A CYTO-TAXONOMIC STUDY IN PALESTINIAN ANAGALLIS ARVENSIS L.

FANIA KOLLMANN AND NAOMI FEINBRUN
(*Department of Botany, The Hebrew University, Jerusalem, Israel*)

ABSTRACT

Four infraspecific taxa of *A. arvensis* L. from Palestine are treated: 1. subsp. *arvensis* var. *arvensis*; 2. subsp. *arvensis* var. *caerulea* (L.) Gouan; 3. subsp. *arvensis* var. *latifolia* (L.) Lange, and 4. subsp. *foemina* (Mill.) Schinz & Thellung.

The controversial nomenclature of these taxa is discussed. *A. caerulea* is typified by B. L. Burtt in an Appendix to this paper.

The infraspecific variability and the reliability of diagnostic characters in *A. arvensis* have been studied on Palestinian plants, both in herbarium and in the field.

The distribution and ecological requirements of the four taxa in Palestine are examined.

The following chromosome numbers have been found in E Mediterranean plants: var. *arvensis* n=20, var. *caerulea* n=20, var. *latifolia* n=40 and subsp. *foemina* n=20.

Chromosome numbers for the whole genus are brought together. It is concluded that all infraspecific taxa of *A. arvensis* are tetraploids, except var. *latifolia* which is an octoploid.

Data from the literature on spontaneous and experimental crosses within *A. arvensis*, which demonstrated the genetical isolation of the two subspecies, are discussed.

NOMENCLATURE

In connection with the preparation of a revised Flora of Palestine, there is need of a revision of *Anagallis*. In the present paper, four taxa of Palestinian *Anagallis arvensis* L. have been cyto-taxonomically investigated. These are:

(1) subsp. *arvensis* var. *arvensis* (corolla scarlet)

(2) subsp. *arvensis* var. *caerulea* (corolla blue)

(3) subsp. *arvensis* var. *latifolia* (corolla blue)

(4) subsp. *foemina* (corolla blue)

The key given below (p. 175) brings out the main differences between these four taxa.

The currently accepted subdivision of *Anagallis arvensis* into two subspecies, subsp. *arvensis* and subsp. *foemina* (Mill.) Schinz & Thellung, was based by Marsden-Jones and Weiss (1938, 1960) on a series of macro- and micro-morphological characters of leaves and flowers (p. 152, 1938).

The most significant diagnostic differences between the two taxa are the number of cells in the glands found on the petal-margin and the shape of the terminal cell of each gland, as well as the number of glands on the petal. Whereas in subsp. *arvensis* the glands are numerous, 3-celled, with a globular terminal cell, in subsp. *foemina* the glands are few, 4-celled and with an elongate terminal cell. These diagnostic differences were found to be constant and reliable in our material and correlated with leaf and flower characters; namely the upper leaves of subsp. *foemina* are usually lanceolate and the pedicels not or only slightly exceeding the leaf-length (Plate 9: 5–8).

In Species Plantarum (1753) Linné described two species of the group concerned, *A. arvensis* and *A. latifolia*. Later, in the Amoenitates (1759) he published *A. caerulea* as a species. The epithet *caerulea* has been subsequently used

by Gouan (1765). Gouan distinguished two varieties of *A. arvensis*: the scarlet-flowered β *phoenicea* and the blue-flowered γ *caerulea*.

Various pre-Linnean authors (Dodoens, 1553, 1557, 1559; Lobel, 1576; Bauhin, 1651) designated the scarlet-flowered form of *A. arvensis* as *Anagallis arvensis mas* and a blue-flowered form as *Anagallis caerulea foemina*.

Miller's *Anagallis foemina* published as a species (1768) was the cause of a later confusion between two blue-flowered forms of *Anagallis* in the literature.

The difficult problem of typification of *A. caerulea* L. and of var. *caerulea* (L.) Gouan is discussed and, in our opinion, solved by Mr. B. L. Burtt in the Appendix to this paper (p. 186). The typification is by Dodoens' illustration 61 (1553, 1559) quoted by Pena & Lobel in the Adversaria (1570). Linné's *A. caerulea* is based on Magnol (1676) who in turn cites Pena & Lobel's Adversaria for *A. caerulea foemina*. The drawing 61 by Dodoens of *A. caerulea foemina* represents, in our opinion, a somewhat compact specimen of var. *caerulea* with rather short flowering pedicels and ovate leaves. Similar specimens have been examined by us in herbaria and proved to be var. *caerulea* (L.) Gouan with 3-celled glands. On the other hand, this drawing does not depict subsp. *foemina* sensu Marsden-Jones and Weiss characterized by lanceolate upper leaves and flowering pedicels not exceeding the leaf in length.

Thus, we accept the epithet *caerulea* as *Anagallis arvensis* L. var. *caerulea* (L.) Gouan for the blue-flowered form of subsp. *arvensis* which, apart from the above mentioned characters of leaves and pedicels, has 3-celled petal-glands.

As to Miller's *A. foemina*, it would certainly be most desirable to examine the petal-glands of his specimens. However, the following remark by Miller (1768) seems to be decisive. It says: "The first (*A. arvensis*) is very common in the fields and other cultivated places in most parts of England. The second sort (*A. foemina*) is sometimes found wild in the fields, but is less common than the first in England. This is supposed to be only a variety of the first but from thirty years cultivating it, I can affirm it never alters, and *plants before they show their flowers are so different as to be easily distinguished from the first*". (Our italics). This remark seems to indicate that Miller's *A. foemina* differed from *A. arvensis* in its macro-morphological characters, i.e. characters of its leaves. Therefore, it most probably represented plants with 4-celled glands and lanceolate leaves.

The epithet *A. caerulea* was later published independently by Schreber (1771). It is, however, a later homonym of *A. caerulea* L. (Nathorst). This, as well as all combinations using "caerulea Schreb." at subspecific level, e.g. *A. arvensis* subsp. *caerulea* (Schreb.) Hartman, subsp. *caerulea* (Schreb.) Vollmann and subsp. *caerulea* (Schreb.) Schinz & Keller, should be abandoned. On the other hand, Schreber's *A. caerulea* is apparently synonymous with *A. foemina* Mill. (cf. Sprengel, Systema Vegetabilium 1: 570, 1825).

The status of subspecies is, in our opinion, appropriate for the plants characterized by 4-celled petal-glands, narrow petals, lanceolate upper leaves and relatively short pedicels. The epithet subsp. *foemina* (Mill.) Schinz & Thellung (1907) used by Marsden-Jones and Weiss (1938, 1960) is, therefore, accepted by us as the valid name of the taxon.

Linné (1753) considered *A. latifolia* a species by itself, though closely related to *A. arvensis*: "Notabilis foliis magnis et latis, caule compresso, *A. arvensi* attamen valde affinis". Several authors, such as Duby (1844) Boissier (1879) and Marsden-Jones and Weiss (1938) doubted whether *A. latifolia* deserved

specific rank, or whether it merely represented particularly vigorous mediterranean specimens of *A. arvensis*. Lange (1860-1865) accorded *A. latifolia* varietal rank. Pax & Knuth followed Lange, while Braun-Blanquet & Maire (1924) treated it as a subspecies.

We accept var. *latifolia* (L.) Lange as a variety of subsp. *arvensis*. It clearly belongs to this subspecies as indicated by its 3-celled glands, and is a gigas form which we later show to be a polyploid with the double chromosome number compared with var. *arvensis* and var. *caerulea*.

In accordance with the evidence brought forth above, we use the following nomenclature for the four taxa of *A. arvensis* L.:

1. subsp. *arvensis* var. *arvensis*
2. subsp. *arvensis* var. *caerulea* (L.) Gouan
3. subsp. *arvensis* var. *latifolia* (L.) Lange
4. subsp. *foemina* (Mill.) Schinz & Thellung

A third subspecies, subsp. *gentianea* (Beck) Domac (1955) (syn.: *A. arvensis* var. "*A. gentianea*" Beck, 1898; *A. arvensis* var. *gentianoides* Hayek, 1928), described from Yugoslavia, is reportedly intermediate between subsp. *arvensis* and subsp. *foemina* and characterized by a truncate petal-margin and 3-celled glands with a globular terminal cell. We can express no opinion with regard to the status of this taxon.

Key to infraspecific taxa of A. arvensis growing in Palestine

Subspecies of *A. arvensis*

1. Petal-glands few, rarely absent, 4-celled, the terminal cell elongate; upper leaves lanceolate; flowering pedicels, as a rule, not or only slightly exceeding the length of leaf; flowers blue; n=20 (Plate 9) . subsp. *foemina*

\+ Petal-glands numerous, 3-celled, terminal cell globular; upper leaves ovate to lanceolate; flowering pedicels considerably longer than leaf; flowers blue or scarlet. (Plate 9) . . . . . subsp. *arvensis*

Varieties of subsp. *arvensis*

1. Flowers scarlet; n=20 . . . . . var. *arvensis*

\+ Flowers blue 2

2. Leaves usually not exceeding 1·5 cm long and 1 cm wide; n=20 var. *caerulea*

\+ Leaves larger, usually 2–3 cm long and 1·5–2 cm wide; plants more robust with larger flowers and capsules than in previous vars.; n=40 var. *latifolia*

Taxonomy

I. Subsp. **arvensis**

1. var. *arvensis*

Syn.: *A. arvensis* L. β *phoenicea* Gouan, Fl. Monspel.: 29–30 (1765).
A. phoenicea Scopoli, Fl. Carn. ed. 2, 1: 139 (1772).
A. arvensis L. subsp. *phoenicea* (Scop.) Vollmann in Ber. Bayer. bot. Ges. 9: 44 (1904).

Duby, the author of Primulaceae in DC. Prodromus, described *A. arabica* Duby from the Yemen and *A. jacquemontii* Duby from the Punjab. These species are probably synonymous with var. *arvensis*.

Selected specimens*: Sharon Plain, env. of Zichron-Ya'aqov, verges of irrigated potato fields, 30 iv 1965, *Feinbrun & Kollmann*; Sharon, Kabbara, ditches, 16 iv 1926, *Zohary & Feinbrun*.

2. var. *caerulea* (L.) Gouan, Fl. Monspel. 29–30 (1765).

Syn.: *A. caerulea* L. (Nathorst) Amoen. Acad. 4: 479 (1759).
A. arvensis f. *caerulea* Lüdi in Hegi, Fl. Mitteleur. 5 (3): 1869 (1927).
A. arvensis f. *azurea* Hylander, Upps. Univ. Arsskr. 7: 256 (1945).

Selected specimens: Judean Mountains, Jerusalem, Mt. Scopus, 18.iii.1931, *I. Amdursky*; Negev, 3 km W of Beersheva, 15 iv 1949, *M. Zohary*; Upper Galilee, SW of Amiad, 8 iv 1960, *M. Zohary*; Gilead, banks of Yabbok river, 500 m, 2 v 1911, *Meyers & Dinsmore*.

3. var. *latifolia* (L.) Lange, Pugill.: 221 (1860–1865); Willk. & Lange, Prodr. Fl. Hisp. 2: 648 (1870); Hayek, Prodr. Pen. Balc. 2: 33 (1928).

Syn.: *A. latifolia* L., Sp. Pl. ed. 1: 149 (1753).
A. arvensis L. subsp. *latifolia* (L.) Br.–Bl. & Maire in Mém. Soc. Nat. Maroc. 8, 1: 214 (1924).

Specimens examined: Sharon Plain, env. of Zichron-Ya'aqov, verges of potato fields, heavy alluvial soil, 3 v 1965, *Feinbrun & Kollmann*. Arabia, Hail, 23 i 1943, *Fitzgerald*.

II. Subsp. **foemina** (Mill.) Schinz & Thellung in Bull. Herb. Boiss. ser. 2, 7: 497 (1907).

Syn.: *A. foemina* Miller, Gard. Dict. ed. 8, n. 2 (1768).
A. arvensis L. subsp. *caerulea* (Schreb.) Vollmann, in Ber. Bayer. Bot. Ges. 9: 44 (1904).

Selected specimens: S Shefela, E of Dvir, verge of a wheat-field, loess, 20 iv 1965, *Feinbrun*; Judean Mountains, between Tsuba and Eshtaol, irrigated fruit grove, 10 v 1965, *Kollmann*.

It is well known that in Western Europe among the various taxa of *A. arvensis* the scarlet-flowered subsp. *arvensis* var. *arvensis* predominates, while blue-flowered forms are comparatively rare. In the Mediterranean region scarlet and blue forms are about equally frequent (Taylor, 1955). In Palestine, on the contrary, the blue-flowered *Anagallis* is much more common than the scarlet-flowered. However, when starting this study, we had no data available to show whether the local blue-flowered *Anagallis* comprises both var. *caerulea* and subsp. *foemina*.

Extensive herbarium material (HUJ) of blue-flowered *Anagallis* from Palestine as well as from Greece, Turkey, Cyprus, Syria, Lebanon, Iraq and Saudi Arabia has been examined. The majority of specimens (ca. 450 sheets) had

* All specimens cited are from the Herbarium of the Hebrew University, Jerusalem (HUJ).

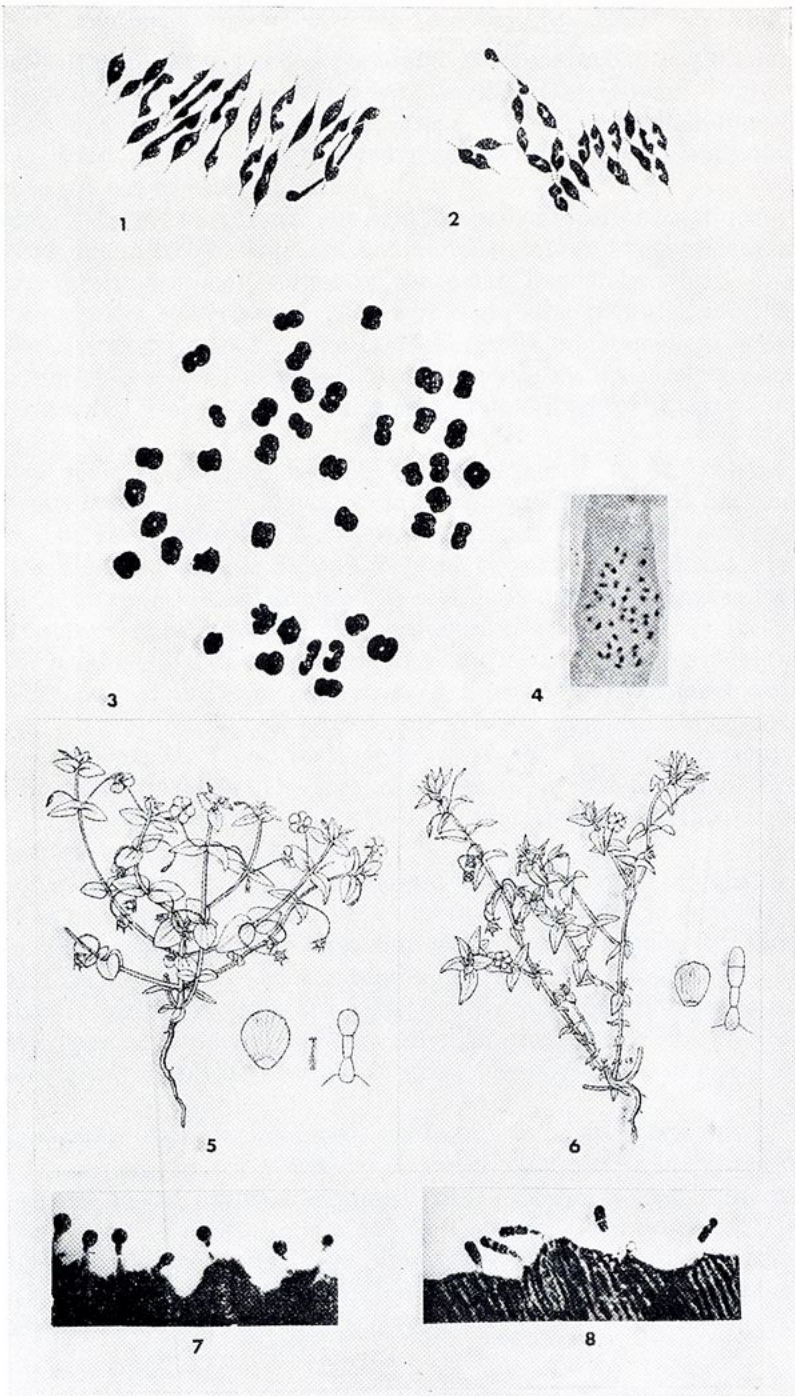

PLATE 9

1–3. Meiosis in *Anagallis arvensis* L. Metaphase I. Magnif. about x 1200.
1. subsp. *arvensis* var. *caerulea* (Israel).
2. subsp. *foemina* (Israel).
3. subsp. *arvensis* var. *latifolia* (Israel).
4. Root tip mitosis in var. *arvensis* (Delos). Magnif. about x 1200.
5. *A. arvensis* subsp. *arvensis* var. *caerulea* (drawn from a living plant coll. in Jerusalem). Plant habit x 0.5; petal about x 1.5.
6. *A. arvensis* subsp. *foemina* (drawn from a living plant coll. in Jerusalem). Plant habit x 0.5; petal about x 1.5.
7. *A. arvensis* subsp. *arvensis* var. *caerulea*. Petal-margin about x 150.
8. *A. arvensis* subsp. *foemina*. Petal-margin about x 150.

petals densely fringed with 3-celled glandular hairs ending in a globular cell and were identified as subsp. *arvensis* var. *caerulea* (L.) Gouan. There were only 15 sheets of subsp. *foemina* (Mill.) Schinz & Thell. from Palestine, Syria and Turkey which had sparingly fringed petals with 4-celled glands and an elongate terminal cell to each gland.

In the spring of 1965 we carried out field studies of local populations which showed that the most stable diagnostic characteristic of both subspecies (subsp. *arvensis* and subsp. *foemina*) is that of the petal glands. In subsp. *arvensis* the glands are always numerous, 3-celled with a globular terminal cell (Plate 9: 5, 7); 4-celled glands never occur. The petal-margin in our specimens is usually crenate-dentate (Plate 9: 7) and not "usually entire or obscurely crenulate" (Marsden-Jones and Weiss); nor is it truncate as described for subsp. *gentianea* Domac (1955).

Our subsp. *foemina* material is quite typical (Plate 9: 6, 8), with 4-celled hairs. Sometimes a few 3-celled glands may occur among 4-celled ones on the same petal, but the terminal cell is always elongate. Rarely specimens with glandless margins are found. Subsp. *foemina* can be distinguished also by shorter pedicels, dense lanceolate upper leaves and somewhat smaller flowers, usually with narrower non-overlapping corolla-lobes.

Unlike the petal-glands, the cells of the staminal hairs, reported as a diagnostic character for each of the two subspecies in Europe by Marsden-Jones and Weiss (1938) and by Šveřepová (1964), showed no significant differences in number in our material. Thus, we counted 5–11 cells in subsp. *arvensis* and 6–12 cells in subsp. *foemina*. The lack of correlation between the number of cells in staminal hairs and that of the petal-margin in Afghanistan plants was also noticed by Wendelbo (1958).

The number of glands on the petal-margin and the number of cells in each gland seem to be important also in the taxonomy of *Anagallis* in general. Thus, *A. linifolia* var. *collina* Schousb. has lanceolate leaves, similar to those of *A. arvensis* subsp. *foemina*, and its petal-margin is also fringed with sparse 4-celled glands; all gland cells are elongate, though longer than in subsp. *foemina*. We have no evidence to show whether this parallelism points to a closer genetic relationship between *A. arvensis* subsp. *foemina* and *A. linifolia* var. *collina*.

In 1965, together with var. *arvensis*, we found vigorous specimens of blue-flowered var. *latifolia* on heavy alluvial soil in the Sharon Plain. These plants were very similar to the Linnean specimen of *A. latifolia* as seen in the photograph of the Linnean Herbarium No. 208. 3. They displayed broad, dark-green leaves, long pedicels, relatively large flowers and larger capsules. The petal-glands in these specimens were 3-celled with a globular terminal cell, the cells larger than in other varieties of subsp. *arvensis*.

Distribution and Ecology

Subsp. *arvensis* var. *caerulea* is widespread in all districts of Palestine. It is a common segetal plant of crop fields, both dry-farmed and irrigated, but grows also in fallow fields and in natural open plant associations such as batha, clearings in the *Quercus calliprinos* maquis as well as open Tabor Oak forests. Concerning its occurrence in the batha, it should be mentioned that var. *caerulea* grows in Palestine in various batha-associations described by Eig (1946) and

Zohary (1962), such as the typical Mediterranean batha (Poterietum spinosi typicum) and its various semi-steppe variants which comprise, in addition to typical Mediterranean associates, a number of Irano-Turanian or Saharo-Arabian species.

As to edaphic conditions, var. *caerulea* occurs on various soil types, e.g. terra-rossa, rendzina, basalt rocky soil, calcareous sandstone, sandy clay, alluvial soils, gray calcareous steppe soils and loess.

Subsp. *arvensis* var. *arvensis* is much rarer in Palestine and limited mainly to wet habitats, e.g. heavy alluvial soils, ditches and river banks found in the Coastal Plain, Upper Galilee, and Coastal and Central Negev. In other Middle-Eastern countries (Syria, Lebanon, Turkey and Cyprus) its habitats seem to be similar.

Other colour variants of subsp. *arvensis*, known from Europe, very seldom occur in Palestine; white-flowered plants were once found in Upper Jordan Valley, a rare lilac-flowered plant was collected on Mt. Carmel and some pink-flowered in the Negev, all among the common blue-ones.

Subsp. *foemina* is much rarer in Palestine than var. *caerulea* and has not been recorded hitherto. We have found it so far only as a segetal plant, often in the same localities as subsp. *arvensis* var. *caerulea*. In Europe its ecological range is narrow compared with that of subsp. *arvensis* (Lehmann, 1952, 1956 and Kornas, 1962). The plant is confined there mostly to calcareous, slightly alkaline soils (pH 7,2–7,3), while subsp. *arvensis* also grows in more acid soils (pH 4,5–7,3).

We found fairly large populations of subsp. *foemina* in the Judean Mountains on terra rossa, in irrigated fruit groves and in ploughed fields. It was also collected in cornfields on loess and heavy alluvial soil in the Negev and Philistean Plain. None has yet been found on sandy clay. In Palestine, soils contain a comparatively high amount of lime, except the sandy clay, which is almost entirely lime-free.

There seems to be a slight difference in phenology between the two subspecies. While in March and April mainly var. *caerulea* is in flower, in May and June, when its flowering is declining, subsp. *foemina* is still in full flower. According to Martinoli (1959), in Sardinia relationships in this respect are quite different; the flowering time of subsp. *foemina* there is shorter and confined to February–June, whereas that of subsp. *arvensis* continues from March to September.

As to their distribution in the Middle East, both *A. arvensis* L. and *A. foemina* Mill. are cited by Rechinger (1959) from Amanus and Syria. Rechinger's statement (1964) that "*A. arvensis* seems to be represented in Iraq exclusively by subsp. *foemina* (Mill.) Schinz & Thellung" is not supported by evidence at hand. Specimens collected by Eig, Zohary and Feinbrun in the environs of Baghdad, Mosul, Kirkuk, all proved to belong to subsp. *arvensis* var. *caerulea*. Also Blakelock (1949) reported only *A. arvensis* L. subsp. *phoenicea* (Scop.) Schinz & Keller var. *caerulea* Lüdi (=var. *caerulea* (L.) Gouan) from Iraq, Baghdad, Daltawa and Bada.

A. arvensis var. *latifolia* (= *A. latifolia*) had been described by Linné from Spain. It is known at present from the Western and Eastern Mediterranean and from the adjoining Irano-Turanian and Saharo-Arabian countries (Mesopotamia, Iran, Arabia, Egypt, Socotra).

Chromosome numbers

The majority of authors who have reported chromosome numbers for *Anagallis arvensis* did not state explicitly which form of the species they had studied. It may be presumed, however, that the most common European form var. *arvensis* was studied when a chromosome count in *A. arvensis* is quoted. Several authors have reported 2n=40 or n=20 for *A. arvensis* (Table 3).

Reese (1957) cited n=20 for a blue-flowered *Anagallis* from the North-Algerian Sahara, which he identified as subsp. *caerulea* (Schreb.) Batt. and considered as a synonym of *A. foemina* Mill. There is, however, no clear evidence as to whether his plant belonged to var. *caerulea* or to subsp. *foemina*.

The number 2n=40 for subsp. *foemina* is quoted by Marsden-Jones (1960) though without any further details on the provenance of the plant examined or any reference to literature.

The present authors carried out chromosome counts in several taxa of *A. arvensis* (Table 1 and Plate 9: 1–4).

Table 1

Chromosome counts

Name	Provenance	Chromosome numbers 2n (mitosis in root tips)	n (Metaphase I and Diakinesis in PMC)
subsp. *arvensis* var. *arvensis*	Greece, Delos	40	
subsp. *arvensis* var. *caerulea*	Jerusalem, University Campus, terra-rossa		20
subsp. *arvensis* var. *latifolia*	Sharon Plain, Zichron Ya'aqov, alluvial soil		40
subsp. *foemina*	(a) N. Negev, Dvir, loess		20
	(b) Jerusalem, University Campus, terra-rossa		20

The chromosomes of var. *arvensis* were counted in somatic mitoses in root-tips of germinating seeds. The root-tips were pre-treated for 24 hours in distilled water at 4°C or for 3 hours in paradichlorobenzene, then fixed in acetic alcohol (1: 3) and squashed in 2% aceto-orcein. In other taxa Diakinesis or Metaphase I were studied in PMCs, squashed in aceto-carmin after a brief fixation in acetic alcohol. Meiosis proceeds very rapidly in *A. arvensis* and division stages were rare.

The results of chromosome counts and details regarding the provenance of the examined plants are summarized in Table 1.

The number n=20 has been found in two varieties of subsp. *arvensis*, var. *arvensis* and var. *caerulea*, as well as in subsp. *foemina*. In var. *latifolia* which can be regarded as a gigas variant of var. *caerulea*, a double chromosome number, n=40, has been counted. Forty more or less equal bivalents were found in Diakinesis and Metaphase I (Plate 9: 3). No multivalents were observed.

The size of stomata has been compared between two specimens of var. *latifolia* in which chromosomes were counted and that of three plants of var. *caerulea*, as shown in Table 2. The result suggests that the mean and the spread of the size of stomata in var. *latifolia* is larger than in var. *caerulea*. An exact statistical test on more plants has not been carried out, however.

The possibility that *A. latifolia* was a polyploid was mentioned by Nilsson (1938) and by Haffner (1946). Our *a priori* assumption of its being an autopolyploid was not corroborated by the regular pairing and by the absence of multivalents observed in our material throughout meiosis.

Table 2

LENGTH OF STOMATA IN MICRONS IN VAR. LATIFOLIA AND VAR. CAERULEA

Plant number	Number of stomata	Mean	Standard Error
var. *latifolia*			
1	30	44.66	0.83
2	30	39.38	0.47
var. *caerulea*			
1	20	32.34	0.48
2	20	32.78	0.57
3	20	33.66	0.54

In another species, *A. linifolia*, Haffner (1964) found that a gigas form, var. *collina*, had a double chromosome number, n=20, and larger stomata than var. *eulinifolia* with n=10. In this case, however, 1% of multivalents appeared and Haffner concluded that var. *collina* was an autopolyploid.

Taylor's (1955) remark in connection with Hedberg's counts in *A. serpens* subsp. *meyeri-johannis* (see our Table 3), that "apparently plants with larger parts have larger numbers of chromosomes" is also applicable to the situation in *A. arvensis* and *A. linifolia*.

Table 3 summarizes all available chromosome counts in *Anagallis*.

In the genus *Anagallis* as a whole two main basic chromosome numbers are found, x=10 and x=11.

The first four taxa of Table 3 belong to subgenus *Anagallis*, whereas *A. tenella* and *A. serpens* subsp. *meyeri-johannis* form part of subgenus *Jirasekia* (Schmidt) P. Tayl. In the two species of the latter subgenus, *A. tenella* and *A. serpens*, varying chromosome numbers were recorded. The basic number of *A. tenella*, a West European and West Mediterranean species, seems to be x=11. In *A. serpens* subsp. *meyeri-johannis*, a mountain species of Central Africa, x=11 appears again, both on the diploid and hexaploid level. On the strength of cyto-taxonomical evidence, Löve (1963) recommended the revival of the genus *Jirasekia* for *A. tenella*.

A. linifolia of subgenus *Anagallis* shows the lowest chromosome number of the genus and the subgenus. The basic number of subgenus *Anagallis* is thus 10. Consequently all subspecific taxa of *A. arvensis* are tetraploids with the exception of var. *latifolia*, which is an octoploid.

Rechinger's (1947) suggestion that *A. latifolia* may be a Mediterranean ancestral form of *A. arvensis* is not supported by the high polyploid level of *A. latifolia* found in our material.

Table 3

SYNOPSIS OF CHROMOSOME NUMBERS IN ANAGALLIS

Name	2n	n	Authors	Provenance
A. arvensis L. *		18	Tischler 1935	Schleswig-Holstein
		20	Wulff 1937	Schleswig-Holstein
		20	A. and D. Löve 1944	Scandinavia
		20	Haffner, in Tischler 1950	Central Europe
	40		A. and D. Löve 1956	Iceland
		20	Chuang et al. 1963	Taiwan
	40		Gadella and Kliphuis 1963	Hoofddijk near Utrecht
subsp. *arvensis*	40		Marsden-Jones and Weiss 1960	?
subsp. *arvensis* var. *arvensis*	40		Present paper	Greece, Delos
subsp. *arvensis* var. *caerulea* (L.) Gouan		20	Present paper	Israel
subsp. *arvensis* var. *latifolia* (L.) Lange		40	Present paper	Israel
subsp. *foemina* (Mill.) Schinz & Thell.		20	Reese 1957	Northern Sahara
	40		Marsden-Jones and Weiss 1960	?
		20	Present paper	Israel
A. linifolia L. var. *eulinifolia* Knuth		10	Haffner 1946	Bot. Gard. Tübingen seeds from Bot. Garden Coimbra and Madrid
var. *collina* Schousb.		20	Haffner 1946	Bot. Gard. Tübingen
A. tenella (L.) Murr.	22		Maude 1940	Britain
		9	Haffner 1946	Bot. Gard. Tübingen
		11	,,	seeds from Bot. Gard.
		10 (rarely)	,,	Coimbra
		20 (rarely)	,,	
A. serpens Hochst. subsp. *meyeri-johannis* (Engl.) Tayl.	20		Hedberg 1957	Elgon; Kilimanjaro
	22		,,	Elgon; Aberdare
	60–64		,,	Mt. Kenya
	66		,,	Aberdare

* Authors cited under *A. arvensis* give no data on the infraspecific taxon examined.

DISCUSSION OF THE BREEDING BEHAVIOUR AND CONCLUSIONS

Information on behaviour in crosses between subsp. *arvensis* and subsp. *foemina* and between varieties of subsp. *arvensis* is found in several papers by Marsden-Jones and Weiss (1935, 1938, 1960). This information is of major interest for the understanding of the taxonomic relationships within *A. arvensis*.

Marsden-Jones and Weiss found that as a rule F_1 hybrids between subsp. *arvensis* and subsp. *foemina* were sterile. These authors summarize their results as follows (1960): "When a large number of crosses were made between the true subspecies it was found that only from the var. *carnea** was it possible to obtain a fertile F_1. When other colours were used only sterile F_1 families resulted. Even with var. *carnea* there was frequently impaired fertility or complete sterility in F_1 and subsequent generations".

Sterility in F_1 hybrids between the two subspecies has been recently corroborated by Šveřepová (1964) in experimental crosses between the scarlet-flowered *A. arvensis* var. *arvensis* and the blue-flowered subsp. *foemina* (cited as *A. caerulea* Nath.).

Here it should be mentioned that the flowers of *A. arvensis* are self-pollinated as a rule and fully self-fertile. A small amount of cross-pollination occurs nevertheless.

Spontaneous hybrids between scarlet-flowered and blue-flowered *A. arvensis* have been reported from Western Europe since the last century. One hybrid has been described as *Anagallis* x *dörfleri* Ronniger (*A. arvensis* x *coerulea*). We were, therefore, glad to examine *A.* x *dörfleri* collected in Austria in 1903 and distributed as No. 4484 of the Herbarium Normale Dörfler along with the putative parents: the scarlet *A. arvensis* L., No. 4483, and the blue *A. coerulea* Schreb., No. 4485. *A.* x *dörfleri* had highly aborted pollen and almost no capsules. The scarlet-flowered *A. arvensis* No. 4483 had ovate leaves and 3-celled glands on the petals, whereas "*A. coerulea*" No. 4485 had the narrow lanceolate leaves and 4-celled glands of subsp. *foemina*. It is worth noting that the sterile hybrid No. 4484 had the 3-celled glands of *A. arvensis* and the lanceolate leaves of subsp. *foemina*. A similar character combination has been noted by Marsden-Jones (1935) in crossing experiments between subsp. *arvensis* and subsp. *foemina*. Šveřepová (1964), however, shows 4-celled glands in her hybrid.

The pollen sterility found in the hybrid between subsp. *arvensis* and subsp. *foemina* (*A.* x *dörfleri*), despite the equal chromosome numbers of the parents, could be ascribed to genic factors or to structural differences in chromosomes. In this connection the following citation of Marsden-Jones and Weiss (1960) is of interest: "When a sterile F_1, obtained by crossing subsp. *arvensis* Grenadine with subsp. *foemina* Grayish Violaceous Blue, was treated with colchicine by Blakeslee, a fertile shoot was produced and seed obtained". Presumably, in this case sterility was caused by structural differences and the doubling of chromosomes restored regular meiosis resulting in fertility.

Thus the two subspecies are practically inter-sterile both in experiment and in the field.

In intervarietal crosses within subsp. *arvensis*, Nilsson (1938) and Marsden-Jones and Weiss (1960) found fertility of the F_1. The flower colour of var. *caerulea* which is the most common taxon of the species in the Eastern Mediterranean, was shown to be recessive in crosses with other varieties of subsp. *arvensis*.

Summing up the data on morphology, distribution, chromosome numbers and breeding behaviour within *A. arvensis*, we come to the following conclusions.

(1) *A. arvensis* has differentiated into two main taxa, subsp. *arvensis* and subsp. *foemina*, separated by reproductive barriers, which restrict free gene

* One of the less common European colour variants of subsp. *arvensis*.

flow between them (sterility of F_1). The two taxa can be usually kept apart by the shape of leaves and length of pedicels; they always differ by the cell number of their petal-glands and by the shape of the terminal cell of the glands.

(2) Despite the existence of genetic barriers between the two taxa, we accept them here as subspecies in accordance with Marsden-Jones and Weiss (1938), and not as species (Hayek, 1913; Hylander, 1945; Janchen, 1958, 1963; etc.).

(3) In Palestine subsp. *arvensis* and subsp. *foemina* grow sympatrically, often in the same habitats, subsp. *foemina* being less common. Subsp. *arvensis* comprises var. *arvensis*, var. *caerulea* and var. *latifolia*. The blue-flowered var. *caerulea* is common almost all over the country, while the scarlet-flowered var. *arvensis* is much rarer and usually confined to wet habitats. The rather rare var. *latifolia* is a gigas variant of var. *caerulea*.

(4) The varieties of *A. arvensis* L. with n=20 are tetraploid and var. *latifolia* with n=40 an octoploid compared with *A. linifolia* L. (n=10) of the same subgenus (subgenus *Anagallis*). Var. *latifolia* can, therefore, hardly be regarded as an ancestral stock of the subgenus.

Acknowledgments

The authors express their sincere thanks to all who contributed in various ways to this study. Special thanks are due to Mr. C. C. Townsend (Kew), to Mr. J. E. Dandy (Brit. Mus. Nat. Hist., London) and to Prof. P. Wendelbo (Göteborg) for their generous help in questions of nomenclature and bibliography. The authors are grateful to Prof. D. Zohary for critically reading parts of the manuscript. Finally, thanks are due to Miss Z. Lookov and Mr. A. Grizi for valuable help in the cytological part and to Miss A. Vered for help with the chromosome drawings.

References

Bauhin, J. (1651). Historia Plantarum Universalis 3, 369. Ebroduni.

Beck von Mannagetta, R. B. (1898). Flora von Südbosnien und der angrenzenden Hercegovina. *Ann. Naturh. Mus. Wien* 13, 3.

Blakelock, R. A. (1949). The Rustam Herbarium, Iraq III. *Kew Bull.* 1949, 519.

Boissier, E. (1879). Flora Orientalis 4. Genevae et Basileae.

Chuang, T. I. et al. (1963). Chromosome numbers of the vascular plants of Taiwan I. *Taiwania* 1, 51–66.

Dodoens, R. (1559). De stirpium historia commentariorum imagines 60, 61.

Domac, R. (1955). Beiträge zur Flora Jugoslaviens. *Phyton* 6, 15–23.

Dörfler, I. (1903). Herbarium normale 4484; Anagallis Dörfleri Ronn.

Duby, I. (1844) in DC. Prodromus 8. Parisiis.

Eig, A. (1946). Synopsis of the phytosociological units of Palestine. *Palest. Jour. Bot., Jerusalem*, Ser. 3, 195–197.

Gadella, Th. W. I. & Kliphuis, E. (1963). Chromosome numbers of flowering plants in the Netherlands. *Acta Bot. Neerl.* 12, 196.

Gouan, A. (1765). Flora Monspeliaca. Lugduni.

HAFFNER, L. (1946). Zytologische Untersuchungen an Anagallis-Arten. Diss. Tübingen.
HARTMAN, J. (1846). Svensk Och Norsk Exc. Fl. Stockholm.
HAYEK, A. (1928). Prodromus Florae Peninsulae Balcanicae 2, Berlin.
HEDBERG, O. (1957). Afroalpine vascular plants. *Symb. Bot. Uppsal.* 15, 149–150.
HYLANDER, N. (1945). Nomenklatorische und systematische Studien über nordische Gefässpflanzen. *Uppsala, Univ. Arsskr.* 7, 256–257.
JANCHEN, E. (1958). Catalogus Florae Austriae 1, Wien.
—— (1963). Geänderte Namen von Gefässpflanzen Oesterreichs. *Phyton* 10, Fasc. 1–2, 47.
KNUTH, R. (1905). in Pax & Knuth. Primulaceae, *Pflanzenreich* 4, Leipzig.
KORNAS, J. (1962). Rodzaj Anagallis w Polsce. Fragm. Fl. et Geobot. 8, 2, 131–138.
LANGE, I. (1860–65). Pugillus Plantarum, Havniae.
LEHMANN, E. (1952). Von der Erforschung einer heimischen Pflanzenart Anagallis arvensis-Gauchheil. *Beitr. zur Biol. der Pflanzen* 29, 208–219.
—— (1956). Zur Unterscheidung der Formen von Anagallis arvensis im Mitteldeutschen Raum. *Wiss. Z. Univ. Halle* 6, 6, 928–929.
LINNÉ, C. (1753). Species Plantarum ed. 1. Holmiae.
LITARDIÈRE, R., (1938). Prodrome de la Flore Corse. 3, Paris.
LOBEL, M. de (1570). Stirpium adversaria nova, 194. Londini.
—— (1576). Plantarum seu stirpium historia, 247–248, Antverpiae.
LÖVE, A. (1963). Cytotaxonomy and generic delimitation. *Reg. Veg.* 27, 45–51
LÖVE, A. & LÖVE, D. (1944). Cytotaxonomical Studies on Boreal Plants III. Some chromosome numbers of Scandinavian plants. *Arkiv för Botanik* 31 A (12), 17.
—— (1956). Conspectus of the Icelandic Flora. *Acta Horti Gothob.* 20, 209.
—— (1961). Chromosome numbers of Central and Northwest European plant species. *Op. Bot.* 5, 277.
LÜDI, W. (1927). Anagallis in Hegi Flora von Mitteleuropa 5 (3). München.
MAGNOL, P. (1676). Botanicum Monspeliense, 17. Lugduni.
—— (1697). Hortus Regius Monspeliensis, 14. Monspelii.
MARSDEN-JONES, E. M. (1935). The genetics of Anagallis arvensis Linn. and Anagallis foemina Mill. *Proc. Linn. Soc. London.* Session 1934–35, part 4, 105–106.
—— (1960). The genetics and pollination of Anagallis arvensis ssp. arvensis and Anagallis arvensis ssp. foemina. *Proc. Linn. Soc. London*, 171, 27–29.
—— & Weiss, F. E. (1938). The essential differences between Anagallis arvensis Linn. and Anagallis foemina Mill. *Proc. Linn. Soc. London*, 150th session, 1937–38, part 3, 146–155.
MARTINOLI, G. (1959). Tassonomia ed ecologia del genere Anagallis della Sardegna. *Webbia* 15, 1–45.
MAUDE, PAMELA, F. (1940). Chromosome numbers in some British plants. *New Phytol.* 39, 17.
MILLER, P. (1768). The Gardener's Dictionary, ed. 8, London.
NILSSON, H. (1938). Anagallis arvensis L. und die Natur ihrer Farben varianten. *Hereditas* 24, 97–108.
NOTHDURFT, H. (1957). Die blaublühenden Sippen des Acker-Gauchheils. *Hess. flor. Briefe* 6, 66, 1–2.

RECHINGER, K. H., fil. (1948). Der Polymorphismus in der ägäischen Flora. *Oesterr. Bot. Zeitschr.* 94, 170, 220–221.
—— (1959). Zur Flora von Syrien, Libanon und angrenzenden türkischen Gebieten. Rel. Samuels. vi. *Ark. Bot.*, Ser. 2, 5, 321.
—— (1965). Flora of Lowland Iraq. Weinheim.
REESE, G. (1957). Ueber die Polyploidiespektren in der nordsaharischen Wüstenflora. *Flora* 144, 609, 617.
SCHINZ, H. & KELLER, R. (1909). Flora der Schweiz, ed. 3, 1. Zürich.
—— & THELLUNG, A. (1907). Beitraege zur Kenntnis der Schweizerflora vii. *Bull. Herb. Boiss.*, Ser. 2, 7, 497.
SCHREBER, J. (1771). Spicilegium Florae Lipsicae. Lipsiae.
SCOPOLI, J. A. (1772). Flora Carniolica, ed. 2, 1. Viennae.
SPRENGEL, C. (1825). Systema Vegetabilium. 1. Gottingae.
ŠVEŘEPOVÁ, G. (1964). Anagallis x doerfleri Ronn. *Preslia* 36, 3, 289–293.
—— (1965). Uebersehene Formen von Anagallis arvensis L. in der Tschechoslowakei. *Preslia*, 37, 333–334.
TAYLOR, P. (1955). The genus Anagallis in Tropical and South Africa. *Kew Bull.* 1955, 321–350.
—— (1958). Primulaceae in Flora of Tropical East Africa. *Kew Bull.* 1958–59, 2–19.
TISCHLER, G. (1935). Die Bedeutung der Polyploidie für die Verbreitung der Angiospermen. *Bot. Jahrb.* 67, 13.
—— (1950). Die Chromosomenzahlen der Gefässpflanzen Mitteleuropas. Gravenhage.
VOLLMAN, FR. (1904). Neue Beobachtungen über die Phanerogamen und Gefässkryptogamenflora von Bayern. *Ber. Bayer. Bot. Ges.* 9, 44.
WENDELBO, P. (1958). Primulaceae in Koeie & Rechinger, Symbolae Afghanicae iv. *Biol. Skr.* 10 (3), 75.
WULFF, H. D. (1937). Chromosomenstudien an der Schleswig-holsteinischen Angiospermen-Flora 1. *Ber. Deutsch. Bot. Ges.* 55, 264.
ZOHARY, M. (1962). Plant Life of Palestine. New York.

APPENDIX

THE TYPIFICATION OF THE EPITHET CAERULEA IN ANAGALLIS

B. L. BURTT

Much confusion and argument has centred on the use of the epithet *caerulea* in *Anagallis*. There are, however, only two questions that need to be answered: what was the first valid use of the epithet at the species level, and what was the first valid use in a rank below that of species.

The name *Anagallis caerulea* was first used by Linnaeus in 1756 in the dissertation of his pupil T. E. Nathorst, Flora Monspeliensis (p. 12; reprinted in Amoenitates Academicae, iv, 479: 1759). Here there is no description, merely a reference to Magnol's Botanicum Monspeliense.* In Magnol, also,

* The references are obtained by adding a serial number to the plants enumerated by Magnol. *Anagallis arvensis* is correctly given as 64, but *A. caerulea* is referred to as 94 (at least in the Amoenitates Academicae reprint which is all I have seen). This, however, is clearly an error for 65 and further on No. 94 is correctly quoted under *Papaver argemone* L.

there is no description and thus Magnol's own specimens, even if they could be found, would not be important. In turn, however, there is another reference: to '*Anagallis caerulea foemina* AD', that is to Pena & Lobel, Adversaria (1570 p. 194) here there are a few very brief words of description and the statement that the two, *Anagallis phoenicea mas* and *A. caerulea foemina*, differ only in colour. There is also a marginal note "Dod. Effig. 60, 61": this refers to Dodoens, De stirpium historia commentariorum imagines, 60, 61: 1559—there is an earlier edition of 1553 which I have not seen. The illustration given by Dodoens of the blue pimpernel is of a somewhat more compact plant than that of the scarlet one. The pedicels are not quite so long, but the upper ones are still decidedly longer than the leaves, which are ovate. There is, in fact, very little significant difference between the two figures, so little that J. Bauhin later (Hist. Pl. iii, 369: 1651) accidentally interchanged them, as pointed out to me by Professor Feinbrun.

Scanty though the descriptive matter may be, there is no adequate reason to reject *Anagallis caerulea* L. as *nomen nudum*. It is typified, through Magnol, by reference to Pena & Lobel and the illustration they cite. If the data so provided is inadequate the name could be rejected as *nomen dubium*, but it is a valid name and any later different use of the epithet for a species is illegitimate.

Another pair of illustrations of the two pimpernels is found in other works of the same period. The first publication seems to have been in Lobel's Plantarum seu stirpium Historia, or Stirpium Observationes as it is called on the running titles (p. 247, 248: 1576); they appear here with a reference to the Pena & Lobel Adversaria, which was reprinted at the end of the same volume. The same figures were reproduced in Dodoens (Hist. Pempt. Sex, 31, 32: 1583 and 1616). These two illustrations are even more alike than are the earlier pair and both of these are clearly *Anagallis arvensis*.

Turning now to the infraspecific level, we find that in 1765 Gouan published *Anagallis arvensis* γ *caerulea* (Flora Monspeliensis, p. 29, 30). Again, there is no original description supplied and therefore the identity of any specimens that Gouan may have had is immaterial. The varietal epithet (there is no reason to doubt that the Greek letter indicates varietal rank) is validated by the references. There are two of these, both to Magnol: to his Botanicum Monspeliense (p. 17) and to his Hortus Monspeliensis (p. 14). The first of these is the same as that given by Linnaeus, leading to Pena & Lobel. The obvious course is to accept this as typifying the variety: then the epithet *caerulea* has the same type at both species and varietal level: in fact because of this the varietal name may well be written *A. arvensis* var. *caerulea* (L.) Gouan.

If Gouan's reference to Magnol, Hortus Monspeliensis is followed up it leads, in the absence of a description, to J. Bauhin, Historia Plantarum (iii 369: 1651). As already mentioned above Bauhin's illustrations are the earlier ones of Dodoens, but he interchanged those of the scarlet and blue pimpernels. As might be expected the text does not mention any significant difference except flower colour. This reference does not, therefore, alter the botanical position and provides no reason against the typification of var. *caerulea* through Magnol's Botanicum Monspeliense to Pena & Lobel and Dodoens illustration they cite. This alone, then, is the basis of the valid use of the epithet *caerulea* in *Anagallis*.