectives between anthers are narrow. Carpels are not compressed, stigmas linear.

Germination and seedling morphology apparently vary within *A. hortensis s.l.* (Fig. 2A). For so-called *A. pavonina* Förster (1999) recorded normal epigeal germination and seedlings with two cotyledons, free petioles and an emerging plumule. However, for *A. hortensis* he described the petioles of the cotyledons as fused into a long cotyledonary sheath. Whereas the rounded–ellipsoid leaf blades of the cotyledons and the first three-lobed primary leaves emerge above the soil surface, the plumule remains underground, a process he called 'intermediate hypogeal germination'. Generally, seedlings of *A. hortensis s.l.* have a thin primary root and a slightly thickened hypocotyl from which the ovoid tuberous rhizome with adventitious roots develops. Juvenile plants produce 3-sected secondary leaves on long petioles (Fig. 2B). According to Madahar (1967), stomata occur mainly on the lower leaf side in *A. hortensis*, but on both leaf sides in the other two species of subsection *Anemone*.

*Anemone hortensis* exhibits considerable morphological, chromosomal (Maïa & Venard, 1976) and genetic variation as demonstrated by restriction site analyses (Hoot *et al.*, 1994) and by *atpB-rbcL* data of morphotypes designated as *A. hortensis* and *A. pavonina* (Figs 8, 9). Nevertheless, experimental $F_1$ hybrids between these types exhibit relatively normal meiosis and fertility (Maïa & Venard, 1976). Variation within *A. hortensis* appears to follow a geographical pattern but has not been sufficiently studied. However, populations on the Croatian mainland and on off-shore islands, isolated for about 10 000 years, exhibit no structural differences in chromosomes, even after a detailed analysis (Mlinarec *et al.*, 2006). Considering all these facts and after a critical survey of specimens classified as *A. pavonina, A. fulgens, A. stellata*, etc. and their assumed morphological differential characters, we prefer to treat them as one polymorphic species, i.e. *A. hortensis s.l*. We also refrain from using infraspecific taxa as long as no detailed morphometric, chromosomal or DNA studies are available from the whole area of the species.

*Distribution and habitat:* East to West Mediterranean, including Southern Europe (Spain, France, Corsica, Sardinia, Sicily, Italy, Slovenia, Croatia, Montenegro, Albania, Bulgaria, Greece, Crete, etc.), South-West Asia (Turkey, Cyprus) and North Africa (Algeria) (Fig. 11). In herbaceous Mediterranean communities, olive groves, fallow and abandoned fields, but also in open rocky places of matorrals (garigue, maquis, phrygana), 100–700 m.

*Specimens examined:* SPAIN: Salinas de Lez, 8.iv.1863, *Huet* (WU); Andalusia, Cadiz, 28.iv.1925, *Zerny* (WU).
FRANCE: Toulon, 27.iii.1861, *Jacquin* (WU); Var: LE Muy, 8.iv.1980, *Litzler* (MARSSJ); Bouches-du-Rhone, iv.1934, *Riedl* (KRAM); Marseille, Vallon du Passe-Temps, 22.ii.1997, *Médail* (MARSSJ); 29.iii.1997, *Ziman & Médail* (KW); Var: Sollies-Ville au Matheron, 2.iii.1997, Médail (MARSSJ); 30.iii.1997, *Ziman & Médail* (KW); Var: Maures Mts, Gonfaron, 30.iii.1997, *Ziman & Médail* (KW); Biot, Massif du Therme, 28.iii.1997, *Ziman & Médail* (KW); Alpes Maritimes, Cap d'Antibes, 31.iii.1975, *Litzler* (MARSSJ); 28.iii.1997, *Ziman & Médail* (KW); Valbonne, 28.iii.1997, *Ziman & Médail* (KW).
ITALY: Sardinia, iv.1854, *Pavillon* (KW); Genova, Castellano, 26.iv.1904, *Ronniger* (WU).
GREECE: Attica: Pentelico, 13.iii.1850, *Orphanides* (KW); 3.iv.1874, *Heldreich* (WU); 17.iii.1891, *Heldreich* (WU); Athene, 6.iii.1976, *Pichler* (W).
CROATIA: Fiume, iii.1969, *Riedl* (KRAM).
BULGARIA: Zwerdec: Veleka, 1976, *Makarova & Cerneva* (KRAM).
TURKEY: Kiretch-Keni, 25.iii.1890, *Ronniger* (WU); Thrakien: Derekoy, 6.v.1967, *Bauer* (WU); Mugla: Farilya Koyu, 22.iii.1969, *Fitz* (WU); Izmir: Gumuldur, 15.iv.1969, *Fitz* (WU).
ALGERIA: Djebel-Ovach, 4.iv1855, *Schultz* (KW); Constantine, Moissons de la valle du Rhummel, 18.iii.1876, *Munby* (K); Kaddous, 19.ii.1969, *Faurel* (WU).

### 4. *ANEMONE PALMATA* L., *SP. PL.*, **1:** 538. 1753

*Type:* 'Habitat Lusitania ad Tagum'. [Lectotype LINN n.710.16, designated here, from the original material listed by Jarvis, 2007. Relevant syntypes are: Herb. Burser Ix: 59 (Ups); Clusius, Rar. Pl. Hist. 1. 248, 1601 (icon); Morison, Pl. Hist. Univ. **2:** 425, s. 4, t. 25, f. 3, 1680 (icon)].
= *A. malvifolia* L., *Sp. Pl.* **1:** 538. 1753.
= *A. lobata* Pers., *Syst. Bot.* **2:** 96. 1883.

*Description* (Fig. 3)*:* Rhizomes tuberous, cylindrical–oblong, 5–7, up to 1 cm deep in the soil, branching, 3–5 × 1.6–2.0 cm, with thin roots. Basal leaves 4–8 (up to 10), petioles 5–15 cm long, scarcely puberulent, petiole base with stipule-like appendages (Figs 3C, 4C), blades monomorphic coriaceous, deeply trilobed, sometimes almost entire, 2–4 × 2.5–6.5 cm, ultimate lobules obtuse or acute, slightly puberulent. Scapes 1–3, 5–2 cm long, slightly puberulent,1- to 2-flowered. Primary involucral leaves 3, dissimilar to the basal ones, sessile, basally connate, blades 3–5-parted or 3–5-lobed, ultimate lobules linear–lanceolate, long–acute. Secondary involucral leaves (bracteoles) small, entire, lanceolate, closely subtending the lateral flowers. Pedicels 5–20 cm long, densely pubescent. Tepals 8–12 (–15), deciduous, elliptic–lanceolate, with wide bases and apices, yellow, but sometimes reddish outside, in two whorls, frequently dimorphic: the outer 18–20 × 5–10 mm, with 3–5 basal veins and 1–3 anastomoses, pubescent, the inner 15–17 × 3–5 mm, with 3 basal veins and without anastomoses, glabrous or subglabrous (Fig. 5C). Stamens 10–15 mm long, with linear filaments, wide connectives and ellipsoid anthers. Pollen grains pantocolpate (Fig. 7C; Huyn, 1970). Carpels ovoid, not compressed, 0.6–1 mm long, densely covered with hairs 0.5–1 mm long, styles straight, 2–3 mm long, stigmas linear (Fig. 5C). Fruiting heads suborbicular, 0.8–1.5 × 1.0–1.5 cm. Achenes ovoid, 3–3.5 × 1–1.2 mm, villous, hairs 2.5–2.5 mm long; styles 2–3.5 mm long; marginal ribs 0.1 mm

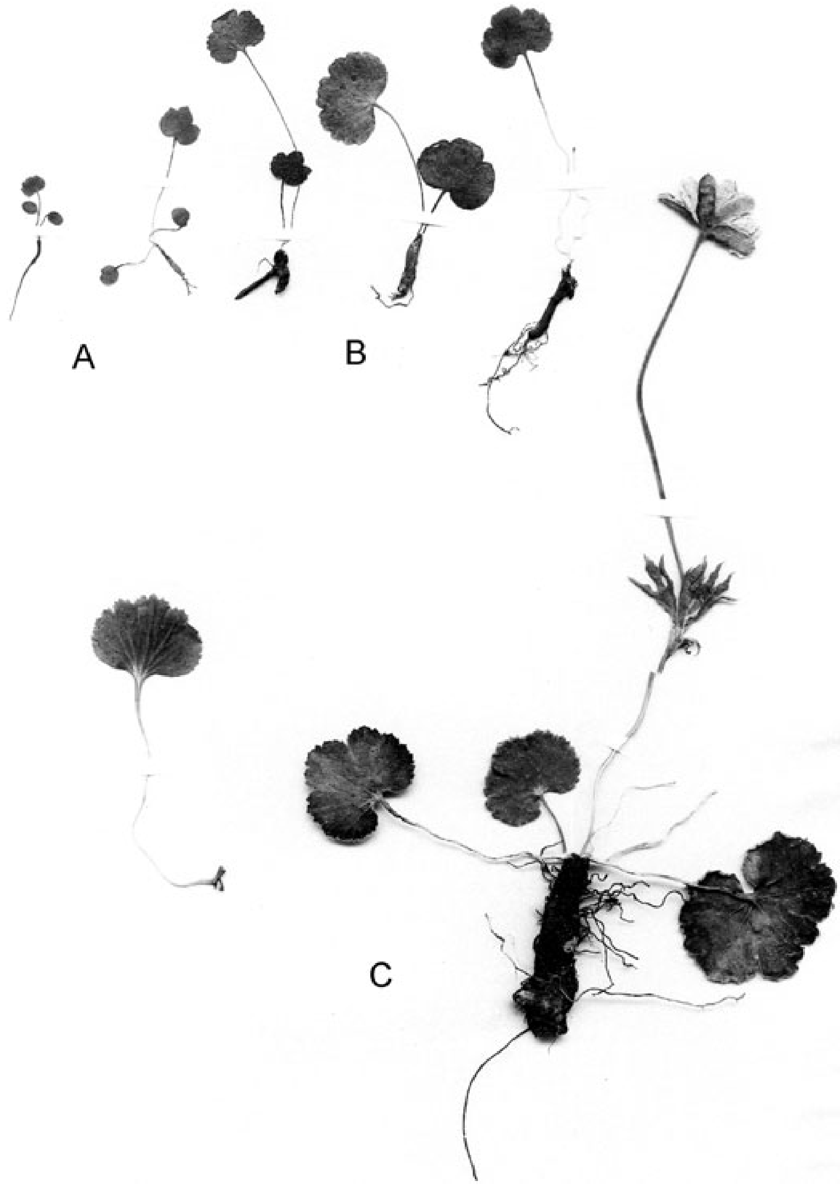


**Figure 3.** Main developmental stages of *Anemone palmata*: A, seedlings. B, juvenile plants. C, adult, reproductive plant and isolated basal leaf with stipule-like 'ears' [Spain, Valencia Co.: Villalonga, Pla de la Llacuna; 3.iv.1997, *Ziman & Boşcaiu* (KW)].



wide (Fig. 6C). Chromosome numbers: $2n = 16$ and 32 (Heimburger, 1959; Madahar, 1967; Baumberger, 1970; Lentini, Romano & Raimondo, 1988; Boşcaiu *et al.*, 1998; Médail *et al.*, 2002, etc.).

*Notes:* Originally Linnaeus (1753: 358) described this species as '*Pulsatilla foliis palmatis*' in his Hortus Cliffortianus (1738). From the relevant sheets in LINN we propose n.710.16 as lectotype. LINN n.710.4 is excluded because it was annotated by Linnaeus himself as 'vernalis 4'. We have not seen the specimen from the Burser herbarium (Ups) and also exclude the less authentic Clusius and Morison icons as possible lectotypes.

*Anemone palmata* has cordate suborbicular and semilobate basal leaves and a 10–12-leaved perianth with obtuse tepals according to Linnaeus (1753) and De Candolle (1817). Later, Pritzel (1841) mentioned the rare occurrence of undivided basal leaves, the 3–5-sected involucral leaves, 1–2-flowered stems, the presence of secondary small involucral bracts and yellow tepals. Germination is hypogeal, the plumule remains underground (Förster, 1999). Our observations show that the seedlings have cotyledons with rounded blades and basally connate petioles, single initial leaves with three-lobed blades, a thickened hypocotyl and thin primary roots (Fig. 3A). The juvenile plants have 2 (3) leaves with three-lobed blades and long, basally dilated petioles, cylindric–ovoid rhizomes and adventitious roots (Fig. 3B). Further developed but still not flowering plants differ by their larger size and the rhizome shape. Adult plants are shown in Figure 3C.

With respect to morphology, karyotype and complete crossing barriers (Maïa & Venard, 1976) and genetic distance (Figs 8, 9), *A. palmata* is somewhat isolated within *A.* subsection *Anemone*. With the exception of the South American *A. decapetala*, *A. palmata* is the only species of section Anemone for which diploid (2×) and obviously autopolyploid (4×) populations with ± identical phenotype have been recorded (Médail *et al.*, 2002). Whereas only 2× plants have been reported for Sicily (Lentini *et al.*, 1988) and Southern France, 4× plants also exist in the Iberian Peninsula (Médail *et al.*, 2002). In Spain 2× plants have been found in the south (Sierra de Cazorla and near Sevilla) and 4× plants in the east (in the area of Valencia). In Portugal, both cytotypes have been recorded. Here, we can report an additional new 2× count ($2n = 16$; M. Lambrou) from a population growing in Southern Spain, north-east of Granada, above Víznar, 1150 m, in Mediterranean grassland [F. & L. Ehrendorfer, 27.04.2003 (WU)].

*Distribution and habitat:* West Mediterranean, South-West Europe (Portugal, Spain, France, Sardinia, Sicily) and adjacent North-West Africa (Algeria, Tunisia and Morocco; indications from Western Greece are erroneous) (see distribution maps Fig. 11 and Médail *et al.*, 2002). In Mediterranean rocky grass- and shrubland or open woods, 100–1200 m.

*Specimens examined:* FRANCE: Var: Maures Mts, La Londe, 6.iv.1978, *Ponel* (MARSSJ); Cavalaire-sur-Mer, Vallon des Collieres, 30.iii.1997, *Ziman & Médail* (KW); Bouches-du-Rhone: Marseille, Calanques Mts, Luminy, 29.iii.1997, *Ziman & Médail* (KW); Allauch, Vallon de l'Equarissage, 29.iii.1997, *Ziman & Médail* (KW); Hyeres, Maures Mts, l'Appie, 30.iii.1997, *Ziman & Médail* (KW).
SPAIN: Alicante: Las Salinas, 8.iv.1863, *Huet* (WU); Andalusia: Cadiz, Puerto de Santa Maria, San Roque, 26.iv.1922, *Grn* (BCC); Cadiz, 28.iv.1925, *Zerny* (WU); Valencia: Montes supra Denia, 7.iv.1957, *Bolos & Mordaus* (VAB); Malaga: Sierra de Enmedio, Sayalonga, 15.iv.1980, *Garcia* (VAB); Albacete: Casas del Gineta, 25.iv.1980, *Piera* (VAB); Mogente, iv.1982, *Mateo* (VAB); Alicante: Vall de Gallinera, iv.1982, *Mateo* (VAB); Caceres: Parque Natur. Montfrague, Finca Causinas, 23.iii.1984, *Crespo* (VAB); Villadangos del Páramo, Leon, 30.iv.1985, *Herrero* (VAB); Casa de Alberola: Carcaixent, Prados, iv.1986, *Piera* (VAB); Peraleja: Bunol, iv.1987, *Villamence* (VAB); Madrid: Aranjuez, 28.iv.1991, *Czimen* (VAB); Valencia Co. Villalonga, Pla de la Llacuna, 3.iv.1997, *Ziman & Boşcaiu* (KW); Ontinyent: Ponce, 3.iv.1997, *Ziman & Boşcaiu* (KW); Benirrama: La Vall de Gallinera, la Carrotxa, 3.iv.1997, *Ziman & Boşcaiu* (KW); Benirrama, 3.iv.1997, *Ziman & Boşcaiu* (KW); Pego: Pla del Mollo, 4.iv.1997, *Ziman & Boşcaiu* (KW); Banyeres: La Rambla, 4.iv.1997, *Ziman & Boşcaiu* (KW).
PORTUGAL: Lisbon, Estremadura, 17.iv.1968, *Miles et al.* (VAB).
ITALY: Sardinia: iv.1854, *Pavillon* (KW).
ALGERIA: Koubba, 3.i850, *Jamin* (K); Djebel-Ovach, 4.iii.1855, *Schultz* (KW); Oran, 1858 (K); Maison-Carree, 27.ii.1879, *Allard* (K); Crescia, 1893, *Jahandier* (Bc); Berruaghia, Leverdo, 7.iv.1937, *Alato* (K); Kaddous, 19.ii.1946, *Faurel* (WU).
MOROCCO: Boulzaut, iii.1931, *Tretewy* (K); Oulmes, ii.1939, *Tretewy* (K); Rabat: Akala, 5.iii.1950, *Vindt* (K).

## III. *ANEMONE* SUBSECTION *BIFLORAE* POPOV

5. *ANEMONE BIFLORA* DC., *SYST.* **1:** 201. 1817, S.LAT

*Type:* 'Habitat in Oriente' (holotype: P).
≡ *A. coronaria* L. var. *biflora* (DC.) Finet & Gagnep., *Bull. Soc. Bot. Fr.* **51:** 75. 1906. See also the synonyms under the varieties of *A. biflora*.

*Description:* Rhizomes tuberous, irregular (asymmetrical), rarely branched, 1.0–2.5 × 1.0–2.5 cm. Roots various, but thickened ones predominate. Basal leaves 3–5 (in adult plants), glabrous; petioles 2–5 cm long; blades once- or twice-ternate, 1.5–5.0 × 1.5–5.0 cm, with primary segments on petiolules 1–10 mm long and 15–35 (up to 80) obovate to almost linear ultimate lobules. Scapes 1–3, 3–5 (up to 20) cm long, glabrous, 1–2-flowered. Involucral leaves 3, with short petiole-like flat bases; blades 3-parted, 1–3 cm long, with 10–20 (up to 30) ultimate lobules, glabrous. Pedicels 2–5 (10) cm long, appressed-pilose. Tepals 5 (6), persistent, ovate to elliptic, apically acuminate, monomorphic, yellow or reddish, 8–15 × 4–9 mm, with 5–9 basal veins and 1–3 anastomoses, densely pubescent (Fig. 5D–G). Stamens 5–6 mm long, with slightly dilated filaments, narrow connectives and ellipsoid anthers. Pollen pantoporate (Ziman *et al.*, 1998). Carpels ovoid, 1–1.5 mm long, slightly compressed (ribs *c.* 0.1 mm wide), more or less densely covered with hairs 1–3 mm long, styles mainly straight, 1–2 mm long, basally densely pubescent, stigmas linear (Fig. 5D–G). Fruiting heads spherical, 1.5–2 cm in diameter. Achenes subovoid, 2.7–4 × 1–1.5 mm, lanate, hairs 2–5 mm long; styles 2–3 mm long, basally pubescent; marginal ribs 0.1 mm wide (Ziman *et al.*, 1998). Chromosome number $2n = 16$ (Madahar, 1967) for '*A. biflora*' and '*A. petiolulosa*').

*Notes:* De Candolle (1817) recognized two varieties within *A. biflora*, var. *bifoliata* DC. and var. *trifoliata* DC., which were not, however, used later. Most following authors considered only a single tuberous species outside of the Mediterranean in Central Asia. Thus, Boissier (1867) described *A. biflora s.l.* with an extensive distribution in South-West Asia. Later, increasing herbarium collections stimulated the recognition and description of several new taxa closely related to *A. biflora: A. gortschakowii, A. eranthioides, A. petiolulosa* Juz., *A. almaatensis* Juz., *A. oligotoma* Juz., etc. In his treatment for the *Flora SSSR*, Juzepchuk (1937) regarded *A. biflora* as an aggregate and recognized several 'micro-species' in Central Asia. Rechinger & Riedl (1992) classified *A. biflora* and *A. petiolulosa* as closely related and often sympatric species in the *Flora Iranica* area.

An examination of many herbarium specimens, including about 150 plants collected by Ziman in 1993–1995 from seven natural populations in Kazakhstan, Tajikistan and Uzbekistan, documented essential similarities in morphological key characters of *A. biflora s.l.*, but also a considerable variability in length of petiolules on primary segments of basal leaves, length of petioles of basal leaves, length of stems and the number of ultimate lobules of basal and involucral leaves. Among the floral characters, the most variable were tepal length and shape and abaxial tepal colour. In addition, changes in many characters during the growing season were observed. All this has stimulated previous descriptions of various narrowly circumscribed taxa within *A.biflora s.l.* We have discussed this situation in a previous paper (Ziman *et al.*, 1998) in which we treated *A. petiolulosa* and *A. eranthioides* as varieties under *A. biflora* and included *A. almaatensis* and *A. oligotoma* as synonyms of *A. gortschakowii*. In this paper, we wish to justify an even wider circumscription of *A. biflora*, treating both *A. gortschakowii* and *A. flexuosissima* Rech.f. as additional varieties of *A. biflora*. This results in the recognition of five ecogeographically differentiated varieties: var. *biflora*, var. *petiolulosa* (Juz.) Ziman, var. *eranthioides* (Regel) Ziman and the new taxa var. *gortschakowii* (Kar. & Kir.) Sinno and var. *flexuosissima* (Rech.f.) Ziman & Ehrendorfer. This corresponds quite well with the independent phenetic analysis by Sinno-Saoud *et al.* (2007), except that they do not consider *A. flexuosissima* and treat var. *eranthioides* as a species. In view of all the uncertainties about taxonomic separation lines within *A. biflora s.l.*and the whole subsection *Biflorae*, we still use the rank of variety for the infraspecific taxa. When more is known about the clade, the rank of subspecies may be more appropriate.

With respect to the distribution of *A. biflora s.l.* in Pakistan (Riedl & Nasir, 1990) and Northern India (Rau, 1993), uncertainties remain as to the correct determination of specimens called *A. tschernjaewii* and *A. biflora* (with its varieties, particularly var. *petiolulosa*), because we have not seen herbarium material from these countries (see further notes under these taxa).

*General distribution and habitat:* South-West and Central Asia, from Iran, Turkmenistan and Afghanistan in the west to Northern Pakistan and Northern India (Jammu and Kashmir) in the south and to Uzbekistan, Tajikistan, Kirgizistan, Kazakhstan and North-West China (West Xinjiang) in the east (Fig. 12). In semi-deserts, steppes, and open woodland, 700–3500 m.

5a. *A. biflora* DC. var. biflora
= *A. subvillosa* Pau, *Trab. Mus. Nac. Cienc. Nat. Madrid Bot.* **10:** 12. 1918.
= *A. biflora* var. *bifoliata* DC., l.c. 1817.
= *A. biflora* var. *trifoliata* DC., l.c. 1817.

*Note:* This variety has all the characters of *A. biflora* as given above. From the other varieties it differs by its short petiolules (1–3 mm) on the primary basal leaf segments, the 3–3.3 mm long achenes with 2–2.2 mm long hairs and the 2–2.2 mm long styles.

*Distribution and habitat:* Iran, Afghanistan, Pakistan and Northern India (Fig. 12). In open slopes, 1000–3300 m.

*Specimens examined:* IRAN: Khorasan: Imam-Guli, 24.v.1896, *Koroviakov* (LE); Azerbajan: Maragi, 13.v.1916, *Shelkovnikov* (LE); Kermanshah: Kazand, 16.iv.1951, *Sharif* (WU); Kazerum: Shiraz, Persepolis, 29.iii.1962, *Furse* (K); Shir Ku: Yezd, 5.iv.1962, *Furse* (K); S Arak: Azna, 14.iv.1962, *Furse* (K); Kurdistan: Bakhtiari, Ushtaran-Kuh, Thiun, 27.iv.1966, *Archibald* (K); Sanandaj, Marivan, 17.v.1966, *Archibald* (K); Ardekan: Shiraz, 7.iv.1969, *Hewer* (K); Kopetdag, 20.iv.1971, *Gibbons* (K); Fars: Firusabad, 5.3.1975, *Iranshar* (WU); Lagharak: Agjah, 1976, *Kukhzd-Narun* (WU); Semnan, 1976, *Riedl* (WU); Sagharak: Agjah, 1976, *Kukhazd-Narun* (WU); Teheran: Lagharak, 30.iv.1976, *Termen & Matin* (WU).
AFGHANISTAN: Herat, 1854, *Aitchinson* (LE); Kazrun, 7.v.1895, *Stapf* (K); Shindand, 1962, *Koie* (WU); Hanna Lake, 20.iii.1953, *Crookshank* (K); Baluchistan: Bandagan Nala, 13.iv.1954, *Crookshank*

KEY TO THE VARIETIES OF *A. BIFLORA*

1a. Tepals densely pubescent; scapes erect or slightly ascending………2
1b. Tepals glabrous or scarcely puberulent; scapes prostrate or ascending………5e. *A. biflora* var. *flexuosissima*
2a. Basal leaf segments mostly petiolulate (sometimes petiolules short, but distinct); tepals 10–25 mm long………3
2b. Basal leaf segments mostly sessile; tepals 5–10 mm long……… 5c. *A. biflora* var. *gortschakowii*
3a. Petiolules of primary basal leaf segments predominately 5–10 mm long; achenes 2.7–2.8 mm long, with hairs 2.5–3.5 mm long………5b. *A. biflora* var. *petiolulosa*
3b. Petiolules of primary basal leaf segments predominately 1–3 mm long; achenes 3–4 mm long, with hairs 2–5 mm long……… 4
4a. Achenes 3.0–3.3 mm long, with hairs 2.0–2.2 mm long and styles 2.0–2.2 mm long….. 5a. *A. biflora* var. *biflora*
4b. Achenes 3.0–4.0 mm long, with hairs 4.0–5.0 mm long and styles 2.5–3.0 mm long………5d. *A. biflora* var. *eranthioides*

*99* (K); 30 mi south of Herat, 22.iv.1964, *Furse 5454* (K); Henan, Baluchistan: Mashad to Faizabad, 19.v.1964, *Furse* (K); Bamian: Bard-i-Amir, 25.v.1969, *Hewer* 1178 (K); Salang Pass, 3.v.1970, *Calteu* (K); Prov. Farah: 11 mi north of Gulestan, 1 mi east of Asfang Valley, 5300 ft, 21.iv.1971, *Gray-Wilson & Gefer 582* (K).

5b. *Anemone biflora* DC. var. *petiolulosa* (Juz.) Ziman, *Thaiszia* **8:** 67. 1998.

*Type:* Western Tien-Shan. 'Ad declivia argillosa prope Ak-tash in montibus Karshan-tau. 12.iv.1922, *Korovin*' (lectotype: LE!).
≡ *A. petiolulosa* Juz., *Fl. Urss* **7:** 259. 1937.
= *A. coronaria* var. *pluriflora* Regel, *Acta Hort. Petropol.* **7:** 689. 1884.

*Notes:* This variety is distinguished by its long–petiolulate primary basal leaf segments, achenes 3–3.3 mm long, with hairs 2–2.2 mm long and styles 2–2.2 mm long. For Pakistan, the localities referred to this taxon and to *A. tschernjaewii* need verification.

*Distribution and habitat:* Uzbekistan, Kazakhstan, Turkmenistan, Iran, Afghanistan, Western Pakistan (Fig. 12). In semi-deserts, semi-savannas, shibliak and steppes, 700–2000 m.

*Specimens examined:* UZBEKISTAN: Pamir Alai: Seravshan Ridge, Amankutan, 20.iv.1913, mi*khelson* (TASH); Distr. Samarkand, Nuratinski Ridge, 5.iv.1954, *Zaprometova* (TASH); Nuratinski Ridge, Urta Sai, Zargar, 11.v.1957, *Momotov* (TASH); Fergana Distr. Arsif, 6.iii.1968, *Rakhimov* (TASH); Chatkalski Ridge: Khodzhikent, 4.iv.1993, *Ziman* (KW); 16.iv.1995, *Ziman* (KW); Majskoe, 15.iv.1995, *Ziman* (KW).
KAZAKHSTAN: Tien-Shan: Karabulak, 28.iv.1935, *Dmitrieva* (TASH); Karzhantau Ridge, Aktash, 3.vi.1940, *Goloskokov* (LE); Talass Alatau, Taldybulak, 15.iv.1947, *Borisenko* (AA); Karzhantau Ridge: Kaplanbek, 8.iv.1954, *Juzepchuk* (LE); Sary Agach, 22.iv.1960, *Pratov* (TASH); Karzhantau Ridge: Birisek, 8.v.1989, *Samoilova* (AA); Karzhantau Ridge: Kaplanbek, 5.iv.1993, *Ziman* (KW).
TURKMENISTAN: Kopetdagh: Nokhur, 17.v.1962, *Gubanov* (LE).
IRAN: Shiraz: Khorasan, Sarakhs, 22.iii.1965, *Martin* 17075 (WU); Sistan: Birjand, 4.iv.1971, *Gray-Wilson* 13490 (WU); Semnan: Shah Pass, Shahrud, 3.v.1974, *Wendelbo* (WU); Damghan-Semnan, 25.iv.1975, *Rechinger 5240* (WU); Khorasan: Rivash, 5.v.1975, *Rechinger 51246* (WU); Tehran: Sabzevar, 19.iv.1976, *Bazarg*an *17490* (WU).
AFGHANISTAN: Maimana, 24.iii.1949, *Koie* (WU).

5c. *Anemone biflora* DC. var. *gortschakowii* (Kar. & Kir.) Sinno, *Bot. J. Linn. Soc.* **153:** 434. 2007.

*Type:* Kazakhstan, 'humid shrubs of Singoriae Hills to River Ai' (lectotype: LE!, isotypes: BM, G, H, K and P).
≡ *A. gortschakowii* Kar. & Kir., *Bull. Soc. Nat. Mosc.* **15:** 131. 1842.
= *A. almaatensis* Juz., *Fl. Urss* **7:** 565. 1937. *Type:* Vicinity of Alma Ata. (holotype: LE!).
= *A. oligotoma* Juz., *l.c.*, 1937. *Type*: Tadjikistan. Pamir Alai: Alai Ridge, Isfairam Valley below the Tengiz-bai Pass (holotype: LE!).

*Notes:* This variety is close to var. *biflora*, but differs by its sessile primary basal leaf segments and smaller flowers (Fig. 5G). However, the shape of the basal leaves is variable and plants with shortly petiolulate (1–3, up to 5 mm long) basal leaf segments sometimes occur. Therefore, we classify *A. gortschakowii* as only a variety of *A. biflora s.l.*

*Distribution and habitat:* Kazakhstan, Tajikistan, Uzbekistan, Kirgizstan, North-West China: West Xinjiang (Fig. 12). In lowland and high-mountain steppes, 700–3500 m.

*Specimens examined:* KAZAKHSTAN: Tien Shan: Talass Alatau, Alma Ata, Kazenni Sad, 20.iv.1921, *Titov* (AA); Chu-Ili Ridge: Talgar, 25.iv.1930, *Granitova* (AA); Vernyi: Kaskelen, 30.iv.1934, Geld (AA); Krasnogorski, 31.v.1942, *Goloskokov* (AA); Dzhambul Distr. Chokpar, 9.v.1951, *Pavlova* (AA); Sjugaty Ravine, 10.iv.1955, *Goloskokov* (AA); Uzun Kargali, 13.v.1963, *Goloskokov* (AA); Myanyi: Betpakdala, 22.iv.1976, *Orazova* (AA); Karaganda Highway, 19.v.1980, *Nelina* (AA); Talgar: Kurganka Mt., 10.iv.1993, *Ziman* (KW).
TAJIKISTAN: Pamir Alai: Petr I Ridge, Ljangarisho, 1952, *Strizhova* (TAD).
UZBEKISTAN: Samarkand Distr. Urgut, 19.iv.1940, *Popov* (Ash); AlaiRidge, Kichik Kuvur-Bulak, 27.vi.1949, *Sakhobiddinov* (TASH); Bukhara Distr. Irmir, Bukan-Tau, 29.iii.1952, *Novikova* (TASH); Padshaat, 21.v.1957, *Galkina* (TASH).
KIRGIZSTAN: Karavan Distr. Dzhida-Sai, 4.v.1952, *Nabiev* (TASH).

5d. *Anemone biflora* DC. var. *eranthioides* (Regel) Ziman, *Thaiszia* **8:** 68. 1998.

*Type:* Tajikistan. 'Darwas: supra castellum Wandsch, 6000 ft, in valle Wandsch, *Mussa*' (lectotype: LE!).
≡ *A. eranthioides* Regel, *Acta Hort. Petropol.* **8:** 691. 1884.

*Notes:* Plants of var. *eranthioides* are characterized by the short petiolules of the primary basal leaf segments, nearly sessile involucral leaves, achenes 3–3.3 mm long with hairs 4–5 mm long, and styles 2–2.2 mm long. Sinno-Saoud *et al.* (2007) regarded *A. eranthioides* as a separate species because the leaves are less dissected than in *A. biflora* var. *biflora*. Nevertheless, the few individuals they analysed phenetically were to *A. biflora* var. *biflora*, var. *gortschakowii* and *A. tschernjaewii* in their scatter diagrams (Figs 1, 2). The matter evidently needs further study.

*Distribution and habitat:* Tajikistan (Fig. 12) and Turkmenistan (Sinno-Saoud *et al.*, 2007). On open slopes, 2000–3000 m.

*Specimens examined:* TAJIKISTAN: Pamir Alai: Hissar Ridge, iii.1884, *Regel* (LE); Hissar Ridge, Anzob Pass, 26.vi.1979, *Ziman* (KW); Maikhura, 21.vi.1991, *Fedoronchuk* (KW); Siakhub, 22.vi.1991, *Fedoronchuk* (KW).
5e. *Anemone biflora* var. *flexuosissima* (Rech.f.) Ziman & Ehrendorfer, stat. et comb. nova
≡ *A. flexuosissima* Rech.f., *Fl. Iran* **169:** 288. 1992.

*Types:* 'Afghanistan. Kabul, base of Khurd Kabul Mt, crevices of rocks, 2.v.1969, *Hedge & Wendelbo & Ekberg* 7539' (holotype: E!). Afghanistan. Parvan: Tob Darrah, Charicar, crevices of rocks, 28.iv.1969, *Hedge & Wendelbo & Ekberg 7370* (isotype: E!).

*Notes:* Based on Rechinger's brief description of *A. flexuosissima* and the type specimen, this taxon is close to *A. biflora* var. *biflora*. It deviates mainly by the glabrous perianth and small tepal size. Essential characters of the type material in E are tuberous rhizomes of irregular shape; basal leaves several, trifoliolate, glabrous with blades 1.5–1.7 × 2–2.5 cm, short–petiolulate segments and obtuse ultimate lobules; involucral leaves 3, sessile, glabrous and similar to the basal leaves; scapes 6–8 cm long, 1–3-flowered; tepals 5, yellow, persistent, glabrous or scarcely puberulent, 6–7 × 3–5 mm with 3–5 basal veins and 1–3 anastomoses; achenes ovoid, *c.* 4 × 2 mm, with hairs 1.5–2 mm long, styles glabrous, 1.3–1.6 mm long, and marginal ribs narrow.

*Distribution and habitat:* Afghanistan (Fig. 12). In rock crevices, 2400 m.

*Specimens examined:* AFGHANISTAN: Kabul, base of Khurd Kabul Mt, crevices of rocks, 2.v.1969, *Hedge & Wendelbo & Ekberg* 7539 (E – holotype); Parvan: Tob Darrah, Charicar, crevices of rocks, 28.iv.1969, *Hedge & Wendelbo & Ekberg* 7370 (E – isotype).

### 6. *Anemone bucharica* (Regel) Finet & Gagnep., *Bull. Soc. Bot. Fr.* **51:** 75. 1906

*Type:* Tajikistan. 'Buchara orientalis. Duwulai supra Kulab. 3–4000 ft, 26.3.1883' (holotype: LE!).
≡ *Anemone coronaria* L. var. *bucharica* Regel, Acta Hort. Petropol. **8:** 689, 1884.

*Description:* Rhizomes irregularly tuberous, rarely branching, 7–12 × 8–15 mm, with thin roots predominating. Basal leaves 2–4(–6), glabrous; petioles 5–8 cm long; blades 2-ternate, 1.5–4.0 × 1.5–4.5 cm, with 30–80 ultimate lobules; primary segments distinctly petiolulate (middle one frequently longer than lateral ones). Scapes 5–15 cm long, glabrous, 1–2-flowered. Involucral leaves 3, with short petiole-like narrow bases; blades 2–5 × 2–3 cm, with 15–35 ultimate lobules, scarcely pubescent. Pedicels 5–10 cm long, densely pubescent. Tepals 5–6, persistent, obovate, with wide bases, purple or red inside and outside, 15–30 × 15–18 mm, with 5–13 basal veins and 7–30 anastomoses (Fig. 5H). Stamens 4–5 mm long, with slightly dilated filaments, wide connectives and elipsoid anthers. Pollen pantoporate. Carpels ovoid, slightly compressed, 1.5–2 mm long, densely covered with hairs 2–3 mm long, styles straight, 1.5–2 mm long, basally densely pubescent, stigmas linear (Fig. 5H). Fruiting heads hemispherical, 1.5–2.5 cm in diameter. Achenes ovoid, 2.5–3 × 1.4–1.8 mm; villous, hairs 2–3.5 mm long; styles 1.7–2.5 mm long, basally densely pubescent; marginal ribs 0.2 mm wide. Chromosome number: $2n = 16$ (Madahar, 1967 as '*A. bucharica*').

*Notes:* According to Rechinger & Riedl (1992), *A. bucharica* differs from *A. coronaria* by the sessile lateral basal leaf segments and from *A. biflora* by its purple anthers. An examination of the herbarium material in W has shown that the length of lateral leaf petiolules varies considerably and is thus not a reliable character. Nevertheless, plants of *A. bucharica* differ throughout their range from those of *A. coronaria* by having no stipule-like appendages at the petiole base and from those of *A. biflora* by their red or purple perianth, much larger tepals with more basal veins and anastomoses and achenes with shorter hairs and styles. The phenetic analyses by Sinno-Saoud *et al.* (2007: Figs 1, 2) demonstrated that *A. bucharica* is relatively distinct within the *A. biflora* complex, but still closer to the other taxa of subsection *Biflorae* than to *A. coronaria* in subsection *Anemone*.

*Distribution and habitat:* Central and South-West Tajikistan (Hissar, Darwaz, Aruktau, Rangontau, Khozretisho, Surkho Ridge), Northern Afghanistan, Northern Iran (Fig. 12). In semi-savanna and shibljak, 700–2000 m.

*Specimens examined:* TAJIKISTAN: Pamir Alai. Rangontau, Baglysai, 30.iv.1806, *Rozhevit*s (AA); Kurgan Tyube, 13.v.1937, *Gomolitski* (AA); Surkho Ridge, Babatag, 19.iv.1928, *Vvedenski* (TASH); 27.iii.1967, *Chukavina* (TAD); Chaltau: Sangtudy, 4.iv.1955, mi*tiakina* (LE); Aruktau: Gandzhino, 5.iii.1958, *Alekseenko* (TAD); Rangontau: Rangontau, 20.vi.1991, *Fedoronchuk* (KW); Tashmechetj,3.iv.1959, *Batritdinova* (TAD); Vakhsh: Dagana, 6.iv.1970, *Sharipov*a (TAD); Sultanabad: Chormazak Pass (18.iv.1970, *Sharipova* (TAD); Khozretisho: Chargy, 15.iv.1971, *Karimo*v (TAD); Fakhrabad Pass, 13.iv.1992, *Ziman* (KW).
IRAN: Kermanshah: Kazand, 1951, *Riedl* (WU); Mazanderan, 12.iv.1960, *Gadd* (LE); Kazerum–Shiraz–Persepolis, 29.iii.1962, *Furse* (K); Azra, 21.iv.1962, *Furse* (K).
AFGHANISTAN: Faisabad, 22.v.1964, *Furse* (K); Masar-Sharif, 6.v.1967, *Riedl* (W); Baghlan: 2 mi east of Banu, 3 mi west of Deh Salah, 7.v.1969, *Hewer* (K).

### 7. *Anemone baissunensis* Juz. ex Sharip., *Fl. URSS* 7: 259. 1937, descr. Ross. in adnot. Latin descr.ex M.M. Sharipova, *Izv. Acad. Sci. Taj. SSR, Otd. Biol. Sci.* 4: 29 (1967) et in *Fl. Tajikistan* 4: 532 (1975)

*Type:* 'Regulum Bucharicum, bejetum Baissunense, Baissun-Tau', 3.iv.1913, mi*chelson* (holotype: LE!).
= *A. verae* Ovcz. & Sharip., *Fl. Tajikistan* **4:** 532. 1975.
= *A. coronaria* var. *intermedia* Regel, *Acta Hort. Petropol.* **8:** 689. 1884.

*Description:* Rhizomes irregularly tuberous, branched, 1.0–2.5 × 1.5–4.5 cm. Basal leaves 2–6; petioles 3–8 cm long, without stipule-like 'ears' (Fig. 4D); blades twice-ternate, 1.5–4 × 1.5–3.5 cm, with 30–80 ultimate lobules; primary segments distinctly petiolulate (petiolules almost always unequal). Scapes 1–3, 5–15 cm long, glabrous, 1–2-flowered. Involucral leaves 3, with petiole-like narrow bases;

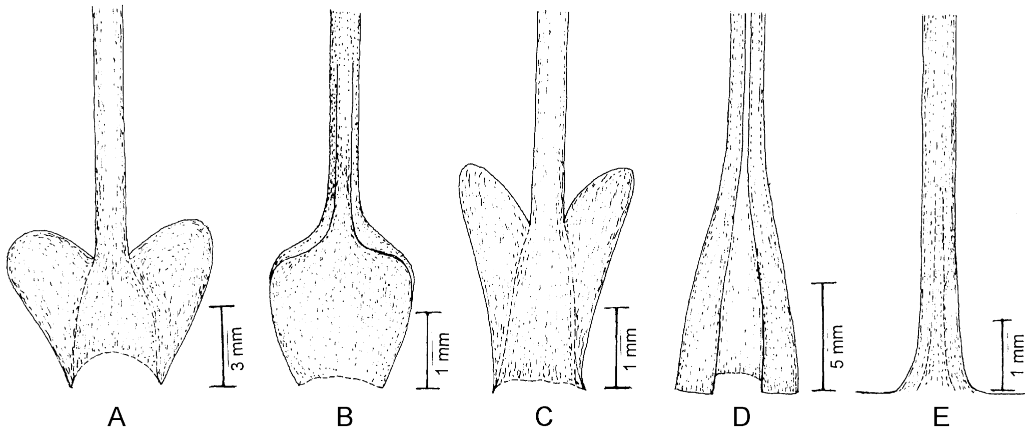


**Figure 4.** Stipule-like bases of basal leaf petioles from species of *Anemone* section *Anemone*: A, *A. coronaria*. B, *A. hortensis*. C, *A. palmata*. D, *A. baissunensis*. E, *A. tscherjaewii*.

blades 3-parted, ultimate lobules 15–35, sparsely puberulent along margins. Pedicels 3–10 cm long, sparsely puberulent. Tepals 5–6, persistent, obovate, basally narrowed, yellow inside and reddish–yellow outside, 15–30 × 8–20 mm, with 5–11 basal veins and 7–15 vein anastomoses, densely pubescent (Fig. 5I). Stamens 5–8 mm long, with distinctly dilated filaments, distinctly wide connectives and ellipsoid anthers. Pollen pantoporate. Carpels ovoid, slightly compressed, 0.5–1.5 mm long, densely covered with hairs 0.5–0.7 1 mm long, styles conic straight, 1–2 mm long, stigmas linear (Fig. 5I). Fruiting heads spherical, 2–2.5 cm in diameter. Achenes ovoid, 3.5–5 × 1.2–1.5 mm; hairs 4–5.5 mm long; styles 2–3 mm long, glabrous; marginal ribs 0.2 mm wide (Ziman *et al.*, 1998). Chromosome number unknown (references in *Index of Plant Chromosome Numbers* are erroneous).

*Notes:* This species is close to *A. bucharica* and sometimes the two species occur sympatrically. They differ mainly by perianth colour, but also by the shape of their tepals, stamens and carpels. For additional comments, see Sharipova (1971). Sinno-Saoud *et al.* (2007) did not study this taxon.

*Distribution and habitat:* Tajikistan (Hissar, Darwaz, Aruktau, Rangontau, Baldzhuan Ridges, Surkho Ridge, etc.), Uzbekistan (Baissun) (Fig. 12). In semi-savanna and shibliak, 600–2000 m.

*Specimens examined:* TAJIKISTAN: Pamir Alai: Surkho Ridge, Chenturi, 20.iv.1928, *Vvedenski* (TASH); Hissar Ridge, Ljuchob, 12.iv.1956, *Grigorjev* (TAD); Aruktau: Burma, 27.iv.1959, *Chukavina* (TAD); Rangontau: Tashmechetj, 30.iii.1971, *Batritdinova* (TAD); Khodzha–Kozjan, 24.iii.1978, *Sharipova* (TAD); Hissar Ridge: Kondara Ravine, 23.vi.1991, *Fedoronchuk* (KW); 10.iv.1992, *Ziman* (KW); 20.iv.1995, *Ziman* (KW); Fakhrabad Pass, 13.iv.1992, *Ziman* (KW).
UZBEKISTAN: Baissun, 10.5.1936, *Lepeshkin* (KW).

### 8. *ANEMONE TSCHERNJAEWII* REGEL, *ACTA HORT. PETROPOL.* **8:** 690. 1884

*Type:* Tajikistan. Ura-Tjube (lectotype: LE!).

*Description:* Rhizomes tuberous, nearly globose, 0.5 × 1.0 cm. Basal leaves solitary; petioles 4–12 cm long, without stipule-like appendages (Fig. 4E); blades 3-parted, 1.5–2.5 × 2–4.5 cm, basally rounded, segments ± sessile and with 8–15 ultimate lobules. Scapes 5–15 (25) cm long, glabrous, 1–2-flowered. Involucral leaves 3, sessile; blades basally connate, with 5–15 ultimate lobules. Pedicels 3–10 (15) cm long, sparsely puberulent. Tepals 5, persistent, elongate–ovoid to lanceolate, with wide bases and apically acuminate, white to pink, purplish or violet, 17–22 × 8–12 mm, with 5–11 basal veins and 5–15 anastomoses, densely pubescent (Fig. 5J). Stamens 5–10 mm long, with slightly dilated filaments apically narrowed connectives longer than and ellipsoid anthers. Pollen pantoporate. Carpels ovoid, not compressed, 0.5–1 mm long, densely covered with hairs 0.5–1 mm long, straight styles, 1.5–2.5 mm long, stigmas linear (Fig. 5J). Fruiting heads spherical, *c.* 2 cm in diameter. Achenes ovoid, 3–3.5 × 1.2–1.4 mm; hairs 5–6 mm long; styles 1.7–2.5 mm long, basally pubescent; marginal ribs 0.1 mm wide (Ziman *et al.*, 1998). Chromosome number unknown (reference in Starodubtsev, 1991 problematical).

*Notes:* The original spelling of the species name by Regel, 1884, was '*A. tschernaewi*'. Here, we follow the more appropriate version '*A. tschernjaewii*' used by Juzepchuk *et al.* (1937) in Flora SSSR. In the new floras for Pakistan (Riedl & Nasir, 1990) and India (Rau *et al.*, 1993), members of section *Biflorae* are listed. For Pakistan, *A. tschernjaewii* is indicated in Baluchistan and Chitral, for Northern India we find *A. biflora* localities in Kashmir and Jammu. The specimens from Baluchistan may be *A. biflora* var. *petiolulosa*, those from Chitral, Kashmir and Jammu *A. tschernjaewii.* On the map, Figure 12, these localities are shown as uncertain and relevant determinations should be verified in the future. The phenetic position of *A. tschernjaewii* (Sinno-Saoud *et al.*, 2007) is relatively distinct but clearly falls within subsection *Biflorae.*

*Distribution and habitat:* Tajikistan, Uzbekistan, Turkmenistan, Afghanistan, Pakistan and Northern India (Fig. 12). In grassland and shibliak, 700–2200 m.

*Specimens examined:* TAJIKISTAN: Baldzhuan, 23.iii.1913, *Michelson* (TAD); Ramit, 12.iv.1956, *Vasak* (TAD); Rangontau: Tashmechetj, 4.iv.1970, *Batritdinova* (TAD); Pamir Alai: Hissar Ridge, Kondara Ravine, 4.iv.1992, *Ziman* (KW); 20. iv.1995, *Ziman* (KW); Fakhrabad Pass, 13.iv.1992, *Ziman* (KW).
UZBEKISTAN: Distr. Fergana: Ankhor, Arpa, 13.iv.1916, *Babenko* (TASH); Tien Shan: Angren, 28.v.1954, *Butkov* (TASH); Distr. Denau: Chobair, 25.iv.1957, *Vvedenski* (TASH); Samarkand Distr. Aman Kutan, 27.iv.1957, *Vvedenski* (TASH); Allajaran: Urgut, 13.v.1979, *Zukervanik* (AA).
AFGHANISTAN: Kurrum: Alikher, 17.iv.1879, *Aitchinson* (K); Upper Zebak Valley, 27.v.1964, *Furse* (LE); Prov. Kabul: Pagham, 23.iv.1965, *Podlech* (LE);

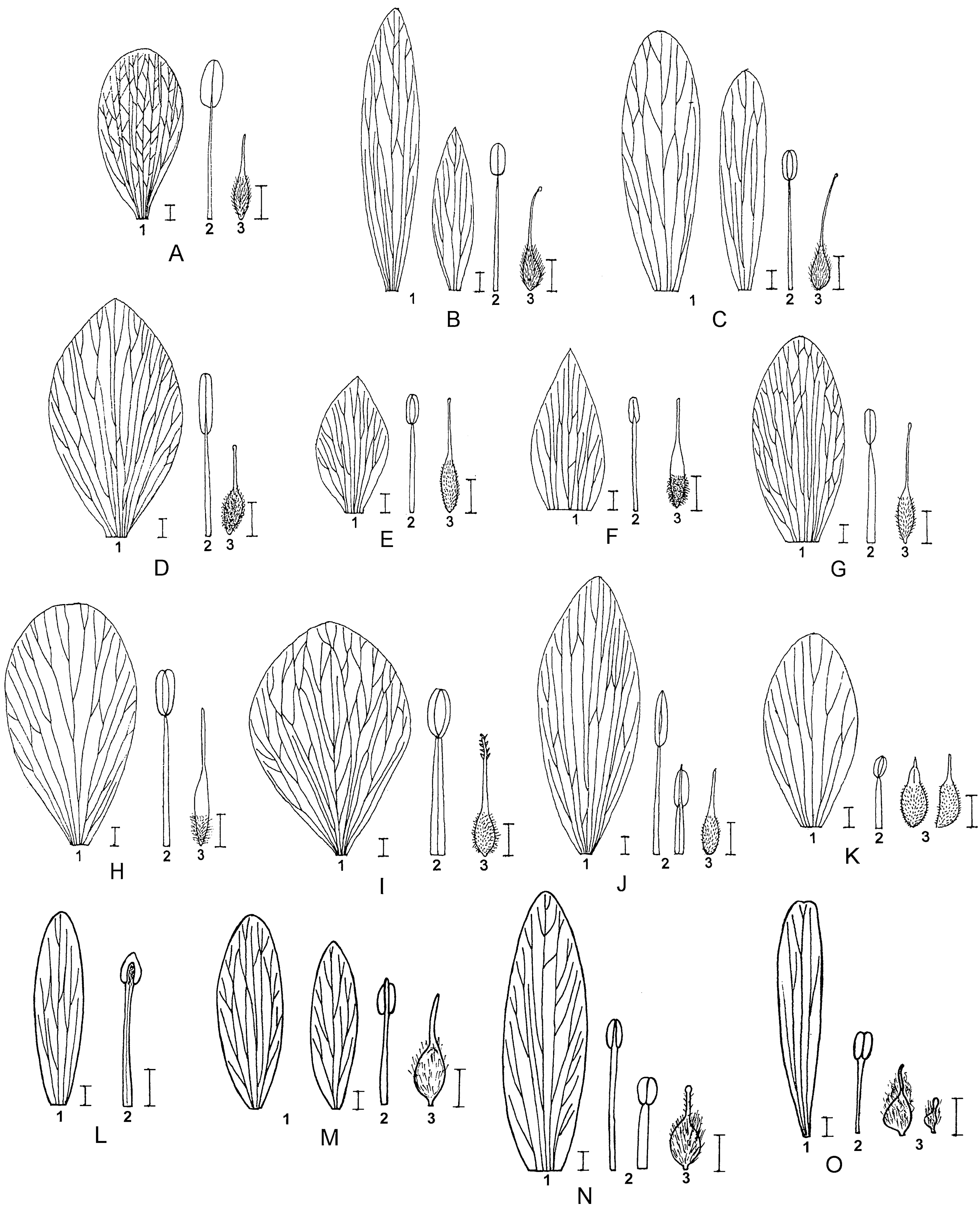


**Figure 5.** Floral parts (1, sepals; 2, anthers; 3, carpels) from taxa of *Anemone* section *Anemone*: A, *A. coronaria*. B, *A. hortensis*. C, *A. palmata*. D, *A. biflora* var. *biflora*. E, *A. biflora* var. *petiolulosa*. F, *A. biflora* var. *eranthioides*. G, *A. biflora* var. *gortschakowii*. H, *A. bucharica*. I, *A. baissunensis*. J, *A. tschernjaewii*. K, *A. serawschanica*. L, *A. caroliniana*. M, *A. tuberosa*. N, *A. decapetala*. O, *A. triternata*. Scale bars, 1 mm.

Kabul, Kargha See, 10.iv.1971, *Anders* (WU); Herat: Kushk, 16.iv.1971, *Gray-Wilson* (K); Ghazni: Dasht-i-Nawar, 30.iv.1971, *Gray-Wilson* (K); Parvan: Kabul, Salang Pass, 3.v.1971, *Gray-Wilson* (K).
PAKISTAN: Baluchistan: Quetta, Khojak Pass, above Shelabad, 8.v.1965, *Lammond 1060* (E).

### 9. *ANEMONE SERAWSCHANICA* KOM., *ACTA PETERSB. SOC. NAT. BOT.* **26:** 49. 1896

*Type:* Tajikistan: Zeravschan Valley, Artuch (holotype: LE!).

*Description:* Rhizomes tuberous, spherical, unbranched, *c.* 0.5 × 0.8 cm, with thin adventitious roots. Basal leaves solitary; petioles 2.5–4.5 cm long; blades 3-sected, segments sessile, with 8–15 ultimate lobules. Scapes 3–8 (10) cm long, glabrous, 1-flowered. Involucral leaves 3, sessile, blades with 12–25 lobes or lobules, puberulent adaxially only. Pedicels 1–3 cm long, sparsely puberulent. Tepals 5, persistent, elongate–elliptic, green or yellowish, 7–8(–10) × 3–5 mm, with 5–7 basal veins and without (or sometimes solitary) anastomoses, glabrous (Fig. 5K). Stamens 3–4 mm long, with linear filaments, wide connectives and rounded anthers. Pollen pantoporate. Carpels ovoid, not compressed, 1–1.5 mm long, scarcely covered with hairs *c.* 1 mm long, styles straight, 0.5–0.7 mm long, stigmas linear (Fig. 5K). Fruiting heads subspherical, *c.* 2 cm in diameter. Achenes ovoid, 2–2.2 × 1 mm, with 1.7–2.3 mm long hairs and *c.* 1.5 mm long glabrous styles; marginal ribs *c.* 0.1 mm wide (Ziman *et al.*, 1998). Chromosome number unknown.

*Note:* This is a distinct local endemic of subsection *Biflorae*. It was not considered in the phenetic study of Sinno-Saoud *et al.* (2007).

*Distribution and habitat:* Tajikistan: Serawschan Ridge (Fig. 12). Between rocks in the shibljak belt, 2000 m.

*Specimens examined:* TAJIKISTAN: Pamir Alai: Hissar Ridge, Sangardarak, 5.vi.1948, *Pjataeva* (TASH); Seravshan Ridge: Osman Tala, 14.vi.1972, *Kochkareva* (TAD).

## IV. *ANEMONE* SUBSECTION *CAROLINIANAE* STAROD

### 10. *ANEMONE CAROLINIANA* WALTER, FL.CAROL. 157. 1788

*Type:* Described from 'Carolina ad ripas missouri', USA, but no type specimen has been located (see below). Neotype: Pyron 2109; 19 March 1938; USA: Georgia: Irwin County: 3 mi south-west of Irwinville (Duke) [designated by Ward, J. Bot. Res. Institute. Texas 2(3): 1280. 2008].
= *A. tenella* Pursh, *Fl. Am. Bor.* **2:** 386. 1814.
= *A. hartiana* Rafin., *Neogen.* 2. 1825.

*Description:* Rhizomes tuberous, small (0.5–10 × 0.5 cm), subglobose, but in early spring stolon-like rhizomes develop, horizontal or ascending, 10–15 × 0.2 cm, bearing 1–2 scales, 2–4 mm long. Basal leaves 1–3 (5), glabrous, their petioles 3–10 cm long and gradually widened towards the basis, but without stipule-like appendages, seasonally dimorphic; outer leaves (which develop in early spring) trilobed to trisected, with wide, slightly lobed or toothed, nearly sessile segments and obtuse ultimate lobules; inner leaves (which develop later) with 1- to 2-ternate blades to 3.5 cm wide; primary segments on petiolules 5–15 mm long with ultimate lobules linear–acute. Scapes 10–30(–60) cm long, scarcely puberulent, 1-flowered. Involucral leaves three, similar to inner basal leaves, sessile, basally connate; blades once-tripartite, with narrow, more or less linear–acute ultimate lobules, scarcely puberulent. Pedicels 10–30 cm long, densely pubscent. Tepals 12–20, deciduous, linear–oblong, white–bluish, 10–20 × 2–5 mm, with five basal veins and without anastomoses, abaxially densely pubescent (Fig. 5L). Stamens 5–7 mm long, with linear filaments, wide connectives and globose anthers. Pollen 3-colpate (Fig. 7E); Huyn (1970). Carpels subspherical, compressed *c.* 1 mm long, densely covered with hairs 1–2 mm long, styles straight, *c.* 1 mm long, stigmas linear (Fig. 5L). Fruiting heads ellipsoid, *c.* 2 × 1 cm. Achenes ovoid, 2.2–2.6 × 0.5–1.1 mm, villous, hairs 3.2–4.7 mm long; styles straight, 1.1–1.7 mm long, basally pubescent; marginal ribs 0.2 mm wide (Fig. 6E). Chromosome number: $2n = 16$ (Joseph & Heimburger, 1966).

*Notes: Anemone caroliniana* was the first tuberous species to be described in detail from North America, but its typification is problematic. As Ward (2007) has shown, the so-called 'Walter herbarium' at the Natural History Museum in London, was brought together by J. Fraser and is of limited value for the typification of the new species described by Walter in his *Flora Caroliniana* (1788). Neither Britton (1891: 220) nor we have found specimens relevant to *A. caroliniana* in this herbarium at BM. The selection of a neotype by Ward was therefore necessary.

*Anemone caroliniana* was first classified by De Candolle (1817) under section *Anemonanthea*, whereas its present placement in section *Anemone*, subsection *Carolinianae*, follows Starodubtsev (1991). Previous descriptions by Pritzel (1841), Britton (1891), Keener (1975), Keener & Dutton (1994) and Dutton, Keener

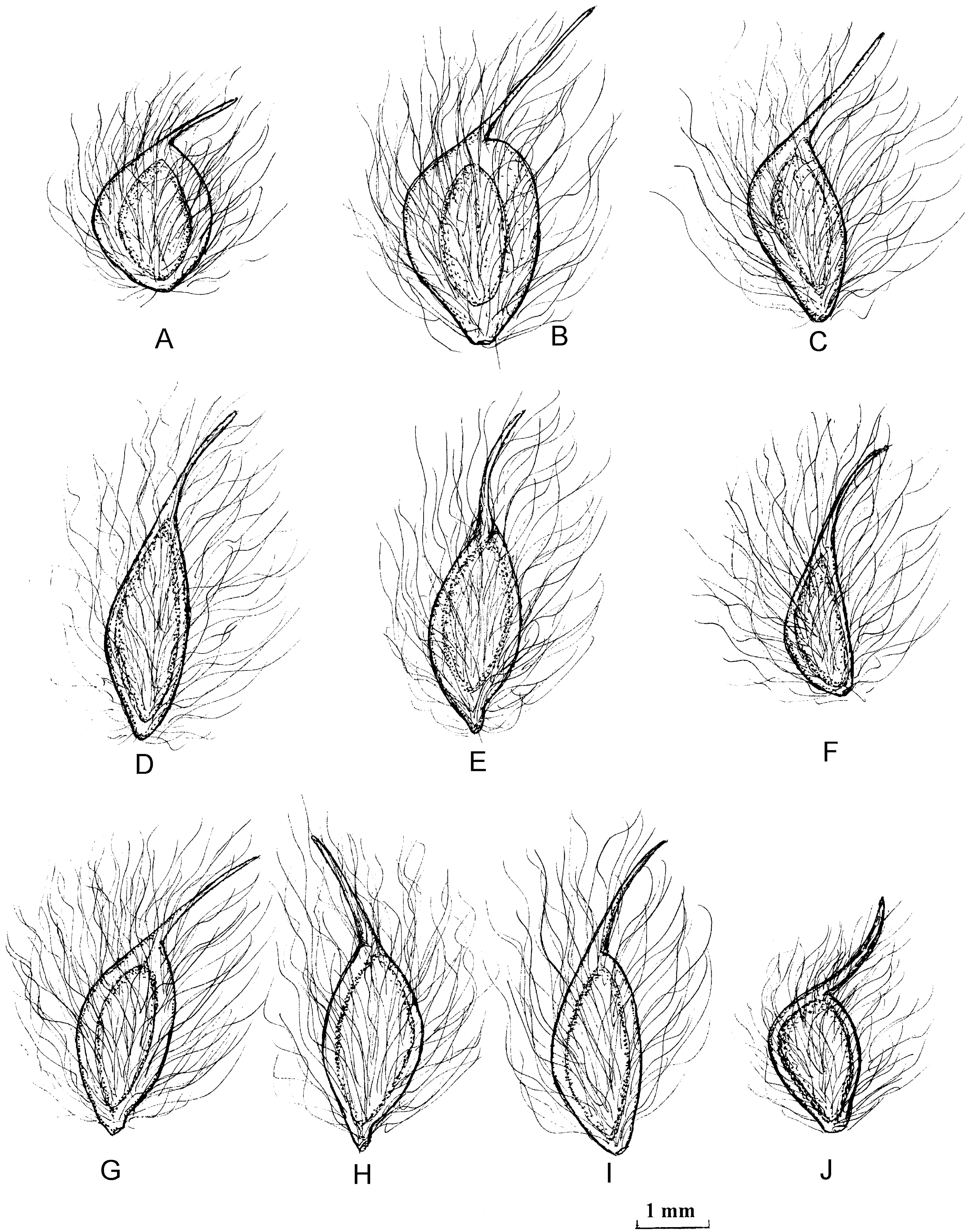


**Figure 6.** Achenes from species of Anemone section Anemone: A, *A. coronaria*. B, *A. hortensis*. C, *A. palmata*. D, *A. somaliensis*. E, *A. caroliniana*. F, *A. berlandieri*. G, *A. edwardsiana*. H, *A. tuberosa*. I, *A. decapetala*. J, *A. triternata*.

& Ford (1997) characterized *A. caroliniana* by its 1- to 2-ternate basal leaves with petiolulate or subsessile primary segments and by the involucral leaves similar to at least some basal leaves. Our data show that the tepals appear occasionally in two whorls and are dimorphic: the outer ones 1.5–2.0 × 5–6 mm, densely pubescent, with five basal veins, the inner 13–15 × 3–4 mm, glabrous, with three basal veins (e.g. *A. caroliniana* f. *violacea* Clute; specimens from South Journey, Oklahoma, 6.04.1908, Brainerd: GH!). Germination corresponds to the normal epigeal type, the seedlings have two cotyledons (Förster, 1999).

*Distribution and habitat:* Mainly in the central and southern parts of the USA (Kansas, Arkansas, Oklahoma, Alabama, Louisiana, Texas, etc.; Fig. 13). In prairies or pastures on stony, sandy or clay soils with *Croton*, *Coreopsis*, *Verbascum*, *Heterotheca* and other herbs, occasionally also in oak-pine woods, 60–700 m.

*Specimens examined:* USA: Alabama: Sumter Co., cd. 2 mi east of Emelle, 10.iv.1966, *Iltis 25107* (LE).
Arkansas: Prescott, 9.iv.1900, *Bush* (GH); Sebastian Co., Little White Oak Ridge, 6.iv.1989, *Thompson et al.* 10274 (GH).
Georgia: Jusper Co., Piedmont Province, 3.5 mi south of Monticello, 25.iv.1952, *Duncan 13445* (LE).
Indiana: Newton Co., Road 14, 1.2 mi west of junction of Road 41, Enos, 9.iv.1938, *Friesner 13025* (LE).
Louisiana: Caddo Parish, Shreveport, 25.iii.1915, *Palmer* (K); 5 mi north of Bastrop, 6.iii.1959, *Kral 8244* (GH).
Minnesota: Washington Co., 5 mi south of Royport, 22.v.1944, *Moore & Bornum* (GH).
Okhlahoma: Lincoln Co., 20.iv.1896, *Maves* (GH); South Journey, 6.iv.1908, *Brainerd* (GH); LE Flore Co., 5 mi south-west of Peteau, 16.iv.1923, Harper (GH); Panhandle Plains, 22.4.1929, *Benke* (BM) Murray Co., near Crusher Spur, 12.iv.1931, *Stevens* (BM); Payne Co., south of Boomer, Stillwate, 12.iii.1938, *Badock* (LE); Osage Co., 6 mi west of Hominy, 15.iv.1969, *Stephens 2955* (GH; Murray Co., Arbuckle Mts, Turner Falls, 15.iv.1989, *Ferguson* (K).
Tennessee: iv.1906, *Gattinger* (GH).
S Dakota: Spink Co. 17.v.1947, *Northwille 47501* (GH).
Texas: Haudlay, 18.iv.1913, *Ruth* (GH); San Augustine, 29.iii.1915, *Palmer* (K); Smith Co., 8 mi northeast of Tyler, 11.ii.1944, *Moore* (GH); Wichita Co., Wichita Falls, 6.iii.1944, *Warnock* (K); Kauffman Co., Elmo, 18.iii.1945, *Moor*e (GH); 4 mi south-southeast of Kauffman, 22.iii.1947, *Vaugh 7621* (GH); Henderson Co., 3 mi north-west of Eustace, 25.iii.1963, Correl (GH); Blanco Co., 16 km north of Johnson City on Federal HW, 19.iii.1986, *Reuter 320* (MHA); Wichita Co., Electra, 30.iii.1995, *Whitenhouse* (NY).
Wisconsin: Pierce Co., Hager City, 2.vi.1935, *Fassett* (NY).

## 11. *Anemone tuberosa* Rydb., Bull. *Torr. Bot. Club* **29:** 151. 1902

*Type:* USA. Arizona, Sierra Tuscon, 1884, *Pringle* (holotype: NY!, isotype: K!).

*Description:* Rhizomes tuberous, vertical, cylindric–oblong, 2.0–4.0 × 1.0–1.5 cm, branching, without stolons but with partly thickened roots. Basal leaves 1–3(–5), monomorphic, glabrous, with gradually widened, but not stipule-like bases; fruiting plants generally lacking basal leaves. Petioles 5–10 cm long; blades 1- or 2-ternate; primary and secondary leaf segments on petiolules (primary chiefly 10–30 mm long, secondary 5–10 mm long) with 50–70 ultimate, acute lobules. Scapes frequently not solitary, 15–30 cm long, glabrous, 1–2 (3)-flowered. Involucral leaves three, similar to the basal leaves, with petiole-like wide (2–5 mm) and flat bases; blades pinnatifid, 2–5 cm long; primary segments petiolulate, with 5–7 long-acute ultimate lobules. Lateral flowers with two small bracts. Pedicels scarcely puberulent or glabrescent, 15–30 cm long. Tepals 6–13, deciduous, linear–oblong, monomorphic, white to pink, 10–20 × 3–5 mm, with 5 basal veins and without anastomoses, more or less densely pubescent (Fig. 5M). Stamens 4–5 mm long, with filiform filaments, narrow connectives and ellipsoid anthers. Pollen grains tricolpate (Huyn, 1970). Carpels subglobose, compressed (ribs *c.* 0.3 mm wide), *c.* 1 mm long, covered with 1–2 mm long hairs, styles staight, *c.* 1 mm long with linear stigmas (Fig. 5M). Fruiting heads cylindrical to ellipsoidal, 1.5–3.0 × 1.0–2.0 cm. Achenes subglobose, compressed, 2.3–2.5 × 2.0–2.5 mm, villous, hairs 2.2–3.5 mm long; styles straight, 0.8–1.5 mm long; marginal ribs *c.* 0.5 mm wide (Fig. 6H). Chromosome number: $2n = 16$ (Joseph & Heimburger, 1966).

*Notes:* This species was described by Rydberg (1902) from Arizona and later treated in his studies of the flora of several other States of the USA. (Rydberg, 1917, etc.). He noted its tuberous roots, 2-ternate basal leaves with oblong–ovate ultimate lobules, involucral leaves similar to basal ones, but with shorter petiolules and with longer ultimate lobules and teeth, 1–2-flowered stems, 8–10 tepals, linear–oblong, white to purplish, ellipsoid fruiting heads and densely woolly achenes having filiform styles about 1.5 mm long. Keener & Dutton (1994), who enlarged and revised the morphological description of *A. tuberosa*, noted the oblong–obovate caudex-like tubers (not roots), the robust habit of the plants, 1–3 (5) basal 1–2-ternate leaves with petioles 5–7 cm long, the blades of primary segments 2–3 × 1–2 cm, predominately sessile leaf segments with broadly acute ultimate lobules, relatively small sepals and densely villous orbiculate flat achenes lacking wings, but with straight styles. We can add that the outer larger tepals are wider and have five basal veins whereas the inner tepals are smaller and narrower with three basal veins.

*Distribution and habitat:* South-West USA (Arizona, California, Nevada, New Mexico, Utah, Texas; Fig. 13) and Northern Mexico (according to TROPICOS. MO). In open limestone, dry rocky ledges and semi-desert grasslands, 800–2500 m.

*Specimens examined:* USA: Arizona: Sierra Tuscon, 8.iii.1884, Pringle (isotype: K); Santa Catalina Mts, 5.iv.1908, *Rose 11797* (K); near Superior, 22.ii.1926, Kearney (K); Mts close to Tuscon, 6.iv.1935, *Nelson* (K); Rocky Mts, Massacre Camp, 12.iv.1935, *Nelson* (GH); Maricopa Co., Adobe, Black Canyon, 28.ii.1960, *Crosswhite* (K); Pima Co., Santa Catalina Estates, Tuscon, 2700 ft, 22.iii.1963, *Beever* (Mha); Vavapai Co., 1.iv.1985, *Ricketson* (NY).
California: Death Valley, Panamint Mt, 30.iii.1891, *Coville 500* (K); San Bernardino, Holy Canyon, 7.v.1940, *Alexander* (GH).
Nevada: Clarc Co., Cedar Basin, 16.iv.1986, *Pinzl* (US).

### 12. *ANEMONE OKENNONII* KEENER & DUTTON, *SIDA* **16:** 198. 1994

*Type:* USA. Texas, Gillespie Co., 2 miles south of Doss, 22.4.1933, *O'Kennon 11390* (holotype: Brit!, isotypes: PAC, Tex).
= *A. tuberosa* Rydb. var. *texana* Enquist & Crozier, *Phytologia* **78:** 428. 1995. Type: USA, Texas, Val Verde Co., on highway 277 north of Del Rio, 25.3.1995, *Enquist & Crozier & Turner 2757* (holotype: Tex-Ll!, isotypes: Taes, Brit).

*Description:* Rhizomes tuberous, vertical or ascending, oblong–obovate, 1–3 × 1 cm, branching, without stolons. Basal leaves 4–10, scarcely pubescent; petioles 5–10 cm long, basis without stipule-like appendages; blades monomorphic, 2–3-ternate; petiolules of primary segments 10–20 mm long, those of secondary segments 1–2 mm long; leaflets with cuneate–acute ultimate lobules. Scapes 20–30 cm long, glabrous, several-flowered. Involucral leaves three, short–petiolate, dissimilar to the basal ones, densely pubescent; blades 3-cleft to pinnatifid, with linear acute ultimate lobules. Pedicels 5–15 cm long, densely pubescent. Tepals 7–10, deciduous, oblong, monomorphic, greenish–white, 6–12 × 2–3 mm, with five basal veins and without anastomoses, densely pubescent. Stamens 3–5 mm long, with filiform filaments, narrow connectives and ellipsoid anthers. No data on pollen grains. Carpels ovoid, slightly compressed, densely covered with hairs *c.* 2 mm long, without ribs, styles straight, *c.* 1 mm long. Fruiting heads oblong-ellipsoid, 1–3 × 0.5–1.0 cm. Achenes subovoid, compressed, densely white–villous, 3.5–4 × 2.5–3 mm; hairs *c.* 2 mm long; styles straight, *c.* 1 mm long; ribs *c.* 0.2 mm wide. Chromosome number not known.

*Notes:* Keener & Dutton (1994), co-authors of this paper, described *A. okennonii* and regarded it as close to both *A. tuberosa* and *A. edwardsiana*. They noted the shape and size of tuber and fruiting head and tepal colour as common to all three taxa. *Anemone okennonii* differs from its nearest presumed congener, *A. edwardsiana*, by leaf dissection, smaller leaflets, tepal number, anther colour, achene pubescence, seedling leaves and relatively later blooming period. From *A. tuberosa* it deviates by its more branched stems, longer tubers, 2- to 3-ternate leaves, appressed–pilose bracts, involucral leaves dissimilar to the basal ones, smaller tepals, shape of fruiting heads and thinner achenes. After re-examination of the tuberous *Anemone* spp. in Texas, Enquist & Crozier (1995) proposed to regard this taxon as *A. tuberosa* var. *texana*. After repeating our examination of all these plants, we confirm the previous consideration of Keener & Dutton (1994) to treat *A. okennonii* as a separate species, not as a variety. Enquist & Crozier overlooked several of its differential characters, i.e. seasonal dimorphism of the basal leaves, much smaller greenish–white tepals with characteristic venation and carpels without marginal ribs.

*Distribution and habitat:* South-east part of the USA (narrow endemic of Central and West Texas; Fig. 13, and adjacent New Mexico according to *New Mexico Botanist*, 1996). In open habitats on sandy loam or limestone, together with *Acacia roemeriana* Scheele, *Delphinium carolinianum* Walter, *Opuntia phaeacantha* Engelm., *Gilia rigidula* Benth., etc., 500–1500 m.

*Specimens examined:* USA: Texas: Gillespie Co., south of Doss, 22.iv.1993, *O'Kennon 11390* (PAC); Kimble Co., south of Llaho River, 9.iii.1992, *O'Kennon* (PAC); Crockett Co., west of Ozona, 14.iii.1949, *Turner & Warnock* (Smu); Val Verde Co. Del Rio, 31.iii.1947, *Vaugh* (Smu); Brewster Co. Glass Mts, 21.iii.1944, *Rose-Innes & Warnock* (Smu).

### 13. *ANEMONE BERLANDIERI* PRITZ., *LINNAEA* **15:** 628. 1841

*Type:* USA. Texas, San Antonio de Bejar (holotype: G, herb. Delessert).

= *A. heterophylla* (Torr. & A.Gray) Nutt. ex A.Wood, *Class-Book Bot.* 202. 1861.
= *A. caroliniana* Walt. var. *heterophylla* Torr. & A.Gray, *Fl. N. Am.* **1:** 12. 1838.
= *A. decapetala* Ard. var. *heterophylla* (Torr. & A.Gray.) Britt. & Rusby, *N. Y. Acad. Sci.* **7:** 7. 1887.

*Description:* Rhizomes tuberous, vertical, elongate, 1.5–2.2 × 0.7–1.2 cm, without stolons, but distally frequently with long, spindle-like roots, especially in young and middle-aged plants. Basal leaves 3–6 (9), scarcely puberulent; petioles 5–20 cm long, at the basis with stipule-like appendages; blades dimorphic (sometimes indistinct): early leaves with less divided blades and sessile or subsessile primary segments, obtuse ultimate lobules; later leaves with more dissected segments on petiolules 15–20 mm long, and with acute ultimate lobules. Scapes (10) 30–50 cm long, scarcely puberulent, 1-flowered. Involucral leaves three, sessile, basally connate, dissimilar to the basal ones; blades 3-cleft, 2–4 (5) cm long, ultimate lobules 3–5, with linear–lanceolate, long–acute divisions (sometimes undivided), scarcely puberulent. Pedicels 10–25 cm long, villous. Tepals 7–12 (17), deciduous, linear–oblong, blue to violet (inside white), monomorphic, 7–15 × 2–3 mm, with three basal veins and without anastomoses, densely pubescent (not glabrous as stated in Britton, 1891). Stamens 3–4 mm long, with filiform filaments, narrow connectives and ellipsoid anthers. Pollen pantocolpate. Carpels subglobose, compressed, *c.* 1 mm long, covered with *c.* 2 mm long hairs, styles curved, *c.* 1 mm long, stigmas linear. Fruiting heads ellipsoid–cylindric, 2.0–3.2 × 1.5–2.0 cm. Achenes subglobose, compressed, 2–3.5 × 2.2–2.5 mm; hairs 4.5–5.7 mm long; styles curved, 0.6–1.3 mm long, pubescent; marginal ribs 0.3–0.4 mm wide (Fig. 6F). Chromosome number: $2n = 16$ (Joseph & Heimburger, 1966, as *A. heterophylla*).

*Notes:* Pritzel described this species in 1841 from the flora of Texas and regarded it as closely related to *A. caroliniana* and *A. decapetala*. He characterized *A. berlandieri* by its tuberous 'roots', numerous pubescent and long–petiolate basal leaves with broad blade divisions, three involucral leaves clasping basally, solitary flowers with linear bluish–white sepals, cylindrical receptacles and woolly achenes with straight styles. Britton (1891) included *A. berlandieri* as a synonym under *A. decapetala s.l.* and postulated its occurrence in both North and South America. As characters, he noted the globose or cylindrical tubers (not roots), petiolulate or rarely sessile primary segments of basal leaves with incised–obtuse or linear–oblong ultimate lobules, involucral leaves with short broad petioles and linear–oblong ultimate lobules, 10–20 bluish linear–oblong glabrous tepals, cylindrical fruiting heads and achenes with subulate styles about 1 mm long. Keener (1975) reinstated *A. berlandieri* because of its priority over *A. heterophylla*. He characterized it by a tuberous rootstock, involucral leaves dissimilar to the basal ones and pubescent pedicels and stems. Later, Keener & Dutton (1994) and Dutton *et al.* (1997) examined *A. berlandieri* in detail and noted its tuber shape (vertical or ascending, oblong) and size (2–4 × 1 cm), 1- to 2-ternate basal leaf blades, sessile to petiolulate primary segments 2–4 cm wide with broad obtuse or acute ultimate lobules, involucral leaves with connate or merely clasping basal parts and linear, acute to acuminate, ultimate lobules, solitary flowers with 7–17 bluish to whitish tepals, etc. Dimorphism of tepals occurs (cf. *A. caroliniana* and *A. tuberosa*) with tepals of the inner whorl frequently being glabrous and having only three basal veins. Occasionally, and especially after flowering, plants may lack basal leaves.

*Distribution and habitat:* USA (Kansas, Arkansas, Oklahoma, Alabama, Texas, etc.; Fig. 13). In prairies, open limestone hills, grassy knolls and stony ground, 60–1100 m.

*Specimens examined:* USA: Alabama: Sumter Co., Emelle, 10.iv.1966, *Iltis* (BM).
Oklahoma: Murray Co., Crusher Spur, 12.iv.1930, *Stevens* (K); Sutton Co., Sonora, 15.iii.1941, *Innes & Warnock* (GH); Bowie Co., 8.5 mi N of New Boston, Red River, 30.iv.1969, *Correll 37136* (GH); Tom Green Co., Jet Limstone, 18.iv.1979, *Lowry Ii* (GH).
Texas: Wilson Co., Sutherland Springs, 8.iv.1934, *Cory* (GH); Sutton Co., 25 miles east of Sonora, 15.iii.1941, *Innes & Warnock 434* (GH); San Patricio Co., Li Rancho, St. Paul, 18.iii.1977, *Hill* (E).

### 14. *Anemone edwardsiana* Tharp, *Amer. midl. Naturalist* **33:** 669. 1945

*Type:* USA, Texas, Travis Co., 22.2.1908, *York* (holotype: Tex).
= *A. edwardsiana* var. *petraea* Correll, *Madroňo* **19:** 189. 1968. *Type:* USA. Texas, Kendall Co., Edge Falls, 31.3.1965, *Correll & Correll 30743* (holotype: Ll).

*Description:* Rhizomes tuberous, vertical, spindle-shaped, branched, 1.2–1.5 × 0.6–0.8 cm, with a narrow terminal part. Basal leaves 3–6, glabrous; petioles 8–15 cm long, base with stipule-like appendages; blades dimorphic (although not always distinct), 2.0–2.5 cm wide with wide–lanceolate obtuse ultimate lobules; early leaves usually with subsessile, little divided primary segments, later leaves 1–2-ternate; leaflets petiolulate (5–20 mm long). Scapes 30–50 cm

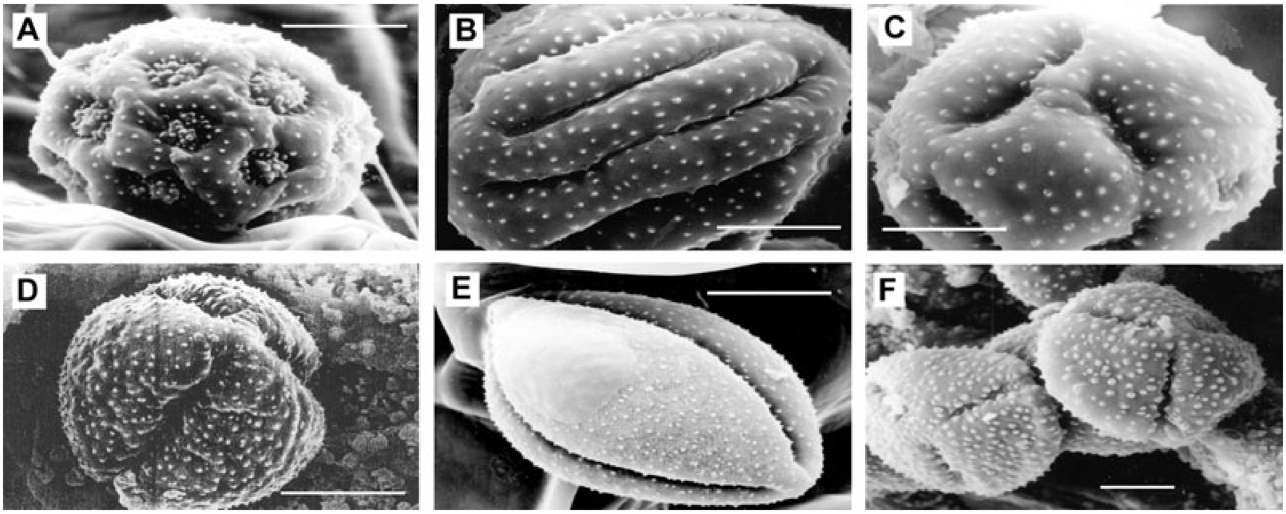


**Figure 7.** Pollen grains of species of *Anemone* section *Anemone* (scanning electron microscopy): A, *A. coronaria*. B, *A. hortensis*. C, *A. palmate*. D, *A. somaliensis*. E, *A. caroliniana*. F, *A. edwardsiana.* Scale bars, 5 μm.

long, glabrous, 2–3-flowered. Involucral leaves three, sessile, glabrous, dissimilar to the basal ones; blades with wide bases, 3-cleft to pinnatifid, 2–5 cm long, with 3–5 obtuse or acute but narrowly linear ultimate lobules, glabrous. Lateral flowers with two small bracteoles. Pedicels 5–15 cm long, densely pubescent. Tepals 6–8 (up to 20), deciduous, oblanceolate, white to bluish, 10–20 × 2–4 mm, with 5 basal veins and without anastomoses, scarcely pubescent. Stamens 4–6 mm long, with linear filaments, narrow connectives and ellipsoid anthers. Pollen tricolpate (Fig. 7F), not pantocolpate as indicated by Huyn (1970). Carpels subglobose, compressed (ribs *c.* 0.5 mm wide), *c.* 1 mm long, covered with hairs *c.* 2 mm long, styles straight, *c.* 1 mm long, stigmas linear. Fruiting heads ellipsoid, 2–3 × 1.5–2 cm. Achenes suboglobose, compressed, 2.8–3 × 2–2.4 mm; hairs 2.2–3.2 mm long (sometimes achenes subglabrous); styles straight or curved, 0.9–1.1 mm long; marginal ribs 0.6–1 mm wide (Fig. 6G). Chromosome number not known.

*Notes: Anemone edwardsiana* was described by Tharp (1945) in 1945 as a restricted endemic occurring only in the Edwards Plateau of Texas. Correll & Johnston (1970), who studied the tuberous species of *Anemone* in Texas, noted its brown, oblong–obovate tubers, several trifoliolate glabrous basal leaves with long petioles, reniform primary segments (or leaflets) up to 2.5 cm wide with crenate ultimate lobules and petiolules up to 25 mm long, three involucral leaves each 3-cleft with linear–oblong ultimate lobules, 3- to 10-flowered stems, the flowers with a whitish to greenish–white perianth 2.5–3.0 cm in diameter, and pubescent to glabrous, broadly ovate achenes with short erect styles. Correll (1968) separated a type with completely glabrous achenes and receptacles as *A. edwardsiana* var. *petraea*. When revising *Anemone* for Texas and for North America, Keener & Dutton (1994), and Dutton *et al.* (1997) treated the characteristics of this species in detail.

*Distribution and habitat:* Endemic to Texas (Edwards Plateau; Fig. 13). In rock crevices of moist and shaded canyons, 200–500 m.

*Specimens examined:* USA: Texas: Dallas, iii.1884, *Reverchon* (K); San Augustine Co., 30.iii.1915, *Palmer* (K); Kendall Co., Spanish Pass, 29.iii.1936, *Cory 18246* (GH); Kendall Co., 7 miles west of Boerne, 4.iii.1938, *Cory 27961* GH); Travis Co., Austin, Bull Creek, 30.i.1941, *Innes 332* (GH); Camp Mabry, 17.iii.1946, *Warnock* (K); 5 miles north of Austin, bluffs of Bull Creek above Colorado River, 25.iii.1947, *Vaugh* (GH); Val Verde Co., near Devil Lake, 20 miles north-northwest of Del Rio, 31.iii.1947, Vaugh 7730 (GH); Kendall Co. Bergheim, 31.iii.1965, *Correll & Correll* (NY); Val Verde Co., 10 miles west of Comstock, 6.iv.1968, *Shinners 32053* (GH).

### 15. *Anemone decapetala* Ard., *Animadv. Bot. Sp. Alt.* **2:** 27. 1764

*Holotype:* n.710–21: LINN! According to A. Lourteig. [*Mem. Soc. Cienc. Nat. La Salle* **16** (44): 200. 1956]: 'De semillas procendentes de Brazil'.
= *A. trilobata* Juss., *Ann. Mus. Hist. Nat. Paris* **3:** 248. 1804.
= *A. jamesonii* Hook.f., *Ic. Pl.* **7:** 670. 1844.

= *A. sphenophylla* Poepp., *Fragm. Syn. Pl.* 27. 1833.
= *A. macrorrhiza* Domb. ex Eichler, *Fl: Bras.* **13:** 151. 1864
= *A. bilobata* Phil., *Cat. Plants Vasc. Chil.* 5. 1881.
= *A. polypetala* Larranaga, *Escritos* **2:** 178. 1922.
= *A. decapetala* Ard. var. *grandifolia* Eichler, *Fl. Bras.* **13:** 152. 1864.
= *A. decapetala* Ard. var. *araucana* Phil., *Anales Univ. Chile* **88:** 62. 1894 and in Reiche, *Fl. Chile* **1:** 8. 1896.
= *A. decapetala* Ard. var. *patagonica* Kuntze, *Revis. General. Pl.* **3**(3): 1. 1898.
= *A. decapetala* Ard. var. *biflora* Arechav., *Anales Mus. Nac. Montevideo*, ser. 2., **1:** 24. 1905.
= *A. decapetala* Ard. var. *majorina* Arechav., l.c. 22. 1905.

*Description:* Rhizomes tuberous, oblong–obovate, 1.7–2.5 × 1.2–1.8 cm. Basal leaves 3–5, dimorphic, 2-ternate, scarcely pubescent, petioles basally gradually widened (6–8 mm) but not stipule-like; early basal leaves with 10–15 broad, primary segments, subsessile or shortly petiolulate (2–3 mm long) and obtuse ultimate divisions; later basal leaves much divided (40–60 ultimate divisions), with petiolules 5–20 mm long and the ultimate leaf lobules broadly obtuse. Fruiting plants sometimes lack basal leaves. Scapes 5–15 cm long, scarcely puberulent, 1–2-flowered. Involucral leaves three, dissimilar to the basal ones, scarcely puberulent, blades 1-ternate with primary segments sessile and 20–30 long–acute linear ultimate lobules. Pedicels 5–25 cm long, scarcely puberulent. Lateral flowers with two small bracteoles. Tepals 10–12, deciduous, linear–oblong, blue or whitish–pink, monomorphic, 15–20 × 5–8 mm, with 5–9 basal veins and 1–2 vein anastomoses (the latter a unique character state within the tuberous species of *Anemone* in the New World), densely pubescent (Fig. 5N). Stamens 4–5 mm long, with linear filaments, narrow connectives and rounded anthers. Pollen tri- to pantocolpate (Huyn, 1970). Carpels subglobose, slightly compressed (ribs *c.* 0.2 mm wide), 0.5–1 mm long, densely covered with 0.7–1 mm long hairs, ribs 0.2 mm wide, styles curved, 0.5–0.7 mm long, stigmas linear (Fig. 5N). Fruiting heads elongate–cylindroid, 2.0–2.5 × 1.5–2.0 cm. Achenes subglobose, 1.3–2.2 × 1.3–1.8 mm; hairs 4.5–5.7 mm long; styles 0.7–1.2 mm long; marginal ribs 0.3–0.6 mm wide (Fig. 6I). Chromosome nuber: $2n = 16$ (Joseph & Heimburger, 1966).

*Notes: Anemone decapetala*, described in 1764 by Arduino from Chile, was recognized early (e.g. by Linnaeus, 1793; De Candolle, 1817; Pritzel, 1841) and in more recent treatments (e.g. Britton, 1892 and Lourteig, 1951). We examined the holotype in LINN which formed the basis for Arduino's description of the species. Seedlings are epigeal and have two cotyledons (Förster, 1999). *Anemone decapetala* is a polymorphic species, closely related to the following *A. triternata*. This makes it difficult to align the synonyms, a problem that also concerns several later described segregate species (e.g. *A. trilobata*, *A. polypetala*, etc.). However, we note that all specimens which we have examined in the herbaria of K, BM, GH, etc. and assembled here under *A. decapetala* share the following differential characters: oblong–obovate tubers, basal leaves dimorphic, early ones 2-ternate, different from the 1-ternate involucral leaves which lack petioles, 1–2-flowered scapes, numerous deciduous, linear–oblong, blue or whitish–pink tepals having 5–9 basal veins with 1–2 anastomoses, and achenes with subulate styles. These differential characters unite all specimens seen of *A. decapetala*, making the recognition of intraspecific taxa unnecessary and allow separation from *A. triternata* (see also there).

*Distribution and habitat:* South America, from South-East Brazil, Uruguay, Argentina, Peru, Chile and the Juan Fernandez Islands (Más a Tierra) (Fig. 14). Rocky slopes, gravelly slopes, and shaded places, 100–3000 m.

*Specimens examined:* ARGENTINA: Tucuman: Santa Maria, 30.viii.1949, *Pederson* (K); San Javier, 10.ii.1950, *Rocha* (WU); Empedrado: Corientes, 22.viii.1971, *Pederson* (GH); Sierra de la Ventana, Cerro Ventruz, 28.ix.1981, *Roig 47037* (K).
CHILE: Concepción, Macrae, x.1825, *Bridges* (K); Santiago, ii.1856 (KW); Valparaiso, 1831, *Cuming* (K); Valparaiso, 1832, *Bridges* (K); Valparaiso, Dürre Ebenen, 5.viii.1895, *Buchtien* (E); Valparaiso, Quintero, ix.1923, *Wenderman* (E); San Martín de los Andes, 3000 m, 3.xi.1926, *Comber 725* (K); Colchagua: San Fernando, Cerro Nicunlanta, ix.1928, *Montero* (K); Coquimbo: Illapel, La Vega Escondida, 20.xii.1938, Morrison (K).
URUGUAY: Montevideo: Cerro Cassabo, ix.1926, *Herter* (GH).

### 16. *Anemone triternata* Vahl, *Symb.Bot.* **3:** 74. 1794

*Type:* Described from 'Uruguay c. Monte-Video ad ostium fluminis Plata'. As no type specimen has been located yet, t. 65 accompanying the protologue by Vahl is here designated as lectotype.
≡ *A. decapetala* Ard. var. *triternata* (Vahl) Kuntze; *Revis: General. Pl.* 3(3): 1. 1898
= *A. fumariaefolia* Juss., *Ann. Mus. Hist. Nat. Paris* **3:** 247. 1804.
= *A. tridentata* Britton, *Ann. N.Y. Acad. Sci.* **6:** 225. 1891.

= *A. cicutifolia* Johnst., *J. Arn. Arbor.* **19:** 248. 1938.
= *A. decapetala* Ard. var. *foliolosa* Eichler, *Fl. Bras.* **13:** 151. 1864.

*Description:* Rhizomes tuberous, elongate–cylindric, 1.5–2.5 × 0.7–1.0 cm. Basal leaves monomorphic, glabrous, long–petiolate, expanded basally but without stipule-like appendages; blades 1–2-ternate; primary segments with 10–25 mm long petiolules long and narrow–linear acute ultimate lobules. Scapes 10–20 cm long, scarcely pubescent, 1-flowered. Involucral leaves similar to basal ones, with petiole-like bases and ultimate lobules linear, acute, scarcely pubescent. Pedicels 5–25 cm long, densely pubescent. Tepals 10–15, persistent, monomorphic, lanceolate, white to pink, 10–15 × 2–3 mm, with three basal veins and without vein anastomoses, only basally densely pubescent (Fig. 5O). Stamens 5–6 mm long, with filiform filaments, narrow connectives and ellipsoid anthers. Pollen tri- to pantocolpate (Huyn, 1970). Carpels subglobose, slightle compressed (ribs 0.2–0.3 mm wide), *c.* 1 mm long, densely covered with hairs *c.* 1 mm long, styles curved, less than 1 mm long, stigmas linear (Fig. 5O). Fruiting heads elongate, 2.0–2.5 × 0.5–1.0 cm. Achenes subglobose, compressed, 1.5–2.2 × 1.5–2.0 mm, densely covered with hairs 4.0–4.5 mm long; styles curved, only 0.4–0.6 mm long, basally pubescent; marginal ribs 0.4–0.6 mm wide (Fig. 6J). Chromosome number: $2n = 16$ (for '*A. decapetala*') and $2n = 32$ (for an unknown taxon, related to *A. cicutifolia*: Joseph & Heimburger (1966).

*Notes:* In her treatment of the South American members of *Anemone*, Lourteig (1951) lumped *A. triternata*, *A. fumariaefolia* and *A. cicutifolia* under *A. decapetala* Ard. var. *foliolosa* Eichler. In the recent treatment of Ranunculaceae for the *Flora de Chile*, Ruiz (2001) followed the same principle. Nevertheless, and in spite of their partly sympatric occurrence and obvious relationships, our data support a specific distinction between *A. decapetala* and *A. triternata*. The latter is characterized by solitary flowers, petiole-like bases of involucral leaves, persistent tepals with three basal veins but without anastomoses and with short curved achene styles. These features are unique within the tuberous *Anemone* spp. of the New World. Nevertheless, *A. triternata* is a polymorphic taxon, and Joseph & Heimburger (1966) even tried to maintain a specific distinction between *A. triternata s.s.* with an eastern and *A. cicutifolia* with a western distribution in southern South America. Furthermore, they report two tetraploid populations from Chile, which they suspected represent another related species. Further critical biosystemtic studies are clearly necessary on the South American members of subsection *Carolinianae*.

*Distribution and habitat:* South America: Southern Brazil, Argentina, Uruguay, Bolivia, Peru and Chile (Fig. 14). In ± open mountain habitats.

*Specimens examined:* ARGENTINA: Buenos Aires: El Soccoro, viii.1926, *Parodi* (K); Tucuman: Burroyaco, Cerro del Campo, 15.xii.1928, *Venturi* (K); Prov. Salta: Department. Guachipas, Alemania, 1300 m, 3.xii.1929, *Venturi 9846* (K); Las Palmas: Buenos Aires, 13.x.1946, *Hunziker 1686* (K); Las Palmas, 14.x.1946, *Krapovickas* (K); Department. Empedrado: Prov. Corrientes, Bella Vista, Toropi, 13.ix.1972, *Schimini* (K); Corrientes, Estancia Las Tres Marias, 22.viii.1975, *Pederson 10723* (K).
URUGUAY: Montevideo, Cerro, viii.1925, *Herter* (K); Concepcion, vii.1877, *Lorentz* (K).
BOLIVIA: Bolivian Plateau, 1891, *Britton & Rusby 1041* (LE); Larecasja: Lorato, Mts Munayapata, Challasuyo, i.1898, *Mandon* (K); Bolivian Plateau, 22.vi.1892, *Britton* (K); Toldos bei Bermejo, 9.xii.1903, *Fiebrig 2375* (K); Rio Grande do Sul, *247* (W); Parana: Galinhas, 27.x.1969, *Hatschbach* (K).
PERU: Department. Cuzco, 13 000 ft, xii.1933, *Stafford 213* (K); Cusco, Santa Rosa, 13 500 ft, 13.ii.1937, *Stafford 516* (K).
CHILE: La Banca, 10.i.1864, *Pearce* (K).

## DNA PHYLOGRAM AND GEOLOGICAL TIMING

In addition to plastid DNA restriction site analyses (Hoot *et al.*, 1994), DNA sequences from the plastid *atpB-rbcL* intergenic spacer are available for taxa of the *Anemone* section *Anemone* clade, the tribe Anemoneae and other members of Ranunculaceae (Ehrendorfer & Samuel, 2001; Schuettpelz *et al.*, 2002; Schuettpelz & Hoot, 2004; Miikeda *et al.*, 2006). This has made it possible to construct a new DNA phylogram (Fig. 8). It allows us to document the phylogenetic position of section *Anemone* and other taxa of Anemoneae and to obtain approximate geological dates for most of their divergence nodes (see MATERIAL AND METHODS).

This phylogram is based on 26 provenances of Ranunculaceae, including four tribes, nine genera and 23 species, of which five represent *Anemone* section *Anemone* (Table 1). It is one of 376 equally most parsimonious trees, corresponding quite well with the 50% majority rule consensus tree (apart from two nodes which collapse in the latter, marked with an asterisk in Fig. 8). Its topology is in good agree-

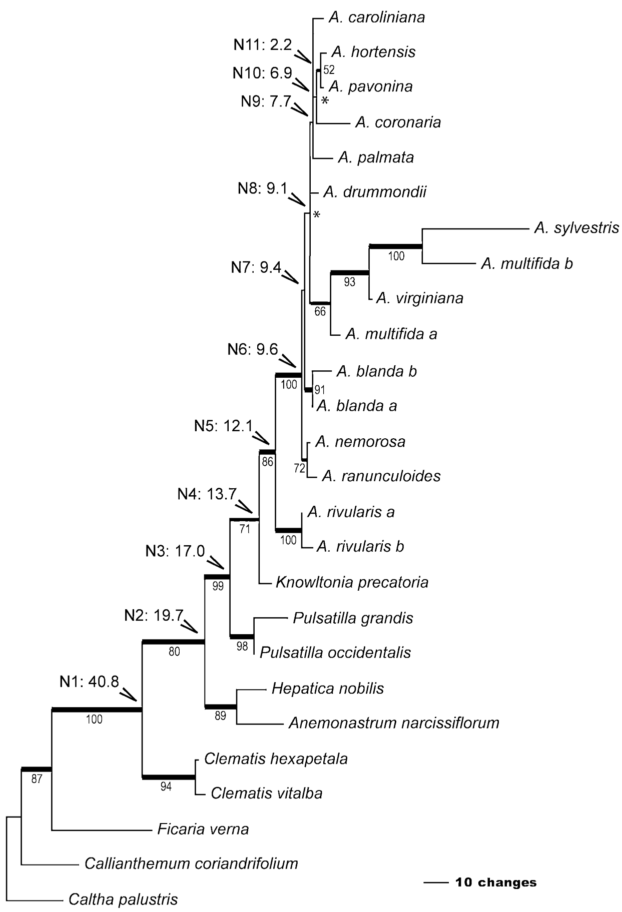


**Figure 8.** Phylogram of Ranunculaceae tribe Anemoneae, based on sequences of the plastid *atpB-rbcL* intergenic spacer (with 164 potentially parsimony informative characters) and with *Caltha* (Helleboreae), *Callianthemum* (Adonideae) and *Ficaria* (Ranunculeae) as outgroups (for provenances see Table 1). One of the 376 most parsimonious trees (length = 499, Ci = 0.84, Ri = 0.82) with the two branches collapsing in the 50% majority rule consensus tree marked *. Bootstrap values are inserted below branches, those > 50% are shown by medium, those > 75% by thick lines. Assumed divergence times in Mya, obtained by the penalized likelihood approach, are inserted at 11 selected nodes (N1-N11).

ment with trees for the whole family (Hoot, 1995a: plastid and nuclear sequences) and for Anemoneae (Hoot *et al.*, 1994: plastid restriction sites) Within Anemoneae, this latter tribe *Clematis* (subtribe Clematidinae) separates at node N1 from the representatives of subtribe Anemoninae which were combined into the single genus *Anemone s.l.* by Hoot *et al.* (1994). In the present treatment, we prefer to circumscribe the genera of this subtribe in a more traditional and narrower manner. At node N2, the clade with the base chromosome number $x = 7$, which includes *Anemonastrum* (= *Anemone* subgenus *Omalocarpus*) and *Hepatica*, separates from all other Anemoninae with $x = 8$. At the following nodes, N3 and N4, the genera *Pulsatilla* and *Knowltonia* split off from the monophyletic *Anemone s.s.* Here, *Anemone rivularis* (subgenus and section *Rivularidium*) appears well separated at N5 from the next, closely related clades at N6–N9, forming the crown group of the tree, corresponding to subgenus *Anemone s.l.* This comprises from N6 *A. nemorosa* and *A. ranunculoides* (section *Anemonanthea*), from N7 *A. blanda* (section *Tuberosa*), from N8 the members of section *Eriocephalus* (with *A. drummondii* in the *A. baldensis* group and the other taxa in the *A. multifida* group) and finally from N9 those of section *Anemone.* Within the clade defined by N9, N10 separates a subclade with *A. coronaria* and *A. hortensis s.l.* (incl. *A. pavonina*) from *A. palmata* and the New World *A. caroliniana* and N11 reflects the infraspecific differentiation within *A. hortensis.*

For the dating of important nodes in the DNA phylogram (Fig. 8) we have used the careful calibrations with reliable fossils and the penalized likelihood (Pl) calculations of Zetzsche (2004: 72). He assumed an Upper Cretaceous age of 80–100 Mya for Ranunculaceae (recent fossil data are even older: Pigg & DeVore, 2005). For the split between the Anemoninae clades with $x = 7$ (represented by '*Anemone*' *antucensis*) and those with $x = 8$ (represented by the genus *Pulsatilla*), Zetzsche (2004) indicated a Pl divergence time of 19.7 Mya (Upper Tertiary, early Miocene). This split corresponds to our node N2 and was used to calculate the approximate age of the other nodes in our phylogram with the r8s software available from Sanderson (2004).

For the present analysis, the crown group of the DNA phylogram (Fig. 8) is particularly relevant. It includes the closely related and more advanced clades corresponding to the *Anemone s.s.* sections *Anemonanthea*, *Tuberosa, Eriocephalus* and *Anemone*. Apparently, they all have diverged within a relatively short geological period, as their nodes N6–N9 are dated approximately between 9.6 and 7.7 Mya, i.e. during the late Miocene. Thus, the separation of the subsections within *A.* section *Anemone*, the Mediterranean subsection *Anemone* and the New World subsection *Carolinianae*, could not have occurred much earlier than *c.* 7 Mya. Species divergence within subsection *Anemone* is relatively old and can be dated at a slightly younger age.

## CLADISTIC CHARACTER ANALYSIS

The character profiles of the 16 species of *A.* section *Anemone* and the outgroup species *A. blanda* (section *Tuberosa*) are presented in Table 2. Columns 1–20 show the 20 taxonomically most significant differential characters. Character states are indicated by abbreviations or by means and partly by ranges in the first subcolumn and in summary form as lower-case letters (a–e) in the second subcolumn as explained in the following section and the legend of Table 2. Quantitative characters are apportioned to classes according to their variance. Column 21 indicates geographical distribution. For the cladistic analysis and the construction of a phylogram for section *Anemone* phylogram (Fig. 9) only differential characters 1–20 were used.

In view of the uncertainties of classifying character states as plesio- or apomorphic, as discussed in the following section, character states were treated as unordered for our calculations. From the 18 most parsimonious trees obtained, one corresponding to the strict consensus tree (apart from two nodes which collapsed in the latter marked with an asterisk) is shown with bootstrap values in Figure 9. It illustrates *A. blanda* as sister to the monophyletic section *Anemone*. Within the section, there are two well-supported clades, the first comprising the three Old World subsections, the second the New World subsection *Carolinianae*. Among the former, the monotypic North-East African subsection *Somalienses* (with *A. somaliensis*) appears as sister to the remaining taxa. It forms a link between the well-supported Mediterranean subsection *Anemone* with *A. coronaria, A. hortensis* and *A. palmata* and the Central Asiatic subsection *Biflorae* with its five, closely related species. Among the New World taxa of subsection *Carolinianae*, the North American *A. caroliniana* and *A. tuberosa* from the first and second branches and *A. okennonii, A. edwardsiana* and *A. berlandieri* form a clade with the South American *A. decapetala* and *A. triternata*.

## CHARACTER DIFFERENTIATION

The following text is based on a detailed study of subtribe Anemoninae (Ehrendorfer, 1995), the relevant literature and the data presented in the preceding sections. Nevertheless, considerations about character evolution (plesiomorphy → apomorphy) within section *Anemone* often remain hypothetical, even if one follows the the principles outlined by Hoot *et al.* (1994: table 4). Because the direction of such character changes is uncertain in many cases and may have occurred in more than one direction, assumed plesio- or apomorphic states are not indicated in Table 2 and are not used for the construction of the phylogram (Fig. 9), which is based on unordered character states. This procedure in turn allows cautious conclusions about character states, more likely plesiomorphic in basal and apomorphic in distal branches of the tree.

Among the vegetative characters of section *Anemone*, the differentiation of the subterranean shoot system (1: rhiz., 2: stol.) is of considerable importance. Variation extends from a regularly branched and often oblique rhizome (1a: br.) via a somewhat branched and ± tuberous rhizome (1b: s. br.) to an unbranched and strongly tuberous rootstock (1c: n. br.). It appears that the character state 1a conveys advantages in ± woody habitats, whereas 1c provides a better adaptation in xeric localities. The outgroup section *Tuberosa* with *A. blanda* is characterized by 1a. The direction of phylogenetic change of this character in section *Anemone* is uncertain, but may be from branched (1a) to unbranched (1c). In contrast, the development of slender stolons from the rootstock or rhizome (2b: +) has to be regarded as an apomorphy compared with the lack of such stolons (2a: –).

Characters 3–5 concern the basal and involucral leaves. Numbers of basal leaves (3: no.leav.) vary from 1 to 8 (11) in section *Anemone*. Two classes have been recognized: with four and more (3a: > 3) or with one to three (3b: ≤ 3) basal leaves. The apomorphic state is uncertain, but in the outgroup *A. blanda* the state is 3b. As a new differential character (Fig. 4), the development of stipule-like appendages at the petiole basis of basal leaves (4: stip. app.) has been observed in several taxa (4a: +). It is found in the outgroup and in some species of section *Anemone* and is probably plesiomorphic in comparison with the lack of such appendages in the majority of taxa (4b: –). The progressive reduction, special differentiation and basal fusion of involucral as compared with basal leaves (5b: sim. leav. –) can be regarded as an apomorphic change relative to their similar development and free bases (5a: sim. leav. +).

The remaining characters concern the reproductive organs of section *Anemone* taxa. With respect to the inflorescences (6: no. flow.) it is obvious that solitary flowers (6b: 1) are the result of a reduction from multi-flowered inflorescences (6a: 1–2 or 6c: 2–3). Therefore, the occurrence of flowering scapes with up to two or even three flowers has to be regarded as plesiomorphic. The great diversity in floral elements is obvious from Figure 5. Tepals (also called 'petaloids' and erroneously 'sepals' in the literature) vary in number between five and 20 within section *Anemone* (7: no. tepals). We separate two classes with means > 7.0 (7a) in *A. blanda* and the majority of section *Anemone* taxa) and < 5.5 (7b: probably apomorphic). The shape of the tepals varies from suborbicular to narrowly elongate or lanceolate and is best expressed by an index of length/breadth (8, tep. l./b.). Taxa with mean values < 3.0 are classified as 8a, those > 3.00 as 8b (also in *A. blanda*; plesiomorphic?). Tepal colour (9: tep. col.)

**Table 2.** Vegetative and reproductive characters (some with means and ranges) and general distribution for all 16 species of *Anemone* section *Anemone* recognized and one outgroup species

| SP | 1 Rhiz. | | 2 Stol. | | 3 No. leav. | | 4 Stip. app. | | 5 Sim. leav. | | 6 No. flow. | | 7 No. tepals | | 8 Tep. l./b. | | 9 Tep. col. | | 10 Tep. postfl. | | 11 Tep. bas. veins | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| SO | n.br. | c | – | a | ≤ 3 | b | – | b | + | a | 1–2 | a | 14 (10–18) | a | 3.0 | a | Blue | c | pers. | b | 4 (3–5) | c |
| CO | br. | a | + | b | > 3 | a | + | a | – | b | 1 | b | 8 (6–13) | a | 1.7 | a | Red | b | dec. | a | 7 (5–9) | a |
| HO | br. | a | – | a | > 3 | a | + | a | – | b | 1 | b | 14 (10–18) | a | 2.9 | a | Red | b | dec. | a | 3.6 (3–5) | c |
| PA | br. | a | – | a | > 3 | a | + | a | – | b | 1–2 | a | 12 (8–15) | a | 2.0 | a | Yellow | a | dec. | a | 4.3 (3–5) | c |
| BI | s.br. | b | – | a | > 3 | a | – | b | + | a | 1–2 | a | 5.1 (5–6) | b | 1.7 | a | Yellow | a | pers. | b | 7.3 (5–9) | a |
| BU | s.br. | b | – | a | ≤ 3 | b | – | b | + | a | 1–2 | a | 5.3 (5–6) | b | 1.8 | a | Red | b | pers. | b | 10.6 (5–13) | a |
| BA | br. | a | – | a | > 3 | a | – | b | + | a | 1–2 | a | 5.2 (5–6) | b | 1.9 | a | Yellow | a | pers. | b | 8.1 (5–11) | a |
| TS | n.br. | c | – | a | ≤ 3 | b | – | b | + | a | 1–2 | a | 5 | b | 1.9 | a | Red | b | pers. | b | 10.1 (5–11) | a |
| SE | n.br. | c | – | a | ≤ 3 | b | – | b | + | a | 1 | b | 5 | b | 1.7 | a | Yellow | a | pers. | b | 6 (5–7) | a |
| CA | n.br. | c | + | b | ≤ 3 | b | – | b | + | a | 1 | b | 16.1 (12–20) | a | 4.7 | b | White | d | dec. | a | 5 | b |
| BE | s.br. | b | – | a | > 3 | a | + | a | – | b | 1 | b | 11.2 (7–17) | a | 5.0 | b | White | d | dec. | a | 5 | b |
| ED | br. | a | – | a | > 3 | a | + | a | – | b | 2–3 | c | 7.1 (6–8) | a | 3.7 | b | White | d | dec. | a | 5 | b |
| TU | br. | a | – | a | ≤ 3 | b | – | b | + | a | 1–2 | a | 9.1 (6–13) | a | 3.7 | b | White | d | dec. | a | 5 | b |
| OK | br. | a | – | a | > 3 | a | – | b | – | b | 2–3 | c | 8.5 (7–10) | a | 3.5 | b | White | d | dec. | a | 5 | b |
| DE | n.br. | c | – | a | > 3 | a | – | b | – | b | 1–2 | a | 11.3 (10–12) | a | 2.5–3 | a | White | d | dec. | a | 5 | b |
| TR | n.br. | c | – | a | > 3 | a | – | b | + | a | 1 | b | 12.2 (10–15) | a | 6.0 | b | White | d | pers. | b | 3 | c |
| BL | br. | a | – | a | ≤ 3 | b | + | a | + | a | 1 | b | 12 (9–15) | a | 4.8 | b | Blue | c | dec. | a | 3.8 (3–5) | c |

Abbreviations for species (SP), vertical: *A.* subsection *Somalienses*: SO, *A. somaliensis*. *A.* subsection *Anemone*: CO, *A. coronaria*; HO, *A. hortensis*; PA, *A. palmata*. *A.* subsection *Biflorae*: BI, *A. biflora*; BU, *A. bucharica*; BA, *A. baissunensis*; TS, *A. tschernjaewii*; SE, *A. serawschanica*. *A.* subsection *Carolinianae*: CA, *A. caroliniana*; BE, *A. berlandieri*, ED, *A. edwardsiana*; TU, *A. tuberose*; OK, *A. okennonii*; DE, *A. decapetala*; TR, *A. triternata*. Outgroup *A.* section *Tuberosa*: BL, *A. blanda*.

Abbreviations, horizontal: 1, rhizome (Rhiz.) branched (br.)/sometimes or rarely branched (s.br.)/unbranched (n.br.); 2, stolons (Stol.); 3, number of basal leaves (No. leav.); 4, presence/absence of stipule-like appendages at petiole basis (Stip. app.); 5, similarity of basal and involucral leaves (Sim. leav.); 6, number of flowers per flowering scape (No. flow.); 7, number of tepals (No. tep.); 8, index length/breadth of tepals (Tep. l./b.); 9, tepal colour (Tep. col.); 10, post-floral behaviour of tepals (Tep. postfl.) deciduous/persistent; 11, number of veins at base of tepals (Tep. bas. veins); 12, number of tepal vein anastomoses (Tep. vein anast.); 13, pollen grain apertures (Poll. gr. ap.) tricolpate/pantocolpate/pantoporate/spiroaperturate; 14, length/breadth of achenes (Ach. l./b.); 15, achene body (Ach. body) ovoid/compressed; 16, width of ripe achene marginal rib in mm (Ach. rib); 17, length of style on ripe achene in mm (Ach. style l.); 18, length of hairs on achenes in mm (Ach. hair l.); 19, number of cotyledons (Cotyl.); 20, germination (Germ.) epigeal/hypogeal; 21, general geographical distribution (Geogr.) (C As, Central Asia; Med., Mediterranean; N Am, North America; S Am, South America). Data for *A. somaliensis* and *A. okennonii* are based on limited material. ? indicates data lacking.

a–c, character states are indicated in summary form as lower-case letters. Further explanations in the text.

varies from yellow (9a) and red (9b) or ± blue (9c) to whitish or white (9d); the latter state is probably apomorphic. Dominant colours in the outgroup section *Tuberosa* are blue to white. In post-floral stages (10: tep. postfl.) tepals may be deciduous from the flower axis (10a: dec.; also in *A. blanda*; probably plesiomorphic) or persistant (10b, probably apomorphic). It has been shown that venation of tepals in section *Anemone* is of considerable taxonomic relevance (Ziman & Bulakh, 2004; fig. 5). The number of basal veins (11: tep. bas. veins) varies from three to 13. With respect to mean values we recognize three classes, 3.0–4.8 (11c), 5 (11b) and 7–10.6 (11a). Great differences exist in the number of tepal vein anastomoses (12: tep. vein anast.), classified into usually > 5 (12b), mostly 1–3 (12a) and none (12c). The outgroup species *A. blanda* corresponds to 11c and 12b, but plesio- or apomorphic states are uncertain.

There is great variation in the pollen grains of *Anemone* and section *Anemone* (Huyn, 1970; Savitski, 1982). This has been verified by additional scanning electron microscopy (SEM) studies (Fig. 7). With respect to apertures (13), there is general agreement that phylogenetic change has proceeded from plesiomorphic tricolpate (13a) via transitions towards pantocolpate (13b) to fixed pantocolpate (13c) and subsequently to pantoporate (13d). A sideline of these increasingly apomorphic developments leads to spiroaperturate pollen grains (13e). 13a characterizes *A. somaliensis*, most of subsection *Carolinianae* and the outgroup taxa from section *Tuberosa*, here *A. blanda*.

An important group of differential characters (14–18) concerns the ripe achenes of section *Anemone* taxa (Fig. 6). Their suborbicular to narrowly ellipsoid outline is best expressed by a length/breadth index (14: ach. l./b.), ranging from 1.1 to 3.6. Two classes

**Table 2.** *Continued*

| 12 Tep. vein anast. | | 13 Poll. gr. ap. | | 14 Ach. l./b. | | 15 Ach. body | | 16 Ach. rib. (mm) | | 17 Ach. style l. (mm) | | 18 Ach. hair l. (mm) | | 19 Cotyl. | | 20 Germ. | | 21 Geogr. | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 2 (1–3) | a | tricol. | a | 3.2 | a | ovoid | a | 0.2 | b | 1.5 (1.2–2.0) | a | 3.2–3.5 | b | ? | – | ? | – | Somalia | b |
| >20 (15–30) | b | p.por. | d | 1.9 | a | ovoid | a | 0.4 | a | 2.0 (1.5–2.5) | a | 3.5–4.5 | b | 2 | a | hypo. | b | Med. | a |
| 1.8 (1–3) | a | sp.ap. | e | 2.0 | a | ovoid | a | 0.2 | b | 2.4 (2.0–2.6) | a | 3.5–5.2 | b | 2 | a | epi./hypo. | a/ b | Med. | a |
| 2.3 (1–3) | a | p.col. | c | 2.8 | a | ovoid | a | 0.1 | b | 2.8 (2.0–3.5) | a | 2.5–4.5 | b | 2 | a | hypo. | b | Med. | a |
| 1.3 (1–3) | a | p.por. | d | 2.6 | a | ovoid | a | 0.1 | b | 2.3 (2.0–3.0) | a | 2.0–5.0 | b | ? | – | ? | – | C As | c |
| >20 (7–30) | b | p.por. | d | 1.8 | a | ovoid | a | 0.2 | b | 2.2 (1.7–2.5) | a | 2.0–3.5 | b | ? | – | ? | – | C As | c |
| 9.2 (7–15) | b | p.por. | d | 3.1 | a | ovoid | a | 0.2 | b | 2.3 (2.0–3.0) | a | 4.5–5.0 | b | ? | – | ? | – | C As | c |
| 8.0 (5–15) | b | p.por. | d | 2.5 | a | ovoid | a | 0.1 | b | 2.3 (1.7–2.5) | a | 5.0–6.0 | b | ? | – | ? | – | C As | c |
| 0.1 (0–1) | a | p.por. | d | 2.1 | a | ovoid | a | 0.1 | b | 1.5 | a | 1.7–2.3 | b | ? | – | ? | – | C As | c |
| 0 | c | tricol. | a | 3.6 | a | comp. | b | 0.2 | b | 1.4 (1.1–1.7) | b | 3.2–4.6 | b | 2 | a | epi. | a | N Am | d |
| 0 | c | tricol. | a | 1.2 | b | comp. | b | 0.4 | a | 0.9 (0.6–1.3) | b | 4.5–5.7 | b | ? | – | ? | – | N Am | d |
| 0 | c | p.col. | c | 1.3 | b | comp. | b | 0.9 | a | 1.0 (0.9–1.1) | b | 2.2–3.2 | b | ? | – | ? | – | N Am | d |
| 0 | c | tricol. | a | 1.0 | b | comp. | b | 0.5 | a | 1.2 (0.8–1.5) | b | 2.2–3.5 | b | ? | – | ? | – | N Am | d |
| 0 | c | ? | – | 1.3 | b | comp. | b | 0.2 | b | 1.0 | b | ~ 2.0 | b | ? | – | ? | – | N Am | d |
| 0 | c | tricol.-> p.col. | b | 1.1 | b | comp. | b | 0.5 | a | 0.9 (0.7–1.2) | b | 4.5–5.7 | b | 2 | a | epi. | a | S Am | e |
| 0 | c | tricol.-> p.col. | b | 1.1 | b | comp. | b | 0.5 | a | 0.5 (0.4–0.6) | b | 4.0–4.5 | b | ? | – | ? | – | S Am | e |
| 4.8 (1–9) | b | tricol. | a | 1.7 | a | comp. | b | 0.2 | b | 0.15 (0.1–0.2) | b | < 1.0 | a | 1 | b | hypo. | b | Med. | a |

are recognized, comprising taxa with values above (14a) and below 1.5 (14b). Achene bodies (15: ach. body) can be classified as ± ovoid (15a) or clearly compressed (15b). Another specialization of achenes relates to the differentiation of their margins (16: ach. rib); these may be inconspicuous and mostly < 0.3 mm broad (16a) as opposed to obviously rib-like and broader than 0.3 mm (16b). States 14a, 15a and 16a occur in the outgroup *A. blanda* and may be plesiomorphic in comparison with 14b, 15b and 16b. Considerable variability exists among taxa of section *Anemone* with respect to to the length of the styles (0.4–2.6 mm) remaining on the ripe achenes (17: ach-.style l.). Styles 1.4 mm or longer are classified as 17a, those shorter as 17b. In *A. blanda* styles are short (about 0.1 mm) and in the other species of section *Tuberosa* they are up to 1.0 mm. The indumentum of ripe achenes (18) of section *Anemone* taxa is formed by relatively long hairs of (1.7) 2.0–5.0(6.0) mm (18b), whereas the outgroup taxa of section *Tuberosa* (including *A. blanda*) are only short puberulent with hairs not longer than 0.1–0.2mm (18a). It is uncertain what is plesio- or apomorphic in characters 17 and 18.

The seedlings of *Anemone* (Ziman, 1985; Förster, 1999) normally develop two cotyledons and that plesiomorphic condition probably applies to all species of section *Anemone* (cotyl. 19a). In contrast, the number of cotyledons has been reduced to only one in section *Tuberosa*, including *A. blanda* (19b). Germination (20: germ.) is normally epigeal (epi. 20a) in *Anemone* acording to Förster (1999), but has been partly changed to intermediate or fully hypogeal (hypo. 20b), where the cotyledons or at least the plumula remain below soil surface.The latter applies to some species of section *Anemone* and section *Tuberosa* (Table 2). Both types apparently occur within *A. hortensis* (with 20a reported for *A. pavonina*, here included in *A. hortensis*). Because of some discrepancies with older observations on the germination behaviour of these *Anemone* taxa by Ziman (1985), further relevant studies are required.

In the final column 21 (geogr., not considered for the phylogram in Fig. 9), taxa are sorted according to their general distribution area, i.e. Mediterranean (21a: Medical.), Somalia (21b: Somal.), South-West to Central Asia (21c: C As.), North America (21d: N Am.) and South America (21e: S Am.).

The above comparative character evaluation of all taxa of section *Anemone* with *A. blanda* from section *Tuberosa* as the most suitable outgroup leads to the following hypothesis about the most plesiomorphic and possibly ancestral character profile of section *Anemone*: epigeal germination of seedlings with two cotyledons; rhizomes branching and ± thick; basal leaves numerous, monomorphic, petiole bases with stipule-like appendages, blades 3-ternately divided, with relatively broad segments; reproductive scapes more than 1-flowered; involucral leaves similar to basal leaves, with free petioles, similar to basal leaves; flower axis relatively long, fruiting heads therefore ± cylindrical; tepals numerous (> 5), deciduous, yellow, red or bluish; pollen tricolpate; achenes sessile, ovoid, not compressed, with inconspicuous

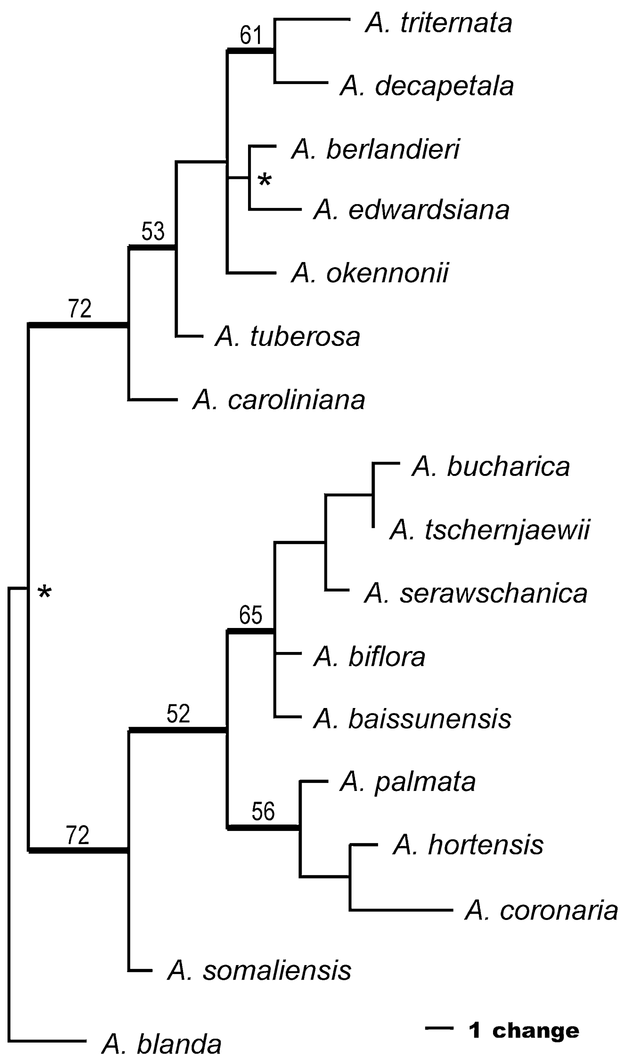


**Figure 9.** Phylogram of *Anemone* section *Anemone*, based on the cladistic analysis of 20 morphological characters (see Table 2) with *A. blanda* from section *Tuberosa* as the outgroup. One of the 18 most parsimonious trees (length = 58, Ci = 0.50, Ri = 0.72) with the two branches collapsing in the strict consensus tree marked *. Bootstrap values are inserted below branches, those > 50% are shown by medium, those > 75% by thick lines.

margins and relatively short hairs; basic karyotype $x = 8$, diploid, with average chromosome length and DNA content, but without conspicuous heterochromatic chromosome banding (as in *A. blanda*). This profile indicates that none of the extant taxa of section *Anemone* or section *Tuberosa* corresponds completely to the postulated plesiomorphic and assumed ancestral character profile of the section, but that *A. somaliensis* and some North American members of subsection *Carolinianae* come relatively close. Thus, the present diversity of section *Anemone* is the result of numerous apomorphic developments, as reflected by the diagnoses of its subsections, species and varieties.

## DISCUSSION

### Monophyly, phylogenetic position and main groups of *Anemone* section *Anemone*

The 16 species of *Anemone* section *Anemone* range from the Mediterranean to Central Asia and from North to South America and share a large number of morphological characters, regarded as apomorphic within the genus. The most important are the tuberous rhizomes, reduced inflorescences (1–3 flowers) and lanate-villose, ± compressed achenes. This unique character profile corresponds to the monophyly of the section demonstrated by plastid and ribosomal DNA restriction analyses (Hoot *et al.*, 1994; Hoot, 1995b). More recently, this has been verified by sequences from plastid and nuclear DNA (Ehrendorfer & Samuel, 2001; Schuettpelz *et al.*, 2002). Further support comes from our new phylogram (Fig. 8, Table 1), based on a sequence analyses of the plastid *atpB-rbcL* intergenic spacer, which also includes approximate geological dates for important nodes.

How do all these data relate to recent efforts towards a phylogenetic classification of *Anemone* and related genera of subtribe Anemoninae (e.g. Hoot *et al.*, 1994; Hoot, 1995b; Tamura, 1995)? First, it is obvious from Figure 8 that the section *Anemone* clade belongs to the crown group of *Anemone s.s.* which emerges from node N6 of our tree and consists of five subgroups of taxa. Their close relationships are not only apparent from the small number of genetic changes which separate them and the chronological proximity of their divergence (N6 = 9.6, N7 = 9.4, N8 = 9.09, N9 = 7.7 Mya), but also from the fact, that some limited hybridization between these subgroups is still possible, as shown by Madahar (1967) for *A. parviflora* michx. (close to *A. drummondii*) × *A. palmata*.

Informal names were already given to most of the five subgroups of the crown group in Figure 8 by Hoot *et al.* (1994): '*Nemorosa*' (*A. nemorosa* and *A. ranunculoides*), '*Blanda*' (*A. blanda*), '*Multifida*' (*A. multifida, A.virginiana* and *A. sylvestris*), '*Baldensis*' (*A. drummondii*) and '*Coronaria*' (*A. coronaria, A. hortensis, A. pavonina, A. palmata* and *A. caroliniana*). Furthermore, Hoot *et al.* (1994) assembled all these subgroups within a broadly circumscribed section *Anemone*, whereas Tamura (1995) delegated them to his heterogeneous subgenera *Anemonanthea* and *Anemone.* In contrast to this, and considering the available data, we propose to arrange these subgroups within only one subgenus *Anemone* as members of the sections *Anemonanthea*, *Tuberosa, Eriocephalus* (with subsections for the subgroups '*Multifida*' and '*Baldensis*') and *Anemone s.s.*, as shown in Table 1.

The '*Nemorosa* group' is named after *A. nemorosa*, the type species of section (or subgenus) *Anemonanthea*. *Anemone nemorosa* is closely related to and forms hybrids with *A. ranunculoides* and both have the chromosome base number $x = 8$. Formerly (e.g. Tamura, 1995), *A.* section *Anemonanthea* was thought to also include taxa with $x = 7$ (e.g. *A. deltoidea* Hook., *A. keiskeana* Ito, *A. baicalensis* Turcz.), but, since the DNA restriction analyses by Hoot *et al.* (1994) became available, it is clear that these taxa have to be separated (Ziman *et al.*, 2004) and placed close to the genera with $x = 7$ (e.g. *Anemonastrum* and *Hepatica*).

The '*Blanda*' group of Hoot *et al.* (1994), including *A. blanda*, *A. apennina* and *A. caucasica*, has often been united with either section *Anemonanthea* or section *Anemone*. Both alternatives are strongly contradicted because the taxa of the '*Blanda* group' have a deviating morphological profile (see INTRODUCTION, Fig. 9 and Table 2) and aberrant seedlings (Förster, 1999) and differ in their karyotypes and DNA contents (Rothfels *et al.*, 1966: Fig. 2; Baumberger, 1970: Abb. 9; Marks & Schweizer, 1974). Taken together, DNA restriction site analysis (Hoot *et al.*, 1994), sequence data (Ehrendorfer & Samuel, 2001; Schuettpelz *et al.*, 2002) and our new DNA phylogram (Fig. 8) clearly support the separation of the '*Blanda*' group as a distinct section *Tuberosa* (Ulbr.) Juz. Schuettpelz & Hoot (2000) suggested a sister relationship between *A. blanda* and *A. thomsonii* Oliver from the alpine zone of the high East African mountains. Nevertheless, this species has no tubers and has stalked carpels and achenes, and is listed under *Anemone* section *Kilimandscharica* (Ulbr.) Tamura by Ziman *et al.* (2006). Its phylogenetic relationships need to be clarified, but it could be distantly related to section *Anemone* and *A. somaliensis.*

According to Tamura (1995) the '*Multifida*' and '*Baldensis*' species groups (the latter represented here by *A. drummondii* only) correspond to section *Eriocephalus* Hook.f. & Thomson and its subsections *Brevistylae* Ulbr. and *Longistylae* Ulbr. The taxa of the former show a relatively high mutation rate compared with the other taxa of the crown group, as shown in Figure 8. The different position of the two provenances of *A. multifida*: (1) from South America and (2) from North America in the phylogram needs to be clarified.

The '*Coronaria*' group (Hoot *et al.*, 1994) corresponds to the present concept of section *Anemone s.s.* Its morphological and cladistic (Fig. 9), cytogenetic and molecular differentiation (Fig. 8) and the distribution pattern of its taxa (Figs 10–14) clearly suggest the recognition of four subsections: (1) subsection *Somalienses* in North-East Africa; (2) subsection *Anemone* in the Mediterranean area; (3) subsection *Biflorae* in South-West and Central Asia; and (4) subsection *Carolinianae* in North and South America. The relationships of these subsections and their taxa and their phylogeography will be discussed in the following sections.

## The North-East African *Anemone* subsection *Somalienses*

The only species of this subsection, *A. somaliensis*, was described by Hepper (1971) as an endemic from northern Somalia, closely related to *A. hortensis*. However, we noted only some differential characters shared with subsection *Anemone* and more correspondence with subsection *Biflorae.* A unique plesiomorphic character of *A. somaliensis* within the Old World members of section *Anemone* is its tricolpate pollen, otherwise found only in the New World subsection *Carolinianae.* Thus, *A. somaliensis* can be regarded as a relatively plesiomorphic and isolated link between the Mediterranean, the South-West + Central Asiatic and even the New World species groups of *A.* section *Anemone*. It is sister to subsections *Anemone* and *Biflorae* in our morphology-based cladistic phylogram (Fig. 9). It is remarkable that the ambivalent relationships of *A. somaliensis* with the two other Old World groups are also evident from a comparative chorological analysis of the flora accompanying this local species in the mountains of northern Somalia, a flora which exhibits both Mediterranean and Asiatic affinities (Fici, 1991). All this justifies subsectional rank for *A. somaliensis* and its classification as a palaeo-Mediterranean relic species. In view of the lack of karyological and DNA-analytical data, further detailed studies, particularly on natural populations of this interesting species, appear very desirable.

## The Mediterranean *Anemone* subsection *Anemone*

The Mediterranean subsection *Anemone* and its three, clearly separated species, *A. coronaria, A. hortensis s.l.* and *A. palmata*, are well characterized by the multidisciplinary data presented. They share several, partly apomorphic features: the tendency towards hypogeal germination (Förster, 1999); the presence of stipule-like appendages at the base of the basal leaves; dissimilar, ± connate and sessile involucral leaves; tepals with 3–9 basal veins; and specialized pollen apertures. The phylogenetic coherence of these species within subsection *Anemone* is clearly

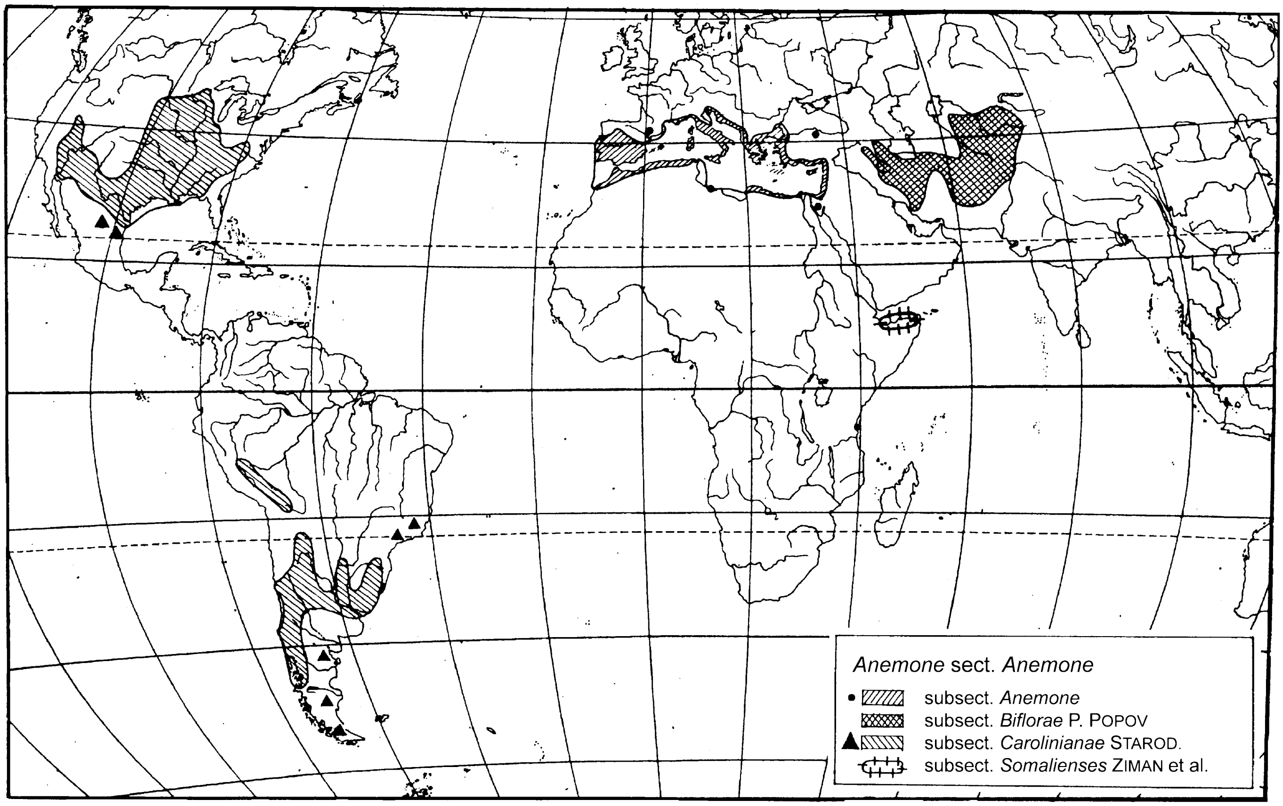


**Figure 10.** Intercontinental distribution of *Anemone* section *Anemone* with its four subsections.

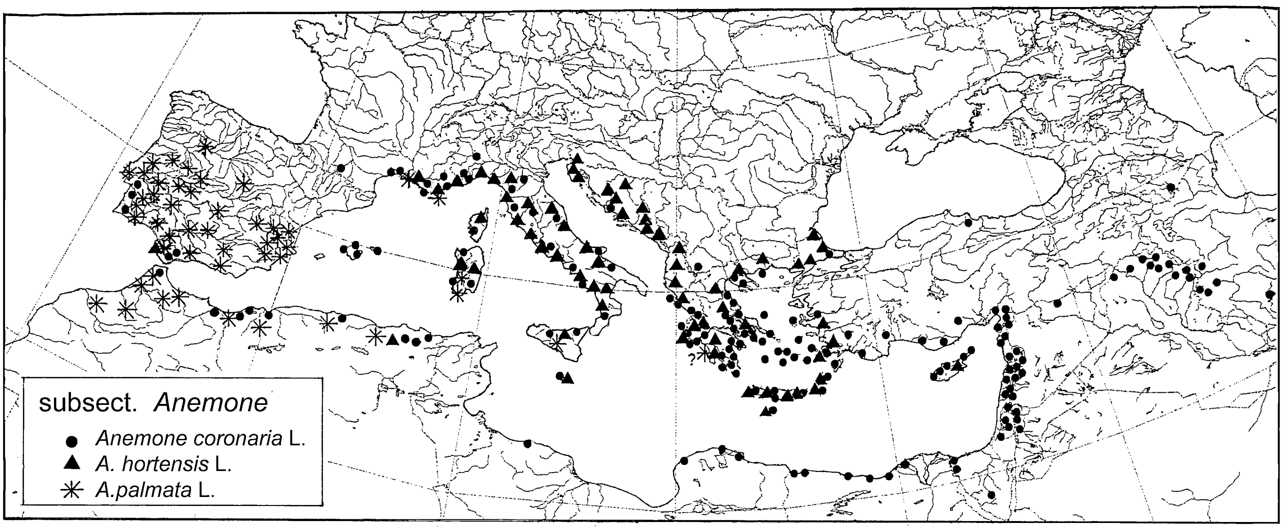


**Figure 11.** Distribution of taxa of *Anemone* subsection *Anemone* in the Mediterranean area and south-west Asia.

documented by previous molecular data (Hoot *et al.*, 1994; Ehrendorfer & Samuel, 2001; Schuettpelz *et al.*, 2002) and by the *atpB-rbcL* phylogram presented here (Fig. 8). Therefore, we regard it as unnecessary to separate *A. palmata* from the other two species as a monotypic subsection *Oriba s.s.*, as proposed by Starodubtsev (1991).

Nevertheless, there is strong phylogenetic divergence between and even within the three species of subsection *Anemone*. This is documented not only by

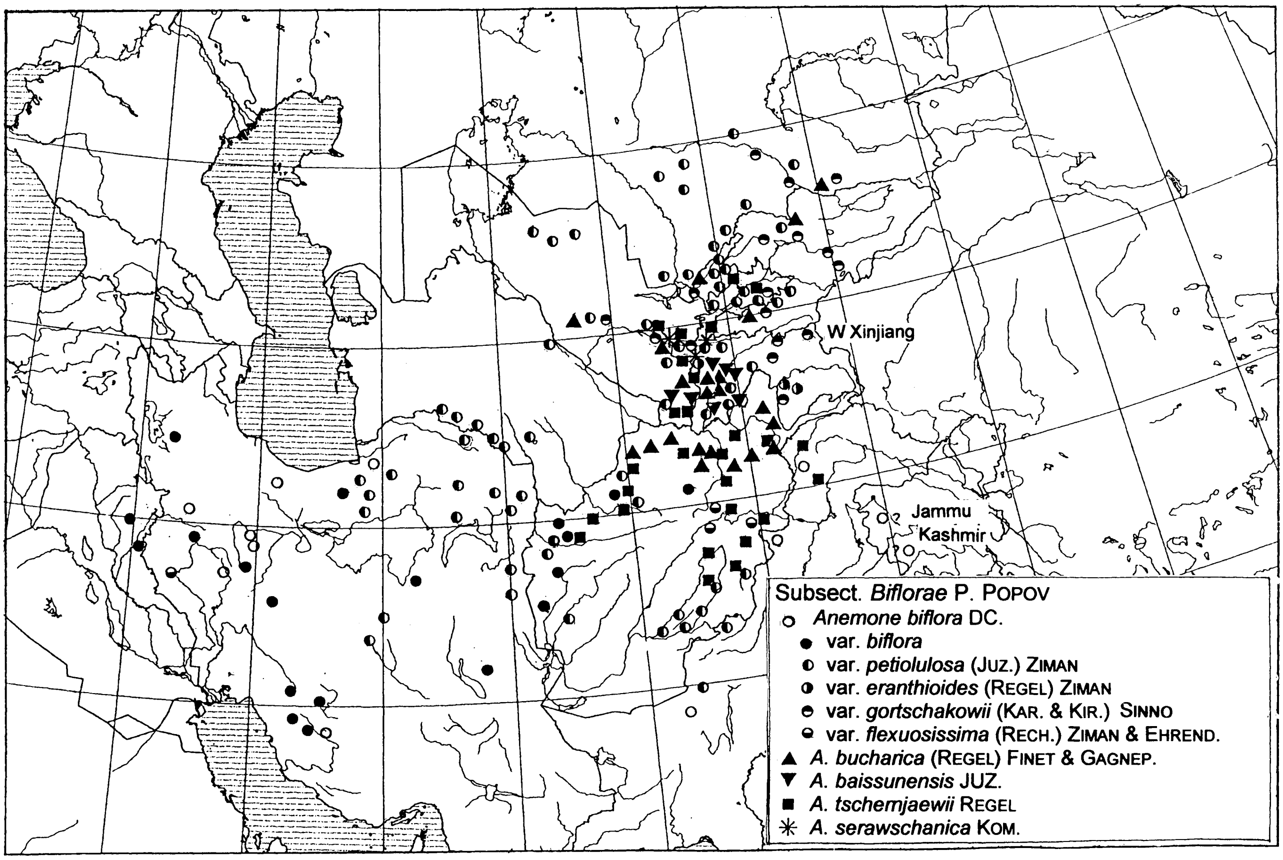


**Figure 12.** Distribtution of taxa of *Anemone* subsection *Biflorae* in south-west and Central Asia. Open circles and regional names indicate localities for which no precise data on varieties or species are available.

our own morphological analyses (Fig. 9) but also by the the phenetic studies of Sinno-Saoud *et al.* (2007) concerning *A. coronaria* and *A. hortensis.* These two species differ in the presence or lack of stolon-like rhizomes, the shape of their leaves and tepals, including number of basal veins and anastomoses, length of achene styles, width of achene ribs and their spiroaperturate vs. pantoporate pollen. The West Mediterranean *A. palmata* deviates from both by its almost entire basal leaves, yellow flowers and pantocolpate pollen.

Karyological and cytogenetic aspects are of great importance for the relationships within subsection *Anemone* (Madahar, 1967 and Maïa & Venard, 1976: scheme of affinities fig. 18). *Anemone hortensis s.l.* (including *A. pavonina*, etc.) exhibits the basic *Anemone* karyotype (Baumberger, 1970: Abb. 6) with four metacentrics, one submetacentric and three acrocentrics (two with satellites), and occasional B chromosomes (Signorini & Mori, 1994). The karyotype of *A. coronaria* is superficially similar, but differs in details: reciprocal translocations have occurred (Baumberger, 1970: Fig. 11), the chromosomes are shorter and the DNA amount is clearly reduced (Heimburger, 1959; Rothfels *et al.*, 1966; Madahar, 1967). *Anemone palmata* exhibits an even more distinct karyotype with four metacentric and four acrocentric chromosome pairs (see also Médail *et al.*, 2002, but disregard Baumberger, 1970: his data and figure 3C and 14.4 are based on a misidentified plant).

As a consequence of all this structural karyotype differentiation within subsection *Anemone*, no hybrids have been obtained in crossing experiments between *A. palmata* and the other taxa. Diploid $F_1$ plants from *A. coronaria* × *A. hortensis* (as *A. pavonina*) exhibit meiotic asyndesis and other disturbances and are sterile, but it was possible to produce an experimental allotetraploid from these $F_1$ plants with normal meiosis and apparent fertility (Maïa & Venard, 1976). In contrast, typical *A. hortenis* and so-called *A. pavonina*, exhibit only slight chromosome structural differences and their hybrids are fertile (Maïa & Venard, 1976); thus, the two form only one biological species. All this corresponds to the relationships of species of subsection *Anemone* in nature: in spite of considerable overlap in their Mediterranean distributions (Fig. 11), only occasional hybrids between *A. coronaria* and *A. hortensis* have been reported.

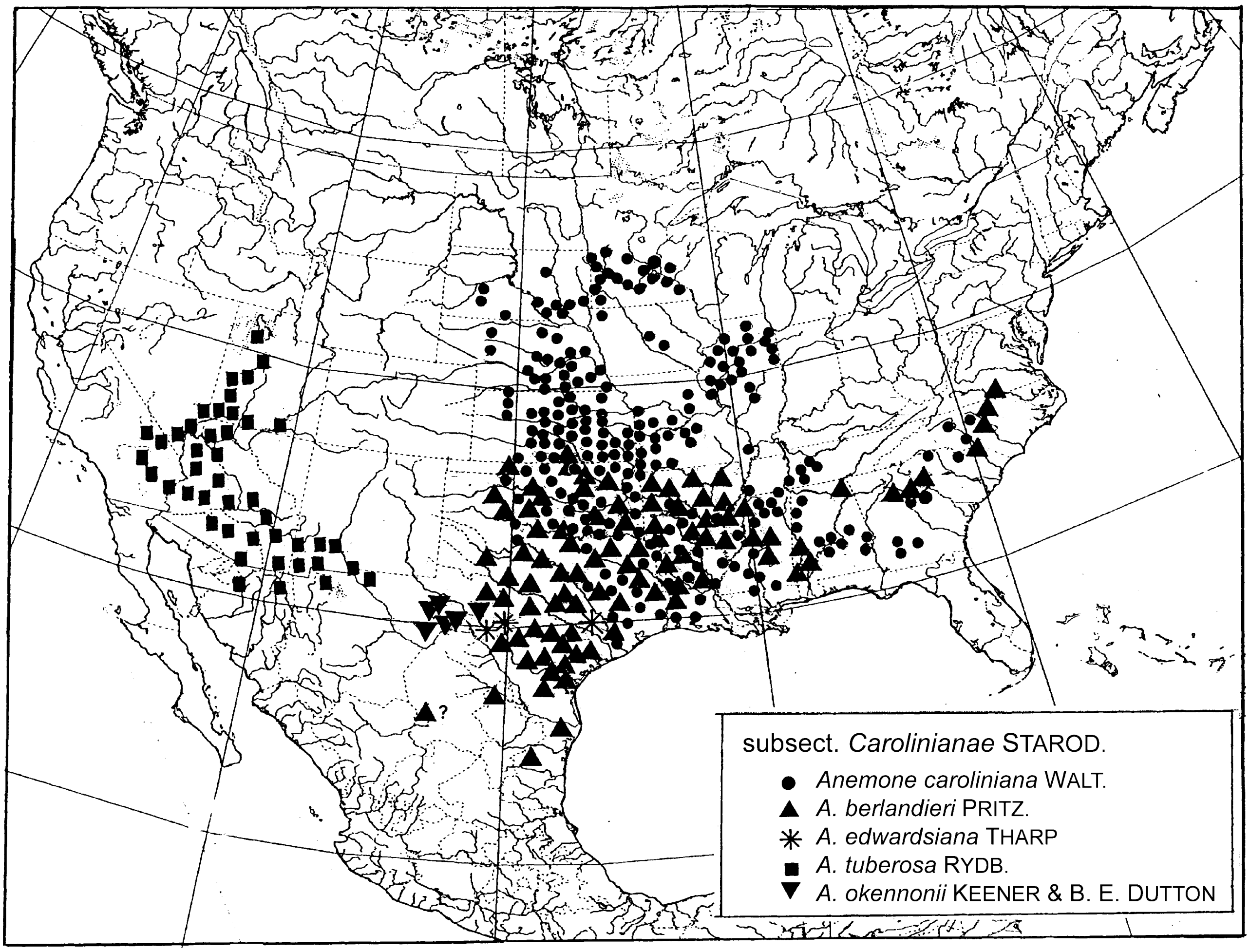


**Figure 13.** Distribution of taxa of *Anemone* subsection *Carolinianae* in North America.

The phylogenetic affinities of subsection *Anemone* are supported by available DNA data. A comparison of their *atpB-rbcL* spacer sequences (Fig. 8) shows that *A. palmata* is separated by 21 substitutions from *A. coronaria* and by 25–29 from *A. hortensis*/*A. pavonina*; *A. coronaria* and *A. hortensis*/*A. pavonina* differ by 16–19 base pair substitutions; but a difference of only five exists between samples determined as *A. hortensis* and *A. pavonina* (Ehrendorfer & Samuel, 2001). With respect to the number of plastid and ribosomal restriction site differences, there are 29 separating *A. coronaria* from *A. hortensis*, but none between the latter and samples determined as *A. fulgens* and *A. pavonina* (Hoot *et al.*, 1994: Fig. 2; no data for *A. palmata*).

Considering the geological dates from the DNA phylogram (Fig. 8), speciation within subsection *Anemone* could have started from ancestors somewhat similar to *A. somaliensis* and *A. hortensis* at about 8 Mya ago, followed by the divergence of *A. palmata* and subsequently of *A. coronaria* and extant *A. hortensis* in the period between 7.5 and 6.5 Mya in the late Miocene. Considerable infraspecific differentiation as documented for *A. hortensis* (2.2 Mya) has continued since the Pliocene to the present.

## THE SOUTH-WEST AND CENTRAL ASIATIC *ANEMONE* SUBSECTION *BIFLORAE*

The five South-West to Central Asiatic species grouped under subsection *Biflorae* in the present survey share the following relevant and partly apomorphic differential characters: leaf petioles without basal stipule-like appendages; involucral leaves not connate at base; flowers with only 5(–6) persistent, elliptic–ovate, yellow to red tepals; pollen pantoporate (Ziman *et al.*, 1998); fruiting heads globose; and achenes ovoid with narrow marginal ribs not more than 0.1–0.2 mm wide. Karyotypes have been studied in three diploid provenances of subsection *Biflorae* determined as *A. biflora*, *A. bucharica* and *A. petiolulosa* (Madahar, 1967). They deviate somewhat from

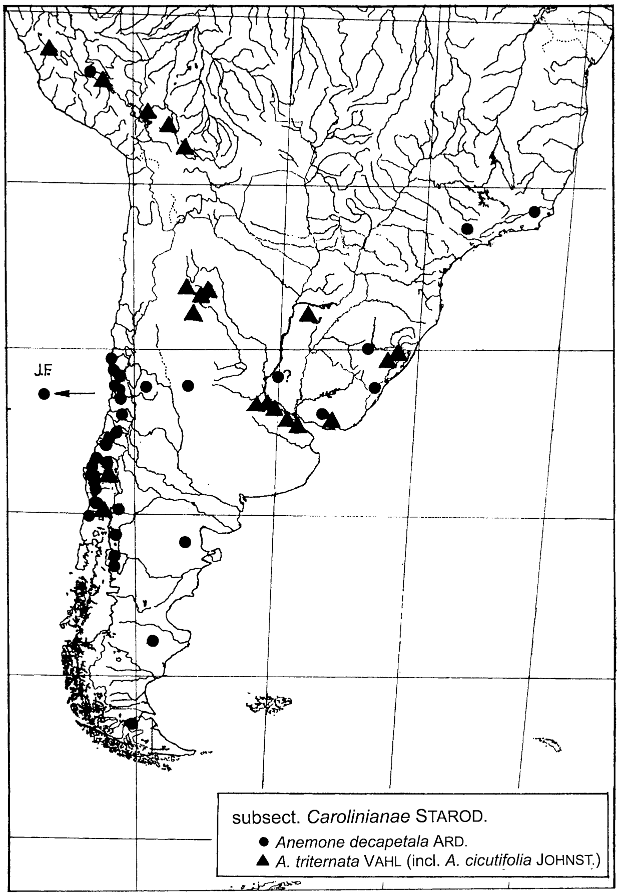


**Figure 14.** Distribution of taxa of *Anemone* subsection *Carolinianae* in South America.

the basic karyotype of section *Anemone* (e.g. *A. hortensis*) by having only three (instead of four) metacentric and two (instead of one) submetacentric, but also three acrocentric, chromosome pairs (two with satellites). Among these provenances, karyotypes exhibit only small structural differences.

The close affinities between members of the *A. biflora* species group and their relatively great distance from *A. coronaria* and *A. hortensis* in subsection *Anemone* was well documented in the recent phenetic study of Sinno-Saoud *et al.* (2007). This, the differential characters, our cladistic phylogram (Fig. 9) and the karyotype homogeneity of the *A. biflora* group support its monophyly and justify its classification as subsection *Biflorae*, separate from subsection *Anemone*.

Molecular data are not yet available for the subsection, but from Figures 8 and 9 we postulate an origin of *A.* subsection *Biflorae* from ancestors similar to *A. somaliensis, A. hortensis and A. coronaria* in the late Tertiary (Pliocene). This divergence was accompanied by shortening of their floral axes and a reduction in tepal number. In contrast to subsection *Anemone*, the taxa of subsection *Biflorae* appear close to each other and more prone to hybridization: Evidently, they are still in an active phase of evolutionary radiation.

Juzepchuk *et al.* (1937) divided subsection *Biflorae* into two series, *Biflorae* and *Tschernjaewianae*, the first with *A. baissunensis*, *A. biflora s.l.* and *A. bucharica*, the second with *A. seravschanica* and *A. tschernjaewii*. This subdivision is only partly supported in Figure 9. Sinno-Saoud *et al.* (2007: Figs 1, 2), in their phenetic analysis, placed *A. eranthioides* (= *A. biflora* var. *eranthioides*) and *A. tschernjaewii* on one side of their diagrams, *A. bucharica* on the other and *A. biflora* with var. *gortschakowii*, var. *biflora* and var. *petiolulosa* in a central position; *A. baissunensis* and *A. serawschanica* were not considered. The complex distribution pattern of the taxa of subsection *Biflorae* is illustrated in Figure 12. Our hypothesis for their phylogenetic differentiation is presented in the section on phylogeography.

### The North and South American *Anemone* subsection *Carolinianae*

A cytotaxonomic revision on the North and South American species of section *Anemone*, corresponding to subsection *Carolinianae*, was published by Joseph & Heimburger (1966). Floristic–taxonomic treatments are available for South America from Lourteig (1951) and for North America from Keener & Dutton (1994) and Dutton *et al.* (1997). Present knowledge about distribution patterns are summarized in Figures 13 and 14. The seven species of subsection *Carolinianae* are united by the following main differential characters: numerous, mostly deciduous tepals, typically with five basal veins but normally lacking vein anastomoses; fruiting heads elongate; achenes subglobose, compressed, with short styles (only 0.4–1.6 mm long) and marginal ribs distinct, mainly 0.5–1 mm wide; and pollen mainly tricolpate. This and our cladistic analysis (Fig. 9) demonstrate the phylogenetic coherence of the subsection. According to Joseph & Heimburger (1966), members of section *Carolinianae* share the basic karyotype of *Anemone* (as in *A. hortensis*). The North American species also have about the same karyotype length and genome sizes, but, in the South American taxa, chromosome size and DNA content are clearly reduced (Rothfels *et al.*, 1966). Successful experimental crosses are possible within subsection *Carolinianae*, but not with other taxa of *Anemone* (Joseph & Heimburger, 1966).

There is also clear evidence from DNA restriction site analyses (Hoot *et al.*, 1994; Hoot, 1995b) that the New World subsection *Carolinianae* is monophyletic and related to Old World members of section *Anemone.* As suggested by the number of separating restriction sites (r.s.; Hoot *et al.*, 1994: Fig. 2), genetic distances are greatest between *A. caroliniana* and *A. berlandieri* (10 r.s.), which are widely sympatric. *Anemone tuberosa* in the west is also far from *A. berlandieri* (9 r.s.), *A. edwardsiana* (7 r.s.) and *A. caroliniana* (7 r.s.) in the east, whereas the vicarious *A. berlandieri* and *A. edwardsiana* are close (4 r.s.). No convincing evidence for a hybrid origin of *A. edwardsiana*, as suspected by Joseph & Heimburger (1966), is available. Comparable molecular data have not yet been obtained for the North American *A. okennonii* and the South American taxa.

The morphological similarities and cytogenetic affinities among species of subsection *Carolinianae* correspond well with the molecular data mentioned above and their distribution pattern (Fig. 13). Within the North American members, *A. caroliniana* in the Central, South and South-East USA is set apart by its small orbicular tubers, stolon-like rhizomes, the presence of stomata on upper and lower leaf sides and ellipsoidal achenes with narrow marginal ribs (as in the Mediterranean *A. coronaria*). The karyotype of *A. caroliniana* is slightly different and shorter than that of the sympatric *A. berlandieri*. Their one hybrid exhibits meiotic disturbances and less than 5% of its pollen is fertile (Joseph & Heimburger, 1966). The following two taxa are characterized by their monomorphic basal leaves without stipule-like bases and petiole-like lower parts of the involucral leaves: *Anemone tuberosa* and the more recently described *A. okennonii* (Keener & Dutton, 1994) form a vicarious species group in the South-West USA. Although similar to *A. tuberosa* (and to *A. edwardsiana*), the specific status of *A. okennonii* is confirmed by our analyses. Another rather distinct specis pair is formed by *A. berlandieri* and *A. edwardsiana*. They are ecogeographically vicarious in the south + south-east and share several essential characters (e.g. leaf petioles with stipule-like bases and dissimilar basal and involucral leaves).

The South American taxa of subsection *Carolinianae* are still imperfectly understood. Since the description of *A. decapetala* by Arduino (1764) from Brazil, this species was considered to be also present in North America (Ulbrich, 1905/1906, and earlier and later authors). Only Joseph & Heimburger (1966), Keener & Dutton (1994) and finally Dutton *et al.* (1997) made it clear that North American plants placed in *A. decapetala* in fact belong to *A. berlandieri* (= *A. heterophylla*) and that the South American populations are specifically distinct. This conclusion is supported by the production of highly sterile South/North American hybrids, produced by Joseph & Heimburger (1966). They obtained experimental diploid $F_1$ hybrids, between *A. triternata* on the one hand and *A. caroliniana* and *A. berlandieri* on the other hand, as well as triploid $F_1$ hybrids between the tetraploid taxon from Chile (treated here under *A. decapetala* and discussed below) and the same North American species. These $F_1$ hybrids exhibited numerous univalents, bridges, fragments, etc. during pollen mother cell meiosis and were nearly 100% pollen-sterile. Thus, North and South American taxa of subsection *Carolinianae* are separated by considerable crossing barriers as a result of structural differentiations of their genomes (inversions, etc.) and by a general decrease in DNA content (Rothfels *et al.*, 1966). These findings are in line with their morphological differences, i.e. the more numerous tepals and the greater length of achene hairs in the South American as compared with the North American species.

Relationships among the South American members of subsection *Carolinianae* are apparently complex, as is evident from the number of species described after the publication of *A. decapetala* and their distribution (Fig. 14). All these species, including *A. triternata*, were treated by Lourteig (1951) as synonyms under two varieties of *A. decapetala*. In contrast, Joseph & Heimburger (1966) maintained not only these two but also *A. cicutifolia* as a third diploid South American species and presented differential morphological characters as well as maps of their distribution. However, one of us (SNZ), after the examination of all available herbarium material of *A. decapetala* and *A. cicutifolia*, found 'acute vs. obtuse tips of the tepals' to be too variable and no other reliable differential characters. Furthermore, Joseph & Heimburger (1966) documented a tetraploid cytotype from Chile (Concepción, Villa San Pedro, where it occurs together with diploid *A. triternata*) and from an unspecified locality, and they suspected this to be an undescribed tetraploid species. With the limited material available to us, the status of these tetraploid populations cannot be evaluated. Thus, at present only the specific separation of two South American species appears possible, with *A. triternata* differing from *A. decapetala* by its similar basal and involucral leaves, solitary flowers and persistent, basally 3-veined tepals. Nevertheless, we are aware that this taxonomic approach is still provisional, as these taxa exhibit peculiar, widely overlapping and disjunct distributions (Fig. 14). Furthermore, the problem of the more northern Andean localities of *A. cicutifolia* and the Chilean tetraploids is still unresolved. There is an obvious need for further studies, particularly on natural populations.

## PHYLOGEOGRAPHY OF *ANEMONE* SECTION *ANEMONE*

From the *atpB-rbcL* phylogram and the approximate geological dates, from the morphological differentiation and the derived cladistic tree and from the distribution of the extant taxa, it is possible to derive a phylogeographic interpretation of the taxa of section

*Anemone* (Figs 8–14). Thus, we hypothesize that progenitors of the section with a plesiomorphic character profile (see above) settled during the Upper Miocene (*c.* 9–8 Mya ago) in open habitats of a subtropical vegetation of South-West Asia and adjacent North-East Africa. Such an Old World origin of the section is supported by three facts: (1) there is much more genetic divergence among the Old than the New World members of section *Anemone*; (2) the sister clade of section *Anemone*, section *Tuberosa*, occurs in the Central and East Mediterranean and adjacent South-West Asia; and (3) the sister group of the Eurasian taxa, *A. somaliensis*, is found in North-East Africa (Fig. 9).

We postulate that the monotypic subsection *Somalienses*, with *A. somaliensis*, is a relic derived from such ancestors of section *Anemone*. It has maintained nearly all of the supposedly plesiomorphic features of section *Anemone* (e.g. involucral leaves similar to basal ones and not connate at the base, numerous tepals, tricolpate pollen) and still grows in local subtropical South-West Asiatic/palaeo-Mediterranean vegetation in the mountains of northern Somalia.

The Mediterranean species of subsection *Anemone* exhibit a more apomorphic character profile (e.g. involucral leaves reduced and connate at base, apertures of pollen grains specialized, etc.). Their common ancestor with a basic karyotype had evidently already evolved 8–7 Mya ago, before the late Miocene Messinian salinity crisis of the Mediterranean. Subsequent allopatric differentiation led relatively quickly to the origin of three taxa with their distribution centres in the East, Central and West Mediterranean area: *A. coronaria, A. hortensis* and *A. palmata*. After considerable structural chromosomal changes and the establishment of crossing barriers, these species of subsection *Anemone* must have achieved their present, widely sympatric distribution. That they have a preglacial age is evident from the infraspecific differentiation in *A. hortensis*, with the split of the deviating *A. pavonina* genotype at N11 being dated at 2.2 Mya in the early Pleistocene.

The expansion of progenitors of subsection *Biflorae* from the South-East Mediterranean to South-West and Central Asia could have occurred during the Pliocene and Pleistocene. This Mediterranean/Oriental–Turanian pattern of distribution is found in many genera; for example, *Asperula* L., *Carthamus* L., *Crucianella* L., *Pistacia* L., *Valerianella mi*ll., the *Asphodelus* L.–*Asphodeline* Rchb.–*Eremurus* M.Bieb. group, etc. For the phylogeographic differentiation of subsection *Biflorae*, the morphology-based phylogram (Fig. 9) and the distribution map (Fig. 12) suggest an early divergence of *A. baissunensis* as a regional endemic in East Uzbekistan and West Tadjikistan. In a second step and from *A. biflora*-like progenitors, the locally endemic and somewhat isolated *A. serawschanica* might have split off, followed by the more southern *A. tschernjaewii* and the more northern *A. bucharica*. In a final phase, we postulate the extension *A. biflora s.l.* over the whole area of the subsection, from Iran to Pakistan and Southern Kazakhstan and its eco-geographical differentiation into var. *biflora* more in the west, var. *petiolulosa* mostly in the centre and north, var. *gortschakowii* in the east and, more locally, of var. *eranthioides* in the central area (Tadjikistan) and of var. *flexuosissima* in the south-east (Central Afghanistan). Today, nearly all these taxa overlap in the mountains from Northern Afghanistan to East Uzbekistan and Northern Tadjikistan, where subsection *Biflorae* has its present centre of diversity.

How can we explain the most remarkable distribution gap within section *Anemone*, the transatlantic disjunction between the Old World subsections and the New World subsection *Carolinianae*? Their morphological divergence is limited to a few apomorphies (reduction of tepal veins and anastomoses, subglobose fruiting heads, compressed achenes, etc.), altogether affecting eight characters (Fig. 9). Many plesiomorphic similarities, including the basic karyotypes in *A. hortensis* and taxa of subsection *Carolinianae*, have persisted to the present day. Nevertheless, there is a complete barrier to hybridization between the Old and New World members of section *Anemone* (Joseph & Heimburger, 1966; Madahar, 1967). In spite of that barrier, there is a relatively low degree of genetic divergence (only 14 plastid and ribosomal DNA restriction sites: Hoot *et al.* 1994). With respect to the *atpB-rbcL* intergenic sequence (Fig. 8), *A. caroliniana* is separated by only nine mutation steps from *A. palmata* and by five from *A. coronaria* + *A. hortensis.* The relevant node N10 is dated at 6.9 Mya, corresponding to the Upper Miocene of the late Tertiary. At that time, the first North American representatives of section *Anemone* must have originated from Mediterranean ancestors. These early migrants evidently brought the plesiomorphic character of tricolpate pollen to the New World. Today, this feature is limited in the Old World to *A. somaliensis*, whereas it is common in present day subsection *Carolinianae*.

Quite an number of transatlantic disjunctions are known which are comparable with the case of *Anemone* section *Anemone*; for example, in *Arbutus* L., *Cercis* L., *Chrysosplenium* L., *Cneorum* L., *Corema* D.Don, *Helianthemum* Gray, *Liquidambar* L., *Pinguicula* L., *Pistacia*, *Styrax* L., *Valerianella*, etc. (see, e.g. Thorne, 1973; Axelrod, 1975; Donoghue, Bell & Jianhua, 2001; Fritsch *et al.*, 2001; Tiffney & Manchester, 2001; Xiang & Soltis, 2001). These authors have discussed the origins of transatlantic disjunctions at temperate and meridional latitudes from various aspects: palaeoclimates, changing palaeogeography (e.g. volcanic islands as 'stepping stones' on the mid-Atlantic Ridge), fossil evidence from the early to the late Tertiary, recent phylogenetic DNA data from various clades, etc., and they arrived at different dates and different explanations for these transatlantic disjunctions. For section *Anemone*, we have to consider its light, long-haired and easily wind-born achenes and the geologically relatively young, late Miocene date of the disjunction. We propose to think of still *A. somaliensis*-like early West Mediterranean representatives of subsection *Anemone* as source populations for a long-distance dispersal event establishing the progenitors of subsection *Carolinianae* in South-East North America. Such an assumption would allow enough time for the following differentiation processes of subsection *Carolinianae* in North America and its subsequent long-distance expansion into South America.

On the base of what is known about the relationships and distribution of subsection *Carolininanae* taxa in the New World (see above and Figs 9, 13, 14), initial phylogenetic differentiation could have started in South-East North America with an east to west eco-geographical divergence between progenitors of *A. caroliniana* and *A. tuberosa*. From the latter, further differentiation apparently resulted in a stepwise expansion back to the east, with *A. okennonii, A. edwardsiana* and *A. berlandieri* now widely overlapping with *A. caroliniana*. Morphological similarities and the results of experimental hybridization strongly support the hypothesis that it was from the *A. berlandieri* + *A. edwardsiana* subgroup that *A. decapetala*-like progenitors reached South America, again by long-distance dispersal. The resulting South American populations of subsection *Carolinianae* are apparently still in a phase of active diversification, including the origin of polyploids.

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