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GEORGIA KAMARI & DIMITRIOS PHITOS

Karyosystematic study of *Fritillaria messanensis* s.l. *(Liliaceae)*

Abstract

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Fritillaria messanensis, in its wide circumscription, is studied karyosystematically across its entire geographical range, including Italy, Serbia-Montenegro, N Albania and Greece. Variation in morphological features, karyotype and ecological preferences are evaluated and its taxonomy is revised. Three subspecies are recognized and a key and descriptions presented. *F. sphaciotica,* a taxon previously considered synonymous with *F. messanensis,* is recognized at subspecific rank and the new combination *F. messanensis* subsp. *sphaciotica* validated. The occurrence of subsp. *gracilis* in Greece (Ionian Islands and W Sterea Ellas) is confirmed. The relationships of *F. messanensis* with taxa occurring in the Mediterranean region are discussed.

Key words: Balkans, S Italy, karyology, phytogeography, taxonomy.

Introduction

Fritillaria L., a genus of *Liliaceae* of considerable diversity in the northern hemisphere, comprises attractive, ornamental species. A total of 145 taxa of *Fritillaria* is recognized worldwide, of which c. 38 have been recorded from Turkey, c. 30 from China and c. 18 from California (Rix 1998). In Greece, the genus is represented by 24 species and 5 subspecies, all belonging to *F.* subg. *Fritillaria* (*F.* sect. *Eufritillaria* sensu Boissier 1884). Kamari & Phitos (2000) concluded that Greece constitutes a secondary evolutionary centre at least for subgenus *Fritillaria,* if not for the whole genus, confirming Rix (1971) who considered Turkey and Greece as secondary evolutionary centre for the genus when only 18 taxa in Greece were known. Its primary evolutionary centre (Rix 1971) is probably Iran, especially its northern parts, where the comparatively small number of 17 species and 4 subspecies (Rechinger 1990) represents four subgenera (*F.* subg. *Fritillaria* L., subg. *Petilium* Engl., subg. *Theresia* (C. Koch) Engl. and subg. *Rhinopetalum* (Fisch. ex Alexander) Engl.). The latter subgenus has recently been segregated as a separate genus by Bakhshi Khaniki & Persson (1997), mainly based on nectary morphology; however, most of the remaining morphological features and also karyological (Bakhshi Khaniki 1998, 2002) and molecular evidence (Rønsted & al. 2005) support its treatment as a subgenus of *Fritillaria* (Rix 2001).

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Fritillaria taxa are distributed throughout Greece, but are particularly common and diverse on the Aegean islands (Kamari & Phitos 2000). On the Ionian Islands, on the contrary, only three *Fritillaria* taxa are found, and this coincides with the comparatively low rate of endemism in the Ionian flora.

Fritillaria messanensis Raf. (*F.* subsect. *Trichostylae* sensu Boissier 1884, Turrill 1937, Turrill & Sealy 1980) has the widest distribution among all Greek *Fritillaria* taxa and is the most common species in the Ionian Islands. It is the name giving member of the circum-Mediterranean *F. messanensis* group (Rix 1971), which comprises taxa with linear and alternate leaves, the uppermost being usually in a whorl of three, broadly campanulate flowers, tessellated perianth segments with or without fascia and a 3-fid style. These characters are shared by *F. involucrata* All. from Italy (Pignatti 1982). From this and other related taxa *F. messanensis* is easily distinguished by its narrow leaves and broadly ovate nectaries.

Here we present the first karyosystematic study of *Fritillaria messanensis* s.l., based on material from its entire geographical range, and a taxonomic revision of the group.

Material and methods

The present study is based on more than twenty years of observations of *Fritillaria,* during which about 260 populations have been sampled and cultivated, most of them from Greece. For *F. messanensis* s.l. alone representatives of 41 populations have been cultivated. Cultivation has been done in pots outdoors, in the experimental Botanical Garden of the University of Patras. The populations karyologically investigated are indicated by an asterisk in the specimen lists, with accession numbers at the end of the specimen citation. The slide preparation technique applied in the study of the karyotype has been described in previous papers (Kamari 1984, Constantinidis & al. 1997). All populations examined are listed under the respective taxa and mapped in Fig. 1. Populations not documented by vouchers and not kept in cultivation are noted as observed (obs.).

Dried material was studied from the herbaria ATH, ATHU, B, C, G, G-BOIS, LJU, LY-Gandog., M, TAU, UPA, W, WU, WU-Hal. (abbreviations according to Holmgren & Holmgren 1998-), from the Museum of Natural History of Cefallonia-Ithaki (abbreviated here as MNHC-I) and the private herbarium of Pinatzi (herb. Pinatzi).

Results and discussion

Distribution

Fritillaria messanensis was originally described from Messina (Italy) and has a scattered distribution in Sicily (Messina), Calabria, Serbia & Montenegro, N Albania and large parts of Greece. The alleged occurrence of *F. messanensis* in Croatia and Herzegovina needs verification, since all the specimens checked by us do not belong to the taxon.

Fritillaria messanensis was first reported from Greece by Margot & Reuter (1839, 1841), from the island of Zakinthos. This report has been confirmed, whereas any reference of other *Fritillaria* taxa on Zakinthos island is erroneous. Boissier (1884: 181) indicated its existence in Peloponnisos (*Orphanides 846,* WU-Hal.!), in Kriti above the village Anopolis *(Heldreich),* in Kerkira *(Mazziari)* and Levkas *(Letourneux)*. The presence of *F. messanensis* on the island of Kerkira has never been confirmed (see also Baxter & Baxter 1974). From Kefallinia island it was first reported by Knapp (1965 as *"F. matthei",* nom. nud.), and later correctly reported by Phitos & Damboldt (1985: 145). The unexpected, somewhat isolated occurrence of *F. messanensis* on Mt Olimbos (its northernmost locality in Greece) is interesting, because these populations are morphologically closer to typical plants from Italy than to those from the Ionian area. In Kriti, *F. messanensis* grows all over the island, in a variety of altitudes and habitats.

According to Gramuglio & Arena (1973), *Fritillaria messanensis* has been the subject of a relatively recent and significant distribution reduction in the Mediterranean region, which frag-

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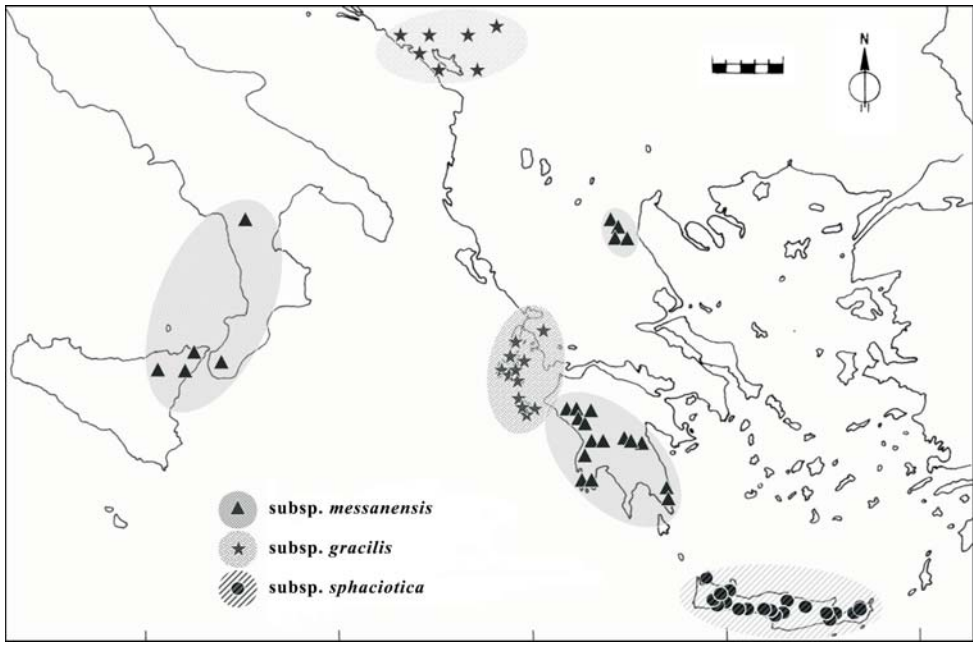


Fig. 1. Revised total geographical distribution of *Fritillaria messanensis* s.l.

mented its populations into small patches, surviving among or under the protection of fruticose perennials. This has been attributed to the major climatic changes that followed the last glacial period, reinforced by the recent, man-made large-scale woodland destruction. The disjunct distribution of *F. messanensis* on Mt Olimbos could be the result of the above process. *F. messanensis* is totally absent from the west, north and east of the Greek mainland, with the exception of Mt Olimbos, most areas of Peloponnisos (not in its N and NE parts) and W Sterea Ellas with Mt Boumistos. It is noteworthy that several other, mostly Ionian taxa (*Teucrium halacsyanum* Heldr., *Heliotropium halacsyi* H. Riedl, *Mentha pulegium* subsp. *cephalonia* Kokkini) or even Italian-Ionian taxa (*Campanula garganica* Ten. s.l., *Lomelosia crenata* subsp. *dalaportae* (Boiss.) Greuter & Burdet) are also found on Mt Boumistos, demonstrating a floristic connection with the Ionian area.

Fritillaria messanensis forms small, scattered populations in various habitats, mostly favouring stony places under a dense shrub canopy. It is often found among bushes of *Arbutus andrachne* L., *A. unedo* L., *Pistacia lentiscus* L., in clearings of *Quercus coccifera* L., woodlands or rarely in openings of *Pinus* or *Fagus* forests and olive groves, usually on calcareous substrates. As an exception, we found *F. messanensis* growing as a weed in cereal plantations of Zakinthos island. Altitudinally, it ranges from almost sea level, as in most Dalmatian and Ionian localities, Peloponnisos and Kriti (Plakias gulf), up to 2000 m in Greece (Mt Olimbos), Italy (Mt Pollino) and Serbia-Montenegro (Cakor pass).

Taxonomy

Fritillaria messanensis s.l. shows considerable variation across its geographical range. Several taxa at subspecific and varietal rank have been described (see Turrill 1937, Turrill & Sealy 1980), most of them attributed today to allies of *F. messanensis.* Because of similarities with related taxa and the difficulty to observe important characters in dry material (e.g., shape and size of the nectaries), plants of *F. messanensis* s.l. were frequently misidentified as *F. tenella* M. Bieb., *F.*

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Fig. 2. *Fritillaria messanensis* – A-B: subsp. *messanensis* from Peloponnisos (pop. no. 163-cult.); C: subsp. *gracilis* from Zakinthos, Ionian Islands (pop. no. 205-cult.).

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nigra Mill., *F. orientalis* Adam, *F. degeniana* Wagner or other synonyms of *F. montana* Hoppe and vice versa. The distribution of these two species, which are partly sympatric in the northern part of the range of *F. messanensis* s.l., adds to this confusion. As an example, Turrill & Sealy (1980) reported under *F. nigra* Mill. (conspecific with *F. montana*) synonyms that apply to typical plants of *F. messanensis* or to subsp. *gracilis.* The same authors noted that "satisfactory morphological criteria for separating *F. tenella, F. montana, F. orsiniana* Parl., *F. gracilis* (Ebel) Asch. & Graebn. and *F. neglecta* Parl., from one another or from *F. nigra* have not been found". This is partly true, particularly for plants of subsp. *gracilis* with very dark perianth segments without fascia from the Balkans (Fig. 3C) or the Ionian Islands (Fig. 3D). These remind of *F. montana* indeed; however, *F. montana* has longer, linear nectaries and a chromosome number of $2n = 18$ instead of $2n = 24$, which is found in all subspecies of *F. messanensis*.

Material reported as *Fritillaria gracilis* from the Dalmatian coast (W and S former Jugoslavia, N Albania) was classified by Rix (1978, 1980) as *F. messanensis* subsp. *gracilis* (Ebel) Rix. Previously, Ronniger (1941) had compared the morphology of his rich *Fritillaria* collections from Zakinthos with the description given by Gussone (1827-28, 1842-45) for *F. messanensis* from Sicily and concluded that the material corresponds to *F. gracilis,* not to *F. tenella* or *F. ionica* Halácsy, which had been reported incorrectly from the area by Boissier (1884: 179) and Halácsy (1904: 219). In that respect, Ronniger (1941) agreed with the view of Margot & Reuter (1839, 1841), who attributed the plants of Zakinthos to *F. messanensis*. Finally, Kamari (1991) stated that "the Ionian plants are closest to subsp. *gracilis*".

Fritillaria messanensis shows also a deviating variation on the island of Kriti. Gandoger (1916) described a new species under the name *F. sphaciotica* Gandog. from the areas of Malaxa and Sphakia (Nomos Chanion), noting that this new taxon differs from *F. messanensis* in characters of the flower, fruit and size of the filament. He also compared the plants of Kriti with material collected by H. de Boissieu on Zakinthos in April 1894 and noted that his plants from Kriti have filaments much longer than the anthers. However, a specimen in Gandoger's herbarium (*12990,* LY!) from Mt Kedros (Nomos Rethimnis) attributed to *F. sphaciotica* and reproduced as such by Rechinger (1943a) clearly belongs to a different genus. Rechinger (1943a) reported two *Fritillaria* species on Kriti, i.e. *F. messanensis* and *F. sphaciotica,* sometimes both from the same locality. Rechinger (1943b) reported again two *Fritillaria* species from the island, but this time he included *F. graeca* Boiss. & Spruner, as new to Kriti. After examining the pertinent specimen (*Rechinger 12231,* W!) we are convinced that it clearly represents *F. messanensis.* Several authors (e.g., Greuter 1973, Turland & al. 1993) followed Rechinger's misidentification and incorrectly mentioned the occurrence of *F. graeca* in Kriti. Whereas *F. graeca* should certainly be excluded from the flora of Kriti on the one hand, the populations of *F. messanensis* on the island clearly differ from the typical species on the other hand, as already reported by Kamari (1991) and Jahn & Schönfelder (1993).

The study of abundant herbarium material and observations on living plants of *Fritillaria messanensis* s.l. from all over its geographical range enabled a clear understanding of its infraspecific variation and permitted the subdivision of the species into three independent entities at subspecific level, as follows:

Fritillaria messanensis Raf. in J. Bot. Agric. 4: 272. 1814. – Described from the meadows of Messina, Sicily

Bulb subglobose to globose, up to 2(-2.5) cm in diameter. *Stem* up to 70(-110) cm tall, glaucous-green or glaucous purplish green. *Leaves* 7-12(-14), glaucous-green or purplish green, shallowly canaliculate, linear to narrowly lanceolate, often suberect, all alternate or the uppermost in a whorl of 3, the lower 0.2-1(-1.4) cm broad and (5-)7-10(-15) cm long. *Flowers* usually 1, rarely 2-3(-4), broadly campanulate to cylindrical, greenish or brownish to dark purplish brown outside, tessellated to obscurely tessellated, sometimes with more distinct purplish brown spots, with or without yellowish green fascia, colours paler inside, segments distinctly upturned at the mouth or not; *outer perianth segments* ovate-lanceolate, usually acute, 2.2-4(-4.5) × (0.9-)1-1.6 cm; *inner perianth segments* apiculate or rounded, 1.2-1.9(-2.2) cm broad. *Nectaries* 0.4-0.6 cm broad and

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Fig. 3. *Fritillaria messanensis* – A: subsp. *messanensis* from Mt Olimbos, Greece (pop. no. 50-cult.); B: subsp. *sphaciotica* from Mt Psiloritis, Kriti (pop. no. 32-cult.); C: subsp. *gracilis* from Mt Orjen, Serbia-Montenegro (photo: V. Stevanović); D: subsp. *gracilis* from Kefallinia, Ionian Islands (pop. no. 84-cult.).

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0.5-0.8(-9) cm long, ovate-lanceolate to broadly ovate, green to brownish green, situated 0.4-0.5 cm above the tepal base. *Filaments* up to 1(-1.3) cm, sparsely papillose. *Style* 1-1.3 cm, 3-fid to 1/3 or more than halfway, smooth. *Capsule* cylindrical, unwinged. *Chromosome number:* 2*n* = 24.

Fritillaria messanensis is a polymorphic species, typically with narrow, usually long leaves, rather broadly campanulate flowers and distinctive, large, broadly ovate (egg-shaped) nectaries, by which it is usually easily distinguishable from its related taxa.

Key to the subspecies of *Fritillaria messanensis*

1. Flowers shortly campanulate, 2.2-2.8(-3.3) cm long, usually obscurely tessellated, with unclear or without fascia; all leaves usually alternate . . . . . b. subsp. *gracilis*
– Flowers campanulate, (2.5-)3-4(-4.5) cm long, usually tessellated, with clear yellowish greenish fascia; the uppermost leaves usually in a whorl of 3 2
2. Stem 20-70(-110) cm tall, glaucous-green; leaves (0.5-)0.7-1(-1.4) cm broad, glaucous-green . . . . . a. subsp. *messanensis*
– Stem 10-20(-25) cm tall, purplish glaucous-green or often purple at the base; leaves 0.2-0.4(-0.6) cm broad, purplish glaucous-green . . . . . c. subsp. *sphaciotica*

a. subsp. ***messanensis***

Stem usually tall (up to 110 cm in humid places), glaucous-green. *Leaves* (0.5-)0.7-1(-1.4) cm broad, glaucous-green, usually narrowly lanceolate, often suberect, the uppermost usually in a whorl of 3. *Flowers* campanulate, 3-4(-4.5) cm long, usually tessellated, with yellowish-greenish fascia, segments distinctly upturned at the mouth. – Fig. 2A-B, 3A.

Variation. – *Fritillaria messanensis* subsp. *messanensis* is a variable taxon, with local forms found throughout its distribution area, and growing under different ecological conditions. The populations on Mt Olimbos (Fig. 3A) are quite similar to those from the locus classicus, particularly with respect to their robustness, the uppermost leaves, which are usually in a whorl of 3, and the usually upturned perianth segments at the mouth of the flowers. Variation is found in the populations growing in Peloponnisos, mainly referring to the number and position of the uppermost leaves. A specimen collected by *Baenitz* (M!) on the island of Kerkira (Corfu) was misidentified as *F. messanensis,* but actually belongs to *F. thessala* subsp. *ionica* (Halácsy) Kamari. *F. thessala* shares the feature of the uppermost leaves usually in a whorl of 3 and is often confused with subsp. *messanensis* in the Balkan Peninsula, where the distribution ranges of the two taxa overlap.

Specimens seen. – Italy: Province Calabria: *Regione Basilicata, Monte Pollino (on Calabrian border), open limestone, W-facing slope, c. 2000 m, 18.6.1997, *Jury 17375 & al.,* no. 206-cult. — Sicily: Province Messina: Messina, *Nicotia* (TAU; herb. Guadagno); *bulbs from the Herbarium Univ. Panormitanae, 22.7.1991, *Raimondo* (UPA), no. 156-cult.; *Monti Peloritani, in prossinuta della Caserma Brugnola (Casalveccio Siculo), sotto Pizzo Varna, 890 m, 13.5.1994, *Raimondo & Gianguzzi* (UPA), no. 190-cult.

Greece: Thessalia: Nomos Pierias: Mt Olimbos: 10.6.1951, *Goulimis 7314* (herb. Pinatzi); 1 km SE of the village Kokkinoplos, 1200-1300 m, 20.6.1970, *Strid & Bothmer 50* (C); supra coenobium Agios Dionisios, in ascensu ad refugium princeps (A), 1800-1900 m, 25.7.1971, *Greuter 9603* (ATH, B); Prionia, in grass among box bushes, 1000 m, 25.5.1972, *Baxter 260* (ATH); Abstieg von Hütte A bis Prionia, 2100-1000 m, 7.6.1972, *Klaus & al. 241* (W); *infra refugium EOS, in saxosis calcareis, 1800 m, 8.8.1973, *Phitos & al. 26997* (UPA), no. 50-cult. (Fig. 3A, 4A); N side, Papa Rema gorge, S of Vrondou, 500-650 m, 12.5.1974, *Strid & Andersen 8392* (C); on ascending path from Prionia to refuge A' "Spilios Agapitos", between *Fagus* forest and the place called Magalia, 1450-1700 m, 26.7.1978, *Stamatiadou 20876* (ATH); NE slopes of Metamorphosis, 1500 m, 23.5.1981, *Strid, Baden & Møller 134* (C); *supra locum Prionia, 1600-1780 m, 12.7.1986, *Tiniakou 1526* (UPA), no. 87-cult.; *NW slopes, at place Kaggelia, c. 1900, 4.8.1986, *Tzini* (UPA), no. 88-cult. — Peloponnisos: Nomos Arkadias: *Inter urbis Sparti et Tripolis,

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c. 6.5 km, in fruticetosis, 800, 14.3.1988, *Phitos & Kamari 20745* (UPA), no. 107-cult. (Fig. 4B). — NOMOS ILIAS: From Pirgos to "Arhea Olymbia" near the village Paleovarvasena, place called Mandres, 80-100 m, 30.3.1969, *Stamatiadou 4975* (ATH); inter pagum Figalia et templum Vasai, in petrosis et in agris ad viam, 20.4.1975, *Phitos & Kamari 18411* (UPA); *village Figalia, close to the branch of the river Neda, 26.3.1988, *Phitos & Kamari 26998* (UPA), no. 163-cult. (Fig. 2A); *between Vasae and Perivolia, close to the branch of the river Neda, in schist, c. 650 m, 19.3.1989, *Phitos & Kamari 26999* (UPA), no. 91-cult.; *Vasai, from the temple of Apollonos to Perivolia (on the right side of the street), *Quercus* forest, in chilly places, serpentine substrate, 650 m, 19.3.1989, *Phitos & Kamari 27000* (UPA), no. 121-cult.; *in ditione pagi Iraklia, 29.3.1980, *Katravas 19429* (UPA), no. 4-cult. (Fig. 4C); *in apertis silvae *Pinus halepensis,* 22.3.1987, *Katravas 21896* (UPA), no. 91-cult. — NOMOS LAKONIAS: In monte Malevo, prope Agios Ioannis, 1000 m, 20.4.1857, *Orphanides 846* (WU-Hal.); Mt Parnon, Peleta bei, 20.4.1971, *Hermjakob 9* (ATH); 7 km SSW of base of Monemvasia peninsula, 20-100 m, 30.3.1980, *Strid & Baden 17193* (UPA); **N* of Monemvasia, along road from the village of Lampokampos to Kremasti, c. 8.5 km before Kremasti close to a chapel, stony slopes with phrygana, limestone, 650-800 m, 13.3.1998, *Constantinidis 7270* (UPA), no. 211-cult.; *S of Monemvasia, around the village of Agios Phokas and SW of it, small meadows, rocky slopes with recently burnt bushes and cliffs facing the sea, limestone, 2-60 m, 14.3.1998, *Constantinidis 7300* (UPA), no. 212-cult. — NOMOS MESSINIAS: Mt Ithome, 23.5.1901, *Zahn 324* (WU-Hal.); *village of Iamia to Charokopio (Methoni & Koroni), in macchia with *Pistacia lentiscus* and *Acer* sp., c. 250 m, 19.2.1989, *Athanasiou & Athanasiou 2118* (UPA), no. 120-cult.; *from Kalamata to village Mesala, in *Quercus* forest, 13.6.1995, *Kamari & al. (Iter Mediterraneum)* (UPA), 195-cult.

b. subsp. ***gracilis*** (Ebel) Rix in Bot. J. Linn. Soc. 76: 356. 1978 ≡ *Lilium gracile* Ebel, Zwölf Tage auf Montenegro 8: t. 1. 1844 ≡ *Fritillaria montana* var. *gracilis* (Ebel) Griseb., Spic. Fl. Rumel. 2: 517. 1844 ≡ *Fritillaria gracilis* (Ebel) Asch. & Graebn., Syn. Mitteleur. Fl. 3: 192. 1905. – Described from Montenegro, "Auf dem Sutormangebirge, an den Abhängen der obern Kalkfelsenhügeln".
? = *F. neglecta* Parl., Fl. Ital. 2: 415. 1852. – Described from Croatia, "Istria, Mt Zagor".

Stem up to 60 cm, glaucous-green. *Leaves* (0.4-)0.6-0.8(-1) cm broad and 6-9(-13) cm long, glaucous-green, usually linear to narrowly lanceolate, often suberect, the uppermost usually alternate. *Flowers* 2.2-2.8(-3.3) cm long, rarely or obscurely tessellated, usually with unclear or without fascia and their segments not upturned at the mouth. – Fig. 2C, 3C-D.

Notes. – The confirmation of the occurrence of *Fritillaria messanensis* subsp. *gracilis* on most of the Ionian Islands is significant, because it extends considerably its geographical range from Montenegro and N Albania to the south (Fig. 1). Ronniger (1941), after studying 36 individuals of *Fritillaria* from Zakinthos, commented on the variability of the flower colour, the variation in shape and size of the perianth segments, the unclear fascia, etc., and concluded that these features correspond to *F. gracilis*. We confirm the variation of these morphological characters and add the variable number of the uppermost leaves, which may range from 1 to 3 in several populations of the Ionian Islands, especially in no. 205-cult. from Zakinthos (Fig. 2C). Certain Ionian plants sometimes recall subsp. *messanensis* in that they have a clear fascia (Fig. 2C). This variation may be attributed to gene infiltration or old hybridisation events and gene flow between subsp. *gracilis* and subsp. *messanensis,* a common feature, even between different species of *Fritillaria* that grow sympatrically and/or parapatrically, which may sometimes result in speciation (Rix 1971, Turrill & Sealy 1980, Zaharof 1987, Kamari 1991). The plants of Kefallinia island are all typical subsp. *gracilis* and usually have dark purplish, shortly campanulate flowers without fascia (Fig. 3D).

Specimens seen. – SERBIA-MONTENEGRO: MONTENEGRO: Djinova Breta, 6.1907, *Bierbach* (M); Straße zwischen Budva und Cetinje, 20.4.1962, *Merxmüller & Wiedmann 5881*(M); Grenzgebirge

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(Bertiscus), Umgeb. d. Cakor passes, 1900-2000 m, Kalk, 6.1969, *Leute 821* (W); in declivitate septentrionali montis Vrsuta (Rumija), supra pag. Virpazar, c. 850 m, 16.5.1982, *Mayer & Mayer 10920* (LJU, M); 1000 m, 16.5.1982, *Mayer & Mayer 10921* (LJU, M); *Mt Orjen, 23.7.1990, *Stevanović* (UPA), no. 146-cult. (Fig. 3C).

Albania: In alpinen Steingerölle zwischen Vermoš und Širokar, c. 1800 m, 12.6.1914, *Dörfler 255* (M); Distr. Scutari, in pratis elatior., Mt Cukali, 16.6.1897, *Baldacci 43* (M).

Greece: Sterea Ellas: Nomos Aitolias-Akarnanias: In Abieto-Quercetis declivium borealiorientalium cacuminis Boumistos, c. 1100 m, 9.6.1963, *Phitos 1050* (M). — Ionian Islands: Levkas: *Inter pagum Eugiros et locum Skidi, 7.5.1979, *Phitos & Kamari 18873* (UPA), no. 45-cult. (Fig. 5C). — Ithaki: *Above the village Ithaki (Vathy), 15.4.1972, *Phitos & Hauser,* no. 47-cult. (Fig. 5B); *ad pagum Perachori, in silva *Quercus ilicis,* 300-400 m, 18.4.1967, *Phitos 5865* (UPA), no. 47a-cult.; Mt Nirito, above the villlage Anogi, 450 m, 7.4.2000, *Katsouni* (obs.). — Kefallinia: Above Sami, next to the monastery at Agrilies area, in bushes, c. 250 m, 11.4.1974, *Fischer* (UPA); *Argostoli, in loco Phanari, in silva *Pinus halepensis,* 15.4.75, *Phitos & Kamari 27001* (UPA), no. 48-cult.; close to the city of Argostoli, area Katavothres, in opening of *Pinus halepensis* forest, 3.4.2004, *Katsouni* (obs.); N-NW slopes of Mt Gioupari (Roudi), 3-4 km of the crossroad to Enos-Sami, place called Vatouna, maquis and *Abies cephalonica* forest, 800-1000 m, limestone, 1.4.1982, *Stamatiadou 22672* (ATH); *in declivibus borealibus cacuminis Roudi, 500 m, 4.9.1985, *Phitos & Kamari 19552* (UPA), no. 84-cult. (Fig. 3D, 5A); *ibid., 19.5.1986, *Phitos & Kamari 27002* (UPA), no. 84a-cult.; between the villages Haliotata and Poulata, close to the road, *Broussalis* (obs.); close to the village Razata, at the place Kiklopia tichi, in *Pinus halepensis* forest, 15.3.1999, *Katsouni 251* (UPA; MNHC-I); *ibid., 2.4.2000, *Phitos & al. 26471* (UPA; MNHC-I), no. 147-cult.; *between Sami and Karavomilos, 30 m, 20.3.2000, *Katsouni 252* (UPA; MNHC-I); between Argostoli and Sami, at the place Lanou, 25.3.2004, *Katsouni 253* (UPA; MNHC-I); close to the village Valsamata, 13.4.2000, *Katsouni 255* (UPA; MNHC-I); close to the village Pastra, at the place named Agios Georgios, *Katsouni* (obs.); close to the monastery Agia Paraskevi Tafiou, *Katsouni* (obs.); close to the village Chavriata, *Katsouni* (obs.); *close to the village Vathi Erissou, 24.3.2004, *Katsouni 459* (UPA; MNHC-I), no. 249-cult. — Zakinthos: Zante, Fuß des Vrachionas, östlich von Mariés, 21.3.1936, *Ronniger* (W); zwischen Kilioménou und Hag. Léon, 22.3.1936, *Ronniger* (W); Nordseite der Insel Pelouso, 23.3.1936, *Ronniger* (W); s. loc., 3.4.1952, *Goulimis 7919* (herb. Pinatzi); *in ditione pagi Volimae, in Pinetis, 31.3.1973, *Tzanoudakis 588* (UPA), no. 43-cult.; *NW part of the island, just SE of Volimes, at the place named Veronika, calcareous substrate, 300-350 m, 6.4.1997, *Phitos & al. 26994* (UPA), no. 205-cult. (Fig. 2C, 5D); *in ditione pagi Gyri, prope locum Megali Spilia, 15.5.1974, *Tzanoudakis 1346* (UPA), no. 44-cult.; *close to the village Gyri, at the edges of uncultivated fields, 5.4.1998, *Phitos & al. 27003* (UPA), no. 216-cult.; *ad Pharos prope pagum Keri, 25.3.1988, *Tzini* (UPA), no. 108-cult.; *between the village Keri and its lighthouse, in clearing of *Pinus* forest and macchie, 5.4.1997, *Phitos & al. 26996* (UPA), no. 203-cult.; *village Korithi, between the lighthouse and the village (in fruit), 13.10.1991, *Phitos & Kamari 27004* (UPA), no. 157-cult.; *ad pagum Korithi, in agris incultis, 45 m, 26.5.1997, *Phitos & Kamari 25434* (UPA), no. 204-cult.; *close to the village of Anafonitria, clay soil in an olive grove and among crops, 3.4.1998, *Phitos & al. 25985* (UPA), no. 215-cult.

c. subsp. ***sphaciotica*** (Gand.) Kamari & Phitos, **comb. & stat. nov.** ≡ *Fritillaria sphaciotica* Gand. in Bull. Soc. Bot. France 62: 156. 1915. – Syntypes: [Greece, Kriti] "Hagia Roumeli", 1000 m, 15.6.1914, *Cousturier 7072* (LY!); "Malaxa, in dumetosis ad podem montium Sphacioticorum", 650 m, 20.4.1914, *Gandoger 4349* (LY!)
– *Fritillaria graeca* auct. fl. graec. [non Boiss. & Spruner in Boisser, Diagn. Pl. Orient. Nov. 1(7): 104. 1846].

Stem short, up to 15(-25) cm, slender, purplish green or often purple at the base. *Leaves* 0.2-0.4(-6) cm broad and 8-12(-15) cm long, purplish glaucous-green, linear and long, often curved

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downwards, the uppermost often in a whorl of 3. *Flowers* (2.5-)2.8-3.5 cm long, rarely or obscurely tessellated, usually with clear fascia and their segments not upturned at the mouth. – Fig. 3B.

Note. – As a rule, subsp. *sphaciotica* is a slender, dwarf plant throughout its distribution, having the longest and narrowest leaves of any *Fritillaria messanensis* taxon and a purple colour prevailing on stems and leaves (Fig. 3B). A similar, considerable size reduction has also been observed in other plants of Kriti, e.g. in several *Crepis* species (Kamari 1992), and is probably an adaptation to the more xeric climate, which developed in Kriti after its separation from the mainland (Greuter 1972, 1979). At lower altitudes (as in Samaria gorge or at Plakias bay) the plants of subsp. *sphaciotica* are somewhat taller but always remain slender and retain the characteristic long, linear leaves, which are often curved downwards. It is noteworthy that no other *Fritillaria* taxon occurs in Kriti.

Specimens seen. – GREECE: KRITI: NOMOS CHANION: Levka Ori, in saxosis calc. ad marginem australem altoplanitiei Omalos, c. 1100 m, 26.4.1942, *Rechinger 12373* (W); N-Hänge der Weissen Berge sdl. ob. Kambi am Weg zum EOS-Katafijio, 850 m, 9.4.1962, *Greuter 4114* (ATH, B, UPA, W); in rupestribus calc. faucium Samaria, 12.5.1963, *Phitos 751* (M); *Samaria gorge, at the end of Xiloskalo, in the base of calcareous rocks, c. 750 m, 28.5.1972, *Kamari & Papatsou 21912* (UPA), no. 31-cult.; between Xiloskalo pass and the chapel of Agios Nikolaos, 1300-700 m, 28.5.1972, *Petamidis 1407* (ATH); Sfakia, road from Anopoli to the Levka Ori, 8.2 km above junction with road to Aradhena in Anopoli, rocky slopes with phrygana, in *Cupressus* woodland, partially rich in soil, 14.4.1994, *Bergmeier & Matthäs 3733* (B, UPA); peninsula Titiron, in saxosis calc., prope Selia, c. 300 m, 21.4.1942, *Rechinger 12231* (W); distr. Kidonia, village Malaxa, 470 m, 13.4.1974, *Goulandri 149* (ATH). — NOMOS RETHIMNIS: Infra pagum Myrthios, in saxosis litoreis, 14.4.1974, *Phitos & al. 16749* (UPA), no. 30-cult.; *ad pagum Plakias, in declivibus maritimis, 10-30 m, 14.4.1974, *Phitos & al. 26992* (UPA), no. 30-cult. (Fig. 6A); above the village Alones, 20.4.1983, *Tzanoudakis* (UPA). — NOMOS IRAKLIOU: MT PSILORITIS: *Supra pagum Gergeri, in faucibus Gafari, prope silvam Rouva *(Quercus coccifera),* 1200-1300 m, 23.4.1972, *Phitos & Kamari 11173* (UPA), no. 32-cult. (Fig. 3B, 6B); *in loco Voskero, 1300-1350 m, 22.4.1974, *Tzanoudakis 1080* (UPA), no. 32a-cult.; in loco Tiganolakos, c. 1300 m, 22.4.1974, *Tzanoudakis 1096* (UPA); in silva Rouva, 1000-1100 m, 22.4.1974, *Tzanoudakis 1097* (UPA); Iraklion, am Berg Strubula bei Marathos, Kalkhänge, 10.4.1954, *Merxmüller & Wiedmann 5886* (M); am Youchtas-SO-Hang, 5.4.1981, *Rehder* (M). — NOMOS LASITHIOU: Kalamafka, Bachufer bzw. lichte Föhrenbestände, 650 m, 11.4.1971, *Malicky-Reisen 7* (W); between the villages Krousta and Kritsa, 4.4.1974, *Goulandri 145* (ATH); *Prinias hill, with low phrygana and rocks, c. 750 m, 8.5.1994, *Anagnostopoulos & Athanasiou* (UPA), no. 122-cult.

Karyology

Fritillaria messanensis shares the chromosome number of $2n = 24$ and its karyotype with most other species of the genus (see Kamari 1991, 1996 for previous references). The standard *Fritillaria* karyotype is asymmetrical, bimodal, consisting of two symmetric (usually one metacentric and one submetacentric) and ten asymmetric (acrocentric to subtelocentric in varying proportions) pairs. Only two taxa of subgenus *Fritillaria,* i.e. *F. montana* and *F. ruthenica* Wikström, have $2n = 18$ chromosomes (Fedorov 1969). This chromosomal reduction is probably the result of successive chromosomal reconstructions and fusion of acrocentric chromosomes into metacentric chromosomes (Darlington 1930, 1936, La Cour 1978a-b, Kamari 1991). The presence, shape and size of satellites on chromosomes vary significantly among members of the genus, and even within the same taxon (Runemark 1970, Bentzer & al. 1971, Mehra & Sachdeva 1976, Koul & Wafai 1980, Kamari 1984, 1991, 1996, Zaharof 1987). These satellites are usually small, spherical and occasionally not visible in all metaphase plates. They are mostly situated on the short arms of the

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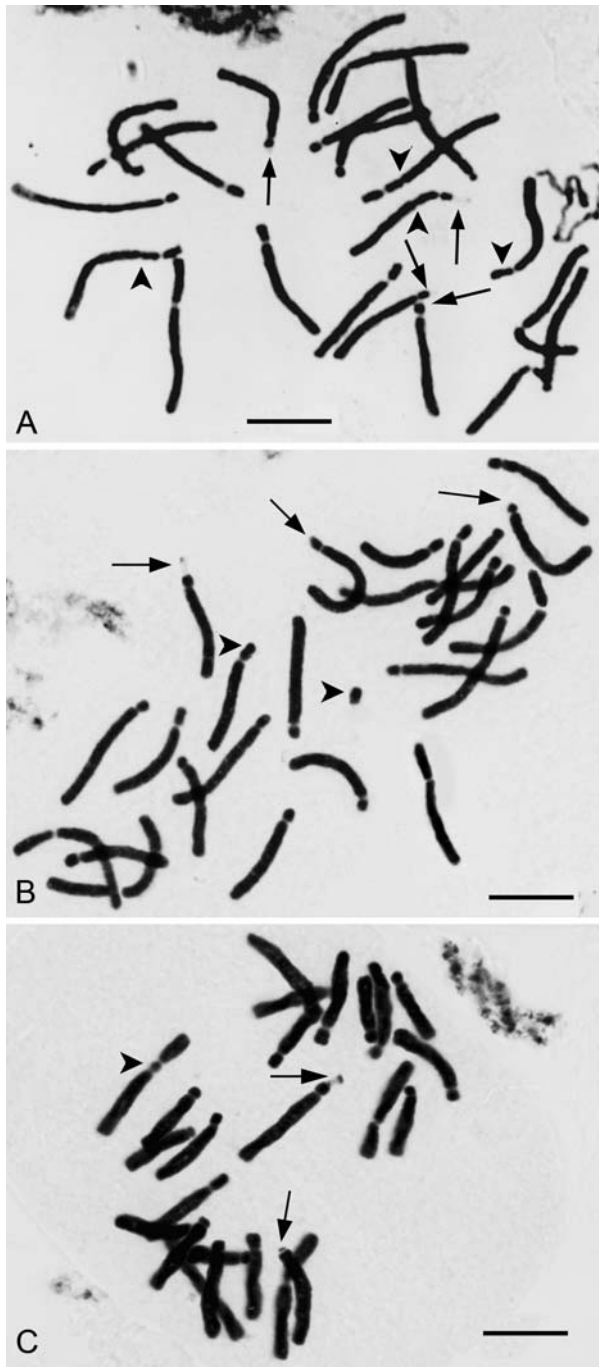


Fig. 4. Microphotographs of mitotic metaphase plates of *Fritillaria messanensis* subsp. *messanensis* – A: Mt Olimbos (pop. no. 50-cult.); B: Nomos Arkadias, Peloponnisos (pop. no. 107-cult.); C: Nomos Ilias, Peloponnisos (pop. no. 4-cult.). – Arrows indicate SAT-chromosomes and arrowheads B-chromosome and secondary constrictions. Scale bars = 10 µm.

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acrocentric or subtelocentric chromosomes, rarely on the shortest arms of the symmetrical chromosomes (Zaharof 1987, 1989, Kamari 1991, 1996). Quite often, one or two secondary constrictions are observed, varying in shape and number (La Cour 1978c, Kamari 1984, 1991, 1996, Zaharof 1987, 1989). In some cases supernumerary B-chromosomes of variable number and morphology are observed, and these are rather common in plants from areas where the distribution ranges of two taxa overlap (La Cour 1978b, Kamari 1984, 1991, Zaharof 1987, 1989). Exceptionally, triploid karyotypes with $2n = 3x = 36$ (Fedorov 1969, La Cour 1978a, Moore 1982, Zaharof 1987) or with $2n = 3x = 27$ (La Cour 1978a-b, Cesca 1986, Kamari 1991) chromosomes are found.

For *Fritillaria messanensis* important karyological information has been published using both Feulgen and C-banding preparations. The first reports were given by La Cour (1951, 1978a-b) in material of *F. messanensis* (sub *gracilis*) from the Balkan coast and N Africa. With respect to the N African populations, the data of La Cour (1951, 1978a-b) and the triploid karyotypes ($2n = 3x = 36$) of Humphries & al. (1978) from the Antiatlas Mts probably refer to the related *F. oranensis* Pomel, which replaces *F. messanensis* in that area. Typical *F. messanensis* has been examined from Messina in Italy by Gori (1958), who presented karyotypes and also a karyogram. A karyotype with $2n = 24$ chromosomes, given by Chichiriccò & Tammaro (1982) under the name *F. orsiniana* Parl. (= *F. montana*), probably belongs to *F. messanensis* and not to *F. montana,* which is characterized by 2n = 18 chromosomes. Confusion between these taxa is quite common in plants from Italy and the N Balkan, especially when the determination is purely based on dry herbarium specimens. Lovka (1975) gave the number of $2n = 24$ and a description of the karyotype for plants from former Yugoslavia that should now be attributed to *F. messanensis* subsp. *gracilis.*

The first chromosome count of *Fritillaria messanensis* in Greece was made by Strid & Franzén (1981) from Mt Olimbos. Kamari & Matthäs (1986) studied material from Kriti (pop. 32-cult.) and published the photograph of a karyotype attributable to subsp. *sphaciotica*. Zaharof (1987, 1989) also studied five populations of *F. messanensis* (two from Mt Olimbos and three from Peloponnisos), and observed that the karyotypes from Olimbos are characterized by two satellited chromosome pairs, in contrast to those of Peloponnisos, where only one pair bears satellites. Similar results have been presented by Kamari (1991), who further reported two pairs of SAT-chromosomes in populations from the Ionian Islands and Kriti. Moreover, she found one B-chromosome in plants from Kefallinia.

The karyotype formula of all *Fritillaria messanensis* subspecies is stable and $2n = 2m + 2sm + 2st\text{-}sat + 8st + 2t\text{-}sat + 8t = 24$ chromosomes. The same karyotype formula was already found by Gori (1958) in material from Messina in Italy and by Zaharof (1987, 1989) in material from Mt Olimbos.

Chromosome counts in 16 populations of *Fritillaria messanensis* subsp. *messanensis* showed that the number and morphology of the satellites varies between the populations studied (Fig. 4A, 4B, 4C), in accordance with the results of Zaharof (1987, 1989) and Kamari (1991). In material from Mt Olimbos (pop. no. 50) we observed satellites on two chromosome pairs (Fig. 4A). The largest satellites marked an acrocentric (st-SAT) pair and smaller satellites were found on a subtelocentric (t-SAT) pair; however, these were not visible in all metaphase plates and commonly only 2-3 satellites were evident (Fig. 4A). In material from Nomos Ilias, Peloponnisos (pop. no. 4) we normally observed one satellited subtelocentric (t-SAT) chromosome pair and additionally an intense secondary constriction on the shorter arm of the submetacentric (sm) chromosomes, close to the centromere (Fig. 4C). Similar observations were reported for plants from Peloponnisos (Zaharof 1987a, 1989), for material from Sicily (Gori 1958) and in some other *Fritillaria* taxa (La Cour 1978c, Kamari 1984, 1991). In material collected between Sparti and Tripoli (pop. no. 107), on the contrary, we observed two satellited chromosome pairs (Fig. 4B), as in the plants from Olimbos, although the satellites were not visible in all metaphase plates. In the same population a small B-chromosome (fragment) was found, its size varying among different plants of the population (Fig. 4B).

We studied 19 populations of *Fritillaria messanensis* subsp. *gracilis*. For this subspecies La Cour (1978a-c) noted that the nucleolar organizing region is heterochromatic and that hetero-

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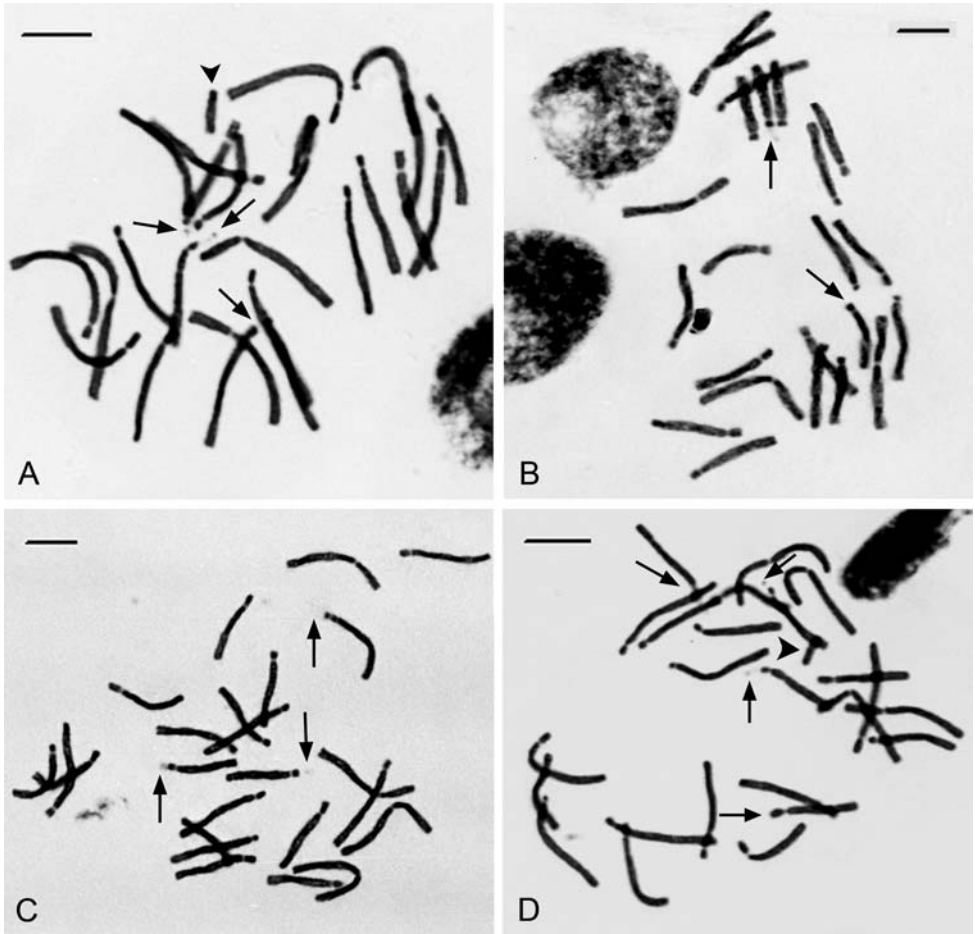


Fig. 5. Microphotographs of mitotic metaphase plates of *Fritillaria messanensis* subsp. *gracilis* from the Ionian Islands – A: Kefallinia (pop. no. 84-cult.); B: Ithaki (pop. no. 47-cult.); C: Levkas (pop. no. 45-cult.); D: Zakinthos (pop. no. 205-cult.). – Arrows indicate SAT-chromosomes and arrowheads the B-chromosomes. Scale bars = 10 µm.

morphy between pairs is apparent at this region, a rather common phenomenon in most satellited chromosome pairs of *Fritillaria*. The Greek material we examined appeared to have two heteromorphic satellited chromosome pairs, but usually only two or three satellites were visible (Fig. 5A-D). Additionally, a B-chromosome (fragment) was observed in one population (Fig. 5A) from Kefallinia (pop. no. 84-cult.) and one (Fig. 5D) from Zakinthos (pop. no. 205-cult.).

The heteromorphy of the satellited chromosomes also appeared in all six populations of *Fritillaria messanensis* subsp. *sphaciotica* examined. The satellites of this subspecies are larger than those of the other two subspecies and usually all visible; two of them are often double, of unequal size, and linked to the main chromosome body by a clearly stained chromonemma. Moreover, several secondary constrictions on the long arms of most chromosomes were evident (Fig. 6A-B).

Thus the variation in karyotype morphology among the different populations of *Fritillaria messanensis,* especially in number and shape of satellites, appears to be in accordance with the morphological variation of the group. The differences in number and shape of satellites on chro-

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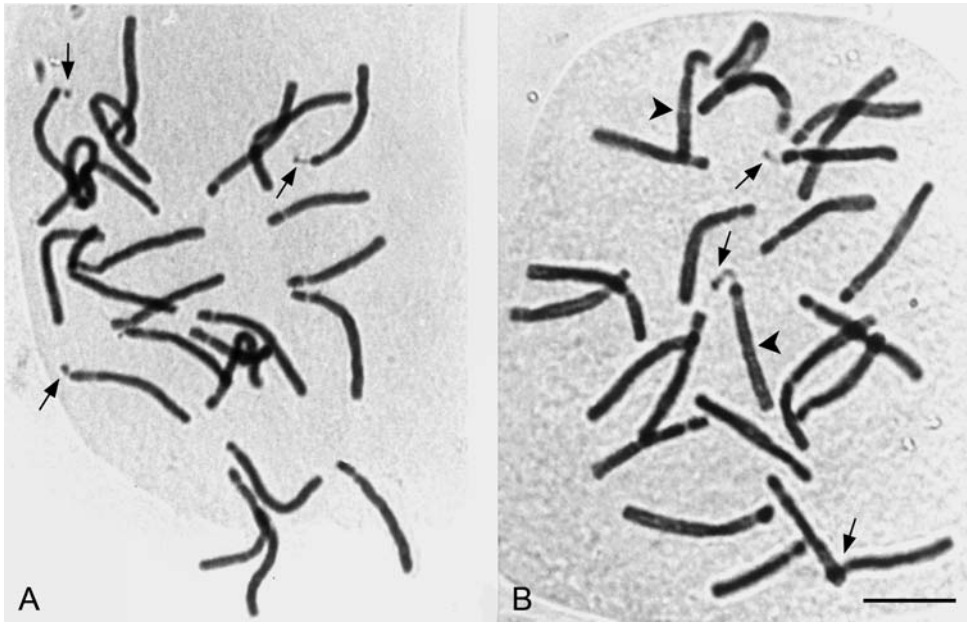


Fig. 6. Microphotographs of mitotic metaphase plates of *Fritillaria messanensis* subsp. *sphaciotica* from Kriti island – A: village Plakias (pop. no. 30-cult.); B: Mt Psiloritis (pop. no. 32-cult.). – Arrows indicate SAT-chromosomes and arrowheads secondary constrictions. Scale bars = 10 µm.

mosome pairs characterize populations rather than taxonomic units. However, some of these may merit more attention: the consistent appearance of the large, double and strongly stained satellites in subsp. *sphaciotica* (Fig. 6A-B) and the intense secondary constriction close to the centromere on the shorter arm of the submetacentric (sm) chromosome pair in populations of subsp. *messanensis* from Peloponnisos (Fig. 4C). The observation of an additional B-chromosome (fragment) in two populations of the Ionian Islands (Fig. 5A-D) and one of Peloponnisos (Fig. 4B) is also significant, because such B-chromosomes, which may vary in number (usually 1-5) and may possess a clear centromere, have usually been observed in populations where two different taxa coexist and may indicate hybridization (Kamari 1984, Zaharof 1987, 1989). It is also noteworthy that no B-chromosome has been observed in the populations of subsp. *sphaciotica* examined. This may suggest a stable karyotype for this subspecies, which corroborates its morphological stability. The use of more sensitive cytogenetic and molecular techniques might be particularly useful to increase our understanding of the genomic relationships and taxonomy of the subspecies of *F. messanensis* throughout their geographical range and their affinities with allied taxa.

Affinities

Rix (1971) treated *Fritillaria messanensis* as name giving member of the circum-Mediterranean *F. messanensis* group, together with *F. pyrenaica* L., *F. lusitanica* Wikström, *F. oranensis* and *F. acmopetala* Boiss. From all of these it differs mainly in nectary size and shape. Later Rix (1974, 1975) concluded that *F. messanensis* is taxonomically closer to the dwarf *F. epirotica* Rix, because the latter has large nectaries similar to those of *F. messanensis*. He also postulated that *F. epirotica* may have evolved as a high altitude ecotype of *F. messanensis*. However, *F. messanensis* is also found at high altitudes on Mt Olimbos (Greece), Mt Pollino (Italy) and Cakor passes (Serbia-Montenegro), usually on limestone substrates, whereas *F. epirotica* grows on ser-

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pentine. Zaharof (1988), after a phenetic study of some Greek *Fritillaria* taxa, placed *F. messanensis* in the same major cluster with *F. montana* and indicated a link of *F. epirotica* to the *F. graeca* group.

Fritillaria messanensis and especially its subsp. *gracilis* has close affinities with *F. montana,* with which it is sometimes confused, particularly in the northern part of its range. Their main distinguishing characters are the shape of the nectaries (large, long-lanceolate in *F. montana* and *F. epirotica;* medium-sized, ovate to egg-shaped in *F. messanensis*) and the leaf arrangement (leaves all alternate in *F. montana* and *F. epirotica;* usually the uppermost leaves in a whorl of three in *F. messanensis,* except subsp. *gracilis*). Furthermore, *F. montana* is characterized by $2n = 18$ chromosomes, in contrast to $2n = 24$ of both *F. messanensis* and *F. epirotica.*

Recently, Persson & Persson (1998) described *Fritillaria sororum* Jim. Perss. & K. M. Perss. from the lowland of Mt Taurus (Anatolia, Turkey). According to these authors *F. sororum* is reminiscent of *F. messanensis* in habit, shape and colour of perianth segments and nectary type. *F. sororum* differs from *F. messanensis* in the presence of leaf tendrils, a feature, however, which we also observed occasionally in plants of subsp. *sphaciotica* on Mt Psiloritis (Tzanoudakis 1097). Also *F. elwesii* Boiss., an E Mediterranean element distributed in S Anatolia and on the Greek island of Kastellorizo, is close to *F. messanensis* from which it mainly differs by its lanceolate nectaries and narrowly campanulate flowers.

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