ΓΕΩΠΟΝΙΚΟ ΠΑΝΕΠΙΣΤΗΜΙΟ ΑΘΗΝΩΝ
ΤΜΗΜΑ ΕΠΙΣΤΗΜΗΣ ΦΥΤΙΚΗΣ ΠΑΡΑΓΩΓΗΣ
ΕΡΓΑΣΤΗΡΙΟ ΣΥΣΤΗΜΑΤΙΚΗΣ ΒΟΤΑΝΙΚΗΣ

Διδακτορική Διατριβή

Βιοσυστηματική μελέτη ειδών του γένους *Fritillaria* L. (LILIACEAE)

Σοφία Α. Σαμαροπούλου

ΠΑΡΑΡΤΗΜΑΤΑ

- **ΠΑΡΑΡΤΗΜΑ Ι**

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Παράρτημα Ι
Μελετηθέντα δείγματα

***Fritillaria bithynica* Baker**

GREECE: EAST AEGEAN ISLANDS: Samos: Mt. Kerkis, NE facing slopes close to Moni Kimiseos Theotokou above Kosmadei, alt. 700 m, 37° 45′ N, 26° 39′ E, ex cultis, 22 Apr. 1975, *D. Tzanoudakis 2183* (Herb. Phitos & Kamari); mons Ampelos, supra pagum Ampelos, alt. 500-700 m, 25 Apr. 1975*, D. Tzanoudakis 2189* (Herb. Phitos & Kamari); mons Ampelos, supra pagum Ampelos, alt. 900 m, 25 Apr. 1975, *D. Tzanoudakis 2190* (Herb. Phitos & Kamari); close to Mitilini, alt. 250-350 m, 37° 43′ N, 26° 54′ E, ex cultis, 2 Mar. 1977*, Gr. Iatrou 183* (Herb. Phitos & Kamari); Mt. Kerkis, N facing slopes above Drakei, alt. 600 m., in *Pinus* woodland, 37° 45′ N, 26° 37′ E, ex cultis, 30 Jun. 1980, *D. Christodoulakis et al. 329* (Herb. Phitos & Kamari); Mt. Kerkis, above the village Drakei, alt. 600-700 m, in *Pinus brutia* forest, 30 Jun. 1980, *D. Christodoulakis, D. Phitos & G. Kamari 1041* (Herb. Phitos & Kamari); **TURKEY**: Olympo, Bithyno*,*1874*, F.W. Noe s.n.* (K); 02. Aydin: d. Karacasu, Baba Dag above Seki, 1100m, *Quercus aegilops* wood in old cemetery, on schist, 22 Apr. 1965, *Davis 41538* (Herb. Phitos & Kamari).

***Fritillaria carica* Rix**

GREECE: EAST AEGEAN ISLANDS: Chios: Mons Provatas, in apertis petrosis silvae *Pinus*, alt. 650-750 m, 19 Apr. 1990, *D. Phitos, G. Kamari, A. Anagnostopoulos & K. Athanasiou 20829* (Herb. Phitos & Kamari); Mons Provatas, ad cacumen, in nanofruticetosis petrosis et saxosis calc., alt. 750-850 m, 19 Apr. 1990, *D. Phitos, G. Kamari, A. Anagnostopoulos & K. Athanasiou 20890* (Herb. Phitos & Kamari); Mons Oros, in declivibus meridio-occidentalibus, alt. 750-850 m, in petrosis et saxosis calc. 38° 30′ N, 26° 00′ E, 24 Apr. 1991, *D. Phitos, G. Kamari, A. Anagnostopoulos & K. Athanasiou 21223* (Herb. Phitos & Kamari).

***Fritillaria conica* Boiss.**

GREECE: PELOPONNISOS: Messinia: Ajios Nicolaos *001911* (ACA); Ep. Kalamon: in declivibus boreo-occidentalibus montis Kalathion, inter pagos Elaeochorion et Arachova, alt. 550 m, ad viam, in fruticetosis, solo calcareo, 19 Apr. 2011, *D. Phitos, G. Kamari, Ch. Kyriakopoulos et al. 27448* (Herb. Phitos & Kamari); in declivibus boreo-occidentalibus montis Kalathion, infra pagum Elaeochorion, alt. 300 m, ad

viam prope Naos Panagitsas Zoodochou Pigis, in fruticetosis, solo calcareo, 19 Apr. 2011, *D. Phitos, G. Kamari, Ch. Kyriakopoulos et al. 27449* (Herb. Phitos & Kamari); in ditione vici Pylos, ad locum Hagios Nikaolas, in nanofruticetosis, solo calcareo, 12 Mar. 1988, *D. Phitos & G. Kamari 19962* (Herb. Phitos & Kamari); in ditione vici Pylos, ad Hagios Nikaolas, in declivibus nanofruticetosis, alt. ca 300 m, 06 Apr. 1983, *D. Phitos & G. Kamari 19130* (Herb. Phitos & Kamari); pr. Hagios Nicolaos, Mar. 1897 *H. Zahn s.n.* (Herb. Phitos & Kamari); at the slopes of Agios Nikolaos, close to Pilos, in shrubs, 39° 55′ N, 21° 42′ E, 6. Apr. 1985*, D. Phitos & G. Kamari 23341* (Herb. Phitos & Kamari); 3 km from Pilos town on the road to Methoni, in phrygana, on rocky slopes, partly grazed by goats, alt. c. 200m, 36° 53′ N, 19° 59′ E, 02 Feb. 1997, *K. Mikkelsen & M.A. Callimassia KM 447* (Herb. Phitos & Kamari); inter vicos Pilos et Methoni, in nanofruticetosis, ca- 200 m, solo calcareo, ex cultis, 12 Mar. 1988, *D. Phitos & G. Kamari 19962* (Herb. Phitos & Kamari); **Sapientza**: north part of the island, in maccchia 36° 47′ N, 21° 42′ E, 24 Mar. 1991, *D. Phitos, G. Kamari, A. Strid & A. Anagnostopoulos 23340* (Herb. Phitos & Kamari); central part of the island, in *Quercus coccifera*, *Acer* sp. etc., woodland, 36° 46′ N, 21° 42′ E, 24 Mar. 1991, *D. Phitos et al. 23339* (Herb. Phitos & Kamari).

***Fritillaria davisii* Turrill**

GREECE: PELOPONNISOS: Lakonia: inter pagos Vathia et Achillion, on calcareis, 11 May 1981, *Gr. Iatrou 1077* (Herb. Phitos & Kamari); inter pagos Ajios Nikon et Itilon, in declivibus occidentalibus cacuminis Miri, alt. ca 250 m, in saxosis calc., 12 Mar. 1988, *Phitos & Kamari 20742* (Herb. Phitos & Kamari)*;* Aeropolis, Profitis Ilias, alt. 800 m, 26 Apr. 1996, *D. Vassiliades s.n*. (Herb. Phitos & Kamari); Mani, Village Pagia, location Keladia, 2 Mar. 1997, *Kirimi s.n*. (Herb. Phitos & Kamari); Mani, Aeropolis, Mar. 2016, *G. Kofinas sub Samaropoulou SF1108* (ACA); **Messinia:** Mani peninsula, Pyrgos (S of Areopolis), olive plantations on plain, 16 Feb. 1940, *P. H. Davis 1152* (E); inter pagos Hag. Nikon et Oetilon, in saxosis calcareis, alt. ca. 300 m, 10 May 1981, *Gr. Iatrou 1000* (Herb. Phitos & Kamari); ibid. *Gr. Iatrou 998* (Herb. Phitos & Kamari).

***Fritillaria drenovskii* Degen & Stoj.**

GREECE: MACEDONIA: Drama: montes Phalakron, prope refugium, alt. 1600 m, 9 Aug. 1978, *D. Tzanoudakis 4962* (Herb. Phitos & Kamari); mons Falakron, alt. 1600 m, 10 Jul. 1989, *A. Tiniakou 1690* (Herb. Phitos & Kamari); mons Falakron, alt. 1800 m, east of the church, *A. Tiniakou s.n* (Herb. Phitos & Kamari); **Kavala:** Mt. Pangeo by the road from the village Akrovouni to the ERT station, alt. 1100 m, Stony (limestone) meadow, large clearing at *Fagus* forest, 10 May 1984, *E. Zaharof F.122* (Herb. Phitos & Kamari); in montis Pangeo ditio Deve Karan, alt. 1800 m, 40° 55' N, 24° 06' E, in clivis praeruptis boreo-orientem spectantibus, in glareosis marmoreis, 17 Jul. 1978, *W. Greuter 16032* (Herb. Phitos & Kamari).

***Fritillaria ehrhartii* Boiss & Orph.**

GREECE: AEGEAN ISLANDS: Evvia: in the valley 1.5-3 km NW of Platanistos, 200-450 m, 11 Apr. 1971, *S. Snogerup & M. Gustafsson S&G42240* (UPA); c. 2 km N of Platanistos, 500-700 m, 11 Apr. 1971, *S. Snogerup & M. Gustafsson S&G42279* (Herb. Phitos & Kamari); between the villages Styra and Marmari, 09 Apr. 2017, *G. Kofinas sub Samaropoulou SF1120* (ACA); **KIKLADES ISLANDS: Andros**: *001912* (ACA); 0.5 km W of the town of Andros, 20-50 m, 3 Mar. 1969, *S. Snogerup & R. v. Bothmer S&B38423* (Herb. Phitos & Kamari); in the valley 2-3 km SW of Akra Gria 50-100 m, 5 Mar. 1969, *S. Snogerup & R. v. Bothmer S&B38510* (UPA); cliffs c. 1 km NE of Ano Gavrion, 500-600 m, 1 Apr. 1971, *S. Snogerup & M. Gustafsson S&G41849* (Herb. Phitos & Kamari); N-slope of Mt. Kouvara (Petalon Oros) 2.5-3 km ESE of Batsi, c. 550 m, 2 Apr. 1971, S*. Snogerup & M. Gustafsson S&G41857* (Herb. Phitos & Kamari); in the valley 0-1 km ENE of Vitali, 50-200 m, 4 Apr. 1971, *S. Snogerup & M. Gustafsson S&G41943* (Herb. Phitos & Kamari); c. 2 km SE of Batsi, c. 450 m, 37° 50′ N, 24° 49′ E, schist, 31 Mar. 1971, *S. Snogerup & M. Gustafsson S&G41856* (UPA); **Kea**: cliffs of hard limestone N-NE of the monastery of Kastriani, 50-150 m, 4 Jun. 1968, *S. Snogerup & R. v. Bothmer S&B34317* (Herb. Phitos & Kamari); **Siros**: Islands of Syra, *Elwes s.n.* (K); insula Syro prope Coïnos (rare), 30 Mar. 1856, *T. G. Orphanides 845* (LD); in insula Syro, 15 Mar. 1885, *B. Tunta s.n*. (Herb. Phitos & Kamari); 1.5 km SE of Kallivari, c. 100 m, 11 Mar. 1969, *S. Snogerup & R. v. Bothmer S&B38887* (Herb. Phitos & Kamari); Mt. Pirgos, the N-part, 4 Apr. 1969, *H. Runemark, A. Strid & M. Gustafsson R,St&G40147* (Herb. Phitos & Kamari); Mt. Nites at Dellagracia, 200-300

m, 5 Apr. 1969, *H. Runemark, A. Strid & M. Gustafsson R,St&G40195* (Herb. Phitos & Kamari); Mt. Siringas, 350-400 m, 5 Apr. 1969, *H. Runemark, A. Strid & M. Gustafsson R,St&G40211* (Herb. Phitos & Kamari); Ajios Dimitris, 23 Mar. 1980, *G. Sfikas 5150* (Herb. Phitos & Kamari); **Tinos**: 1 km NE of Falatados, 250-300 m, 29 Mar. 1969, *H. Runemark, A. Strid & M. Gustafsson R,St&G39680* (UPA); 3 km NE of Falatados, 400 m, 29 Mar. 1969, *H. Runemark, A. Strid & M. Gustafsson R,St&G39698* (Herb. Phitos & Kamari); 1 km of Agapi, 29 Mar. 1969, *H. Runemark, A. Strid & M. Gustafsson R,St&G39720* (Herb. Phitos & Kamari); between Koumaros and Loutra, 29 Mar. 1969, *H. Runemark, A. Strid & M. Gustafsson R,St&G39729* (Herb. Phitos & Kamari); Tsimenas, the plateau at the church, 550 m, 31 Mar. 1969, *H. Runemark, A. Strid & M. Gustafsson R,St&G39873* (UPA); 3 km of Aetofolia, 2 Apr. 1969. *H. Runemark, A. Strid & M. Gustafsson R,St&G399967* (Herb. Phitos & Kamari); Choris Pirgos, 400 m, 2 Apr. 1969, *H. Runemark, A. Strid & M. Gustafsson R,St&G39980* (UPA); supra pagum Stavria, alt. ca. 400 m, in phrygana, solo schistoso, 19 Apr. 1986, *G. Kamari 20798* (Herb. Phitos & Kamari); prope pagum Stavria, alt. ca 400 m, in phrygana, solo schistose, 19 Apr. 1986, *G. Kamari 20799* (Herb. Phitos & Kamari); prope pagum Kataporiani, alt. ca. 350m, in phrygana, solo schistoso, 19 Apr. 1986, *G. Kamari 20800* (Herb. Phitos & Kamari); 500 m after the village Isternia and towards Katapoliani, open area with ruined windmills, schistolithic substrate, 360 m, 37° 37' 34'' N, 25° 3' 01'' E, 20 Mar. 2016, *S. Samaropoulou & I. Patrikios SF1102* (ACA); **SPORADES ISLANDS**: **Koulouri** (ditio insulae Skyros): in saxosis calc., 17 Mar. 1969, *D. Phitos 8667* (Herb. Phitos & Kamari); **Skiros**: 2.5 – 3 km NNW of the top of Mt. Kochilas, rocky phrygana, NE-slope, c. 100 m, 1 Mar. 1969, *S. Snogerup & R. v. Bothmer S&B39060* (Herb. Phitos & Kamari); the islands of Valacha, the S part 0-100 m, 17 Mar. 1969, *S. Snogerup & R.v.Bothmer S&B39094* (Herb. Phitos & Kamari); NE of Kochilas, close to Ajios Artemios, in phrygana, 17 Jun. 1977, *G. Kamari s.n.* (Herb. Phitos & Kamari); mons Kochilas, in declivibus boreo-orientalibus, 200-500 m, 17 Jun. 1977, *G. Kamari 13676* (Herb. Phitos & Kamari).

***Fritillaria elwesii* Boiss.**

GREECE: EAST AEGEAN ISLANDS: Kastellorizo: (Megisti), Polje of Agios Georjios (Vounou), fallow fields SW of Ajios Georjios monastery, marly soil (terra rosa) with abundant *Narcissus*, *Asphodelus* and phrygana, 23 Mar. 1974, *E. Stamatiadou 17521* (Herb. Phitos & Kamari); Kastellorizo (Megisti), Mandhraki village, SE and above of

the cemetery, place named Eleonas, alt. 20-70 m, stony ground with *Olea europaea*, *Amygdalus communis* and phrygana, 22 Mar. 1974, *E. Stamatiadou 17497* (Herb. Phitos & Kamari); **TURKEY**: Adrasan: Antalya: along the side of a dry stream bed. Along a goat trail overhung by *Styrax, Pinus brutia, Cotinus coggygria* and *Fontanesia,* 50m, 27 Mar. 1998, *Ann Eustace 9* (E).

***Fritillaria epirotica* Turrill ex Rix**

GREECE: EPIRUS: Ioannina: Katara Pass, prope ekchionistikos stathmos, alt. 1750 m, in apertis (*Pinus, Buxus* etc.), solo serpentinico, 4 May 1990, *D. Phitos & G. Kamari 21348* (Herb. Phitos & Kamari); Eparchia Metsovou, Katara Pass, close to the second snowplow station, c. 13.5 km of Metsovon along the road to Trikala, slopes with *Pinus nigra* and *Buxus sempervirens* ophiolithic substrate, alt. c. 1640 m, 39° 47' N 21° 13' E, 24 Jun. 1998, *Th. Constantinidis 7919* (Herb. Phitos & Kamari); Katara Pass, rocky bare slopes, serpentine, about 500 m. from the snowplow station, 17 May 1983, *Brousalis s.n*. (Herb. Phitos & Kamari); **MACEDONIA: Grevena:** Mt. Smolikas, 2438 m, 30 Jun. 1937, *E.K. Balls & W.B. Gourlay 3434* (K); Mt. Vasilitsa, alt. 1764 m, 17 May 2015, *G. Kofinas sub Samaropoulou* SF1076 (ACA); Mt. Smolikas, alt. 2200 m, Aug. 2015, *G. Kofinas sub Samaropoulou* SF1097 (ACA). **THESSALIA: Trikala:** Ep. Kalampakas, Mt. Chasia (Kratsovo), stony slopes close to a forest road, c. 3.0–3.5 km from Kakoplevri village, serpentine, alt. c. 1100–1180 m, 39° 48' N, 21° 24' E, 15 Jun. 2000, *D. Phitos, G. Kamari & Th. Constantinidis s.n.* (cult. no. 235, Herb. Phitos & Kamari); Ep. Kalampakas, Mt. Chasia (Mt. Kratsovon), c. 3.1 km WNW of Kakoplevri village on the foothills of the mountain, hills with low *Buxus sempervirens* and *Juniperus oxycendrus,* serpentine substrate, alt. 1120–1160 m, 39° 49' N, 21° 24' E, 24 Jul. 2006, *Th. Constantinidis s.n.* (cult. no. 235, Herb. Phitos & Kamari).

***Fritillaria euboeica* Rix**

GREECE: AEGEAN ISLANDS: Evvia: Mt. Kandili, alt. 1000 m, in shrubs, 38° 41′ N, 23° 27′ E, 18 Apr. 1983, *D. Phitos & G. Kamari 19163* (Herb. Phitos & Kamari); ibid. 23 Mar. 1984, *D. Phitos & G. Kamari 23342* (Herb. Phitos & Kamari); Mt. Kandili, around Moni Sotiros above Prokopi, alt. 700-750m, 38° 42′ N, 23° 26′ E, ex cultis, 23 Mar. 1984, *D. Phitos & G. Kamari 23342a* (Herb. Phitos & Kamari); Mt. Kandili, alt. 1000 m, in shrubs, 38° 41′ N, 23° 27′ E, ex cultis, 18 Apr. 1983, *D. Phitos & G. Kamari 19163* (Herb. Phitos & Kamari).

***Fritillaria graeca* Boiss & Spruner**

GREECE: **AEGEAN ISLANDS: Evvia:** Ep. Chalkidas, mons Skotini, supra pagum Metochi alt. 1200 m, 38° 35' N, 23° 59' E, in saxosis calc. 27 Apr. 1989, *D. Phitos & G. Kamari 20395* (Herb. Phitos & Kamari); Mt. Oksilithos, 17 Apr. 2015, *N. Kalogiannis sub Samaropoulou SF1000/1* (ACA); **PELOPONNISOS: Achaia:** Ep. Lakedemonos, mons Klokos, supra pagum Pteri, alt. 1350-1400m, in apertis silvae Abietis cephalonicae, solo calcareo, 38° 08' N, 22° 03' E, 26 Apr. 1987, *D. Phitos & G. Kamari 19943* (Herb. Phitos & Kamari); Ep. Patron, mons Panachaikon, in declivibus meridio-occidentalibus, alt. 1450 m, 38° 10' N, 21° 52' E, *D. Phitos & G. Kamari 21774* (Herb. Phitos & Kamari); Ep. Kalavriton, mons Chelmos, in declivibus borealibus, alt. ca. 1800 m, in saxosis calc. 38° 03' N, 22° 09' E, 18 May 1996, *G. Kamari 24687* (Herb. Phitos & Kamari); Mt. Chelmos, next to the shelter, 2080 m, 37° 59.427′ N, 22° 11.534′ E, 23 May 2015, *P. Trigas sub Samaropoulou SF1078* (ACA); **Arcadia:** Mons Parnon, in declivibus occidentalibus, alt. 1400-1500 m., in apertis silvae Abietis, 17 April 1979, *D. Phitos, G. Kamari, Gr. Iatrou & D. Tzanoudakis 16489* (Herb. Phitos & Kamari); Ep. Mantinia, Mt. Menalon, slopes W and NW of the plateau with the ski resort, alt. 1600-1800 m, 37° 39' 15'' N, 22° 15' 20'' E, sparse *Abies cephalonica* wood and bare slopes, on limestone, 4 Jun. 1995, *G. Kamari, C. Beurton, T. Constantinidis, M. A. Garcia Garcia, R. Jahn, N. Jogan, U. Matthas, P. Mazzola, M. Popova, E. Rico, K. Siems, V. Stevanovic, W. Strasser, S. Savic & K. Sutory 1233* (Herb. Phitos & Kamari); Ep. Mantinia, Mt. Menalon, slopes E and SE of the plateau with the ski resort, toward Mt. Ostrakina, alt. 1650-1850 m, 37° 38' 50'' N, 22° 15' 20'' E, sparse *Abies cephalonica* wood and bare slopes, on limestone, 4 Jun. 1995, *G. Kamari, C. Beurton, T. Constantinidis, M. A. Garcia Garcia, R. Jahn, N. Jogan, U. Matthas, P. Mazzola, M. Popova, E. Rico, K. Siems, V. Stevanovic, W.*

Strasser, S. Savic & K. Sutory 1212 (Herb. Phitos & Kamari); Mt. Mainalon, plateau Ostrakina, behind the shelter "Panos Alexopoulos", 1570 m, 37° 38′ 12′′N, 22° 16′ 08′′E, 08 May 2016, *S. Samaropoulou & I. Patrikios SF1110* (ACA); **Korinthos:** Mt. Killini, Ziria, 10 May 2015, *G.Kofinas sub Samaropoulou SF1073* (ACA); **STEREA ELLAS:** Apr. 1841, *P. E. Boissier* s.n. (G); **Attiki**: Mt. Hymettus, Apr. 1841, *E. Boissier s.n.* (K); Mt. Hymettus, Apr. 1903, *W. Spruner s.n.* (K); Mt. Parnes, supra Metochi, l.d Prioni, Mar. 1911, *001915* (ACA); Mt. Parnitha summit, Alalades, 26 May 1917, *P. Tsevas 001915* (ACA); Ins. Salamis, in collibus saxosis, 27 Mar. 1965, *D. Phitos 2695* (Herb. Phitos & Kamari); Ins. Salamis, prope pagum Selinia, in declivibus petrosis, 20 Mar. 1966, *D. Phitos s.n.* (Herb. Phitos & Kamari); Ins. Salamis, ad Mavrovounion, ca. 200 m, in saxosis calcareis, 19 Apr. 1973, *D. Phitos 19585* (Herb. Phitos & Kamari); Ep. Megaridos, Mt. Gerania, the summit Makriplagi, calcareous substrate, alt. c. 1340-1351 m, 38° 01' N, 23° 08' E, 07 May 1995, *Th. Constantinidis & A. Iliadis 5509* (Herb. Phitos & Kamari); Isl. Salamina: Ampelakia, Ep. Selinia, Mt. Mavrovounio, slopes with phrygana, 160 m, 37° 55′ 34.5′′ N, 23° 30′ 34.8′′ E, 18 Mar. 2015, *S. Samaropoulou & A. Samaropoulos SF1051* (ACA); Mt. Kithaironas: at the summit of the mountain, Profitis Ilias, just before the entry of the old airport base, stony substrate, 1387 m, 38° 10' 58" N, 23° 14' 58′′ E, 29 Apr. 2015, *S. Samaropoulou & A. Samaropoulos SF1066* (ACA); Eparchia Spata, Hill Perati: 160 m, 37° 54′ 48.10′′ N, 24° 01′ 22.10′′ E, 01 Apr. 2015, *S. Samaropoulou & A. Samaropoulos SF1056* (ACA); Eparchia Spata, Hill Palati, 155 m, 37° 52' 59.60" N, 23° 52' 02.80′′ E, 01 Apr. 2015, *S. Samaropoulou & A. Samaropoulos SF1057* (ACA); Mt. Imittos, above Argiroupoli, alt. ca 310 m, 37° 54' N, 23° 46' E, 15 Apr. 2015, *S. Samaropoulou, A. Samaropoulos & G. Kofinas SF1062* (ACA); Mt. Parnitha, shelter of Mpafi, 1198 m, 38° 10' 05" N, 23° 43' 35′′ E, 22 Apr. 2015, *S. Samaropoulou & I. Patrikios SF1063* (ACA); **Voitia:** Mt. Elikonas, alt. c. 1500 m, 05 May 1996, *D. Vassiliades s.n.* (Herb. Phitos & Kamari).

***Fritillaria gussichiae* (Degen & Dörfl.) Rix**

GREECE: MACEDONIA: Florina: Mt. Vitsi, by the road from the village Drosopigi to the top of the mountain (army base), clearings at *Fagus* forest with *Pteridium*, alt. 1250 m, 16 May 1983, *Zaharof F-072* (ATH); Florina – Kastoria, summit area of Mt. Vitsi SW of the village Drosopigi, place called Magovits (WSW of Radar station on the peak), alt. 1750-1870 m, massive rocks and grazed meadows in opening of *Fagus* forest, gneiss and micaceous schist, grassland among rocks, 27 Jul. 1985,

Stamatiadou 23131 (ATH); **Pella:** Mt. Voras, *Voliotis s.n.* (Herb. Phitos & Kamari); **Serres:** Sintikis, SW part of Mt. Kerkini (Belles), by the end forest road 12 km WNW of the village Platanakia towards the military post "Neon Triethnes", alt. 1100 m, *Fagus* woodland, micaceous schist, in woody opening with abundant *Pteridium*, 3 Jul. 1981, *Stamatiadou 22417* (ATH); **Thessaloniki:** Mt. Hortiatis. alt. ca 1000 m, 2017, *A. Karydas sub Samaropoulou SF1121 (*ACA).

Fritillaria messanensis* Rafin subsp. *messanensis

GREECE: MACEDONIA: Pieria: Mt. Olimpos: 10 Jun. 1951, *Goulimis 7314* (Herb. Pinatzi, ACA); 1 km SE of the village Kokkinoplos, 1200-1300 m, 20 Jun. 1970, *Strid & Bothmer 50* (C); supra coenobium Agios Dionisios, in ascensu ad refugium princeps (A), 1800-1900 m, 25 Jul. 1971, *Greuter 9603* (ATH, B); Prionia, in grass among box bushes, 1000 m, 25 May 1972, *Baxter 260* (ATH); Abstieg von Hütte A bis Prionia, 2100-1000 m, 7 Jun. 1972, *Klaus & al. 241* (W); montes Olympos, infra refugium EOS, in saxosis calcareis, 1800 m, 08 Aug. 1973, *Phitos & al. 26997* (Herb. Phitos & Kamari); N side, Papa Rema gorge, S of Vrondou, 500-650 m, 12 May 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 Jul. 1978, *Stamatiadou 20876* (ATH); NE slopes of Metamorphosis, 1500 m, 23 May 1981, *Strid, Baden & Møller 134* (C); montes Olympos, supra locum Prionia versus refugium Spilios Agapitos, alt. 1600-1780 m, 12 Jul. 1986, *A. Tiniakou 1526* (Herb. Phitos & Kamari); slopes, at place Kaggelia, c. 1900, 04 Aug. 1986, *Tzini s.n.* (Herb. Phitos & Kamari); **PELOPONNISOS: Arkadia:** Inter urbis Sparti et Tripolis, in fruticetosis, alt. ca. 800 m, 14 Mar. 1988, *Phitos & Kamari 20745* (Herb. Phitos & Kamari); Leonidio, May 2017, *G. Kofinas sub Samaropoulou SF1122* (ACA); **Ilia:** From Pirgos to "Arhea Olymbia" near the village Paleovarvasena, place called Mandres, 80-100 m, 30 Mar. 1969, *Stamatiadou 4975* (ATH); inter pagum Figalia et templum Vasai, in petrosis et in agris ad viam, 20 Apr. 1975, *Phitos & Kamari 18411* (Herb. Phitos & Kamari); prope pagum Iraklia, in apertis silvae *Pinus halepensis*, 29 Mar. 1980, *H. Katravas 19429* (Herb. Phitos & Kamari); in prope pagum Iraklia, in apertis silvae Pinus halepensis, 22 Mar. 1987, *Katravas 21896* (Herb. Phitos & Kamari); village Figalia, close to the branch of the river Neda, 26 Mar. 1988, *Phitos & Kamari 26998* (Herb. Phitos & Kamari); between Vasae and Perivolia, close to the branch of the river Neda, in schist, c. 650 m, 19 Mar. 1989, *Phitos & Kamari 26999* (Herb. Phitos & Kamari); 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 Mar. 1989, *Phitos & Kamari 27000* (Herb. Phitos & Kamari); **Lakonia:** in monte Malevo, prope Agios Ioannis, 1000 m, 20 Apr. 1857, *Orphanides 846* (WU-Hal.); Mt. Parnon, Peleta bei, 20 Apr. 1971, *Hermjakob 9* (ATH); 7 km SSW of base of Monemvasia peninsula, 20-100 m, 30 Mar. 1980, *Strid & Baden 17193* (Herb. Phitos & Kamari); 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 Mar. 1998, *Constantinidis 7270* (Herb. Phitos & Kamari); 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 Mar. 1998, *Constantinidis 7300* (Herb. Phitos & Kamari); Mt. Parnonas, 05 Apr. 2015, *G. Kofinas sub Samaropoulou SF1067* (ACA); **Messinia:** Mt. Ithome, 23 May 1901, *Zahn 324* (WU-Hal.); village of Iamia to Charokopio (Methoni & Koroni), in macchia with *Pistacia lentiscus* and *Acer* sp., c. 250 m, 19 Feb. 1989, *Athanasiou & Athanasiou 2118* (UPA); from Kalamata to village Mesala, in *Quercus* forest, 13 Jun. 1995, *Kamari & al. Iter Mediterraneum* (Herb. Phitos & Kamari); **THESSALIA: Larisa:** Kato Olympus, Livadaki, North of Kallipefki, alt. ca 1407 m, 39° 57' 00" N, 22° 29' 32'' E, 30 May 2015, *S. Samaropoulou, I. Patrikios & K. Tamvakas SF1085* (ACA); Kato Olympus, Livadaki, North of Kallipefki, alt. ca 1414 m, 39° 56' 58" N, 22° 29' 33" E, 30 May 2015, *S. Samaropoulou, I. Patrikios & K. Tamvakas SF1086* (ACA); Kato Olympus, Livadaki, North of Kallipefki, alt. ca 1438 m, 39° 56' 52" N, 22° 29' 33" E, 30 May 2015, *S. Samaropoulou, I. Patrikios & K. Tamvakas SF1087* (ACA); Kato Olympus, Livadaki, North of Kallipefki, alt. ca 1415 m, 39° 56' 54" N, 22° 29' 13" E, 30 May 2015, *S. Samaropoulou, I. Patrikios & K. Tamvakas SF1088* (ACA); **Pieria:** Mt. Olympos: at the summit of the mountain, Prionia, opposite of the shelter, forest of *Pinus* sp., *Abies* sp. and *Fagus* sp, alt. ca 1115 m, 40° 05' 02" N, 22° 24' 25'' E, 29 May 2015, *S. Samaropoulou, I. Patrikios & L. Kipopoulos SF1082* (ACA); Mt. Olympos: along the road from Litochoro towards the top of the mountain, Prionia, alt. ca 1113 m, 40° 05 '17" N, 22° 24' 35'' E, 29 May 2015, *S. Samaropoulou, I. Patrikios & L. Kipopoulos SF1083* (ACA); Mt. Olympos, along the road from Litochoro towards the top of the mountain, Prionia, alt. ca 633 m, 40° 06' 47" N, 22° 28' 49'' E, 29 May 2015, *S. Samaropoulou, I. Patrikios & L. Kipopoulos, SF1084* (ACA).

***Fritillaria messanensis* Rafin. subsp. *gracilis* (Ebel) Rix**

GREECE: IONIAN ISLANDS: Ithaki: ad pagum Perachori, in silva *Quercus ilicis*, 300-400 m, 18 Apr. 1967, *Phitos 5865* (Herb. Phitos & Kamari); above the village Ithaki (Vathy), 15 Apr. 1972, *Phitos & Hauser s.n.* (Herb. Phitos & Kamari); Mt. Nirito, above the villlage Anogi, 450 m, 07 Apr. 2000, *Katsouni* (Herb. Phitos & Kamari.). **Kefalonia:** above Sami, next to the monastery at Agrilies area, in bushes, c. 250 m, 11 Apr. 1974, *Fischer* (Herb. Phitos & Kamari); Argostoli, in loco Phanari, in silva *Pinus halepensis*, 15 Apr. 1975, *Phitos & Kamari 27001* (Herb. Phitos & Kamari); close to the city of Argostoli, area Katavothres, in opening of *Pinus halepensis* forest, 3 Apr. 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, 01 Apr. 1982, *Stamatiadou 22672* (Herb. Phitos & Kamari); in declivibus borealibus cacuminis Roudi, 500 m, 4 Sep. 1985, *Phitos & Kamari 19552* (Herb. Phitos & Kamari); ibid., 19 May 1986, *Phitos & Kamari 27002* (Herb. Phitos & Kamari); between the villages Haliotata and Poulata, close to the road, *Broussalis s.n.* (Herb. Phitos & Kamari); close to the village Razata, at the place Kiklopia tichi, in *Pinus halepensis* forest, 15 Mar. 1999, *Katsouni 251* (Herb. Phitos & Kamari; MNHC-I); ibid., 2 Apr. 2000, *Phitos, Kamari & Katsouni 26471* (Herb. Phitos & Kamari; MNHC-I); between Sami and Karavomilos, 30 m, 20 Mar. 2000, *Katsouni 252* (Herb. Phitos & Kamari; MNHC-I); between Argostoli and Sami, at the place Lanou, 25 Mar. 2004, *Katsouni 253* (Herb. Phitos & Kamari; MNHC-I); close to the village Valsamata, 13 Apr. 2000, *Katsouni 255* (Herb. Phitos & Kamari; MNHC-I); close to the village Pastra, at the place named Agios Georgios, *Katsouni s.n.*(Herb. Phitos & Kamari); close to the monastery Agia Paraskevi Tafiou, *Katsouni s.n.* (Herb. Phitos & Kamari); close to the village Chavriata, *Katsouni s.n.* (Herb. Phitos & Kamari); close to the village Vathi Erissou, 24 Mar. 2004, *Katsouni 459* (Herb. Phitos & Kamari; MNHC-I); **Lefkada:** inter pagum Eugiros et locum Skidi, 07 May 1979, *Phitos & Kamari 18873* (Herb. Phitos & Kamari); 1.5 km πριν από τη διασταύρωση για Σύβοτα (από Νυδρί προς Βασιλική) alt. c. 182 m, 38º 64' N, 20º 675', *Ε. Τρίγκου & Κουγιουμτζής 317* (Herb. Phitos & Kamari); Hortata, Apr. 2015, G. Kofinas *sub Samaropoulou SF1061* (ACA); from village Karya towards Livadi, at the edge of the road, 398 m, 38° 45.767' N, 020° 39.205' E, 01 Apr. 2016, *D. Phitos, G. Kamari & E. Katopodi sub Samaropoulou SF1126/7* (ACA); Olive groves at Paraspori – Hortata, along with *Paeonia* sp. and *Ornithogalum* sp., 38° 43.869' N, 020° 36.150' E, 01 Apr. 2016, *D. Phitos, G. Kamari & E. Katopodi sub*

Samaropoulou SF1126/8 (ACA); **Zakinthos:** Zante, Fuß des Vrachionas, östlich von Mariés, 21 Mar. 1936, *Ronniger* (W); zwischen Kilioménou und Hag. Léon, 22 Mar. 1936, *Ronniger* (W); Nordseite der Insel Pelouso, 23 Mar. 1936, *Ronniger* (W); s. loc., 3 Apr. 1952, *Goulimis 7919* (Herb. Pinatzi); in ditione pagi Volimae, in Pinetis, 31 Mar. 1973, *Tzanoudakis 588* (Herb. Phitos & Kamari); NW part of the island, just SE of Volimes, at the place named Veronika, calcareous substrate, 300-350 m, 37° 45' N, 20° 55' E, 06 Apr. 1997, *Phitos, Kamari, Constantinidis, Callimassia, Mikkelsen 26994* (Herb. Phitos & Kamari); in ditione pagi Gyri, prope locum Megali Spilia, 15 May 1974, *Tzanoudakis 1346* (Herb. Phitos & Kamari); close to the village Gyri, at the edges of uncultivated fields, 5 Apr. 1998, *Phitos & al. 27003* (Herb. Phitos & Kamari); ad Pharos prope pagum Keri, 25 Mar. 1988, *Tzini s.n.* (Herb. Phitos & Kamari); between the village Keri and its lighthouse, in clearing of *Pinus* forest and macchie, 5 Apr. 1997, *Phitos, Kamari, Constantinidis, Callimassia, Mikkelsen 26996* (Herb. Phitos & Kamari); village Korithi, between the lighthouse and the village (in fruit), 13 Oct. 1991, *Phitos & Kamari 27004* (Herb. Phitos & Kamari); ad pagum Korithi, in agris incultis, 45 m, 26 May 1997, *Phitos & Kamari 25434* (Herb. Phitos & Kamari); close to the village of Anafonitria, c. 340 m, 37° 50' N, 20° 39' E, 3 Apr. 1998, *Phitos, Kamari & Constantinidis 25985* (Herb. Phitos & Kamari); close to the village of Giri and NE of it, c. 550 m, 37° 48' N, 20° 44' E, 3 Apr. 1998, *Phitos, Kamari & Constantinidis 26995* (Herb. Phitos & Kamari); ad pagum Korithi, alt. ca 45 m, in agris incultis, 37° 56' N, 20° 43' E, 26 May 1997, *Phitos & Kamari 25434* (Herb. Phitos & Kamari); **STEREA ELLAS: Aetoloakarnania:** in Abieto-Quercetis declivium borealiorientalium cacuminis Boumistos, c. 1100 m, 09 June 1963, *Phitos 1050* (M).

***Fritillaria messanensis* Rafin. subsp. *sphaciotica* (Gand). Kamari & Phitos**

GREECE: KRITI: Chania: Lefka Ori, Kallikratis, 30 Apr. 2017, *G. Kofinas sub Samaropoulou SF1119* (ACA); peninsula Titiron, in saxosis calc., prope Selia, c. 300 m, 21 Apr. 1942, *Rechinger 12231* (W); Levka Ori, in saxosis calc. ad marginem australem altoplanitiei Omalos, c. 1100 m, 26 Apr. 1942, *Rechinger 12373* (W); N-Hänge der Weissen Berge sdl. ob. Kambi am Weg zum EOS-Katafijio, 850 m, 09 Apr. 1962, *Greuter 4114* (ATH, B, UPA, W); in rupestribus calc. faucium Samaria, 12 May 1963, *Phitos 751* (M); Samaria gorge, at the end of Xiloskalo, in the base of calcareous rocks, c. 750 m, 28 May 1972, *Kamari & Papatsou 21912* (Herb. Phitos & Kamari); between Xiloskalo pass and the chapel of Agios Nikolaos, 1300-700 m, 28 May 1972,

Petamidis 1407 (ATH); distr. Kidonia, village Malaxa, 470 m, 13 Apr.1974, *Goulandri 149* (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 Apr. 1994, *Bergmeier & Matthäs 3733* (B, Herb. Phitos & Kamari); **Iraklio**: Iraklion, am Berg Strubula bei Marathos, Kalkhänge, 10 Apr. 1954, *Merxmüller & Wiedmann 5886* (M); Supra pagum Gergeri, in faucibus Gafari, prope silvam Rouva *(Quercus coccifera),* 1200-1300 m, 23 Apr. 1972, *Phitos & Kamari 11173* (UPA); montes Psiloritis, supra pagum Gergeri, in loco Voskero, alt. 1300-1350 m, 22 Apr. 1974, *D. Tzanoudakis 1080* (UPA); in loco Tiganolakos, c. 1300 m, 22 Apr. 1974, *Tzanoudakis 1096* (UPA); Ep. Kenourgiou, Mt. Psiloritis, supra pagum Gergeri, in silva Rouva (*Quercus coccifera*), alt. 1000-1100 m, 22 Apr. 1974, *D. Tzanoudakis 1097* (UPA); am Youchtas-SO-Hang, 05 Apr. 1981, *Rehder s.n.* (M); **Lasithi:** Mt. Thripti, 29 May 2017, *G. Kofinas sub Samaropoulou SF1118* (ACA); Kalamafka, Bachufer bzw. lichte Föhrenbestände, 650 m, 11 Apr. 1971, *Malicky-Reisen 7* (W); between the villages Krousta and Kritsa, 04 Apr. 1974, *Goulandri 145* (ATH); Prinias hill, with low phrygana and rocks, c. 750 m, 08 May 1994, *Anagnostopoulos & Athanasiou s.n.* (Herb. Phitos & Kamari); **Rethimno**: Infra pagum Myrthios, in saxosis litoreis, 14 Apr. 1974, *Phitos, Kamari & Tzanoudakis 16749* (Herb. Phitos & Kamari); ad pagum Plakias, in declivibus maritimis, 10-30 m, 14 Apr. 1974, *Phitos & al. 26992* (Herb. Phitos & Kamari); above the village Alones, 20 Apr. 1983, *Tzanoudakis s.n.* (Herb. Phitos & Kamari).

***Fritillaria montana* Hoppe ex W.D.J. Koch**

GREECE: MACEDONIA: Florina: montes Triklarion, in declivibus boreo-occidentalibus cacuminis Boutsi, in apertis saxosis calc. alt. 1450-1550 m, 19 May 1987, *D. Phitos* & *G. Kamari 19865* (Herb. Phitos & Kamari); **Kastoria:** Mt. Boutsi: alpine meadow, calcareous substrate, 1549 m, 40° 38' 33" N, 21° 09' 25'' E, 31 May 2015, *S. Samaropoulou, I. Patrikios & A. Ioannou SF1092* (ACA); **Kozani:** mons Vourinos, in declivibus orientalibus cacuminis, alt. 1300-1350 m, in apertis ad viam et in silva Abietis et Pinetis, solo ophiolithico, 09 Jul. 1981, *T.R. Dudley, D. Phitos, D. Tzanoudakis, Gr. Iatrou & D. Christodoulakis 16765* (Herb. Phitos & Kamari); **THESSALIA: Larissa:** Mt. Kato Olympos, Livadaki, alt. 1400 m, May 2006, *K. Tamvakas 253* (Herb. Phitos & Kamari); Mt. Kato Olympos, Livadaki, north of Kallipefki, alt. ca 1407 m, 39° 57' N, 22° 29' E, 30 May 2015, *S. Samaropoulou, I.*

Patrikios & K. Tamvakas SF1089 (ACA); Kato Olympus, Livadaki, North of Kallipefki, 18 Apr. 2017, *P. Bareka & Ch. Lampropoulos sub Samaropoulou SF1116* (ACA).

***Fritillaria mutabilis* Kamari**

GREECE: IONIAN ISLANDS: Kephalonia: Mt. Roudi: Location Thea, 25 Apr. 2015, *D. Phitos, G. Kamari & G. Ismailos SF1070* (ACA); **Lefkada:** mons Elati, supra pagum Exanthia, alt. 600-900 m, 23 Apr. 1975, *D. Tzanoudakis 19427* (Herb. Phitos & Kamari); **PELOPONNISOS: Achaia:** monte Chelmos, prope pagum Vrachni in regione Abietina, alt. ca 1100 m, 28 Apr. 1974, *D. Tzanoudakis 1145* (UPA); Mt. Erimanthos, valley of the river Tethrea, rocks E of Alepochori, alt. 800 m, 13 Apr. 1998, *G. Maroulis 944* (UPA); Mt. Erimanthos, N slopes of Ntesmena, *Ostrya carpinifolia* forest, alt. 1100, 29 Apr. 2002, *G. Maroulis 811* (Herb. Phitos & Kamari); Mt. Erimanthos, E of Kertazi, Ntesmena top, *Ostrya carpinifolia* forest, alt. 1000 m, May 2002, *G. Maroulis 2534* (UPA); Mt. Chelmos, 2015, *D. Tzanoudakis sub Samaropoulou SF1080* (ACA); **STEREA ELLAS: Aetoloakarnania:** Mt. Boumistos, Sgouriouri, east of Boumistos' highest peak. Forested of *Arbutus adrachne*, *Q. ilex*, *F. ornus*, alt. c. 950 m, 38° 44′ N, 21° 03′ E, 12 May 1997, *S. Vlachos 242* (Herb. Phitos & Kamari); **Fokida:** Material cultivated in the Botanical Garden. Lund, dried 1976-77: 6 km ENE of Lidorikion, 1750 m, meadow with boulders, 16 May 1975, *E. Nilsson s.n.* (Herb. Phitos & Kamari); Material cultivated in the Botanical Garden. Lund, dried 1976-77: 7 km NNE of Lidorikion, 1850 m, S-slope, clay with pebbles, 17 May 1975, *E. Nilsson s.n.* (Herb. Phitos & Kamari); Mt. Vardousia, ad lacum Pyrgos, supra pagum Athanasios Diakos, in apertis silvae Abietis cephalonicae et in pratis montanis, alt. 1400-1600 m, 19 May 1985, *D. Phitos & G. Kamari 19959* (LD); mons Giona, in declivibus borealibus, supra pagum Kaloskopi, alt. 1950-2050 m, in pratis, 4 Jun. 1985, *A. Tiniakou 1201* (UPA); Mt. Iti, 1529 m, 13 May 2017, *G. Kofinas sub Samaropoulou SF1123* (ACA); Mt. Vardousia, 14 May 2017, *G. Kofinas sub Samaropoulou SF1125* (ACA); **Fthiotida:** mons Iti, in regione abietina supra pagum Pavliani, alt. 110-1300m, 21 May 1975, *D. Tzanoudakis 7184* (Herb. Phitos & Kamari); mons Iti, in regione abietina prope locum Katavothres, alt. ca 1500 m, 20 Jun. 1981, *D. Tzanoudakis 6847* (Herb. Phitos & Kamari); Material cultivated in the Botanical Garden. Lund, dried 1976-77: 5 km NW of Pavliani 1525 m, among boulders on S-facing slope, 26 May 1975, *E. Nilsson s.n.* (Herb. Phitos & Kamari); Material cultivated in the Botanical Garden. Lund, dried 1976-77: 7 km SSE of Ipati, 2050-2100 m, meadow with boulders, schist, 23 Jun. 1975, *E. Nilsson s.n.*

(Herb. Phitos & Kamari); mons Iti, inter locum Katavothres et livadies, in montanis Pasturis, alt. ca 1500m, 20 Apr. 1981, *D. Tzanoudakis 6838* (Herb. Phitos & Kamari); mons Iti, in declivibus borealibus cacuminis Katavothra, supra pagum Pavliani, in apertis silvae Abietis, alt. 1550 m, 28 May 1988, *D. Phitos & G. Kamari 21804* (Herb. Phitos & Kamari); **Viotia:** Levadhia, in parto austro-occidentali montis Parnassos ad meridiem vallis Lipokesa, alt. 1600 m, in clivis rupestribus calcareis graminosis et partim silvaticis septemtriones spectantibus, solo atro humifero, 16 Jun. 1963, W. *Greuter 5995* (UPA); mons Elikos, supra locum Arvanitsa, alt. 1450 m, 25 May 1974, *D. Tzanoudakis & Gr. Iatrou 1374* (Herb. Phitos & Kamari); Material cultivated in the Botanical Garden. Lund, dried 1976-77: 6 km NE-ENE of Arachova, 1900 m, meadow on stabilized scree on S-facing slope, 12 May 1975, *E. Nilsson s.n*. (Herb. Phitos & Kamari); Material cultivated in the Botanical Garden. Lund, dried 1976-77: 6.5 km N of Arachova, 1850 m, meadow vegetation among scree on W-SW-facing slope, 15 May 1975, *E. Nilsson s.n.* (Herb. Phitos & Kamari); mons Elikos, inter pagos Kyriaki, et Koukoura, alt. ca 1000 m, 20 Apr. 1977, *D. Tzanoudakis 6635* (Herb. Phitos & Kamari).

Fritillaria obliqua* Ker-Gawler subsp. *obliqua

GREECE: AEGEAN ISLANDS: Evvia: Ep. Karistias, mons Ochtonia, supra pagum Ochtonia, alt. 320 m, in nanofruticetosis, saxosis calc., 38° 32' N, 24° 10' E, 17 Apr. 1993, *D. Phitos & G. Kamari 23270* (Herb. Phitos & Kamari); Oktonia, 01 Apr. 2015, *N. Kalogiannis sub Samaropoulou SF1058* (ACA); Ohtonia, 01 Apr. 2015, *N. Kalogiannis sub Samaropoulou SF1059* – ex cultis (ACA); **STEREA ELLAS: Attiki:** Lykabetto, 1851, *Mart 2230* (K); in submontosis Atticae ad latus septentrionale m, Parnethos, 1855, *Mart 458* (K) - as *Fritillaria tristis*; Tourkovounia, 2 Mar. 1917, *P. Tsevas 001906* (ACA); in collibus Tourkovounia, prope Athina, in saxosis calc., 05 Mar. 1971, *G. Kamari 16746* (Herb. Phitos & Kamari); in collibus Tourkovounia, prope Athina, in saxosis calc., 05 Mar. 1972, *G. Kamari 16747* (Herb. Phitos & Kamari); mons Parnis, in declivibus borealibus, supra pagum Hagios Merkourios, 720 m, 24 Mar. 1974, *D. Tzanoudakis, 1703* (Herb. Phitos & Kamari); mons Parnis, supra pagum Malakasa, alt. 720 m, 24 Mar. 1974, *D. Tzanoudakis 1703*i (Herb. Phitos & Kamari); ad oppidum Athina, in collibus Tourkovounia, in saxosis calc., 27 Mar. 1983, *D. Phitos & G. Kamari 19134* (Herb. Phitos & Kamari); peninsula Kynosura, prope Marathon, in nanofruticetosis, saxosis calc. 38° 08′ N, 24° 03′ E, 26 Feb. 1995, *D. Phitos & G. Kamari 24266* (Herb. Phitos & Kamari); Marathonas: Peninsula of

Kinosoura, maquis shrubland, 30 m, 38° 08′ 42′′ N, 24° 03′ 20′′ E, 20 Mar. 2015, *S. Samaropoulou & A. Samaropoulos SF1052* (ACA); Tourkovounia: At the top of the hill and around the edges of Attiko Alsos, by the side of Galatsi, 290 m, 38° 00′ 19′′ N, 23° 45′ 42′′ E, 27 Mar. 2015, *S. Samaropoulou & A. Samaropoulos SF1054* (ACA); Mt. Parnitha: Korakovouni, Ippokratios Politia, 672 m, 38° 13' 04" N, 23° 47' 49′′ E, 06 Apr. 2015, *S. Samaropoulou & A. Samaropoulos SF1060* (ACA).

***Fritillaria obliqua* Ker-Gawler subsp*. tuntasia* (Heldr.) Kamari**

GREECE: KIKLADES ISLANDS: Gyaros: 23 May 1977, *D. Tzanoudakis 3195* (Herb. Phitos & Kamari); supra Panagia, alt. 250 m, 23 May 1977, *D. Tzanoudakis 3146* (Herb. Phitos & Kamari); 10 Apr. 1978, *D. Tzanoudakis 3663* (Herb. Phitos & Kamari); alt. ca 200 m, 11 Apr. 1978, *D. Tzanoudakis 3748* (Herb. Phitos & Kamari); **Kithnos**: ad Ag. Elias, phrygana, Apr. 1900, *B. Tuntas 001908* (ACA); 16 Mar. 1901, *B. Tuntas 001907* (ACA); 1-2 km S of Merixas, 11 Apr. 1969, *H. Runemark, A. Strid & M. Gustafsson R,St&G40451* (Herb. Phitos & Kamari); Kithnos, Ormos Flampourion, 11 Apr. 1969, *H. Runemark, A. Strid & M. Gustafsson 40472* (Herb. Phitos & Kamari); NE of Merixas, 14 Apr. 1969, *H. Runemark, A. Strid & M. Gustafsson 40587* (Herb. Phitos & Kamari); Kithnos, in collibus ad meridiem pagi Merichas spectantibus, alt. c. 50 m, in nanofruticetosis, solo schistose, 20 May 2007, *D. Phitos & G. Kamari 28004* (Herb. Phitos & Kamari); **Serifos:** The SC part of the island, N of Megalo Chorio, along the road from Megalo Livadi to Avessalos, grazed phrygana, substrate: schists, 318 m, 37° 9' 13.5''N, 24° 27' 11.48'' E, 04 Apr. 2015, *K. Kougioumoutzis SF1064* – ex cultis (ACA); The N part of the island, N of Panagia village, along the road to Sikamia beach, Grazed phrygana, substrate: schists, 203 m, 37° 11' 29.70'' N, 24° 29' 4.60'' E, 03 Apr. 2015, *K. Kougioumoutzis SF1065* – ex cultis (ACA).

***Fritillaria pelinaea* Kamari**

GREECE: EAST AEGEAN ISLANDS: Chios: Mt. Pelineon, W facing rocky slopes above Spatounda, alt. 760 m, under *Acer* sp. 38° 32′ N, 26° 00′ E, 22 Apr. 1990, *D. Phitos, G. Kamari, A. Anagnostopoulos & K. Athanasiou 21122* (Herb. Phitos & Kamari); Mt. Pelineon NE facing slopes above Amades, 350-550 m, in shrubs, 38° 34′ N, 26° 02′ E, ex cultis, 26 Apr. 1990, *A. Anagnostopoulos & K. Athanasiou 3634* (Herb. Phitos & Kamari); Mt. Pelineon W facing slopes, above Spartounda, alt. 800-1000 m, under

Acer sp. 38° 32′ N, 26° 00′ E, 23 Feb. 1979, *G. Kamari & D. Christodoulakis 15833a* (Herb. Phitos & Kamari); Mt. Perdikas, towards Volisso, alt. 100 m, 01 Apr. 2000, *P. Saliaris s.n.* (Herb. Phitos & Kamari); mons Pelineon, supra pagum Vikion, alt. 480 m, in apertis silvae *Pinus brutia*, solo argilloso, 38° 34′ N, 26° 00′ E, 25 Jul. 1992, *D. Phitos & G. Kamari 23096* (Herb. Phitos & Kamari).

***Fritillaria pontica* Wahlenb.**

BULGARIA: Haemus orientalis, intra fruticeta ad l.d. "Karandila", prope urb. Sliven, 22 Apr. 1975, *M. Markova, Z. Cerneva & P. Gerginov s.n.* (Herb. Phitos & Kamari); Strandza, in lapidosis intra fruticeta ad rivum Veleka, distr. Vic. Zvezdec, 20 Apr. 1975, *M. Markova, Z. Cerneva & P. Gerginov* (Herb. Phitos & Kamari); **GREECE:** *Koch* 1344 (G); **AEGEAN ISLANDS: Thasos:** supra pagum Sotir, alt. 450 m, (ex cultis), 27 May 1975, *D. Tzanoudakis 3606* (Herb. Phitos & Kamari); Mt. Ypsarion, NE slopes of Potamia, small forest of *Castanea* sp., *Quercus* sp., *Pinus* sp., *Platanus* sp., alt. c. 400 m, schist, 10 Jul. 1992, *A. Tiniakou & L. Tiniakos s.n.* (Herb. Phitos & Kamari); **MACEDONIA: Chalkidiki:** Hagion Oros inter Roussico – Careys, 13 Jun. 1961, *17569* (Herb. Phitos & Kamari); monte Athos, castanetes inter Vatopedi – Caryes, 1 Jul. 1963, *L. Pinatzi 18890* (Herb. Pinatzi, ACA); mons Athos, inter coen. Hag. Athanasios et Panaghia, alt. 1000-1400 m, 04 Jul. 1976, *Th. Georgiadis 208* (Herb. Phitos & Kamari); Hagion Oros, mons Athos, supra Kerasia, alt. 900-1050 m, 05 Jul. 1976, *Th. Georgiadis & H. Katravas 3524* (Herb. Phitos & Kamari); mons Athos, supra monasterium Hagia Anna Kerasia, alt. 500-600 m, 05 Jul. 1976, *Th. Georgiadis & H. Katravas 3486* (Herb. Phitos & Kamari); mons Athos, ad Karyes, in fagetis, alt. 370-400 m, 19 Apr. 1986, *D. Phitos 19945* (Herb. Phitos & Kamari); mons Athos, supra coenobium Agia Anna, alt. 500-800 m, in apertis petrosis, 20 Apr. 1986, *D. Phitos 19946* (Herb. Phitos & Kamari); mons Athos, supra coenobium Agia Anna, alt. 800-850 m, in apertis petrosis, 30 Apr. 1986, *D. Phitos 19944* (Herb. Phitos & Kamari); Agion Oros, Kerasia, alt. 600 m, in saxosis calcareis, 19 Apr. 1996, *D. Babalonas 129* (Herb. Phitos & Kamari); Ajios Antonios, Agion Oros, ca 600 m, in saxosis calcareis, 19 Apr. 1996, *D. Babalonas AO 140* (Herb. Phitos & Kamari); **Drama:** Mt. Menoikio, May 2016, *G. Kofinas sub Samaropoulou SF1111* (ACA); **Kavala**: Ep. Pangeou, Mt. Pangeo, meadows in openings of *Fagus sylvatica* woodland around the barracks of forest authorities, alt. 1300 m, 40° 54' N, 24° 06' E, 12 Jun. 1991, *A. Anagnostopoulos & A. Athanasiou 2095* (Herb. Phitos & Kamari); **THRAKI: Rodopi**: Komotini, *Quercus* sp. and *Fagus* sp. forest, 21

May 2015, *S. Ispikoudis sub Samaropoulou SF1077* (ACA); **TURKEY:** *Berggern s.n.* sub S06-4282 and S06-4283 (S); Instabul – Sarier, 20 Apr. 1959, *F. Yaltirik 1469* (E); Instabul, Belgrade forest, near Kos Bend, 02 May 1961*, F. Yaltirik s.n.* (E); Ordu, Fatsa, hills above town, 60 m, northern exposure, open oak scrub, slopes, 23 Apr. 1963, *C. Tobey 45* (E); Bolu, about WSW of Bolu, 07 May 1965, *B. Mathew & J. Tomlinson 4049* (E); Sinop, Ince Burum, 30 m, heavy forest, boxwood, oak and *Arbutus unedo*, 23 Apr. 1966, *C. Tobey 1644* (E); Samsun, Cetirli Pinar Köy, Bafra, *C. Tobey 44* (E).

***Fritillaria rhodocanakis* Orph. Ex Baker**

GREECE: STEREA ELLAS: Attiki: Idra: 03 Apr. 1876, *Heldreich* s.n. (K); 2 km E of the town, the upper monastery, garigue-slope, 02 May 1969*, M. Gustafsson G41581* (UPA); 500 m W of the town, Prof. Elias, 02 May 1969, *M. Gustafsson G41592* (UPA); supra vicum Hydra, in saxosis calcareis, alt. ca 30 m, 10 Mar. 1972, *D. Phitos & G. Kamari 16748* (Herb. Phitos & Kamari); along the road towards the summit Profitis Ilias, stony substrate, *Pinus* forest, 225 m, 37° 20′ 31′′ N, 23° 27′ 56′′ E, 21 Feb. 2016*, S. Samaropoulou & I. Patrikios SF1104* (ACA).

***Fritillaria spetsiotica* Kamari**

GREECE: PELOPONNISOS: Argolida: Nafplio, beside the castle of Palamidi, slopes with phrygana, 195.5 m, 37° 33′ 31′′ N, 22° 48′ 30′′ E, 24 Feb. 2016, *S. Samaropoulou & I. Patrikios SF1098* (ACA); **STEREA ELLAS: Attiki: Spetses:** Eparchia Trizinies, ad locum Zagoria, in apertis silvae *Pinus halepensis*, alt. ca. 50 m, 37° 36' N, 23° 24' E, 10 Mar. 1972, *D. Phitos & G. Kamari 18942* (Herb. Phitos & Kamari).

Fritillaria spetsiotica* × *F. rhodocanakis

GREECE: PELOPONNISOS: Argolida: in ditione pagi Nea Epidavros, in nanofruticetosis, alt. ca 100 m, 13 Mar. 1985, *G. Kamari & M. Tzini 19432* (Herb. Phitos & Kamari); inter Mon. Agnountos et pagum Nea Epidauros, in fruticetosis, alt. ca. 100 m, 13 Mar. 1985, *G. Kamari & M. Tzini 19430* (Herb. Phitos & Kamari); ad Iera Moni, 3 km ab urbem Navplion, in fruticetosis, alt. ca. 150 m., 13 Mar. 1985, *G. Kamari & M. Tzini 19431* (UPA) sub *F. spetsiotica*; prope pagum Didymon, alt. 160 m, 16.III.1988, L. Tiniakos 19968 (UPA) sub *F. spetsiotica*; Didima: Along the road towards the village, cultivated fields with olive trees, along with *Tulipa* sp., 167.5 m, 37° 27′ 15′′ N, 23° 10′ 16′′ E, 23 Feb. 2016, *S. Samaropoulou & I. Patrikios SF1100* (ACA); Moni Agnountos, 500 m after the monastery, towards Epidavros, macchie with *Juniperus* sp. alt. ca. 190 m, 37° 42′ 28′′ N, 23° 7′ 43′′ E, 24 Feb. 2016, *S. Samaropoulou & I. Patrikios SF1099* (ACA); **STEREA ELLAS: Attiki: Poros:** open Pinus woodland, alt. 100 m, 37° 30′ N, 23° 28′ 1′′ E, 16 Mar. 1984, *E. Zaharof F-079* – isotypus (sub 289634 G) sub *Fritillaria rhodocanakis* subsp. *argolica*.

***Fritillaria sporadum* Kamari**

GREECE: SPORADES ISLANDS: Yioura: c.1 km SW-WSW of the top 10 - 300 m, 24 Apr. 1972, *S. Snogerup* & *D. Phitos 43319* (UPA); the top area, 500-570 m, 25 Apr. 1972, *S. Snogerup S.43378* (Herb. Phitos & Kamari)-isotypus; in apertis silvae *Quercus cocciferae* ad borealem spectantibus, alt. 400 m, 17 Apr. 1985, *D. Phitos* & *G. Kamari 19446* (Herb. Phitos & Kamari); in apertis silvae *Quercus cocciferae*, ad locum Patimata, alt. 370-470 m, 17 Apr. 1985, *D. Phitos* & *G. Kamari 19447* (Herb. Phitos & Kamari); ad locum Manolis, in saxosis calc. ad orientem spactantibus, alt. 540 m, 17 Apr. 1985, *D. Phitos* & *G. Kamari 19448* (Herb. Phitos & Kamari); ad ditionem loci Patimata, in Quercetis alt. 470 m, in saxosis calc., 19 Apr. 1985, *D. Phitos* & *G. Kamari 19691* (Herb. Phitos & Kamari); supra locum Spilia, in apertis silvae *Quercus coccifera*, alt. 150 m, in petrosis calc. 39° 22′ N, 24° 09′ E, 05 Apr. 1991, *D. Phitos* & *G. Kamari 22225* (Herb. Phitos & Kamari); supra locum Spilia, in apertis silvae *Quercus coccifera*, alt. 150 m, in saxosis calc. 39° 22′ N, 24° 09′ E, 08 Apr. 1991, *D. Phitos* & *G. Kamari 22261* (Herb. Phitos & Kamari); **Kira Panagia**: in declivibus orientalibus collium Papavardia, alt. ca 100 m, 05 May 1988, *D. Phitos, G. Kamari* & *A. Anagnostopoulos 20300* (Herb. Phitos & Kamari); Ormos Ajios Petros, in fruticetosis

saxosis calc. declivium orientalium, alt. 50-100 m, 05 May 1988, *D. Phitos, G. Kamari* & *A. Anagnostopoulos 20031* (Herb. Phitos & Kamari).

***Fritillaria theophrasti* Kamari & Phitos**

GREECE: EAST AEGEAN ISLANDS: Lesvos: Mytilene, 1937, *Guiol 4204* (Herb. Pinatzi); ins. Lesbos, 22 May 1952, *Pinatzi 7920* (Herb. Pinatzi), insula Lesbos, in olivertis, 11 Apr. 1957, *Pinatzi 14136* (UPA, Herb. Pinatzi); W-SW of Sanatorion, 600 m, 13 Mar. 1969, *Stamatiadou 4832* (ATH); Mt. Olympos, SW of the Sanatorium of Agiassos, 600 m, 17 May 1969, *Stamatiadou 6302* (ATH); Agiassos, alt. 600 m, on schist, 03 May 1973, *Eustratiou s.n.* (Herb. Phitos & Kamari); close to the village of Agiassos and Prof. Elias, 500 m, 05 May 1973, *G. Kamari cult*. *No 16* (Herb. Phitos & Kamari); Agiassos, 08 May 1977, *H. Baumann s.n.* (Herb. Phitos & Kamari); Mt. Olimpos, at the area Sanatorion, ca 3 km towards Palaeochorion, 24 Feb. 1979, *G. Kamari & D. Christodoulakis cult. no*. *15* (Herb. Phitos & Kamari); Ep. Plomariou, near Megalochorion, c. 500m, disused terraced fields, 39° 01', 26° 22', 27 Apr. 1987, *Strid & al. 26151* (Herb. Phitos & Kamari); Ep. Plomariou: Near Megalochorion, c. 500 m, disused terraced fields, 39° 01′ N, 26° 22′ E, 27 Apr. 1987, *K.I. Christensen, K.B. Moller* & *A. Strid Strid&al26151* (Herb. Phitos & Kamari); Agiassos at Plomari, in schist, 700-800 m, 25 Jul. 1989, *Anagnostopoulos & Athanasiou* cult. *no 137* (Herb. Phitos & Kamari); Kalloni near Moni Limonos, 15 Mar. 1994, *Markou s.n.* (ATH); 4 km N of the vil. Agra towards the vil. Fterounda, in ravine with *Platanus orientalis*, volcanic substrate, 600-650 m, 16 Jun. 1998, *Bazos 3280* (ATHU); 1 May 2015, *G. Kofinas sub Samaropoulou SF1071* (ACA).

Παράρτημα ΙΙ

Χάρτες εξάπλωσης

***Fritillaria* taxa με σκούρα πορφυρά-καφέ άνθη:**

Χάρτης 1. (△) *F. davisii*, (●) *F. obliqua* subsp. *obliqua*, (⊘) *F. obliqua* subsp. *tuntasia*, (■) *F. sporadum*.

Fritillaria taxa με εσωτερικά κίτρινα και εξωτερικά σκούρα πορφυρά-καφέ άνθη:

Χάρτης 2. (△) *F. drenovskii*, (●) F. *ehrhartii*.

***Fritillaria* taxa με γραμμοειδή και κατ' εναλλαγή φύλλα:**

Χάρτης 3. (●) *F. messanensis* subsp. *messanensis*, (⊘) F. *messanensis* subsp. *gracilis*, (⊖) *F. messanensis* subsp. *sphaciotica*, (△) *F. elwesii*.

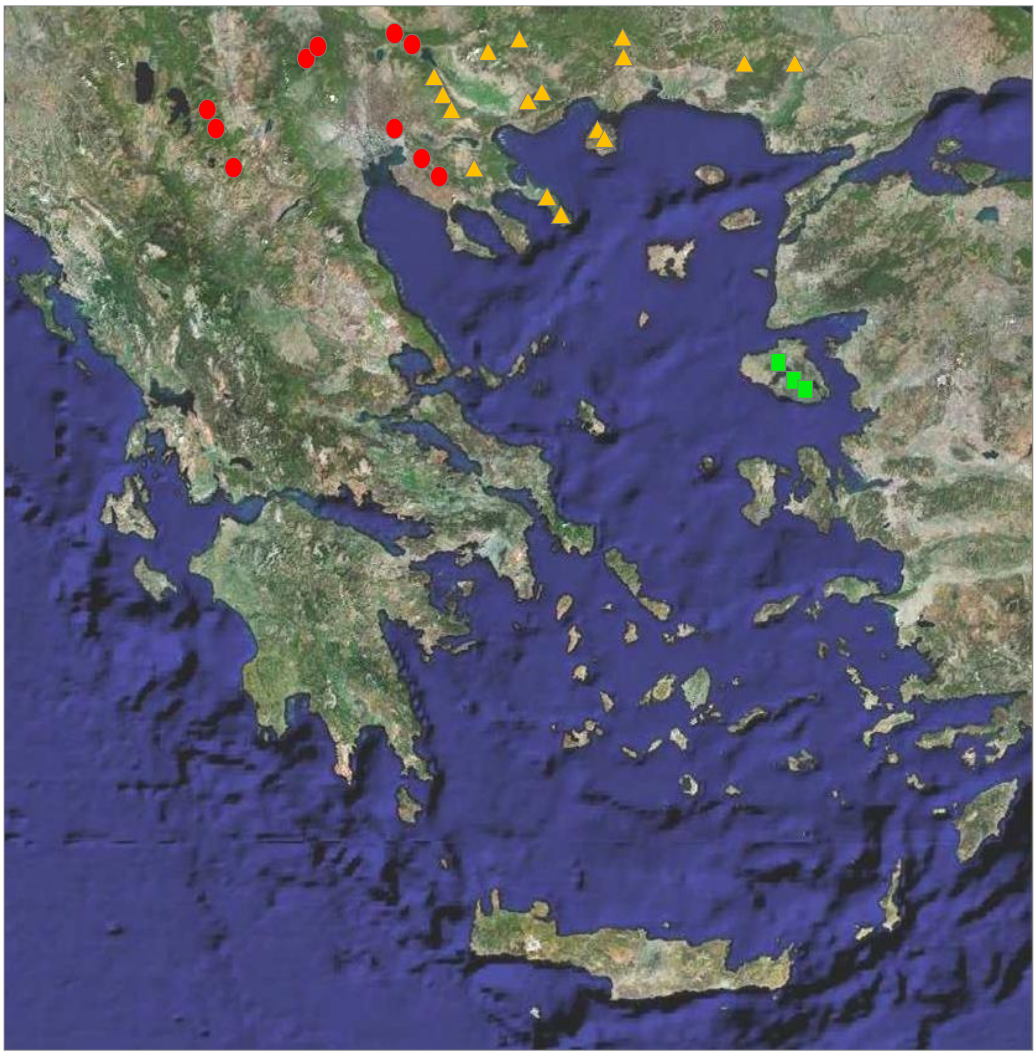
Fritillaria taxa στενοενδημικά του Αργοσαρωνικού Κόλπου:

Χάρτης 4. (■) *F. rhodocanakis*, (▲) F. *spetsiotica*, (●) *F. spetsiotica* × *F. rhodocanakis* (2*n* = 2x), (⊘) F. *spetsiotica* × *F. rhodocanakis* (2*n* = 3x), (★) *F. spetsiotica* × *F. graeca*.

Fritillaria taxa με σκούρα πορφυρά-καστανά, ασαφώς ψηφιδωτά (tessellated) άνθη:

Χάρτης 5. (△) *F. epirotica*, (●) *F. montana*.

***Fritillaria* taxa με χαρακτηριστικά πτερύγια στις κάψες:**



Χάρτης 6. (△) *F. pontica*, (●) *F. gussichiae*, (■) *F. theophrasti*.

Fritillaria **taxa με σκούρα πορφυρά-καφέ κωδωνοειδή άνθη με στενή έως πλατιά κίτρινη/κιτρινοπράσινη ζώνη (fascia)**

Χάρτης 7. (△) *F. graeca*, (●) *F. mutabilis*, (■) *F. ionica* subsp. *ionica*, (▨) *F. ionica* subsp. *thesssala*, (▤) *F. ionica* subsp. *reiseri*.

Fritillaria taxa με κίτρινα/κιτρινοπράσινα άνθη:

Χάρτης 8. (△) *F. bithynica*, (●) *F. carica*, (■) *F. conica*, (◆) *F. euboeica*, (★) *F. forbesii*, (▽) *F. pelinaea*, (✸) *F. phitosia*, (⬢) *F. rhodia*, (✚) *F. sibthorpiana*.

Παράρτημα ΙΙΙ

Δημοσιεύσεις

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RESEARCH ARTICLE

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Karyomorphometric analysis of *Fritillaria montana* group in Greece

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Abstract

Fritillaria Linnaeus, 1753 (Liliaceae) is a genus of geophytes, represented in Greece by 29 taxa. Most of the Greek species are endemic to the country and/or threatened. Although their classical cytotaxonomic studies have already been presented, no karyomorphometric analysis has ever been given. In the present study, the cytological results of *Fritillaria montana* Hoppe ex W.D.J. Koch, 1832 group, which includes *F. epirotica* Turrill ex Rix, 1975 and *F. montana* are statistically evaluated for the first time. Further indices about interchromosomal and intrachromosomal asymmetry are given. A new population of *F. epirotica* is also investigated, while for *F. montana*, a diploid individual was found in a known as triploid population. Paired t-tests and PCoA analysis have been applied to compare the two species.

Keywords

Fritillaria epirotica, *Fritillaria montana*, karyotype analysis, PCoA, endemics, Greek flora, karyograms

Introduction

The genus *Fritillaria* Linnaeus, 1753 (Liliaceae) comprises approximately 150 taxa of geophytes, found in the temperate zones of the Northern Hemisphere (Kamari and Phitos 2006). Most of them are distributed across Eurasia while about 20 species occur in

California. Only one species, *F. camschatcensis* (L.) Ker Gawler, 1809 links both groups by its distribution in both North America and eastern Asia (Fay and Chase 2000, Ambrozova et al. 2011).

According to its latest revision (Rix 2001), the genus is divided into eight subgenera, *Fritillaria* Rix, 2001 (including two sections, *Olostyleae* Rix, 2001 and *Fritillaria* Rix, 2001); *Davidii* Rix, 2001; *Liliorhiza* (Kellogg) Bentham & Hooker, 1883; *Japonica* Rix, 2001; *Rhinopetalum* Fischer, 1835; *Petilium* Baker, 1874; the monotypic *Theresia* K. Koch, 1849 and *Korolkowia* Rix, 2001. Although Iran (and more precisely its northern part as well as the neighbouring countries) is relatively poor in species (17 species and 4 subspecies), it is considered to be the centre of *Fritillaria* diversity above species level (Rix 1977), because those taxa belong to four out of five main subgenera (Jafari et al. 2014).

In Greece, the genus is also characterized by high diversity and is represented by a multitude of taxa (24 species and 5 subspecies), all belonging to the subgenus *Fritillaria* (Kamari and Phitos 2006).

Out of the 29 taxa found or described in Greece so far, 18 taxa (14 species and 4 subspecies) are endemic to the country and no less than 17 species and 2 subspecies occur in the Aegean archipelago and the surrounding continental region (Kamari and Phitos 2000). Moreover, Turkey is the richest country concerning the number of *Fritillaria* with 35 species and 6 subspecies, 19 of which are considered endemic (Tekşen and Aytaç 2011, Advay et al. 2015, Özhatay et al. 2015). Eighteen of those species and 4 subspecies are distributed in the Mediterranean, 12 of which are endemic. Taking into consideration the total number of *Fritillaria* taxa as well as the number of the endemic ones, Greece, along with W Turkey (Rix 1984, Özhatay 2000, Tekşen 2012), constitutes a secondary evolutionary center at least for this subgenus, if not for the whole genus. As a result, the Aegean archipelago can be considered as the heart of the secondary biodiversity center for the subgenus *Fritillaria* (Kamari and Phitos 2000).

Among the *Fritillaria* taxa occurring in continental Greece two species constitute the *Fritillaria montana* group (Kamari 1991a): *Fritillaria epirotica* Turrill ex Rix, 1975, which is endemic to NW Greece and *Fritillaria montana* Hoppe ex W.D.J.Koch, 1832, which has a wide distribution in S and SE Europe. Both species of the above group are characterized by their long (2/3 of the tepal length) nectaries, as well as by their obscurely tessellated tepals.

Fritillaria epirotica is a very short plant (up to 15 cm) with dark purplish, obscurely tessellated flowers, which almost touch the ground and it grows on ophiolithic substrates, usually at high altitudes (up to 2600 m). On the contrary, *F. montana* is tall (up to 60 cm), characterized by alternate or subopposite linear, slightly canaliculated leaves, with dark purplish distinctly tessellated flowers, and it grows usually on limestone substrate at an altitude up to 1600 m.

Fritillaria epirotica is included in the Red Data Book of Rare and Threatened Plants of Greece (Phitos et al. 1995 & 2009), in the IUCN Red List of Threatened Species, Version 2014.2. and also in the Council Directive 92/43/EEC on the conservation of natural habitats and of wild fauna and flora. It is protected by the Presidential Decree

67/81, characterized as Endangered (EN) by IUCN and as Vulnerable (VU) in the Red Data Book of Rare and Threatened Plants of Greece (Kamari 1995, Kamari and Phitos 2009). *Fritillaria montana* is characterized, according to IUCN Red List of Threatened Species, Version 2014.2., as a Data Deficient (DD) species. In Greece, some of its populations are included in Natura 2000 sites. Despite its wide distribution, the species is Rare (R) in Italy (Peruzzi et al. 2008) and included in the regional Red Lists of Italian threatened species (Conti et al. 1997). As already known, the misapplied nomenclature of the *F. montana* complicates botanical literature (Lozina-Lozinskaja 1935, Zahariadi 1966, Kamari 1991a, b, Tomovic et al. 2007). Several locations in Italy have recently been further studied and *Fritillaria montana* populations are getting distinguished, while more biometric details for the species are provided (Peruzzi and Bartolucci 2009, Bartolucci et al. 2009, Mancuso et al. 2012, Peruzzi et al. 2012). An indicative example of the situation is the very low production of fruits during fruiting season in 2008 observed by Mancuso et al. (2012). Moreover, *Fritillaria montana* is characterized as an Endangered (EN) species listed in the third edition of the Red Book of Ukraine (Chorney et al. 2009), as a Rare (R) one in Bosnia and Herzegovina (Šilić 1996), Vulnerable (VU) in Serbia (IUCN Red List of Threatened Species) and protected at a national level in France. Tomovic et al. (2007) referred that the species was listed as Rare in the Red Data Book of the PR Bulgaria (Velchev 1984 sub *F. orientalis* Adam), but the latest version does not include it anymore (Petrova and Vladimirov 2009).

Concerning the cytology of the genus, *Fritillaria* has been studied for many years due to the interest of its large chromosomes and vast genome size (Darlington 1935, 1937, Frankel 1940). Indeed, 1C values (DNA content of the unreplicated haploid chromosome complement) in *Fritillaria* are among the largest reported for all angiosperms (Bennett and Smith 1976, Sharma and Raina 2005). The karyotype is quite stable, asymmetrical and usually diploid, with a basic chromosome number of x = 12. Only a few species are an exception to this, with x = 9 (3 species), x = 11 (2 species) and x = 13 (2 species), but without a special pattern (Darlington 1937, Noda 1964, Li and Shang 1989, Jafari et al. 2014). However, the presence and the morphology of satellited chromosomes vary among the species or even among populations of the same taxon (Runemark 1970, Bentzer et al. 1971, Mehra and Sachdeva 1976, Koul and Wafai 1980, Kamari 1984a, 1991a, 1996, Zaharof 1987, Kamari and Phitos 2006). In addition, secondary constrictions and supernumerary B-chromosomes are observed very often (La Cour 1978b, 1978c, Kamari 1984a, 1991a, 1991b, Zaharof 1987, 1989, Kamari and Phitos 2006). As a result, that type of differentiations is always emphasized and specific chromosome pairs are studied as markers, in order to spot the differences among the generally stable and similar karyotypes (Kamari 1984b, Zaharof 1989, Kamari and Phitos 2000, 2006). Finally, a few triploid karyotypes have been reported with 2n = 3x = 36 (Fedorov 1969, La Cour 1978a, Moore 1982, Marchant and Macfarlane 1980, Zaharof 1987, Peruzzi et al. 2009) or with 2n = 3x = 27 chromosomes (Cesca 1986, Kamari 1991a).

Recently many questions have arisen, regarding the classification and phylogeny of the genus, especially for the species appearing in Greece. Although several molecular phylogenetic studies have been published (Fay and Chase 2000, Rønsted et al. 2005,

Turktas et al. 2012, Metin et al. 2013) none of them refer to the total of Greek taxa. Even though classical cytotaxonomic studies of the genus in Greece have already been published (Kamari 1984a, 1984b, 1991a, 1991b, 1996, Zaharof 1987, 1989, Kamari and Phitos 2000, 2006), neither karyomorphometric analysis, nor statistical evaluation of the cytological results, have ever been given so far. In the present study, an attempt for further karyomorphometric analysis of chromosome features has been made, concerning the two members of *Fritillaria montana* group.

Material and methods

Living plants of the *Fritillaria montana* and *F. epirotica* populations were collected (Table 1) and cultivated in the Experimental Gardens of the University of Patras and Agricultural University of Athens. Vouchers are deposited in UPA and ACA.

The cytological study is based on the squash technique and the chromosome counts were made from root tip metaphases (Östergren and Heneen 1962, Kamari 1976). The root tips were pretreated in a mixture of 1:1 8-hydroxyquinoline (0,002% w/v):colchicine (0.3 w/v) for 3 hrs (Kamari 1984a) and fixed in 3:1 (v/v) absolute ethanol:glacial acetic acid for 24 hours at 4 °C. Fixed root tips were stored at -20 °C at 75% ethanol.

Before staining, the root tips were hydrolyzed in 1N HCl 60 °C for 15 min and stained in Feulgen for 3 hrs (Darlington and La Cour 1969). Prior to squashing, the stained root tips were put on a slide with a drop of 45% (v/v) acetic acid. The slides were observed with AXIOLAB Zeiss microscope and photos were taken with Canon EOS 600D digital camera.

At least five metaphase plates of each species were analysed and indices were calculated with Microsoft Office Excel 2007, IBM SPSS Statistics version 22 and Past 3.03. Chromosome terminology follows Levan et al. (1965), Stebbins (1971) and Kamari (1976), taking into consideration comments and suggestions by Sybenga (1959), Bentzer et al. (1971) and Favarger (1978). For each taxon there is a presentation of the karyotype formula, maximum and minimum length of the chromosomes, total and average chromosome length and total haploid length of the chromosome set, along with their standard deviation. The interchromosomal asymmetry (CV_{CL}), is estimated according to Paszko (2006) and the intrachromosomal asymmetry (M_{CA}) according to Watanabe et al. (1999), Peruzzi and Eroğlu (2013) and Peruzzi and Altinordu (2014). Additionally the coefficient of variation of centromeric index (CV_{CI}) measuring the centromere position heterogeneity is estimated following Paszko (2006) and Peruzzi and Altinordu (2014). A multivariate analysis (Principal Coordinate Analysis - PCoA) was made concerning six karyological parameters: 2n, x, THL, CV_{CL}, CV_{CI} and M_{CA} (Peruzzi and Altinordu 2014). When marker chromosomes are observed (metacentric, submetacentric, SAT-chromosomes and secondary constrictions) r-index, R-length, Centromeric index and Arm difference ratio are also given. Finally, t-tests are given, regarding the indices of TCL, ACL, CV_{CL}, $M_{CA,}$ in order to check statistically significant differences between the two species.

Table 1. Origin, chromosome numbers (2n) and voucher number of *Fritillaria* material.

Taxon	Origin	2n	Voucher number, Herbarium
F. montana	Mt. Vourinos (W Macedonia)	18	16765, UPA
	Mt. Kato Olympos (Thessalia)	18	SF1089, ACA cult. no. 253, UPA
	Mt. Boutsi (NW Macedonia)	27 and 18 (1 individual)	SF1092, ACA 19865, UPA
F. epirotica	Katara Pass (Epirus)	24	21348, UPA 7919, UPA
	Mt. Vasilitsa (N Pindos)	24	SF1076, ACA
	Mt. Smolikas (N Pindos)	24	SF1097, ACA
	Mt. Kratsovo (W Thessalia)	24	cult. no. 255, UPA

Results

Fritillaria montana Hoppe — 2n = 2x = 18 + 0-3B (Figs 1, 2).

Populations karyologically studied:

Greece: Macedonia: Nomos Kozanis: mons Vourinos, in declivibus orientalibus cacuminis, alt. 1300-1350 m, in apertis ad viam et in silva Abietis et Pinetis, solo ophiolithico, 9 Jul 1981, T.R. Dudley, D. Phitos, D. Tzanoudakis, Gr. Iatrou & D. Christodoulakis 16765 (UPA); **Thessalia: Nomos Larissis:** Mt. Kato Olympos, Livadaki, north of Kallipefki, alt. ca. 1407 m, 39°57'N; 22°29'E, 30 May 2015, S. Samaropoulou, I. Patrikios & K. Tamvakas SF1089 (ACA); Mt. Kato Olympos, Livadaki, alt. 1400 m, May 2006, K. Tamvakas 253 (UPA).

Fritillaria montana is the only Greek species with a basic chromosome number of x = 9, having 2n = 18 chromosomes (Fig. 1). Its karyotype includes two metacentric (m) chromosome pairs that can be characterized as markers, the longer and the shorter ones (Table 3, chromosome pairs no. 1 and no. 5, numbered according to their chromosome length), because they bear characteristic secondary constrictions close to the end of the short arm (Fig. 2). Secondary constrictions are also observed to the rest of the metacetric chromosomes, however, they are not always visible. For this reason, the other three metacentric chromosome pairs cannot be characterized as markers.

The karyotype formula of the studied populations is given as 2n = 10m + 2st + 6t = 18 (Fig. 2). The chromosome size ranges between 24.41 μm and 11.26 μm and the total chromosome length is 316.34 μm. The karyotype is more symmetric (Table 2) concerning the variation in chromosome length (CV_{CL} = 25.2) rather than the centromere position (M_{CA} = 41.42), while the parameter CV_{CI} is even higher (CV_{CI} = 56.21). Up to three B-chromosomes were found, all of them acrocentric (st) in the studied material.

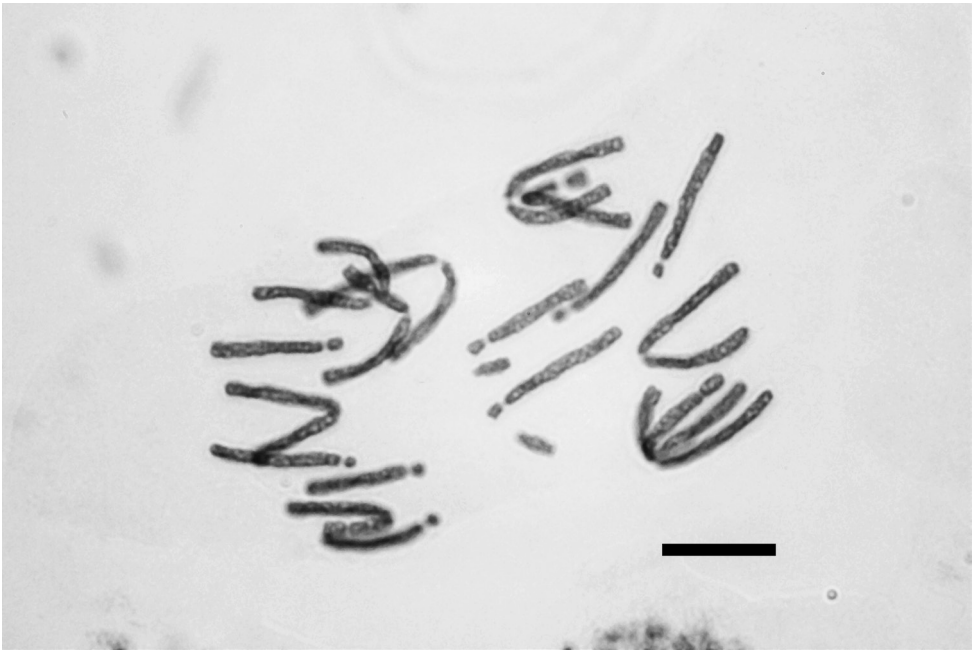

Figure 1. Photomicrograph of mitotic metaphase plate of *Fritillaria montana* from Mt. Vourinos, 2n = 2x = 18. Bar = 10 μm.

Table 2. Studied species with karyomorphometric indices. Chromosome number (2n), total (TCL) and average (ACL) chromosome length, total haploid chromosome length (THL), maximum (max l + s) and minimum (min l + s) chromosome length, karyotype asymmetry indices (CV_{CL}, CV_{CI} and M_{CA}).

Species	*F. montana*		*F. epirotica*
Chromosome number	2n = 2x = 18	2n = 3x = 27	2n = 2x = 24
Karyotype formula	10m + 2st + 6t	15m + 3st + 9t (10m + 4st + 4t, 1 individual)	2m + 2sm + 14st + 6t
TCL (μm) **(SD)**	316.34 (30.22)	363.23 (53.47)	324.39 (51.12)
THL (μm) **(SD)**	158.17 (15.11)	121.08 (17.82)	162.2 (25.56)
ACL (μm) **(SD)**	17.57 (1.68)	13.45 (1.98)	13.52 (2.13)
max l + s (μm)	24.41	22.86	18.44
min l + s (μm)	11.26	8.00	10.00
CV_{CL} **(SD)**	25.26 (1.12)	31.07 (3.61)	16.85 (2.43)
CV_{CI} **(SD)**	56.21 (0.99)	54.79 (3.57)	51.66 (2.99)
M_{CA} **(SD)**	41.42 (0.35)	40.41 (1.18)	63.33 (1.25)

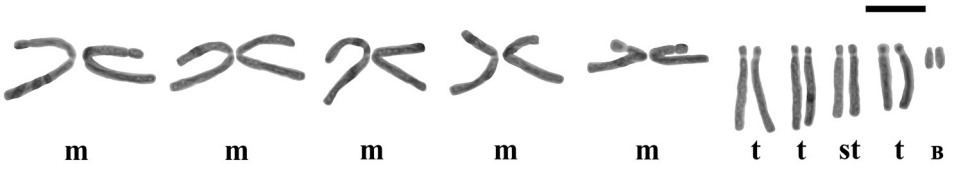

Figure 2. Karyogram of *Fritillaria montana* from Mt. Vourinos, 2n = 2x = 18. Bar = 10 μm.

Table 3. Karyomorphometric indices of marker chromosomes for each species, marker chromosome pairs (numbered according to their chromosome length), long arm's length (l), short arm's length (s), chromosome length (l + s) with minimum and maximum prices, r- index, Centromeric index, Arm difference ratio, R-length.

Species	***Fritillaria montana***		***Fritillaria epirotica***			
Chromosome number	2n = 18		2n = 24			
marker chromosomes	Pair no. 1	Pair no. 5	Pair no. 1	Pair no. 2	Pair no. 3	Pair no. 5
l (μm) **(SD)**	12.84 (1.00)	10.71 (1.09)	9.68 (1.05)	10.51 (1.04)	12.19 (1.07)	10.87 (1.23)
s (μm) **(SD)**	11.15 (0.79)	6.93 (0.67)	6.86 (0.82)	5,27 (0.63)	1.60 (0.44)	1,82 (0.36)
l + s (μm) **(SD)**	23.99 (1.71)	17.65 (1.66)	16.53 (1.73)	15.77 (1.49)	13.79 (1.18)	12.42 (1.51)
min l + s (μm)	20.88	15	13.53	12.94	11.47	8.40
max l + s (μm)	26.47	20	19.12	18.24	15.59	15
r-index **l/s**	1.15	1.54	1.40	2.03	8.06	6.24
Centromeric index **l/l + s**	0.54	0.61	0.58	0.67	0.88	0.85
Arm difference ratio **l - s/l + s**	0.70	0.21	0.17	0.34	0.77	0.71
R-length **l + s/Sn(l + s)**	0.08	0.06	0.05	0.05	0.04	0.04

Fritillaria montana Hoppe — 2n = 3x = 27 and 2n = 2x = 18 (1 individual) (Figs 3, 4).

Populations karyologically studied:

Greece: Macedonia: Nomos Florinas: Montes Triklarion, in declivibus boreo-occidentalibus cacuminis Boutsi, in apertis saxosis calc., alt. 1450-1550 m, 19 May 1987, D. Phitos & G. Kamari 19865 (UPA); Mt. Boutsi, alpine meadow, calcareous substrate, alt. ca. 1549 m, 40°38'33"N; 21°09'25"E, 2 Jun 2015, S. Samaropoulou, I. Patrikios & A. Ioannou, sub Samaropoulou SF1092 (ACA).

The triploid population previously reported for the first time by Kamari (1991a), is now further examined. The karyotype formula is given as 2n = 15m + 3st + 9t = 27 (Figs 3, 4) and the chromosome length ranges from 22.86 μm to 8 μm, while the TCL equals to 363.23 μm (Table 2). The interchromosomal asymmetry of the triploid karyotype (CV_{CL}

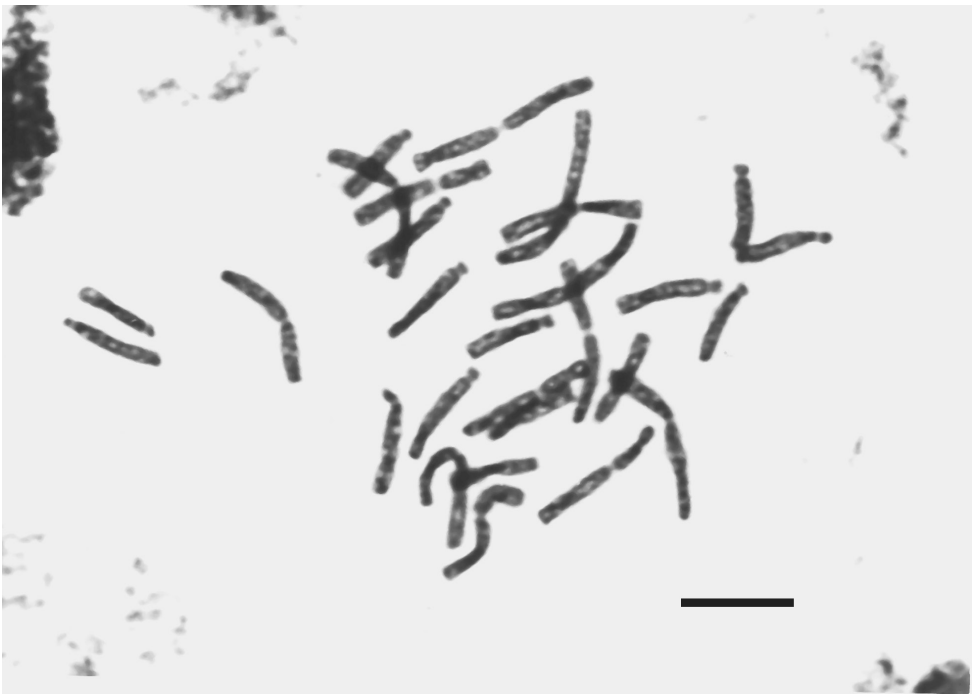

Figure 3. Photomicrograph of mitotic metaphase plate of *Fritillaria montana* from Mt. Boutsi, 2n = 3x = 27. Bar = 10 μm.

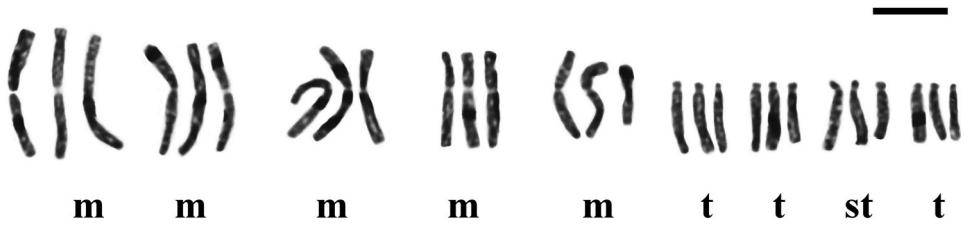

Figure 4. Karyogram of *Fritillaria montana* from Mt. Boutsi, 2n = 3x = 27. Bar = 10 μm.

= 31.07) is higher than the diploid, but the intrachromosomal is lower (M_{CA} = 40.41). The heterogeneity of the centromere position is lower than the diploid (CV_{CI} = 54.79). Even though secondary constrictions were observed again, their number and position varies in several plates, making the distinction of marker chromosomes very difficult.

It is noteworthy that a diploid individual was found for the first time at the studied triploid population. The karyotype of this individual comprises 2n = 10m + 4st + 4t = 18 chromosomes, with an additional pair of acrocentric (st) chromosomes compared with the other diploid populations studied and without B-chromosomes in contrast with the population of Mt. Vourinos. The secondary constrictions were also unclear as in the triploid individuals.

Fritillaria epirotica Turrill ex Rix — 2n = 2x = 24 (Figs 5, 6).

Populations karyologically studied:

Greece: Epirus: Nomos Ioanninon: Katara Pass, prope ekchionistikos stathmos, alt. 1750 m, in apertis (*Pinus* Linnaeus, 1753; *Buxus* Linnaeus, 1753 etc), solo serpentinico, 4 May 1990, D. Phitos & G. Kamari 21348 (UPA); Eparchia Metsovou, Katara Pass, close to the second snowplow station, c. 13.5 km of Metsovon along the road to Trikala, slopes with *Pinus nigra* Arnold, 1785 and *Buxus sempervirens* Linnaeus,1753; ophiolithic substrate, alt. c. 1640 m, 39°47'N; 21°13'E, 24 Jun 1998, Th. Constantinidis 7919 (UPA); **Macedonia: Nomos Grevenon:** Mt. Vasilitsa, alt.

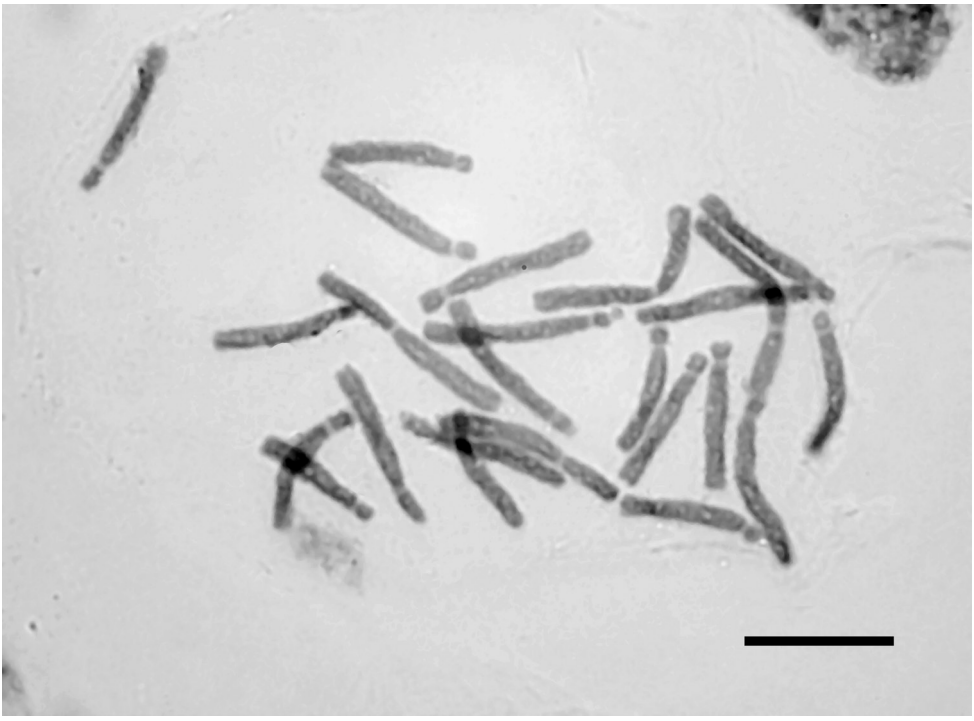

Figure 5. Photomicrograph of mitotic metaphase plate of *Fritillaria epirotica* from Mt. Smolikas, 2n = 2x = 24. Bar = 10 μm.

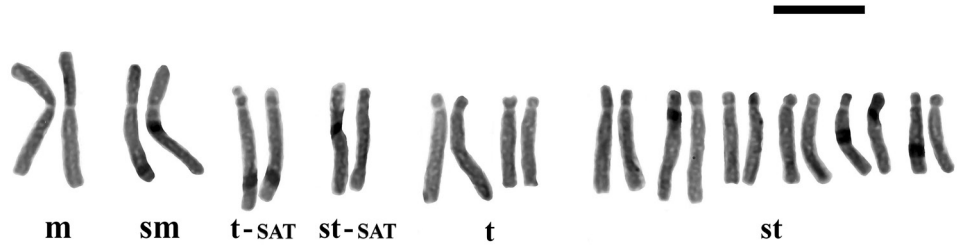

Figure 6. Karyogram of *Fritillaria epirotica* from Mt. Smolikas, 2n = 2x = 24. Bar =10 μm.

1764 m, 17 May 2015, G. Kofinas s.n. (cult. no. SF76, ACA); Mt. Smolikas, alt. 2200 m, Aug 2015, G. Kofinas s.n. (cult. no. SF97, ACA). **Thessalia: Nomos Trikalon:** Ep. Kalampakas, Mt. Chasia (Kratsovo), stony slopes close to a forest road, c. 3.0–3.5 km from Kakoplevri village, serpentine, alt. c. 1100–1180 m, 39°48'N; 21°24'E, 15 Jun 2000, D. Phitos, G. Kamari & Th. Constantinidis s.n. (cult. no. 235, UPA); Ep. Kalampakas, Mt. Chasia (Mt. Kratsovon), c. 3.1 km WNW of Kakoplevri village on the foothills of the mountain, hills with low *Buxus sempervirens* and *Juniperus oxycendrus* Linnaeus,1753; serpentine substrate, alt. 1120–1160 m, 39°49'N; 21°24'E, 24 Jul 2006, Th. Constantinidis s.n. (cult. no. 235, UPA).

Unlike *Fritillaria montana*, *F. epirotica* has the same basic somatic number as the rest of the Greek *Fritillaria* taxa, x = 12. The karyotype consists of 2n = 2m + 2sm + 14st + 6t = 24 chromosomes (Figs 5, 6), which range in size between 18.44 and 10 μm, while the TCL is 324.39 μm (Table 2). The index for interchromosomal asymmetry is small (CV_{CL} = 16.85) contradicting the big intrachromosomal one (M_{CA} = 63.33), while the centromere position heterogeneity is 51.66. Satellites on the short arms of one telocentric (t) and one acrocentric (st) pair of chromosomes (Table 3, chromosome pairs no. 3 and no. 5) are observed. However, in most metaphase plates, three of them are usually visible.

According to paired t-tests made (Table 4), the two species display an interesting similarity regarding their total chromosome length, but as far as the interchromosomal and intrachromosomal asymmetries are concerned (Table 5), the species seem to be

Table 4. Paired t-tests between the three species regarding the TCL and ACL, along with degrees of freedom (df) and Significance (Sig) for every parameter. Bold characters are used for P values (Sig 2-tailed) under 0.01, which reveal significant statistical difference.

Species in comparison		TCL			ACL		
		t	df	Sig (2-tailed)	t	df	Sig (2-tailed)
F. epirotica 2n = 2x = 24	*F. montana* 2n = 2x =18	0.379	18	0.709	-4.347	18	**0.000**
F. epirotica 2n = 2x = 24	*F. montana* 2n = 3x = 27	-1.427	16	0.173	0.057	16	0.955
F. montana 2n = 2x = 18	*F. montana* 2n = 3x = 27	-1.947	10	0.080	3.898	10	**0.003**

Table 5. Paired t-tests between the three species regarding the CV_{CL} and M_{CA}, along with degrees of freedom (df) and Significance (Sig) for every parameter. Bold characters are used for P (Sig 2-tailed) under 0.01, which reveal significant statistical difference.

Species in comparison		CV_{CL}			M_{CA}		
		t	df	Sig (2-tailed)	t	df	Sig (2-tailed)
F. epirotica 2n = 2x = 24	*F. montana* 2n = 2x = 18	-8.598	18	**0.000**	44.847	18	**0.000**
F. epirotica 2n = 2x = 24	*F. montana* 2n = 3x = 27	-9.754	16	**0.000**	34.473	16	**0.000**
F. montana 2n = 2x = 18	*F. montana* 2n = 3x = 27	-4.066	10	**0.002**	1.995	10	0.074

clearly distinct. The only insignificant difference was revealed between the two cytotypes of *Fritillaria montana*, 2n = 18 and 2n = 27, as expected, since they both bear a lot of metacentric chromosomes (by Robersonian fusions).

Discussion

In the present study a detailed karyomorphological analysis of *Fritillaria montana* and *Fritillaria epirotica*, in material from Greece, was implemented focusing specifically to the study of the inter- and intrachromosomal asymmetry, as well as the detailed analysis of the marker chromosomes.

The study of marker chromosomes (Table 3) is always important since it can provide further information concerning genome organization and the differentiation of the karyotype between related species. Moreover, especially in the case of the genus *Fritillaria*, marker chromosomes are helpful for the distinction of the chromosome homologues, which is very difficult since the karyotype usually consists of mostly acrocentric and subtelocentric chromosomes with similar size.

Marker chromosomes were observed in both *F. epirotica* with 2n = 2x = 24 and *F. montana* with 2n = 2x = 18 chromosomes. However, when it comes to triploid karyotypes of the same species, the secondary constrictions are not stable in number and position.

Fritillaria epirotica (2n = 24) has four marker chromosome pairs (Fig. 6). The first two chromosome pairs, which are the longest ones of the complement, have a different morphology than all the other chromosomes of the karyotype, which are acrocentric (st) and subtelocentric (t). The longest chromosome pair is metacentric (m) (no. 1), while the second one is the second in range of length and a submetacentric (sm) one (no. 2). The third marker chromosome pair (no. 3) is telocentric and bears small spherical satellite on the short arm of the homologues. Finally, the last marker chromosome pair is the fifth in length, comprising of two acrocentric satellited (st-SAT) chromosomes. The results are in agreement with previous studies by Kamari (1991a). Zaharof (1989) reported the heteromorphism of satellites' length in one out of two SAT-chromosome pairs.

Fritillaria montana (2n = 18) has two marker chromosome pairs with secondary constrictions. The karyotype formula given here (2n = 10m + 2st + 6t = 18) differs from the previously reported karyotype of 2n = 10m + 8t = 18 chromosomes given by Zaharof (1989). This is the only one species in Greece with 18 chromosomes and this chromosomal reduction has already been claimed as the result of successive chromosomal reconstructions and Robersonian-fusion of six acrocentric chromosomes into three metacentric ones (Darlington 1936, La Cour 1978a, 1978b, 1978c, Kamari 1991a). Zaharof (1989) explained the secondary constrictions, which are also observed in the present study, with the above hypothesis. Recently, Peruzzi et al. (2016) studied an Italian population with 2n = 2x = 18 chromosomes, further confirming the chromosome number of *F. montana*, while the presence of up to three B-chromosomes is already referred by Kamari (1991a, 1991b).

The triploid chromosome number of *F. montana* (2n = 3x = 27) is known in Greece from only one population, but it has also been reported from Italy by Cesca (1986, under the name *F. tenella* Marschall von Bieberstein, 1808), for a Calabrian population (S Italy).

Paired t-tests have revealed similarities among the three karyotypes. Especially the similarity between TCL of the diploid *F. epirotica* 2n = 24 and *F. montana* 2*n* = 18 reinforces the hypothesis, apart from the secondary constrictions, that the second species has derived after successive chromosomal reconstructions and Robersonian-fusions. Less similar indices of TCL between *F. montana* 2n = 2x = 18 and *F. montana* 2n = 3x = 27 can also be explained since it is known that polyploidy usually comes with gene loss and genome amount reduction (Kamari 1992, Leitch and Bennett 2004, Adams and Wendel 2005, Buggs et al. 2009). Another proof for gene loss, is the fact that the triploid cytotype of *F. montana* has the lower price of THL.

The results concerning the heterogeneity of centromere position CV_{CI} and the intrachromosomal asymmetry M_{CA} are nothing but expected. Following the explanation of this index by Zuo and Yuan (2011), the higher price of CV_{CI} found here, belongs to *Fritillaria montana*, because the karyotype comprises of mostly metacentric chromosomes. On the contrary, the higher price of M_{CA} belongs to *F. epirotica*, as it has a typical asymmetrical karyotype according to Stebbins (1971).

In total, the multivariate analysis PCoA confirms all above findings. More precisely, it presents all the accessions belonging to the same species close to each other. The two cytotypes of *Fritillaria montana* overlap, while the two species are clearly separated (Fig. 7).

Generally, karyological characteristics, as chromosome number, ploidy level, centromere position, and the number and location of satellites and secondary constrictions, can be used in elucidating taxonomical relationships of several plant taxa (Bareka et al. 2008, 2012 see for references). Although, karyomorphometrics is able

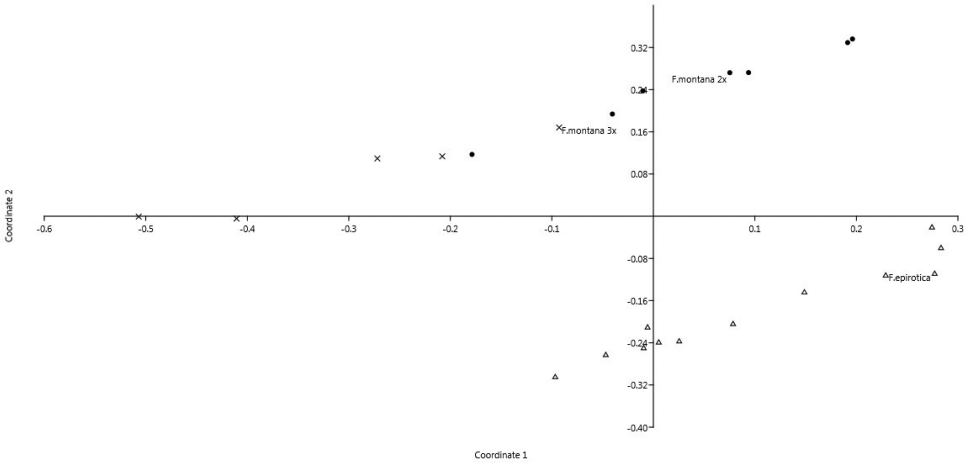

Figure 7. PCoA analysis based on six quantitative karyologial parameters. Triangle depicts *F. epirotica*, 2n = 2x = 24; dots *F. montana*, 2n = 2x = 18 and x *F. montana*, 2n = 3x = 27.

to provide more information about the studied taxa, the conclusions can be used only as additional evidences to the primary hypothesis. However, molecular chromosomal markers and fluorescence in situ hybridization (FISH) could provide additional information concerning genome organization in the genus and differentiation among its species and are recommended as a safer way to reveal whether our assumption for the origin of the reduced chromosome number 2n = 18 is correct. Moreover, this method is desirable to be carried out because it will unveil the type of polyploidy for 2n = 3x = 27, as an autopolyploidy or allopolyploidy (Bareka et al. 2012).

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Seed morphology in the genus *Fritillaria* (Liliaceae) from Greece and its taxonomic significance

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Abstract

The genus *Fritillaria* is represented in Greece by 31 taxa, more than a half of which are endemic to the country. This is the first report studying the seed morphology of this genus in Greece, in an attempt to prove its taxonomic importance. Seeds from 59 Greek populations, representing 25 taxa have been studied concerning 11 morphological parameters. All examined taxa have numerous seeds per capsule that are flat and characterised by the presence of a peripheral wing. Their shape is ovate to widely ovate-triangular, with the exception of *F. epirotica* which is more hemispherical. The smallest seeds of all studied taxa belong to *F. montana*. The morphometric data, along with the multivariate analysis (PCA) and paired t-tests, can lead to interesting conclusions concerning the taxonomic relationships among several taxa. For example, taxa currently considered as synonyms, like *F. sporadum* within *F. ehrhartii* and *F. theophrastii* within *F. pontica* are found statistically different concerning seed morphology. On the other hand, taxonomically well distinct taxa, such as *F. ionica* subsp. *thessala*, *F. graeca*, and *F. messanensis* subsp. *gracilis*, share similar seed morphology. Finally, the two—very similar—subspecies of *Fritillaria obliqua* share the same seed features, rising again questions upon their taxonomic distinctiveness.

Key words: biosystematics, micromorphology, morphometry

Introduction

The genus *Fritillaria* Linnaeus (1753: 303), belonging to Liliaceae, consists of approximately 130 geophyte taxa, distributed in the Northern Hemisphere (Peruzzi 2016). This genus is very diverse in Greece, where 31 taxa (26 species and 5 subspecies) occur, all of them belonging to *F.* subg. *Fritillaria*, and their majority (15 species and 3 subspecies) is endemic to the country (Samaropoulou *et al.* 2016, Kamari *et al.* 2017).

Even though this genus in Greece has been the subject of research for many years (Rix 1971, 1974a, 1974b, 1975, 1978, 2001, Kamari 1984a, 1984b, 1986, 1991a, 1991b, 1996, Zaharof 1987a, 1987b, 1988, 1989a, 1989b, Kamari & Phitos 2000, 2006, Samaropoulou *et al.* 2016, 2019, Kamari *et al.* 2017), there are still open questions upon its classification and phylogeny. A variety of intermediate forms has been observed, and proved to emerge through hybridisation, polyploidy and chromosome rearrangements (Kamari 2009b, Kamari & Phitos 2009a, 2009b, Samaropoulou *et al.* 2016, 2019). Nowadays, some species are considered as synonyms (Dimopoulos *et al.* 2013), such as *F. sporadum* Kamari (1984b: 331) and *F. ehrhartii* Boiss. & Orph. in Boissier (1859: 105), but a general taxonomic revision of this genus is still lacking (Kamari *et al.* 2017).

Due to the commercial, medicinal, or horticultural, importance of *Fritillaria* species, their seeds have been examined mostly in an effort to provide protocols for their germination (see Çakmak *et al.* 2016, for references), rather than to describe their morphology and taxonomic value. To our knowledge, seeds from all Iranian *Fritillaria* have been studied morphologically (Khaniki 2003), but the author concluded that the fruits rather than the seeds are of taxonomic importance at subgeneric level. Even though Khaniki (2003) noticed differences among species in seeds shape and in size of testa cells, he treated them as taxonomically insignificant. Furthermore, information has been provided for *F. montana* Hoppe ex Koch (1832: 476) from Italy (Mancuso *et al.* 2012) and for *F. tubaeformis* Grenier & Godron (1855:

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13) subsp. *moggridgei* (Boiss. & Reuter ex Planchon 1873: 116) Rix (1978: 356) by Carasso *et al.* (2012). The features commonly examined are the shape and the size of the seeds (length and width), weight and thickness. In addition, Hill (2011–2018) has published a great amount of photographed seeds, including 26 Greek taxa. However, this is the first contribution devoted to the morphometry of seeds of *Fritillaria* from numerous Greek populations. The purpose of the study is to evaluate the seed morphology as an identification tool among taxa, useful to clarify taxonomic and evolutionary relationships. In addition, this study aims to examine whether seed morphological parameters are in agreement with current classification of the genus in Greece, especially focusing on taxonomically disputed taxa.

Materials and methods

Seeds were extracted from ripening capsules and dried with heat lamps along with the corresponding plant material that has been deposited to Herbarium ACA (acronym follows Thiers 2019) and Herbarium Phitos & Kamari. Totally 25 taxa have been studied from 59 populations, all from the Greek territory (Table 1). At least 5 capsules were randomly selected in each population and 10 seeds of different sizes per capsule, depending on their position inside the capsule, were examined in equal proportion. The seeds were observed using Zeiss Stemi 2000-c stereomicroscope and photographed with Canon EOS 600D digital camera (Fig. 1).

TABLE 1. Sources of material studied.

Taxa	Locality along with accession - cultivation number
1. *F. bithynica*	East Aegean Isl. Samos, Mt. Kerkis, close to Moni Kimiseos Theotokou. 37°43N, 26°41´E. **F12**
	East Aegean Isl. Samos, Mt. Kerkis, above the village Drakei. 37°45´N, 26°37´E. **F13**
2. *F. conica*	Peloponnisos. Nomos Messinias. Sapientza islet, north part of the island. 36°47´N, 21°42´E. **F150**
	Peloponnisos. Nomos Messinias. Pylos, Agios Nikaolas hill. 36°53´N, 21°41´E. **F9**
3. *F. davisii*	Peloponnisos. Nomos Lakonias. Mani Peninsula, Village Pagia. 36°30´N, 22°22´E. **F201**
	Peloponnisos. Nomos Lakonias. Between the villages Vathia and Achillion. 36°26´N, 22°28´E. **F7**
4. *F. drenovskii*	Macedonia. Nomos Dramas. Mt. Falakron. 41°18´N, 24°03´E. **F128**
	Macedonia. Nomos Dramas. Mt. Falakron towards the ski resorts. 41°18´N, 24°04´E. **F129**
5. *F. ehrhartii*	Kiklades Isl. Andros, above the village Batsi. 37°51´N, 24°47´E. **SF1127**
	Kiklades Isl. Tinos, between the villages Isternia and Katapoliani. 37°37´N, 25°03´E. **F75**
	Kiklades Isl. Tinos, above the village Katapoliani towards Stavria. 37°37´N, 25°03´E. **F74**
	Sporades Isl. Skyros, Mt. Kochilas, NE slopes, at Agios Artemios. 38°51´N, 24°35´E. **F51**
6. *F. epirotica*	Macedonia. Nomos Grevenon. Mt. Smolikas, close to Drakolimni. 39°59´N, 20°47´E. **SF1097**
7. *F. euboeica*	Aegean Isl. Evvia, Mt. Kandili, at the summit area. 38°39´N, 23°33´ E. **F20**
	Aegean Isl. Evvia, Mt. Kandili, above the village Prokopi. 38°43´N, 23°28´E. **F57**
8. *F. graeca*	Peloponnisos. Nomos Achaias. Mt. Chelmos, above the village Kalavryta. 38°02´N, 22°09´E. **F8**
	Peloponnisos. Nomos Argolidos. Nafplio, Mt. Arachneon. 37°40´N, 22°57´E. **F182**
	Peloponnisos. Nomos Arkadias. Mt. Menalon, Ostrakina. 37°38´N, 22°16´E. **F130**
	Peloponnisos. Nomos Korinthou. Akrokorinthos hill. 37°53´N, 22°52´E. **F5**
	Peloponnisos. Nomos Lakonias. Mt. Parnonas, above the village Agios Petros. 37°13´N, 22°36´E. **F3**
	Sterea Ellas. Nomos Attikis. Mt. Imittos, radar area. 37°57´N, 23°49´E. **F41**
	Sterea Ellas. Nomos Attikis. Mt. Imittos, W slopes, above Argiroupoli. 37°54´N, 23°47´E. **F152**
	Sterea Ellas. Nomos Attikis. Mt. Pateras, south of the summit. 38°04´N, 23°21´E. **F39**
	Sterea Ellas. Nomos Attikis. Salamina isl., Selinia. 37°55´N, 23°30´E. **F38**
9. *F. gussichiae*	Macedonia. Nomos Florinas. Mt. Triklario, Boutsi. 40°38´N, 21°09´E. **F133**
	Macedonia. Nomos Florinas. Mt. Triklario, Boutsi, NW of Vatochori. 40°40´N, 21°08´E. **F166**
10. *F. ionica* subsp. ***ionica***	Macedonia: Nomos Florinas. Prespes Lake, towards the village Psarades. 40°49´N, 21°01´E. **F144**
11. *F. ionica* subsp. ***reiseri***	Sterea Ellas. Nomos Etoloakarnanias. Mt. Koutsilaris. 38°18´N, 21°08´E. **F1**

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TABLE 1. (Continued)

Taxa	Locality along with accession - cultivation number
12. ***F. ionica*** subsp. ***thessala***	Epirus. Nomos Ioanninon. Katara pass. 39°47′N, 21°11′E. **F135**
	Macedonia. Nomos Kastorias. Mt. Voion, above the village Pentalofos. 40°11′N, 21°08′E. **F100**
13. ***F. messanensis*** subsp. ***messanensis***	Peloponnisos. Nomos Ilias. Above the village Iraklia. 37°41′N, 21°34′E. **F4**
	Peloponnisos. Nomos Ilias. Above the village Vasai. 21°53′N, 37°25′E. **F121**
14. ***F. messanensis*** subsp. ***gracilis***	Ionian Isl. Kefalonia, Mt. Roudi. 38°12′N, 20°31′E. **F84**
	Ionian Isl. Zakynthos, above the village Keri, Pharos area. 37°39′N, 20°48′E. **F108**
	Ionian Isl. Zakynthos, above the village Korithi. 37°54′N, 20°41′E. **F204**
	Ionian Isl. Zakynthos, above the village Veronika. 37°52′N, 20°39′E. **F45**
15. ***F. messanensis*** subsp. ***sphaciotica***	Aegean Isl. Crete. Nomos Chanion. Samaria gorge. 35°18′N, 23°55′E. **F31**
	Aegean Isl. Crete. Nomos Rethymnis. Mt. Psiloritis, above the forest Rouvas. 35°07′N, 24°57′E. **F32**
16. ***F. montana***	Thessalia. Nomos Larissas. Mt. Kato Olympos, Livadaki, N of Kallipefki. 39°57′N, 22°29′E. **F253**
	Thessalia. Nomos Trikalon. Kalambaka, Mts. Chasia (Mt. Kratsovon). 39°49′N, 21°24′E. **F256**
17. ***F. mutabilis***	Sterea Ellas. Nomos Etoloakarnanias. Mt. Bardousia, above the village Athanasios Diakos. 38°41′N, 22°10′E. **F105**
	Sterea Ellas. Nomos Etoloakarnanias. Mt. Boumistos, above the village Komboti. 21°04′N, 38°44′E. **F132**
	Ionian Isl. Lefkada, Radar area (Atrakli). 38°44′N, 20°39′E. **F27**
18. ***F. obliqua*** subsp. ***obliqua***	Aegean Isl. Evvia. Mt. Ochtonia. 38°30′N, 24°09′E. **F167**
	Sterea Ellas. Nomos Attikis. Athens, Tourkovounia hills. 38°00′N, 23°45′E. **SF55**
	Sterea Ellas. Nomos Attikis. Marathonas, Kinosoura Peninsula. 38°08′N, 24°03′E. **F192**
	Sterea Ellas. Nomos Attikis. Mt. Parnitha, Agios Merkourios. 38°13′N, 23°47′E. **F56**
19. ***F. obliqua*** subsp. ***tuntasia***	Aegean Isl. Kiklades. Kithnos, above the port Merichas. 37°22′N, 24°25′E. **F58**
	Aegean Isl. Kiklades. Serifos, cross road towards mega Chorio and Avyssalo. 37°09′N, 24°26′E. **F169**
	Aegean Isl. Kiklades. Serifos, towards Chora. 37°09′N, 24°29′E. **F168**
20. ***F. pelinaea***	East Aegean Isl. Chios. Mt. Pelineon, W facing slopes, above Spartounda. 38°32′N, 25°59′E. **F14**
21. ***F. pontica***	Macedonia. Nomos Chalkidikis. Athos Peninsula, close to the Moni Agias Lavras. 40°10′N, 24°23′E. **A157**
22. ***F. rhodocanakis***	Sterea Ellas. Nomos Attikis. Dokos isl. 37°20′N, 23°18′E. **F185**
	Sterea Ellas. Nomos Attikis. Idra isl. 37°20′N, 23°27′E. **F33**
	Sterea Ellas. Nomos Attikis. Poros isl. 37°30′N, 23°27′E. **F34**
23. ***F. spetsiotica***	Sterea Ellas. Nomos Attikis. Spetses isl., above the village Zagoria. 37°16′N, 23°06′E. **F35**
24. ***F. sporadum***	Sporades Isl. Gioura, at place Tragorema. 39°22′N, 24°09′E. **F112**
	Sporades Isl. Kira Panagia, Bay Agios Petros. 39°19′N, 24°03′E. **F109**
25. ***F. theophrasti***	East Aegean Isl. Lesvos, Mt. Olympos, between the villages Agiassos and Prof. Ilias. 39°04′N, 26°22′E. **F16**

The morphometric study includes 11 parameters (Fig. 2): total length of the seed (TL), total width (TW), total length/total width ratio (TL/TW), seed width (SW), seed wing coverage width (WW), seed/wing width index (SW/WW), seed length (SL), seed length/width (SL/SW), length from the crossing point of the major axes (length and width) up to the closest edge of the seed (crossing point location, CPL), total length/crossing point location ratio (TL/CPL) and seed weight (WT). For the calculation of the dry weight, seeds were randomly selected and weighed in lots of 15.

In order to illustrate and compare the range of the values, line charts were created separately for every parameter per species, representing the mean values along with standard deviation (Figs. 3–6). Eventually, above parameters were used for a multivariate PCA analysis. Whenever the results of the PCA analysis diverged from current taxonomy and/or revealed interesting distribution among taxa, the findings were further discussed. In the case of diverse distribution between taxonomically disputed taxa, paired t ‑ tests were carried out so as to detect the existence of statistically significant differences. For the statistical study Microsoft Office Excel was used, PCA analysis was extracted from PAST 3.25 (Hammer *et al.* 2001), while paired t ‑ tests were made through SPSS Statistics 25.

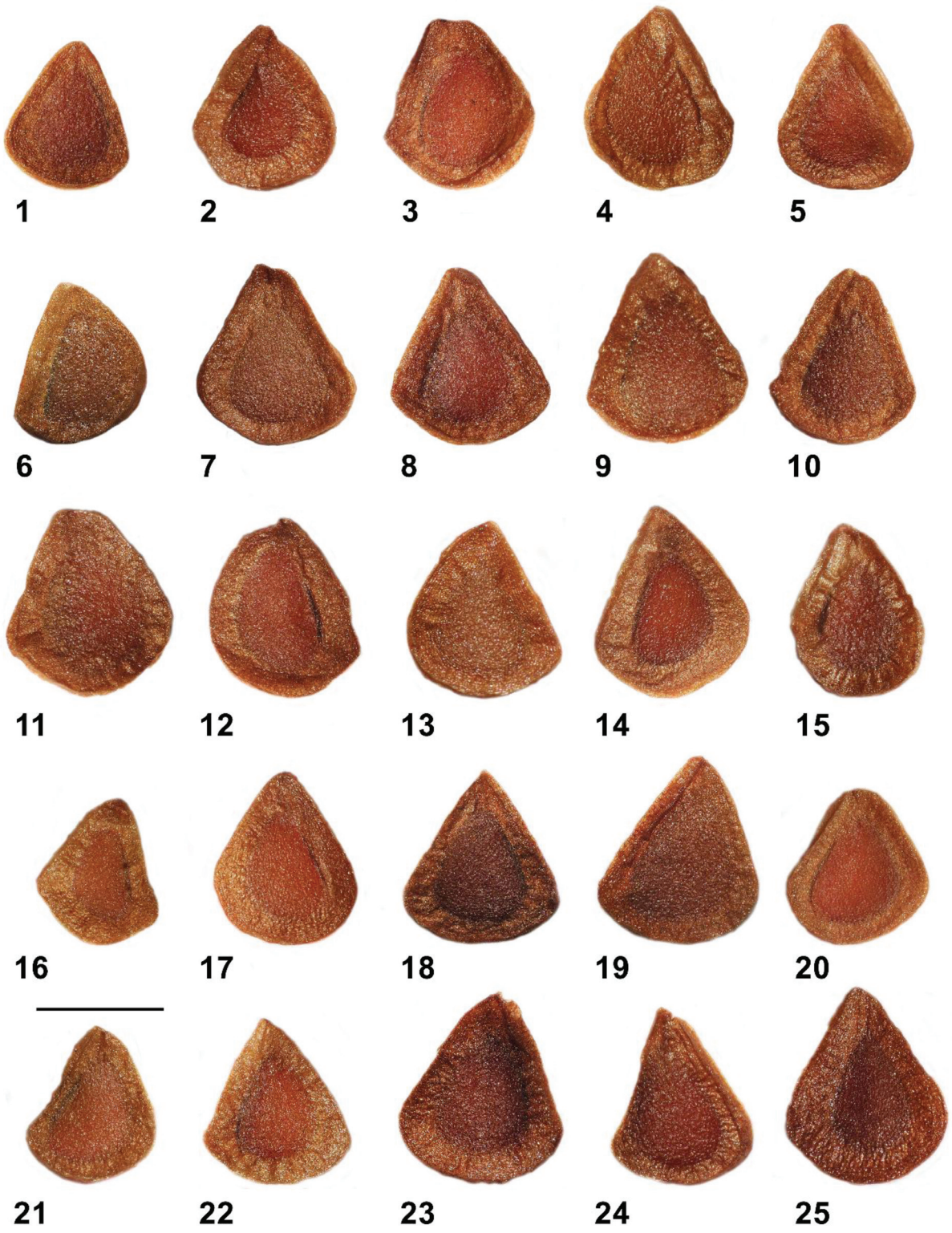

FIGURE 1. Examples of seed of Greek *Fritillaria* species. (1) *F. bithynica*; (2) *F. conica*; (3) *F. davisii*; (4) *F. drenovskii*; (5) *F. ehrhartii*; (6) *F. epirotica*; (7) *F. euboeica*; (8) *F. graeca*; (9) *F. gussichiae*; (10) *F. ionica* subsp. *ionica*; (11) *F. ionica* subsp. *reiseri*; (12) *F. ionica* subsp. *thessala*; (13) *F. messanensis* subsp. *messanensis*; (14) *F. messanensis* subsp. *gracilis*; (15) *F. messanensis* subsp. *sphaciotica*; (16) *F. montana*; (17) *F. mutabilis*; (18) *F. obliqua* subsp. *obliqua*; (19) *F. obliqua* subsp. *tuntasia*; (20) *F. pelinaea*; (21) *F. pontica*; (22) *F. rhodocanakis*; (23) *F. spetsiotica*; (24) *F. sporadum*; (25) *F. theophrasti*.

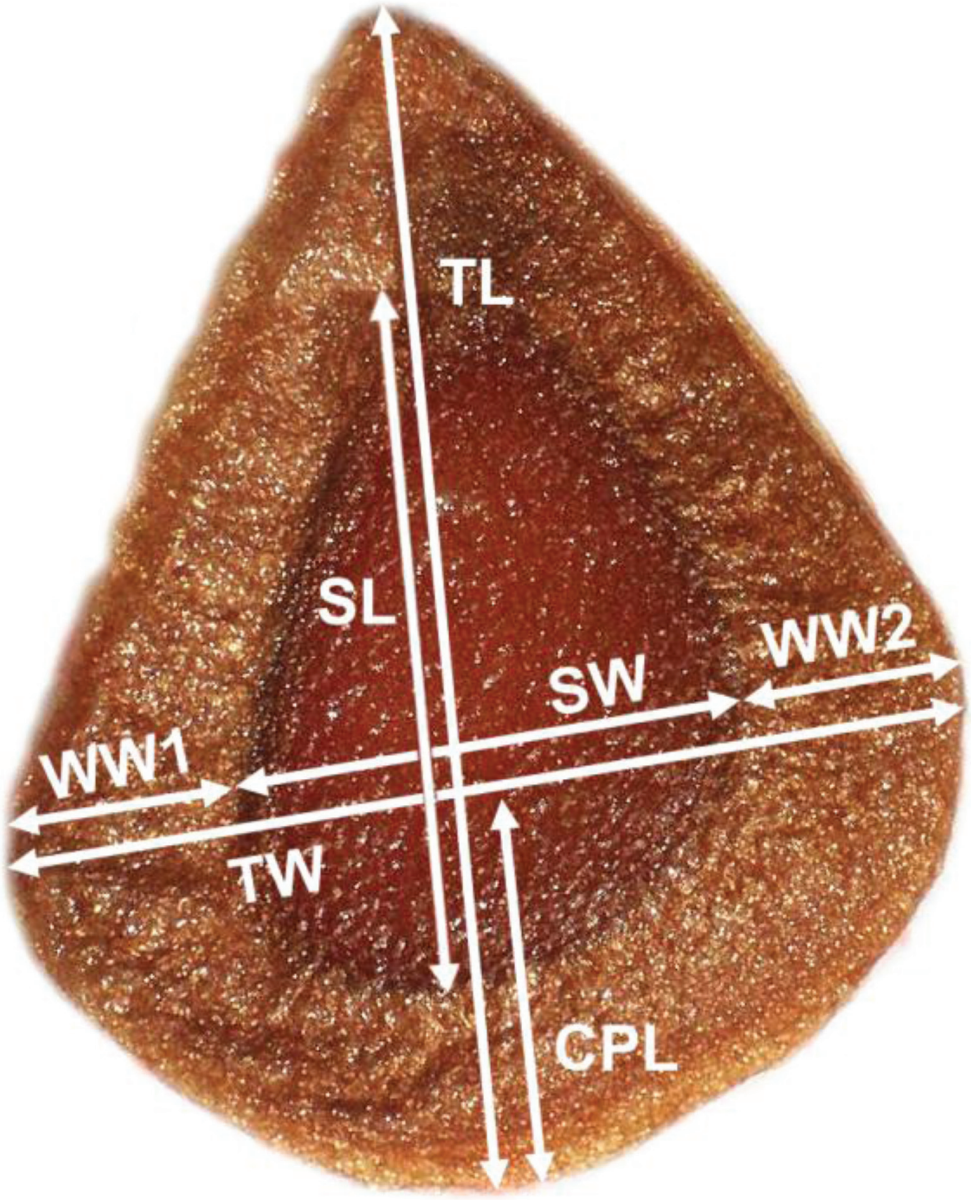

FIGURE 2. Seed morphological parameters examined. (TL) Total Length, (TW) Total Width, (SL) Seed Length, (SW) Seed Width, (WW = WW1 + WW2) Width of the seed wing coverage, (CPL) Length between the crossing point of (TL) & (TW) to the nearest edge of the seed.

Results

All *Fritillaria* fruits (capsules) contain numerous seeds, which are flattened with ovate to widely ovate-triangular shape and characterised by the presence of a peripheral wing that most probably allows anemochory (Fig. 1).

Fritillaria theophrasti Kamari & Phitos (2000: 70) is observed with the maximum mean TL (Table 2), while *F. conica* Boissier (1846: 105) with the maximum mean TW (Fig. 3). However, *F. drenovskii* Degen & Stojanov (1931: 142) is found with the longest and widest seed, whereas *F. montana* is proved to have the smallest seeds (5.481 × 4.805 mm). Accordingly, *F. montana* has the smallest SL values, whilst *F. obliqua* subsp. *tuntasia* (Heldr. ex Halácsy 1904: 222) Kamari (1991a: 259) the largest (Fig. 5).

TABLE 2. Morphological features of the seeds of the studied *Fritillaria* taxa: Total Length (TL); Total Width (TW); Total Length/Total Width (TL/TW); Seed Width (SW); Wing Width (WW); Seed/Wing Width (SW/WW); Seed Length (SL); Seed Length/Seed Width (SL/SW); Weight (WT); Crossing point length (CPL); Total Length/Crossing point Length (TL/CPL). Standard deviation is given inside the brackets.

Taxa	**Morphological Features (SD)**										
	TL (mm)	**TW (mm)**	**TL/TW**	**SW (mm)**	**WW (mm)**	**SW/WW**	**SL (mm)**	**SL/SW**	**WT (gr)**	**CPL (mm)**	**TL/CPL**
F. bithynica	6.370 (0.627)	5.465 (0.473)	1.167 (0.083)	3.630 (0.403)	1.835 (0.221)	2.007 (0.337)	4.375 (0.705)	1.203 (0.112)	0.0560 (0.0020)	1.782 (0,357)	3.661 (0.529)
F. conica	7.433 (1.224)	6.257 (0.901)	1.188 (0.093)	2.867 (0.529)	3.391 (0.701)	0.875 (0.19)	3.905 (0.700)	1.399(0.336)	0.0480 (0.0120)	1.923 (0.287)	3.911 (0.684)
F. davisii	7.310 (1.519)	6.095 (1.103)	1.195 (0.067)	3.270 (0.473)	2.825 (0.768)	1.215 (0.257)	4.7 (1.081)	1,429 (0.227)	0.049 (0.0110)	2.058 (0.412)	3.572 (0.413)
F. drenovskii	7.406 (1.558)	6.233 (1.274)	1.188 (0.052)	3.678 (0.766)	2.556 (0.634)	1.469 (0.236)	4.888 (1.008)	1.334 (0.125)	0.0640 (0.0460)	2.085 (0.458)	3.563 (0.21)
F. ehrhartii	6.254 (0.756)	5.225 (0.732)	1.205 (0.128)	3.067 (0.492)	2.158 (0.782)	1.320 (0.657)	4.177 (0.597)	1.376 (0.171)	0.0470 (0.0120)	1.743 (0.293)	3.635 (0.439)
F. epirotica	6.567 (0.458)	5.800 (0.561)	1.138 (0.099)	3.707 (0.563)	2.093 (0.788)	2.019 (0.839)	4.5 (0.535)	1.225 (0.139)	0.0630 (0.0001)	1.656 (0.204)	4.016 (0.52)
F. euboeica	6.905 (0.855)	6.162 (0.862)	1.125 (0.061)	3.833 (0.785)	2.329 (0.300)	1.670 (0.374)	4.786 (0.799)	1.262 (0.134)	0.0810 (0.0001)	1.714 (0.231)	4.057 (0.453)
F. graeca	6.839 (0.691)	5.971 (0.577)	1.148 (0.086)	3.291 (0.528)	2.680 (0.437)	1.269 (0.330)	4.521 (0.8)	1.379 (0.160)	0.0560 (0.0080)	1.886 (0.311)	3.705 (0.604)
F. gussichiae	7.119 (0.675)	6.050 (0.559)	1.178 (0.062)	3.442 (0.459)	2.612 (0.378)	1.346 (0.274)	4.673 (0.616)	1.366 (0.157)	0.0670 (0.0060)	1.917 (0.289)	3.759 (0.39)
F. ionica subsp. *ionica*	6.771 (0.807)	5.743 (0.742)	1.181 (0.035)	3.286 (0.696)	2.457 (0.217)	1.344 (0.287)	4.428 (0.958)	1.353 (0.122)	0.0600 (0.0001)	1.65 (0.337)	4.228 (0.878)
F. ionica subsp. *reiseri*	7.533 (1.039)	6.207(0.586)	1.214 (0.131)	3.180 (0.563)	3.027 (0.423)	1.079 (0.268)	4.367 (0.812)	1.387 (0.202)	0.0890 (0.0001)	2.293 (0.209)	3.296 (0.455)
F. ionica subsp. *thessala*	6.900 (1.288)	5.975 (0.950)	1.152 (0.090)	3.287 (0.619)	2.687 (0.496)	1.244 (0.256)	4.583 (1.10)	1.390 (0.199)	0.0610 (0.0130)	1.861 (0.48)	3.844 (0.697)
F. messanensis subsp. *messanensis*	6.252 (0.927)	5.505 (0.743)	1.137 (0.085)	2.919 (0.495)	2.586 (0.545)	1.172 (0.280)	3.881 (0.74)	1.333 (0.164)	0.0490 (0.0120)	1.737 (0.361)	3.657 (0.394)
F. messanensis subsp. *gracilis*	7.075 (0.506)	5.945 (0.447)	1.211 (0.084)	3.253 (0.296)	2.692 (0.395)	1.240 (0.247)	4.425 (0.397)	1.368 (0.149)	0.0630 (0.0130)	2.060 (0.262)	3.472 (0.365)
F. messanensis subsp. *sphaciotica*	6.809 (0.503)	5.245 (0.234)	1.301 (0.116)	2.964 (0.201)	2.282 (0.340)	1.339 (0.300)	4.227 (0.344)	1.435 (0.178)	0.0700 (0.0001)	1.901 (0.195)	3.606 (0.327)
F. montana	5.481 (0.618)	4.805 (0.536)	1.145 (0.094)	2.519 (0.400)	2.286 (0.339)	1.124 (0.260)	3.548 (0.522)	1.424 (0.198)	0.0260 (0.0040)	1.586 (0.276)	3,514 (0.454)
F. mutabilis	6.603 (0.681)	5.486 (0.496)	1.205 (0.086)	3.294 (0.524)	2.397 (0.422)	1.326 (0.267)	4.542 (0.498)	1.478 (0.158)	0.0550 (0.0150)	2.048 (0.779)	3.448 (0.638)
F. obliqua subsp. *obliqua*	7.057 (0.933)	6.137 (0.879)	1.155 (0.084)	3.680 (0.602)	2.457 (0.461)	1.535 (0.314)	5.08 (0.772)	1.39 (0.147)	0.0720 (0.0040)	1.97 (0.326)	3.65 (0.633)
F. obliqua subsp. *tuntasia*	7.036 (0.968)	6.168 (0.842)	1.142 (0.066)	3.738 (0.571)	2.430 (0.565)	1.614 (0.418)	5.149 (0.667)	1.387 (0.113)	0.0730 (0.0160)	2.045 (0.405)	3.517 (0.559)
F. pelinaea	6.085 (0.640)	5.023 (0.295)	1.211 (0.093)	3.069 (0.413)	1.954 (0.270)	1.621 (0.415)	4.423 (0.572)	1.453 (0.181)	0.0570 (0.0001)	1.884 (0.424)	3.311 (0.454)
F. pontica	6.133 (0.485)	5.058 (0.358)	1.217 (0.111)	2.942 (0.360)	2.117 (0.379)	1.405 (0.388)	4.167 (0.389)	1.439 (0.254)	0.0370 (0.0001)	1.704 (0.386)	3.728 (0.658)
F. rhodocanakis	6.630 (0.983)	5.567 (0.697)	1.189 (0.076)	3.139 (0.524)	2.427 (0.489)	1.345 (0.357)	4.545 (0.804)	1.455 (0.182)	0.0440 (0.0090)	1.752 (0.346)	3.851 (0.525)
F. spetsiotica	7.256 (1.081)	6.111 (0.823)	1.188 (0.089)	3.544 (0.515)	2.567 (0.441)	1.412 (0.300)	4.197 (0.827)	1.391 (0.159)	0.0640 (0.0001)	1.884 (0.367)	3.928 (0.667)
F. sporadum	6.723 (0.838)	5.307 (0.705)	1.195 (0.097)	3.259 (0.396)	2.048 (0.542)	1.759 (0.772)	4.222 (0.560)	1.299 (0.122)	0.0624 (0.0180)	1.547 (0.333)	4.209 (0.741)
F. theophrasti	7.625 (0.543)	6.058 (0.911)	1.285 (0.202)	3.050 (0.243)	3.008 (0.729)	1.127 (0.530)	4.917 (0.417)	1.615 (0.113)	0.0470 (0.0001)	2.024 (0.217)	3.796 (0.376)

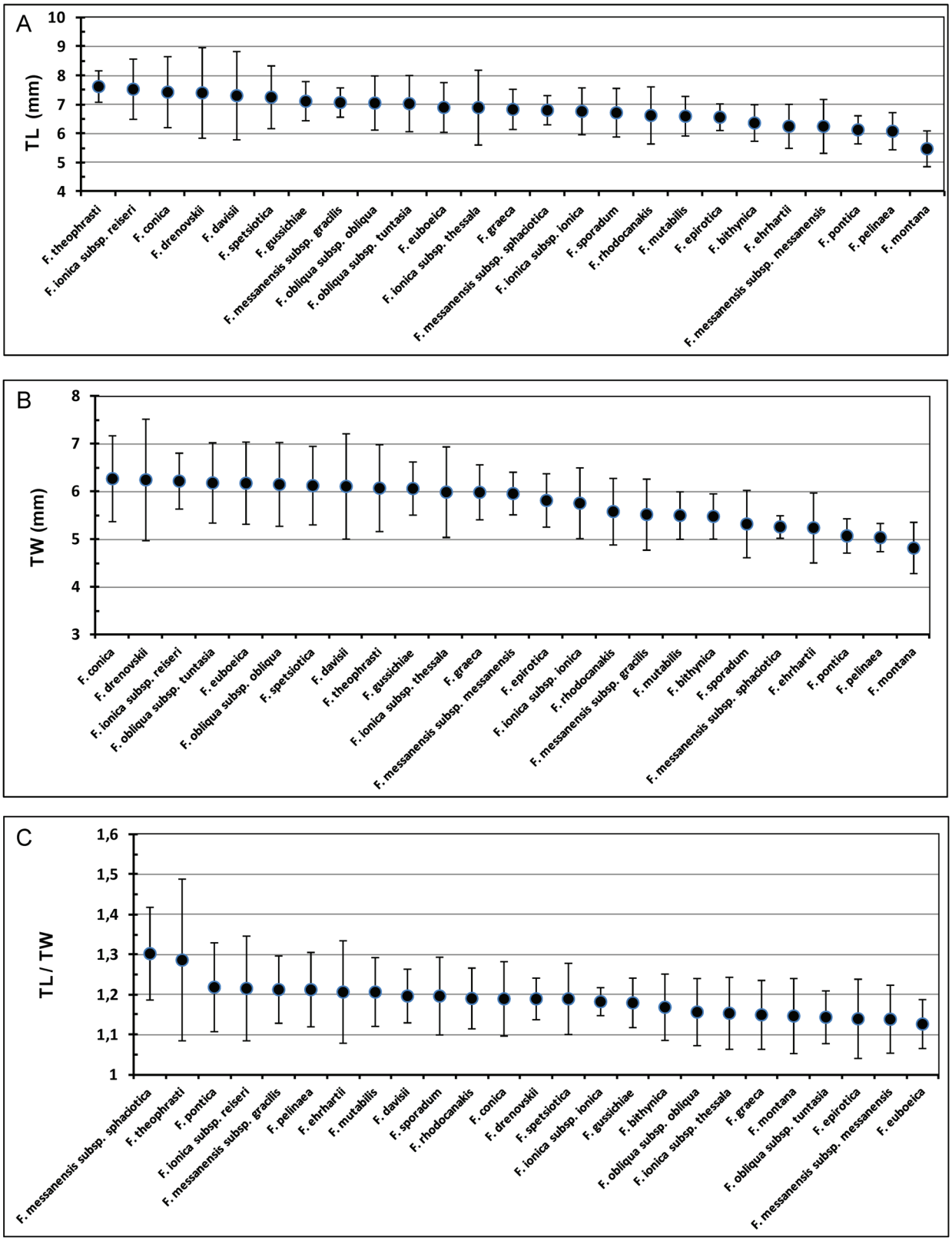

FIGURE 3. Line charts of: A. TL; B. TW; C. TL/TW. The point represents the mean value. Above and below whiskers demonstrate standard deviation.

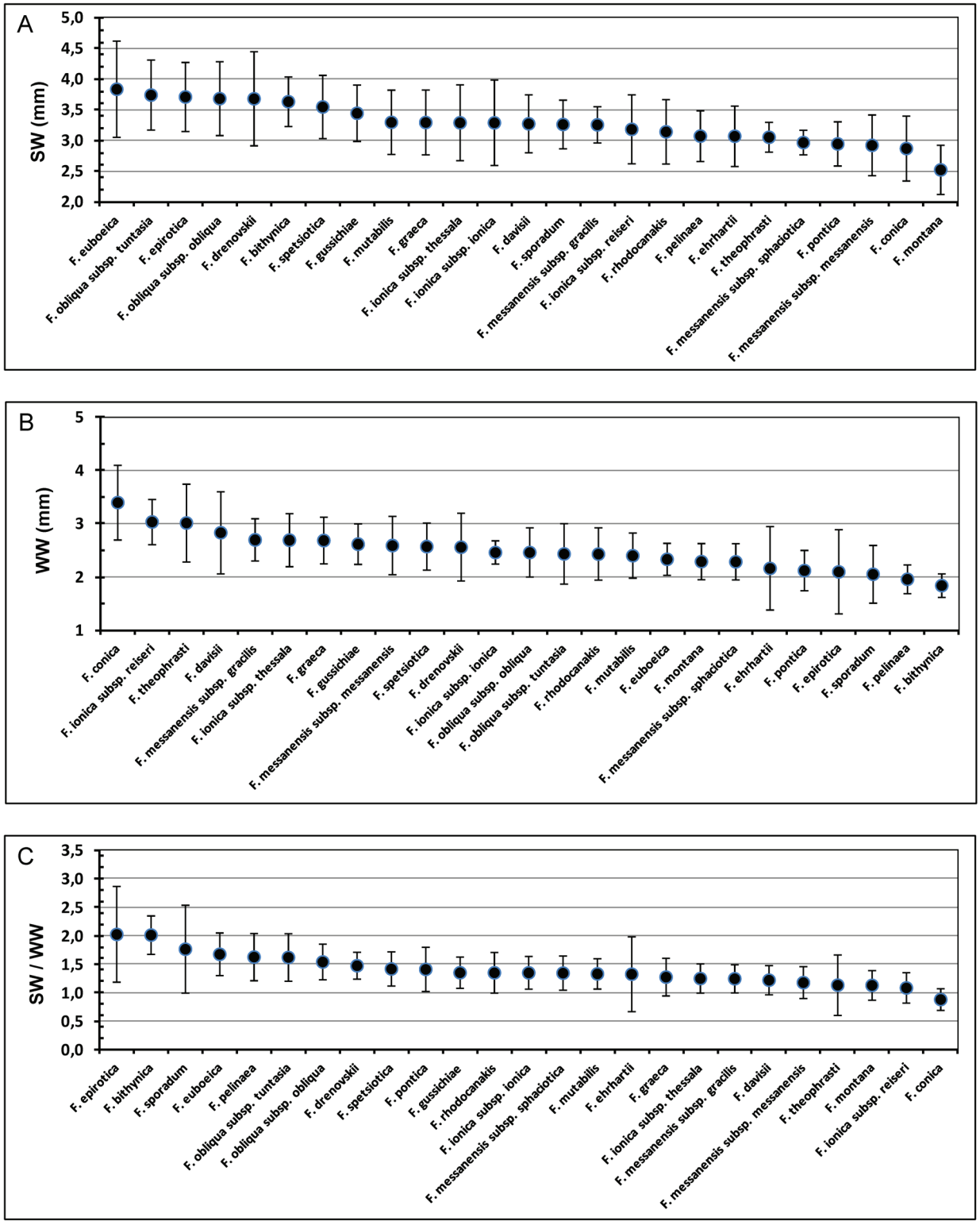

FIGURE 4. Line charts of: A. SW; B. WW; C. SW/WW. The point represents the mean value. Above and below whiskers demonstrate standard deviation.

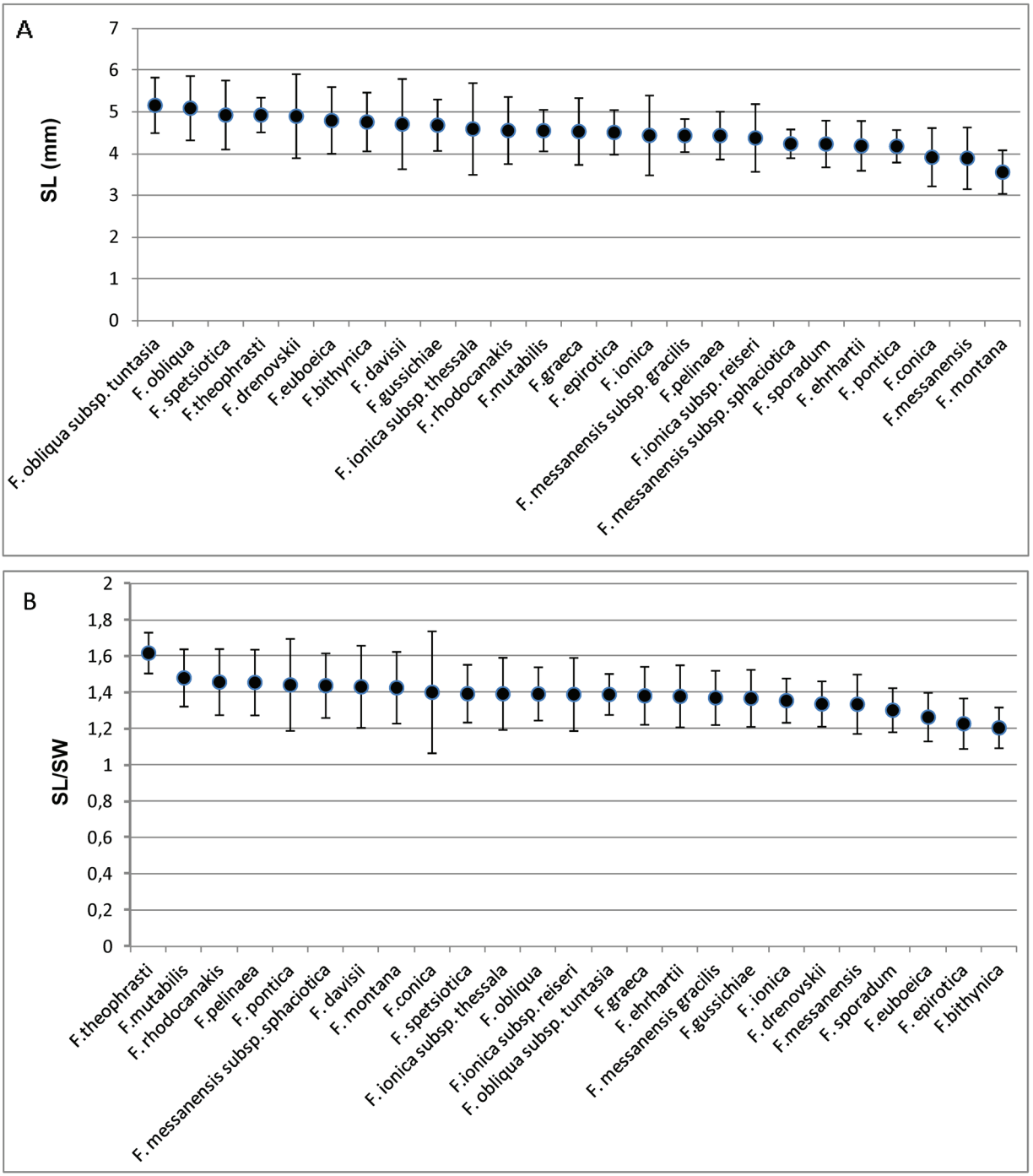

FIGURE 5. Line charts of: A. SL; B SL/SW. The point represents the mean value. Above and below whiskers demonstrate standard deviation.

Even though the presence of the peripheral wing at the seeds is a common feature of all Greek *Fritillaria* taxa, WW (Fig. 2) varies a lot among taxa (Table 2). *Fritillaria conica* bears the widest WW (mean 3.391 mm), even wider than the seed (2.867 mm), leading to the smallest SW/WW (0.875) ratio. On the other hand, *F. bithynica* Baker (1874: 264) has the narrowest WW, whose mean equals to 1.835 mm (Fig. 4).

Concerning the weight (Table 2), *F. ionica* Halácsy (1904: 219) subsp. *reiseri* (Kamari 1991b: 682) Kamari (2016: 429) shows the heaviest seeds, and *F. montana*, the lightest, while *F. drenovskii* presents the highest variation (Fig. 6).

The maximum TL/TW ratio is found in *F. messanensis* Rafinesque (1814: 272) subsp. *sphaciotica* (Gandoger 1915: 156) Kamari & Phitos (2006: 225) that has indeed a distinctly ovate shape (Fig. 3). *Fritillaria ionica* subsp. *reiseri* comes with the greatest CPL, even though this taxon is characterised by the smallest TL/CPL ratio (Fig. 6), leading to the most widely-ovate shape (Fig. 2).

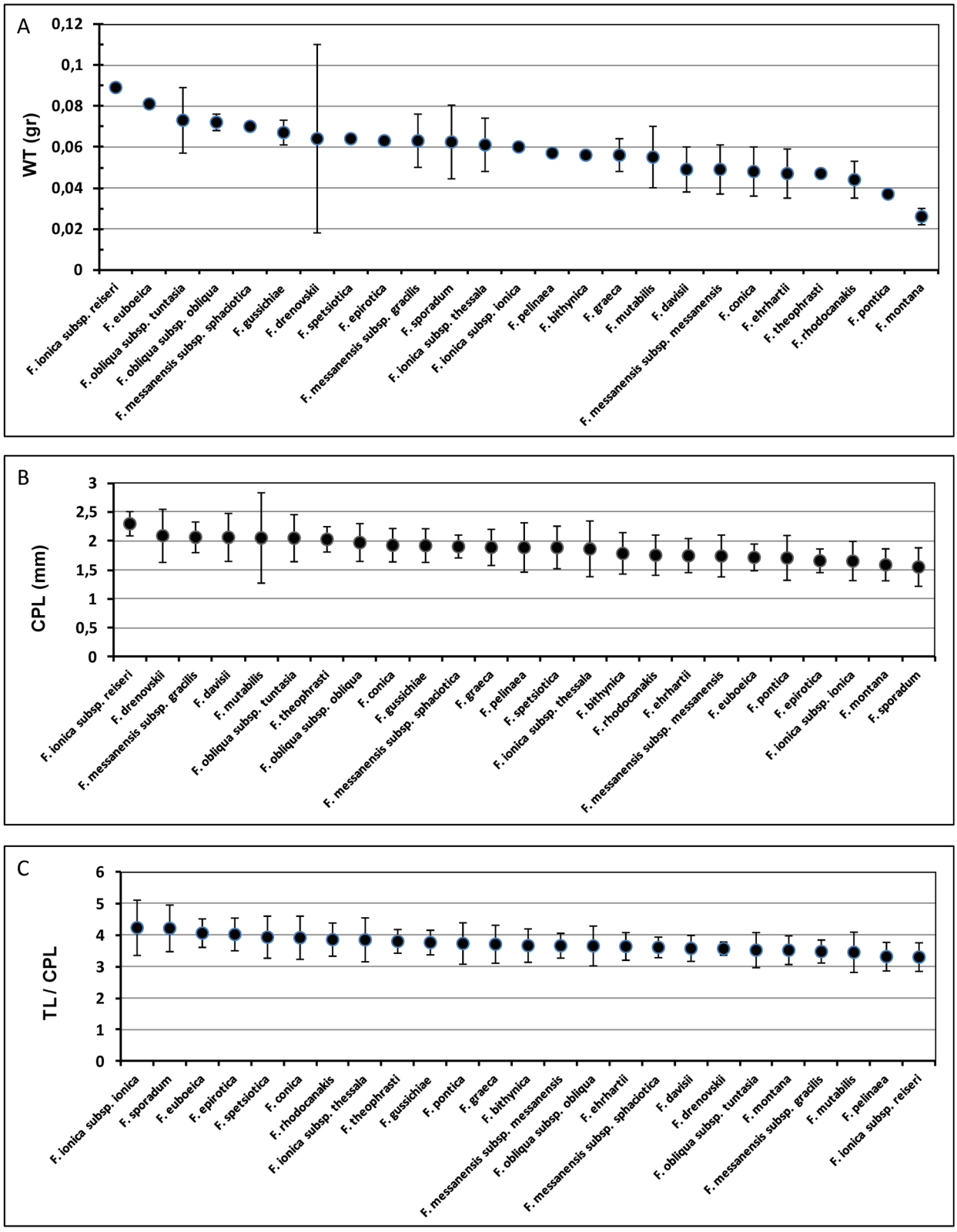

FIGURE 6. Line charts of: A. WT; B. CPL; C. TL/CPL. The point represents the mean value. Above and below whiskers demonstrate standard deviation.

According to the PCA analysis (Fig. 7), taxa with yellowish flowers, such as *F. bithynica*, *F. conica*, *F. pelinaea* Kamari (1996: 227), and *F. euboeica* are widely intermingled with taxa showing both yellow and purplish flowers, either as fascia [e.g., *F. graeca* Boiss. & Spruner in Boissier (1846: 104), *F. messanensis*, *F. ionica*, and *F. mutabilis* Kamari (1991b: 679)], half coloured, as *F. rhodocanakis* Orph. ex Baker (1878: 323), or yellow inside/purple outside, as for instance *F. ehrhartii* and *F. drenovskii*.

Among taxa with yellowish flowers, *Fritillaria conica* and *F. bithynica* have the most different seeds, due to significant differences in TL, TW, SW, WW, and SW/SW. Secondly, *F. conica* is different from *F. euboeica* due to SW, WW, and SW/WW. Likewise, *F. epirotica* Turrill ex Rix (1975: 160) and *F. montana*, that are both characterised by tessellated flowers, show a wide difference in their PCA position, due to TW, SW, SW/WW, WT, and TL/CPL, according to paired t - tests. *Fritillaria ehrhartii* is also well distinct from *F. sporadum*. The most variable parameter is the TL/CPL ratio. Additionally, *F. theophrasti* occupies a position in the PCA well distinct from *F. pontica* Wahlenberg (1826: 27), due to differences in the parameters TL, TW, and WW (Table 3).

On the other hand, paired t-tests failed to highlight significant differences in the case of the taxonomically doubtful species *F. spetsiotica* and *F. mutabilis* from *F. rhodocanakis* and *F. ionica* subsp. *thessala,* respectively, despite they occupy different positions in the PCA (Fig. 7).

TABLE 3. Paired t - tests among *Fritillaria* species, along with degrees of freedom (df) and Significance (Sig) for every parameter. Only the couples with P (Sig 2-tailed) < 0.01, revealing statistically significant differences, are reported.

Species couple		parameter	T	df	Sig (2-tailed)
F. conica	***F. bithynica***	TL	-3.474	39	0.001
		TW	-3.497	39	0.001
		SW	5.182	39	0.000
		WW	-9.485	39	0.000
		SW/WW	13.334	39	0.000
F. conica	***F. euboeica***	SW	-4.681	40	0.000
		WW	6.384	40	0.000
		SW/WW	-8.645	40	0.000
F. sporadum	***F ehrhartii***	TL/CPL	-4.222	73	0.000
F. theophrasti	***F. pontica***	TL	-7.098	22	0.000
		TW	-3.539	22	0.002
		WW	-3.759	22	0.001
F. epirotica	***F. montana***	TW	5.388	34	0.000
		SW	7.410	34	0.000
		SW/WW	4.608	34	0.000
		WT	9.519	3	0.002
		TL/CPL	3.081	34	0.004

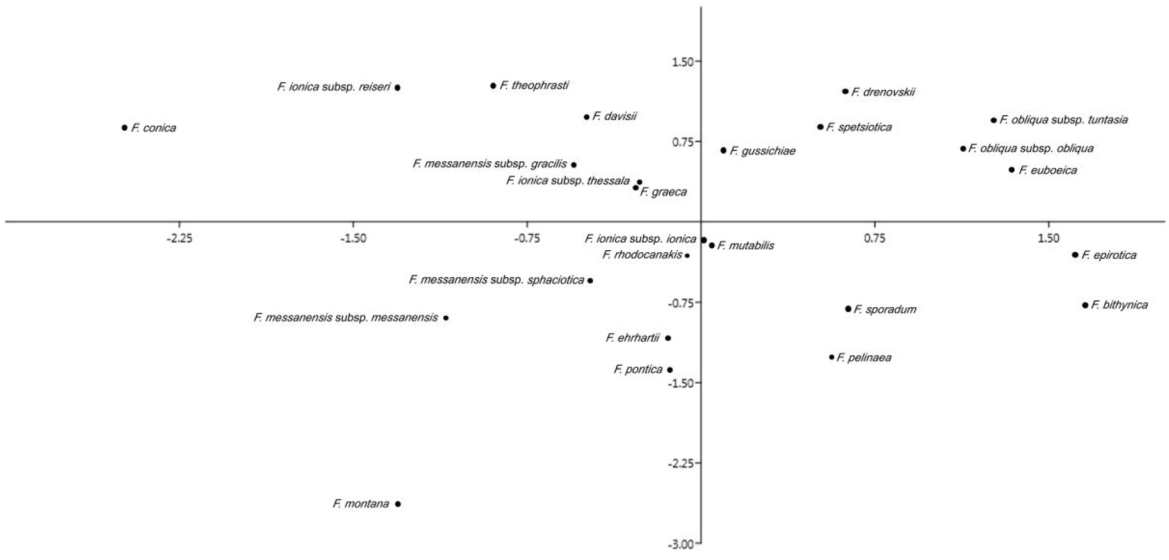

FIGURE 7. PCA analysis based on eleven morphological parameters. For each accession, only the mean value is plotted. The cumulative percentage of variation by the first two components is 80%.

Discussion

The seed morphometry proved that seed features cannot be used as a key to the identification of *Fritillaria* taxa. However, interesting taxonomic conclusions can be drawn when the parameters are analysed together (PCA analysis).

Discrimination among *Fritillaria conica*, *F. bithynica* and *F. euboeica*:—*Fritillaria conica* has an isolated geographical distribution and it was sometimes related to *F. bithynica* and *F. euboeica* (Kamari & Phitos 2009a). However, nowadays, *F. conica* is a distinct species mainly due to the colour and arrangement of its leaves, division of style and shape of capsules (Kamari 1996). Its seeds are also different from those of the other two taxa. In addition, as already mentioned above, *F. conica* is characterised by the widest seed wings of all Greek *Fritillaria* taxa studied.

Discrimination between *Fritillaria epirotica* and *F. montana*:—In the past, *F. epirotica* was thought to be a taxon derived from *F. messanensis* (Rix 1974b, 1975), or a species relative to *F. graeca* (Zaharof 1988). Nowadays, *F. epirotica* is grouped together with *F. montana* since they share intensely tessellated flowers, as well as the same shape of nectaries and leaf arrangement (Kamari 1991a, Kamari & Phitos 2006). However, they are clearly two different species that prefer different habitats (*F. epirotica* is found on serpentine, while *F. montana* on limestone or ophiolithic substrate, Kamari 1991b). *Fritillaria montana* is a very robust plant, contrary to *F. epirotica*, whose flowers almost touch the ground. The morphological parameters of their seeds are also distinct, with *F. epirotica* showing a more hemispherical shape and *F. montana* showing the smallest seeds (Fig. 1). They also have a different chromosome number, as *F. montana* is the only Greek *Fritillaria* species with a basic chromosome number $x = 9$, $2n = 18, 27$ (Zaharof 1989b, Kamari 1991a, 1991b, Samaropoulou *et al.* 2016), contrary to the common $x = 12$ and $2n = 24$, which is also typical of *F. epirotica*. Seeds from Greek populations of *F. montana* are very similar to those from Italy (Mancuso *et al.* 2012).

Discrimination between *Fritillaria sporadum* and *F. ehrhartii*:—*Fritillaria sporadum* is a taxon firstly described by Kamari (1984b), occurring at N. Sporades islands. Recently, it has been considered by A. Strid (Dimopoulos *et al.* 2013, Strid 2016) as a synonym of *F. ehrhartii*, even though they differ in the flower shape, in the division of the style and in the size, shape and arrangement of the leaves (Kamari 1984b). Seed morphology is an additional distinctive feature of this couple of taxa, reinforcing their original classification as separated species.

Discrimination between *Fritillaria theophrasti* and *F. pontica*:—*Fritillaria theophrasti* was described by Kamari & Phitos (2000) from plants of Lesvos island that were firstly considered as *F. pontica.* Since 1898, morphological differences have been observed by Candargy, who described *F. theophrasti* as *F. pontica* var. *substipetala* Candargy (1898: 450). Afterwards, Pinatzi labelled his specimens as *"F. lesbia"* (Herb. Pinatzi specimen no. 4204, 7920, 14136), and Broussalis (1978) pointed out the whorled leaves as an additional distinctive character-state. Recently, this species has been considered by A. Strid (Dimopoulos *et al.* 2013, Strid 2016) as a synonym of *F. pontica*, based on observations made in cultivated material. According to the seed morphology, *F. theophrasti* is distinct from *F. pontica*, supporting the former as a separate species. Another taxon related to *F. theophrasti* and *F. pontica* due to their winged capsules is *F. gussichiae* (Degen & Dörfler 1897: 738) Rix (1978: 356), whose seed features are clearly distinct from the former two species (Fig. 7), and also from *F. graeca*, although it was previously classified as *F. graeca* var. *gussichiae* Degen & Dörfler (1897: 738).

Discrimination between *Fritillaria obliqua* subspecies:—*Fritillaria obliqua* Ker Gawler (1805: 857) includes two subspecies, *F. obliqua* subsp. *obliqua* and *F. obliqua* subsp. *tuntasia* that are morphologically very similar. They have been considered synonyms (Kamari 1984a), but later they were separated (Kamari 1991a), mainly due to their isolated geographical distribution (Sterea Ellas and Evvia for the typical species, and some of the North Kiklades islands for *F. obliqua* subsp. *tuntasia*), and secondarily because of the division of the style and the leaf number and shape (Kamari 2009a, Kamari *et al.* 2009). Their seeds are very similar, raising again the question whether the difference between these two taxa is enough to rank them as two distinct subspecies (Kamari 1991a), and certainly not as distinct species (Halácsy 1904, Zaharof 1988, Rix 2000).

Discrimination among *Fritillaria taxa usually* with clear fascia on their flowers:—The three studied subspecies of *F. messanensis* [*F. messanensis* subsp. *messanensis*, *F. messanensis* subsp. *gracilis* (Ebel 1842: 8) Rix (1978: 356) and *F. messanensis* subsp. *sphaciotica*] and those of *F. ionica* [*F. ionica* subsp. *ionica*, *F. ionica* subsp. *reiseri* and *F. ionica* subsp. *thessala* (Boissier 1882: 182) Kamari (2016: 429)] are well distinct concerning their seed morphology. However, *F. messanensis* subsp. *gracilis* and *F. ionica* subsp. *thessala* are very close with each other, as well as with *F. graeca*, according to PCA analysis (Fig. 7). This is not so unexpected, since these particular taxa have confused botanists in the past concerning their taxonomy. *Fritillaria ionica* subsp. *thessala* has been described as *F. graeca* var. *thessala* Boissier (1882: 182), *F. graeca* subsp. *thessala* (Boiss.) Rix (1978: 356) and also as *F. pontica* var. *ionica*

Turrill (1948: 8), until it was considered as *F. thessala* (Boiss.) Kamari (1991b: 680) and later as *F. ionica* subsp. *thessala* (Kamari 2016), pointing at differences from *F. graeca* on the colour of the flower, shape of the nectaries, shape and arrangement of the leaves. *Fritillaria ionica* subsp. *thessala* is easily distinguished from *F. pontica* mainly when their capsules are observed, with the first one being unwinged and the second one winged (Turrill & Sealy 1980, Kamari 1991a). Their seeds are very distinct too, as proved by PCA (Fig. 7). Similarly, *F. mutabilis* was not separated from *F. ionica* subsp. *thessala* until Kamari (1991b) described its variability in flower colour and number of the uppermost leaves, but pointed out its morphological differences comparing to *F. ionica* subsp. *thessala* and *F. graeca* (colour, arrangement and shape of the leaves, colour of the flowers and shape of the nectaries). According to Dimopoulos *et al.* (2013), *F. mutabilis* is an accepted taxon, but doubtfully distinct from *F. ionica* s.l. This is probably because *F. mutabilis* is considered to be an old hybrid between *F. ionica* and *F. graeca*, when the two taxa coexisted in the same area before the separation of Peloponnisos and Sterea Ellas (Kamari 1991b). PCA seemingly supports current taxonomy (Fig. 7), albeit none of the parameters is statistically different when paired t ‑ tests are attempted. *Fritillaria messanensis* subsp. *gracilis*, as Kamari & Phitos (2006) reported, has been misidentified in the past and recorded also as *F. thessala*, probably because the distribution ranges of both taxa in Adriatic-Ionian zone and Ionian Islands overlap and they share the same number of the uppermost leaves, usually in a whorl of three, even though with different shape. Apart from that, they also share seed features. In addition, *F. messanensis* subsp. *gracilis* has been placed in the same cluster with *F. montana* (Zaharof 1988). The latter species however differs significantly in seed morphology.

Discrimination between *Fritillaria rhodocanakis* and *F. spetsiotica*:—Finally, another couple of taxa worth comparing are *F. rhodocanakis* and *F. spetsiotica* Kamari (1991a: 259), which are distributed on the Islands of the Argosaronic gulf (endemic to Idra and Spetses, respectively) and they have the ability to hybridise when they co-exist. The two taxa met at Argolida Peninsula and along with *F. graeca* at the north, ended up to hybridogenous populations with numerous morphologically intermediate forms and karyotype formulae (Kamari 2009b, Kamari & Phitos 2009b, Samaropoulou *et al.* 2019). According to Dimopoulos *et al.* (2013) and Strid (2016), *F. spetsiotica* is considered as a synonym of *F. rhodocanakis* Orph. ex Baker subsp. *argolica* Zaharof (1987a: 348), a hybrid between *F. graeca* and *F. rhodocanakis*. Although *F. spetsiotica* shares similar karyotype morphology with *F. rhodocanakis*, it is distinguished by stable morphological features (shape and colour of flowers and leaves, etc.). Concerning their seed morphology, the two species are rather distant in PCA (Fig. 7), but no statistically significant difference was observed following the paired t ‑ tests.

Conclusions

Fritillaria is a very interesting, valuable and variable genus. Turrill (1937) wrote that "it is often impossible to draw hard and fast lines, since many of them overlap in various characters in a most perplexing manner". Through the years, important studies have been carried out and still the variety of morphological features arises doubts on the taxonomy at species level. The results of this study agree with and support previous studies based on classical morphological and karyological data (Kamari 1991a). The study of the seed morphology has managed to contribute by providing taxonomic remarks.

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Hybridization and karyotype variability of three endemic *Fritillaria* L. (Liliaceae) in Argolis Peninsula (Greece)

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ABSTRACT

The Argolis Peninsula covers the north-eastern part of Peloponnisos and is surrounded by the Gulf of Argosaronic. The area hosts three species of the genus *Fritillaria*: *F. graeca*, *F. rhodocanakis* and *F. spetsiotica*. *Fritillaria graeca* is a Greek endemic taxon and its distribution includes Peloponnisos, C & E Sterea Ellas, C Evia and in proximity to Sterea Ellas, Salamis and Kea islands, while the stenoendemic *F. rhodocanakis* and *F. spetsiotica* are mainly found on Idra and Spetses islands respectively. The last two taxa are included in the Red Data Book of Rare and Threatened Plants of Greece, while *F. rhodocanakis* is also included in the IUCN Red List. Hybridization among them is a common phenomenon in the areas where they coexist, leading to an array of morphologically and karyologically intermediate forms. The current study presents the taxa's karyomorphometric analysis for the first time and reveals hybrids' cytological variety, including differences in marker chromosomes, polyploidy and the number of B-chromosomes.

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Fritillaria graeca; *F. rhodocanakis*; *F. spetsiotica*; karyomorphometry; polyploidy; endemism; B-chromosomes

Introduction

Fritillaria L. is a genus of perennial bulbous plants, very important from a taxonomic, pharmaceutical, horticultural and karyological point of view due to its vast genome size (Li et al. 2006; Bennett and Leitch 2012). It includes over 160 taxa, most of them distributed in the European and Asiatic area (Samaropoulou et al. 2016; Kamari et al. 2017 and literature cited therein). According to Rix (2001), the genus is divided into eight subgenera: i.e. *Fritillaria* Rix, *Davidii* Rix, *Liliorhiza* (Kellogg) Bentham & Hooker, *Japonica* Rix, *Rhinopetalum* Fischer, *Petilium* Baker and the monotypic *Theresia* K. Koch and *Korolkowia* Rix.

Greece has been recognized as an evolutionary centre of the subgenus *Fritillaria* L. (Kamari and Phitos 2006) since there are at least 31 taxa (26 species and 5 subspecies), all belonging to the subgenus *Fritillaria* (Rix 2001) and most of them (15 species and 3 subspecies) are endemic to the country (Kamari et al. 2017). At least 21 taxa occur particularly in the Aegean Archipelagos and its surrounding mainlands (Kamari and Phitos 2005).

Following both morphological and biogeographical data, the Greek *Fritillaria* taxa can be subdivided into smaller groups (Kamari 1991a). The current study deals with *Fritillaria* taxa occurring in Argolis Peninsula and Argosaronic Islands (Table 1) and they are known to hybridize intensively with each other when they co-exist (Kamari 2009). The group includes *F. graeca* Boiss. & Spruner, with quite a wide distribution in Greece and two stenoendemic *Fritillaria* taxa, *F. rhodocanakis* Orph. ex Baker and *F. spetsiotica* Kamari, as well as their hybrids.

Fritillaria graeca is a Greek endemic taxon (Figure 1) common in Peloponnisos, in central and eastern parts of Sterea Ellas, in central Evia and on some islands in proximity to Sterea Ellas (Salamis and Kea). It grows on rocky slopes with phrygana, shrubs, in clearings of coniferous forests or in rocky places, usually on limestone, from near sea level to 2000 m altitude (Kamari 1991b). The taxon is listed under Appendix I of the Convention on the Conservation of European Wildlife and Natural Habitats (Bern Convention). Some populations are also found in Natura 2000 sites. Morphologically, it can be distinguished by the presence of a clear fascia on the purplish-brown tepals, its longer lanceolate nectaries and its narrowed, lanceolate, deeply glaucous leaves (Figure 2A). It is noticed that *F. graeca* has a greater ability than other *Fritillaria* Greek representatives to hybridize [*F. conica* × *F. graeca* (Kamari and Phitos 2009a), *F. spetsiotica* × *F. graeca* (Kamari 1986, Kamari and Phitos 2009b), etc.].

Fritillaria rhodocanakis is a stenoendemic taxon, mainly occurring on Idra Island (Figure 1) and the smaller islands between Idra and East Peloponnisos (Poros, Dokos etc.), on rocky limestone areas with phrygana or low maquis and clearings of *Pinus halepensis* Mill. forest, olive groves or vineyards, usually in open vegetation but often under shrubs. Morphologically, it is a very distinct species among Greek *Fritillaria*, especially concerning the color of the perianth segments which is dark-brown at the base up to the half-length, whereas it is yellow at the other half (Figure 2B). *Fritillaria*

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Table 1. Most important morphological features of the parental species: *F. graeca*, *F. rhodocanakis* and *F. spetsiotica*.

Species	*F. graeca*	*F. rhodocanakis*	*F. spetsiotica*
Perianth	Purplish-brown with clear fascia	Bicolor: dark purplish-brown with yellow apical almost the half	Dark purplish-brown or obscurely tessellated outside, slightly or more tessellated inside
Fascia	Yellowish-green, distinct, narrow	Absent	Absent or indistinct
Tessellated flower	Slightly tessellated outside and inside	Inside slightly tessellated only at the base	Obscurely tessellated
Shape of the nectaries	Linear to oblanceolate	Linear-lanceolate	Ovate to elliptic
Color of the nectaries	Green or brown sometimes green with brown base	Brown to dark green	Brown or dark green
Shape of the leaves	Oblong-lanceolate	Lanceolate	Ovate-lanceolate to broadly lanceolate
Color of the leaves	Glaucous	Glaucous-green	Glaucous
Style	3-fid, glabrous	3-fid, usually papillose but sometimes smooth	3-fid, sometimes glandular papillose
Capsule	Subglobose, unwinged	Subglobose, unwinged, usually brownish red on top	Subglobose, unwinged

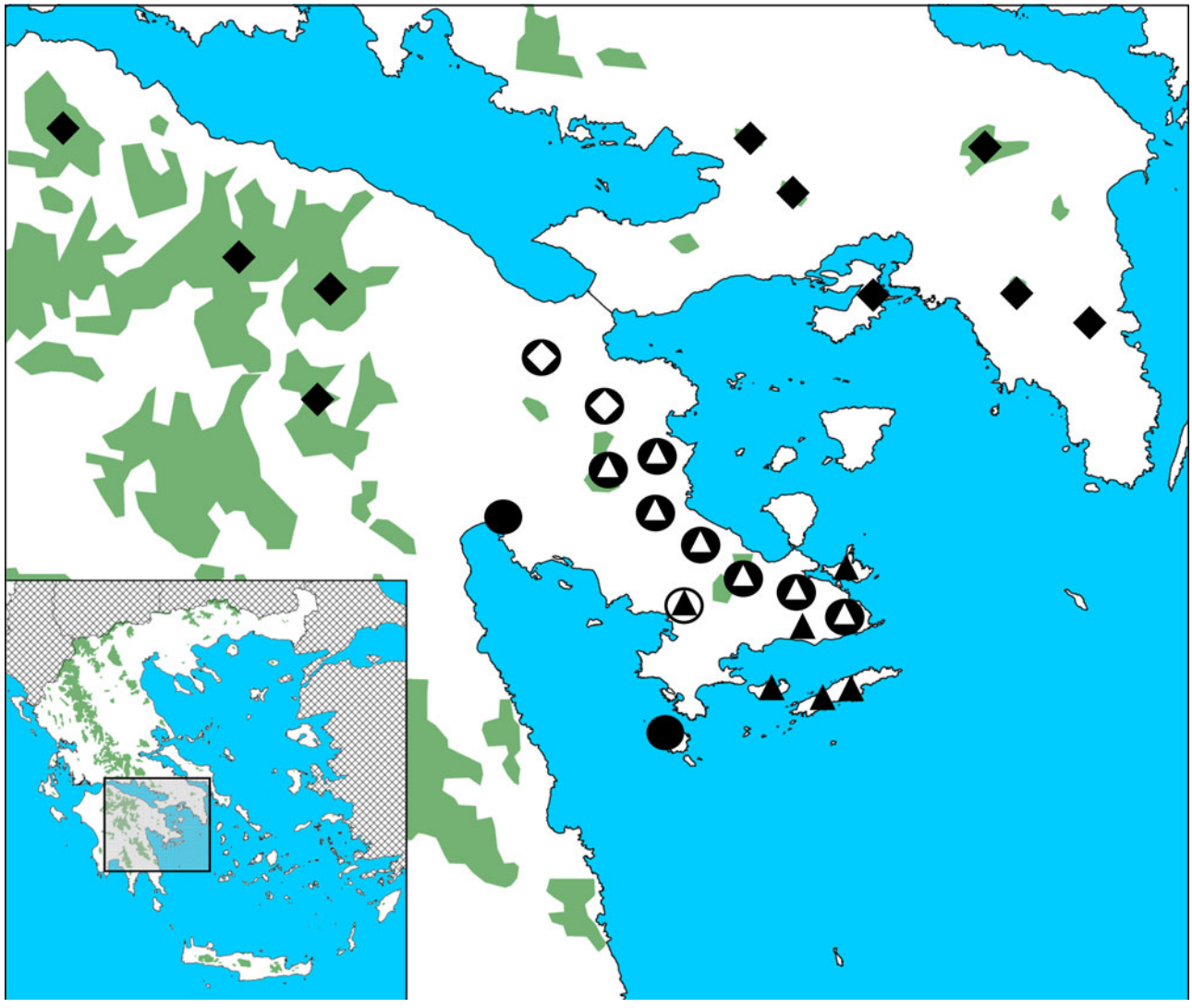

Figure 1. Distribution map of: (◆) *F. graeca*; (▲) *F. rhodocanakis*; (●) *F. spetsiotica*; (◇) *F. spetsiotica* × *F. graeca*; (▲) *F. spetsiotica* × *F. rhodocanakis* ($2n = 2x$); (▲) *F. spetsiotica* × *F. rhodocanakis* ($2n = 3x$).

rhodocanakis resembles *F. michailovskyi* Fomin and *F. reuteri* Boiss., which are distributed in NE Turkey to Caucasus region and SW Iran, respectively (Kamari 2009). *Fritillaria rhodocanakis* is categorized as Vulnerable (VU) in the Red Data Book of Rare and Threatened Plants of Greece (Kamari 1995a, 2009) and as Endangered (EN) according to the latest version of IUCN's Red List of Threatened species (Kamari 2011). Moreover, it is under protection by the Bern Convention, Council Directive 92/43/EEC and the Presidential Decree 67/81.

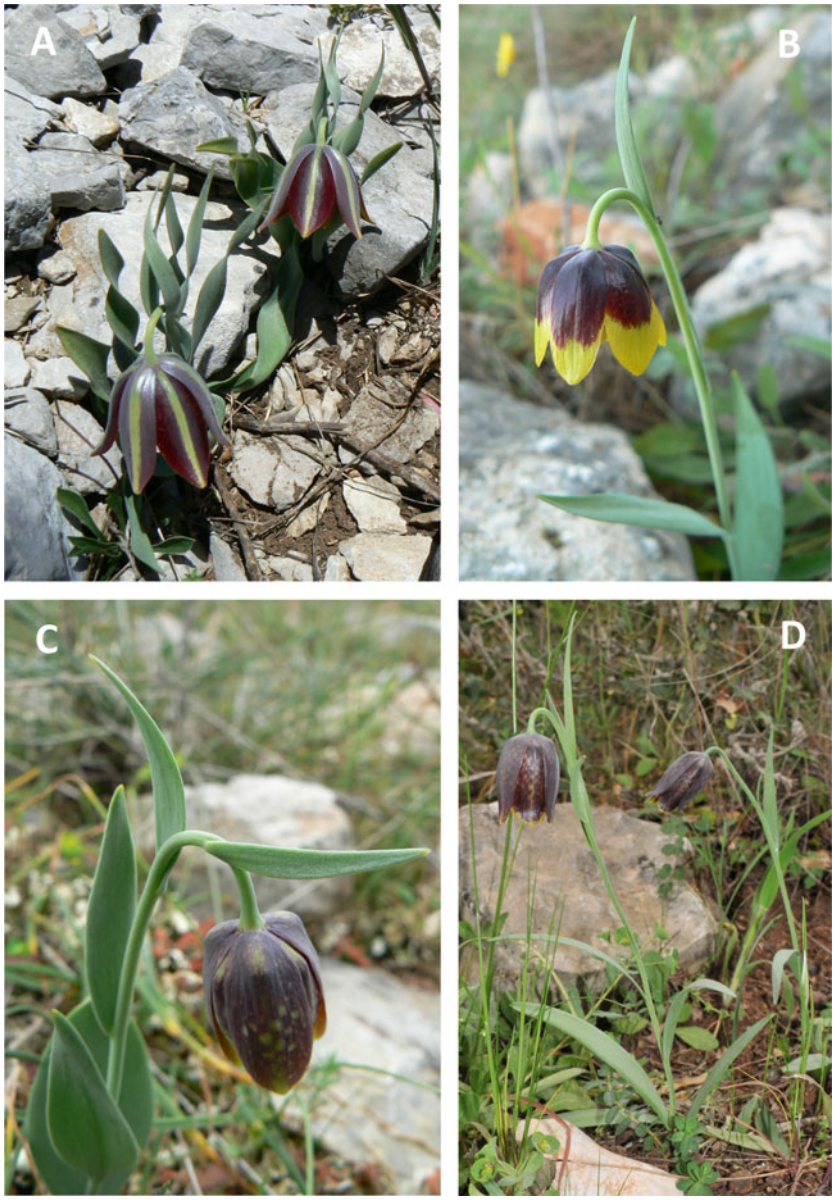

Figure 2. Individuals of the typical species: A, *Fritillaria graeca*; B, *F. rhodocanakis*; C and D, *F. spetsiotica*.

Fritillaria spetsiotica has dark (outside slightly/inside more intense) tessellated tepals and broadly lanceolate to ovate glaucous leaves (Figure 2C,D). The taxon's main distribution covers Spetses Island (Figure 1), found on rocky limestone places with phrygana or low macchia, uncultivated fields and at the edges of *Pinus halepensis* forest and olive groves, usually in open vegetation but often under shrubs. *Fritillaria spetsiotica* is included in the Red Data Book of Rare and Threatened Plants of Greece (Kamari 1995b; Kamari and Phitos 2009b) and characterized as Vulnerable (VU). The taxon is not included in the IUCN (2019) Red List of Threatened Species even though its populations are very restricted and threatened by grazing, urbanization, tourism development, hybridization and reduction of mature individuals.

Argolis is a peninsula located in the north-eastern part of Peloponnisos, sharing northern borders with Korinthos and the south-western ones with Arkadia. Eastward, it is surrounded by Argolic bay and southernly by Saronic bay, commonly called together Argosaronic Gulf. Its substrates mostly consist of limestone. Three mountains characterize the area, i.e. Arachnaio, Didima and Aderes, with the highest peak belonging to Arachnaio (1200 m). Very few stenoendemic species are located in the region, such as *Alkanna sartoriana* Boiss. & Heldr. (EN/Endangered), while some of the most important threatened taxa found in the area (Phitos et al. 2009a, 2009b) reveal a phytogeographical link with the following areas: East Peloponnisos and Sterea Ellas, as testified by the common presence of *Astragalus maniaticus* Kit Tan & Strid (NT/Near Threatened) and *Consolida tuntasiana* (Halácsy) Soó (EN/Endangered); North Peloponnisos, as witnessed by *Colchicum peloponnesiacum* Rech.f. & P.H. Davis (NT/Near Threatened); Central and East Aegean Islands, as testified by *Myosurus heldreichii* Heldr. (VU/Vulnerable).

In the southern parts of Argolis, close to Nafplio, which is right opposite Spetses, there is one population in which only morphologically typical forms that match the selected type specimen (typical) of *F. spetsiotica* exist (Kamari and Phitos

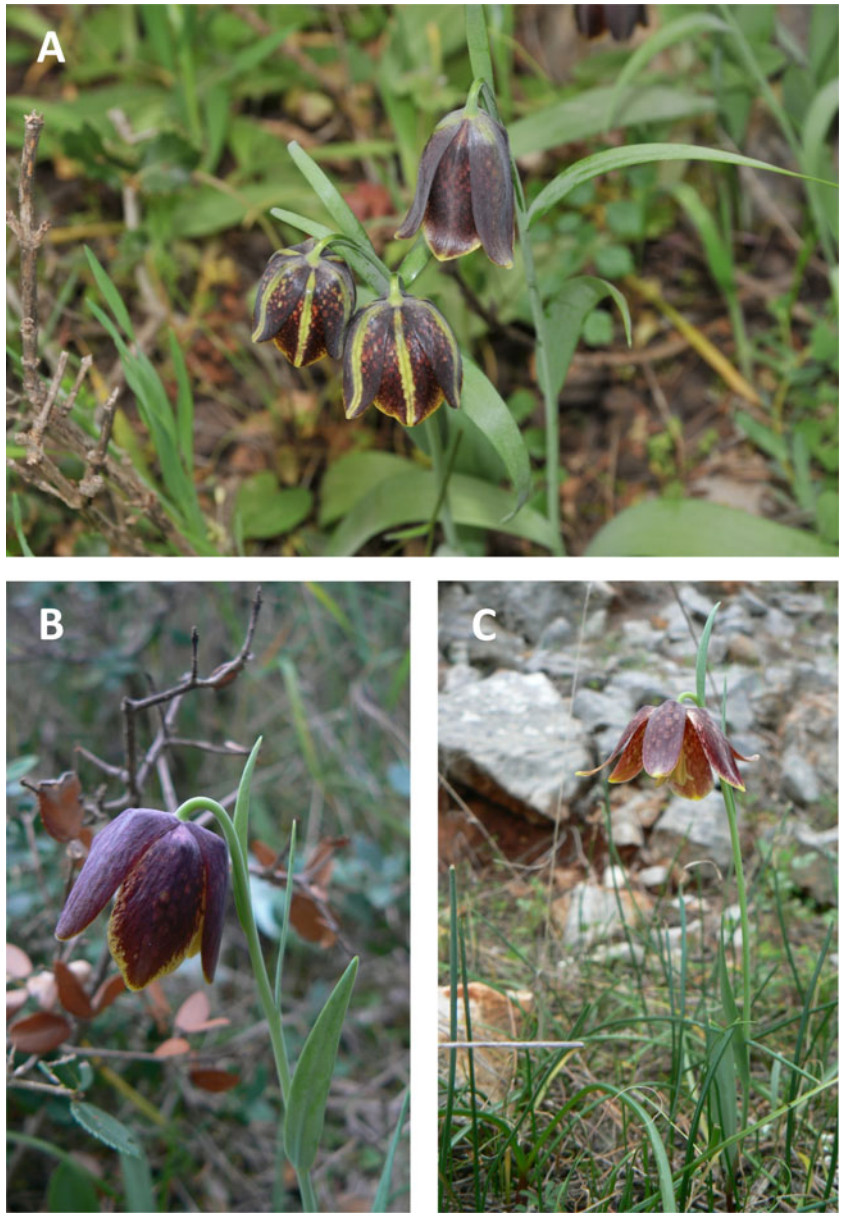

Figure 3. Intermediate forms of hybrids: A and B, *Fritillaria spetsiotica* × *F. graeca*; C, *F. spetsiotica* × *F. rhodocanakis*.

2009b). In the south and south-eastern parts of the Argolis peninsula, *F. spetsiotica* meets *F. rhodocanakis* and nowadays they are well hybridized, while in the northern part of Argolis, it is mainly hybridized with *F. graeca* (Figure 1). As a result, most of the Argolis populations consist of hybrids with all kind of morphologically intermediate forms between the typical parental species (Figure 3). To our knowledge, no typical forms have been observed mixed with the intermediate ones. The subsequent reduction of the typical populations introgressing with the increasing hybridized ones is the reason why the stenoendemic taxa are considered Vulnerable (VU). Zaharof (1987a) raised a hybrid to subspecies and described it as *F. rhodocanakis* subsp. *argolica* Zaharof, concluding that parental species are *F. rhodocanakis* and *F. graeca*, without taking *F. spetsiotica* into account. The selected individual by Zaharof as subspecies has morphological features closest to *F. rhodocanakis* and although she didn't find any karyological variability, she stated that her proposal could be regarded as subjective. In the latest Vascular Plants Checklist of Greece (Dimopoulos et al. 2013), *F. spetsiotica* is reported as a synonym of *F. rhodocanakis* subsp. *argolica*. However, where *F. spetsiotica* does not overlap with other species (i.e. Spetses and Nafplio) it shows stable morphological features according to the original description, different from those of other species. *Fritillaria rhodocanakis* presents the same stability in morphological features in Idra and the other smaller islands between Idra and Peloponnisos. According to Hill (2011), apart from *Fritillaria rhodocanakis* subsp. *argolica*, another two *Fritillaria* hybrids have been described as taxa (Macfarlane 1978; Meyers et al. 2006). The chromosome number $2n = 2x = 24$ is known for all of the currently studied species. Their number as well as their morphology follow the most common for the Greek *Fritillaria* taxa, which have diploid, asymmetrical karyotypes with the basic chromosome number $x = 12$ (Kamari 1984a, 1984b, 1986, 1991a, 1996; Zaharof 1987b, 1989;

Table 2. Studied species with karyomorphometric indices: Chromosome number (2*n*), total (TCL) and average (ACL) chromosome length, total haploid chromosome length (THL), maximum (max. l + s) and minimum (min. l + s) chromosome length, karyotype asymmetry indices (CV_{CL} and M_{CA}) and variation of centromeric position (CV_{CI}).

Species	2*n*	Karyotype formula	Max. (μm) (SD)	Min. (μm) (SD)	TCL (μm) (SD)	THL (μm) (SD)	ACL (μm) (SD)	CVCI (SD)	CVCL (SD)	MCA (SD)
F. graeca	24	2m + 2sm + 6st + 10t + 4t-SAT	19.44 (1.91)	10.94 (0.79)	350.01 (22.75)	175.01 (11.38)	14.58 (0.95)	65.17 (9.03)	17.46 (2.29)	67.02 (1.27)
F. rhodocanakis	24	2m + 2sm + 8st + 10t + 2t-SAT	18.53 (1.45)	9.81 (0.71)	319.36 (22.77)	159.68 (12.47)	13.31 (0.95)	66.69 (3.76)	17.42 (0.90)	67.89 (1.67)
F. spetsiotica	24	2m + 2sm + 8st + 10t + 2t-SAT	18.06 (3.82)	9.32 (1,58)	309.58 (62.9)	154.79 (35.16)	12.9 (2.62)	65.34 (2.87)	17.63 (1.36)	65.67 (1.97)
F. spetsiotica × ***F. rhodocanakis***	24	2m + 2sm + 8st + 12t	17.73 (2.48)	10.15 (1.46)	311.58 (47.32)	155.79 (21.6)	12.98 (1.97)	63.29 (3.17)	17.8 (1.21)	65.33 (1.49)
	36 + 0–2B	3m + 3sm + 15st + 15t	17.81 (1.57)	8.59 (0.89)	433.91 (17.54)	144.64 (5.23)	12.05 (0.49)	58.65 (1.72)	23.46 (3.69)	64.44 (1.28)
F. spetsiotica × ***F. graeca***	24 + 0–5B	2m + 2sm + 10st + 2st-SAT + 8t	16.26 (2.72)	9.38 (1.09)	286.89 (37.98)	143.44 (16.45)	11.95 (1.58)	57.05 (3.55)	17.14 (1.99)	63.45 (1.1)

Kamari and Phitos 2000, 2006; Samaropoulou et al. 2016; Kamari et al. 2017). The karyotype formulas mostly consist of st and t chromosomes, apart from one m and one sm chromosome pair. However, karyotypes vary among the species due to the presence and morphology of chromosomes either with satellites or secondary constrictions. As a consequence, specific chromosome pairs can be distinguished and considered as markers in order to compare similar karyotypes (Kamari 1984b; Zaharof 1989; Kamari and Phitos 2000, 2006).

In the context of a broader biosystematic and cytological study of the genus in Greece, carried out by the first author for her doctoral dissertation, this is the second in-line paper (Samaropoulou et al. 2016). The aim of the current study is to examine further the phenomenon of hybridization amongst *Fritillaria* taxa, and Argolis Peninsula is considered a case study of this phenomenon. The main goal is to reveal whether the morphological variety observed in hybrids is accompanied by karyological diversity.

Materials and methods

Living plants were collected and their cultivation took place in the Laboratory of Systematic Botany of Agricultural University of Athens. Parental species were collected from populations including only typical individuals, while hybrids were chosen according to their intermediate morphological characters. All populations karyologically studied are listed in the Appendix.

Root tips were pretreated in colchicine (0.05 w/v) for 6 h at room temperature and overnight at 4 °C, then fixed in 3:1 (v/v) absolute ethanol:glacial acetic acid for 24 hours at 4 °C and stored in 70% ethanol at -20 °C. Pretreated material was hydrolyzed in 1 N HCl at 60 °C for 11 min, and staining was achieved after 2.5 h in Feulgen (Darlington and La Cour 1969). The stained root tips were put on a slide with a drop of 45% (v/v) acetic acid and then squashed according to Östergren and Heneen (1962) and Kamari (1976).

Chromosome plates were observed with AXIOLAB Zeiss microscope or Zeiss Axiophot photomicroscope. Ten individuals per population were examined and at least five plates per individual were measured. Chromosome terminology follows Levan et al. (1965), Stebbins (1971) and Kamari (1976), taking into consideration comments and suggestions by Sybenga (1959), Bentzer et al. (1971) and Favarger (1978). The karyomorphometric results were statistically analysed using Microsoft Office Excel 2007 and they include the karyotype formula, mean values of maximum (max) and minimum (min) length of the chromosomes, total (TCL) and average (ACL) chromosome length, total haploid length of the chromosome set (THL) and karyotype asymmetry (Table 2): CV_{CL} according to Paszko (2006) and M_{CA} according to Peruzzi and Eroğlu (2013). Moreover, centromere position heterogeneity was measured using the index CV_{CI} according to Paszko (2006). Multivariate analysis (Principal Coordinate Analysis – PCoA) was performed on six karyological parameters (2*n*, *x*, THL, CV_{CL}, CV_{CI}, M_{CA}; see Peruzzi and Altinordu 2014) using Past 3.03 (Hammer et al. 2001). Marker chromosomes (metacentric, submetacentric, SAT-chromosomes and secondary constrictions) are given (Table 3) with their total (l + s), long (l) and short (s) arm's length, arm ratio (r-index l/s), the proportion of the long arm regarding the whole chromosome (centromeric index (l/l + s), arm difference ratio (l − s/l + s) and relative chromosome length [R-length l + s/Sn(l + s)].

Results

Fritillaria graeca 2n = 2x = 24 — *Figures 4A and 6A*

The species shares the most common chromosome number reported for *Fritillaria* species, i.e. 2*n* = 24, and the karyotype formula is usually 2*n* = 2 m + 2sm + 6st + 10t + 4t-SAT = 24. *Fritillaria graeca* is diploid with a high intrachromosomal (M_{CA} = 67.02) and a low interchromosomal karyotype asymmetry (CV_{CL} = 17.46). The position of the centromere is variable (CV_{CI} = 65.17). The chromosomes range in size from 10.94 to 19.44 μm. The total chromosome length is 350.01 μm, while the average length is 14.58 μm (Table 2). Four chromosome pairs can be distinguished as markers (Figure 6A): the longest one, which is m with a secondary constriction on the long arm next to the centromere, the sm, as well as two t-SAT chromosome pairs bearing a small satellite on the short arm (Table 3). Due to their small size, satellites can be easily removed after squashing and often three out of four satellite t chromosomes are observed (Figure 4A).

Table 3. Karyomorphometric indices of marker chromosomes for each species. Marker chromosome pairs, long arm's length (l), short arm's length (s), chromosome length (l + s), r-index, centromeric index, arm difference ratio, R-length.

Species	Marker chromosome pairs	l (μm) (SD)	s (μm) (SD)	l + s (μm) (SD)	r- index (l/s) (SD)	centromeric index (l/l + s) (SD)	arm difference ratio (l-s/l + s) (SD)	R-length [l + s/Sn(l + s)] (SD)
F. graeca	m-secondary constriction	11.61	7.87	19.45	1.51	0.6	0.2	0.06
		(1.18)	(1.11)	(1.7)	(0.3)	(0.08)	(0.004)	(0.004)
	sm	11.78	5.47	17.25	2.2	0.68	0.37	0.05
		(0.78)	(0.93)	(1.58)	(0.29)	(0.03)	(0.06)	(0.003)
	t-SAT	14.80	1.38	17.01	12.36	0.92	0.83	0.05
		(1.85)	(0.56)	(1.67)	(5.22)	(0.03)	(0.05)	(0.006)
	t-SAT	11.73	1.67	13.39	7.67	0.87	0.75	0.04
		(1.62)	(0.46)	(1.53)	(2.75)	(0.04)	(0.04)	(0.005)
F. rhodocanakis	m-secondary constriction	10.85	7.42	18.27	1.47	0.59	0.19	0.06
		(1.31)	(0.83)	(1.9)	(0.16)	(0.03)	(0.05)	(0.003)
	sm	11.17	5.48	16.65	2.05	0.67	0.34	0.05
		(0.57)	(0.34)	(0.61)	(0.18)	(0.02)	(0.04)	(0.003)
	t-SAT	13.78	1.45	15.23	9.47	0.9	0.81	0.04
		(1.23)	(0.08)	(1.32)	(0.31)	(0.003)	(0.006)	(0.002)
	st-secondary constriction	9.52	2.71	12.23	3.56	0.78	0.55	0.04
		(1.33)	(0.31)	(1.27)	(0.72)	(0.035)	(0.07)	(0.002)
F. spetsiotica	m-secondary constriction	9.87	7.59	17.47	1.28	0.56	0.12	0.06
		(3.02)	(1.56)	(4.52)	(0.18)	(0.035)	(0.07)	(0.004)
	sm	9.85	5.19	15.05	1.91	0.66	0.31	0.05
		(1.8)	(1.02)	(2.76)	(0.17)	(0.02)	(0.04)	(0.002)
	t-SAT	12.22	1.27	13.49	10.45	0.9	0.8	0.04
		(2.25)	(0.48)	(2.34)	(3.88)	(0.03)	(0.06)	(0.004)
	st-secondary constriction	9.16	2.47	11.63	3.86	0.79	0.6	0.04
		(2.76)	(0.72)	(3.28)	(1.26)	(0.04)	(0.09)	(0.004)
F. spetsiotica* × *F. rhodocanakis	m-secondary constriction	10.58	7.15	17.73	1.49	0.59	0.19	0.06
		(1.63)	(1.06)	(2.48)	(0.17)	(0.09)	(0.18)	(0.007)
2n = 2x	sm	10.02	5.17	15.19	1.94	0.66	0.31	0.05
		(1.76)	(0.87)	(2.55)	(4.55)	(0.11)	(0.22)	(0.005)
	st-secondary constriction	9.87	2.52	12.38	3.99	0.79	0.59	0.04
		(1.95)	(0.35)	(1.98)	(1.06)	(0.03)	(0.07)	(0.003)
F. spetsiotica* × *F. rhodocanakis	m-secondary constriction	10.32	7.48	17.81	1.39	0.58	0.16	0.04
		(1.12)	(0.87)	(1.57)	(0.19)	(0.03)	(0.07)	(0.003)
2n = 3x	sm	9.50	5.01	14.51	1.91	0.65	0.31	0.03
		(1.04)	(0.56)	(1.36)	(0.25)	(0.03)	(0.05)	(0.004)
F. spetsiotica* × *F. graeca	m-secondary constriction	9.27	6.99	16.26	1.35	0.57	0.16	006
2n = 2x		(1.36)	(1.34)	(2.54)	(0.18)	(0.03)	(0.08)	(0.004)
	sm	9.65	4.68	14.33	2.06	0.67	0.35	0.05
		(1.28)	(0.61)	(1.86)	(0.08)	(0.009)	(0.02)	(0.002)
	st-SAT (double satellite)	11.26	1.64	12.89	6.92	0.87	0.75	0.04
		(1.96)	(0.35)	(2.3)	(0.32)	(0.005)	(0.01)	(0.003)

Fritillaria rhodocanakis 2n = 2x = 24 — *Figures 4B and 6B*

The species is diploid with $2n = 2\,m + 2sm + 8st + 10t + 2t\text{-}SAT = 24$ chromosomes, ranging between 9.81 and 18.53 μm (Figure 4B). The TCL is 319.36 μm and ACL 13.31 μm (Table 2). As in most *Fritillaria* taxa, the two longest chromosome pairs are markers, one m and one sm. An intense secondary constriction is observed on the shorter arms of the metacentric chromosomes, very close to the centromere (Figure 6B). Moreover, one t-SAT chromosome pair bears a small satellite on the short arm and one st pair comes with a very intense, close to the centromere, secondary constriction on the short arm, which is often broken due to squash technique, so it may be confused with B-chromosomes (Table 3). Karyotype is intrachromosomally asymmetric ($M_{CA} = 67.89$) and interchromosomally symmetric ($CV_{CL} = 17.42$). Centromere position is heterogeneous among chromosomes ($CV_{CI} = 66.69$).

Fritillaria spetsiotica 2n = 2x = 24 — *Figures 4C and 6C*

The species is diploid with $2n = 2\,m + 2sm + 8st + 10t + 2t\text{-}SAT = 24$ chromosomes (Figure 4C). The total and average chromosome lengths of the karyotype are TCL = 309.58 μm and ACL = 12.9 μm respectively (Table 2). The karyotype shows asymmetry in its intrachromosomal component ($M_{CA} = 65.67$), while it is symmetric as concerns its interchromosomal component ($CV_{CL} = 17.63$). Centromere position is heterogeneous among chromosomes ($CV_{CI} = 65.34$). Four chromosome pairs can be characterized as markers (Figure 6C). Similar to *F. rhodocanakis*, the markers are the longest and metacentric chromosomes (m) with a secondary constriction beside the primary ones, the second longest and submetacentric pair (sm), one st pair with a secondary constriction close to the centromere and two t-SAT chromosomes with a small satellite on their short arms. Usually, one of the two satellites is visible (Table 3).

Fritillaria spetsiotica × *F. rhodocanakis* 2n = 2x = 24, 2n = 3x = 36 + 0 − 2B — *Figures 5A,B and 6D,E*

Both diploid and triploid populations are found. The diploid karyotype consists of $2n = 2x = 2\,m + 2sm + 6st + 2st\text{-}SAT + 12t = 24$ chromosomes. The chromosomes vary in size between 10.15 and 17.73 μm, while their average length is

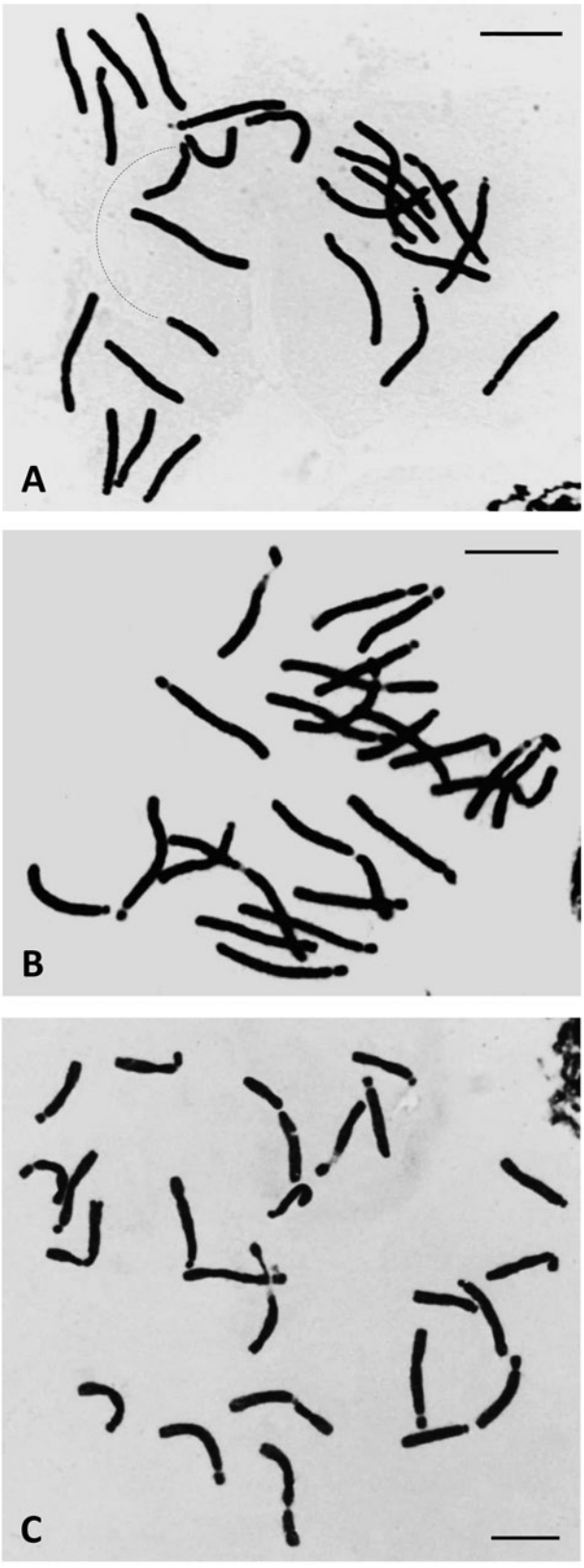

Figure 4. Microphotographs of mitotic metaphase plates of: A, *F. graeca* ($2n = 2x = 24$); B, *F. rhodocanakis* ($2n = 2x = 24$); C, *F. spetsiotica* ($2n = 2x = 24$). – Scale bars = 10 μm.

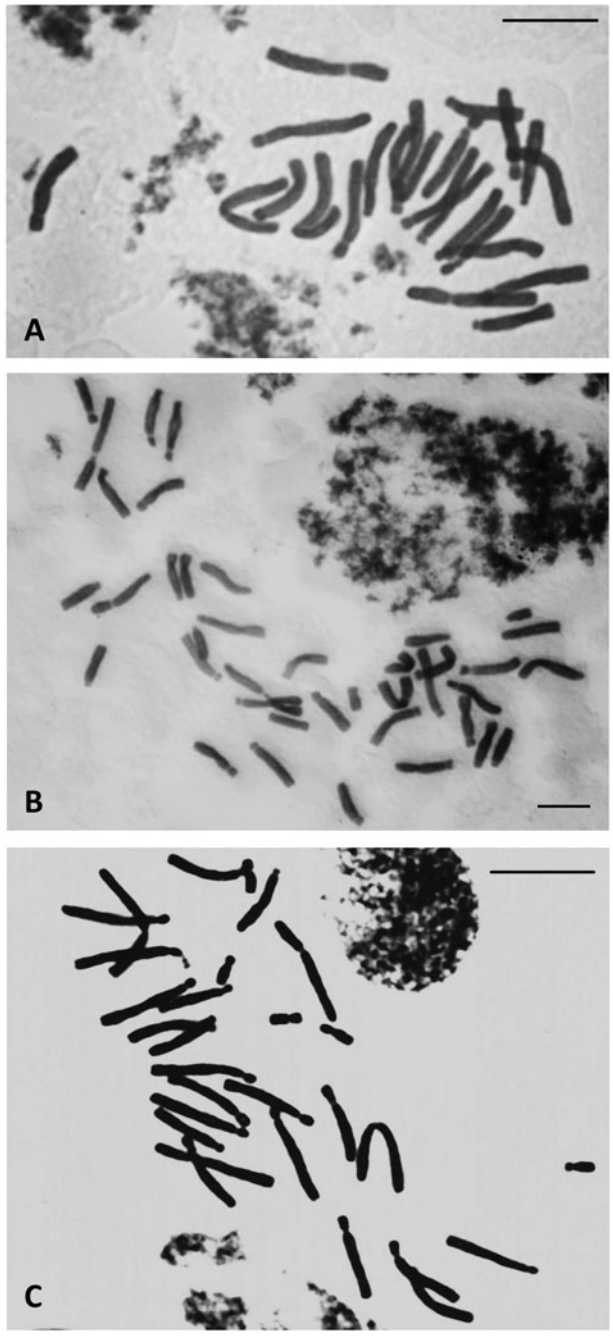

Figure 5. Photomicrograph of mitotic metaphase plates of: A, *F. spetsiotica* × *F. rhodocanakis* ($2n = 2x = 24$); B, *F. spetsiotica* × *F. rhodocanakis* ($2n = 3x = 36 + 0$–$2B$); C, *F. spetsiotica* × *F. graeca* ($2n = 2x = 24 + 0$–$5B$). – Scale bars = 10 μm.

12.98 μm (Figure 5A). Total chromosome length is 245.05 and the indices of asymmetry are: M_{CA} = 65.33 and CV_{CL} = 17.8. CV_{CI} is 63.29 (Table 2). Concerning the marker chromosomes (Figure 6D), there are two m which are the longest and have a secondary constriction close to the centromere and two sm ones, like those of the parental taxa. Moreover, there are two st chromosomes with a secondary constriction on the short arm and close to the centromere (Table 3).

The triploid population from Didima is found with $2n = 3x = 3\,m + 3sm + 15st + 15t = 36 + 0$–$2$ B chromosomes. Six chromosomes are observed as markers (Figure 6E), three metacentric (m) with the usual secondary constriction on the short arm, next to the centromere and three submetacentric (sm) ones (Table 3). As expected the total chromosome length is bigger, TCL = 433.91 μm with an

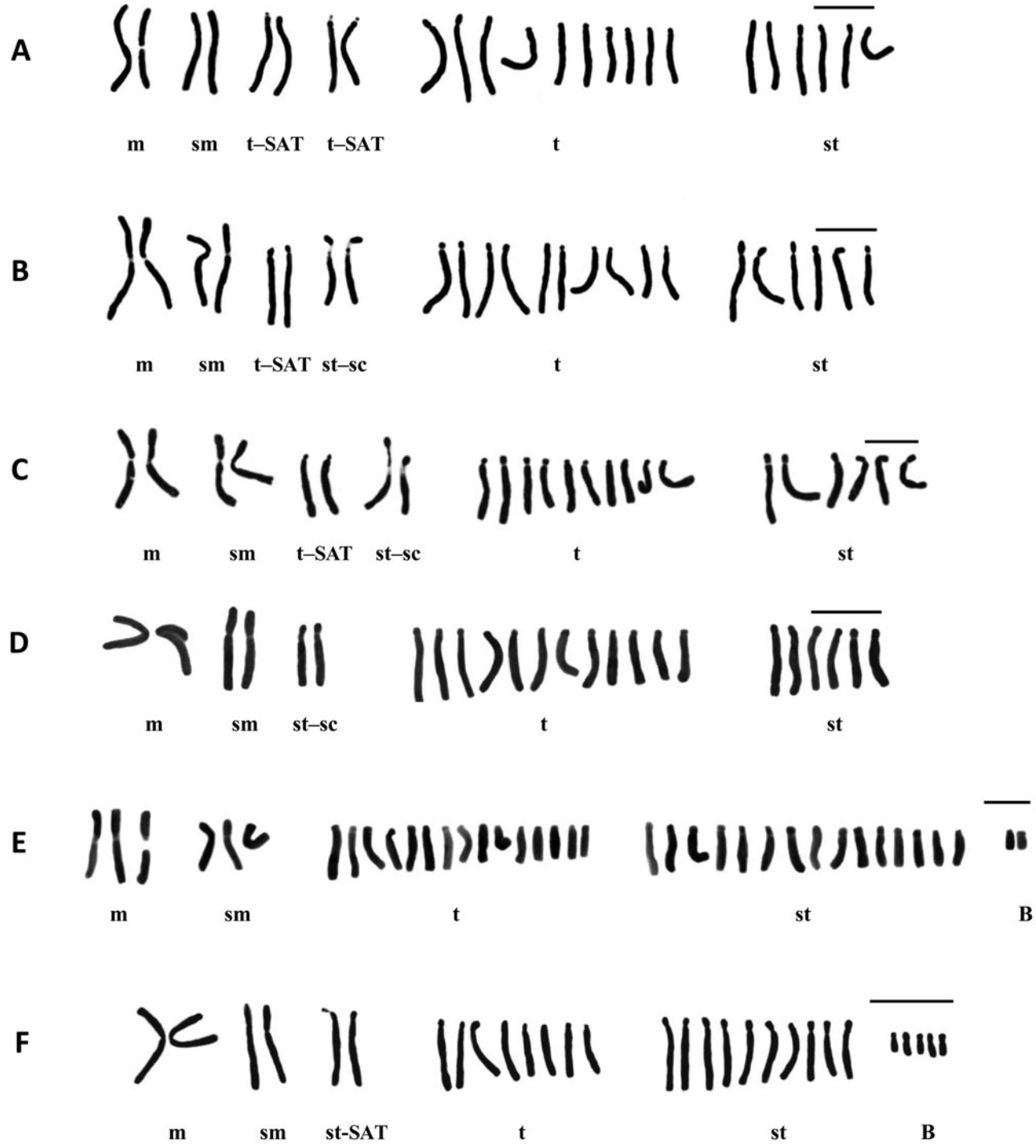

Figure 6. Karyograms of: A, *F. graeca*; B, *F. rhodocanakis*; C, *F. spetsiotica*; D, *F. spetsiotica* × *F. rhodocanakis* (2*n* = 2*x*); E, *F. spetsiotica* × *F. rhodocanakis* (2*n* = 3*x*); F, *F. spetsiotica* × *F. graeca*. sc: secondary constriction.

average length of 12.05 μm. The mean longest chromosome is 17.81 μm and the shortest 8.59 μm. The average length of B-chromosomes, which are either sm or st, is 4.57 μm. The accessory chromosomes are euchromatic and apart from the obvious primary constriction, they also bear secondary constrictions (Figure 5B). The karyotype is, of course, asymmetrical in the morphology's view (M_{CA} equal to 64.44), but symmetrical when it comes to the chromosome size (CV_{CL} = 23.46). The index for the heterogeneity of the centromere position (CV_{CI}) is equal to 58.65 (Table 2).

Fritillaria spetsiotica × *F. graeca* 2n = 2x = 24 + 0 − 5B — *Figures 5C and 6F*

The hybrids of *Fritillaria spetsiotica* × *F. graeca* from Sofiko (N Argolis Peninsula) are characterized by the common metacentric and submetacentric chromosome markers. Moreover, there is a third st marker chromosome with a small, double satellite on the short arm, which is not observed in the parental species (Figure 6F). Up to five B-chromosomes are counted, sizing around 4.05 μm, with distinct primary

constrictions that make them m or sm (Figure 5C). The karyotype formula is usually $2n = 2x = 2\,m + 2sm + 10st + 2st\text{-}SAT + 8t = 24$ with the following indices of asymmetry: $M_{CA} = 63.45$ and $CV_{CL} = 17.14$. CV_{CI} is 57.05 (Table 2). The chromosome size varies from 7.35 to 12.82 μm and their average length is estimated to be 9.39 μm. The total chromosome length is equal to 225.32 μm.

Discussion

Argolis Peninsula is a hybridization zone for three *Fritillaria* taxa and in the framework of the current study, a thorough examination of the karyotype variability among the typical species and their hybrids is attempted.

Hybridization

Generally, hybridization in the genus *Fritillaria* is thought to be rare (Hill 2011), even though at least 16 cases have been reported (Hill 2011). Argolis is apparently a hybridization area where *Fritillaria* taxa end up with a vast variation of morphological characters (Figure 3). At first, the hybridization of *F. spetsiotica* was known, either with *F. rhodocanakis* or *F. graeca*. After years of observations and cultivation, apart from hybrids with intermediate characters between the two parental species, individuals bearing all combinations of the three taxa have been found since hybrids keep fertilizing with each other. However, in the frame of this study, no population with intermediate forms only between *F. rhodocanakis* and *F. graeca* was observed. Following our findings, karyotypes vary mostly in the morphology of the marker chromosomes according to different hybrids and parental species.

Karyomorphometric study

Even though chromosome numbers of the examined taxa have already been referred, this is the first time their karyomorphometric study is carried out. The observed karyotype of *F. graeca* has four marker chromosome pairs. As in all cases studied here, the longest four chromosomes are m and sm. The metacentric pair is found to bear a secondary constriction close to the centromere. The other marker chromosomes are t-SAT with a small spherical satellite on the short arm. The satellite on the fourth t marker chromosome is not always visible (Figure 6A).

Fritillaria rhodocanakis and *F. spetsiotica* are two morphologically distinguished taxa. However, they appear to be very similar karyologically. Both of them are found to share the same marker chromosomes: two m with secondary constriction on the short arm, next to the centromere, two sm, two t-SAT with small satellites on the short arms and two st with secondary constrictions on the short arms, too (Figure 6B & 6C). In the case of *F. rhodocanakis*, the constriction of the st is more vivid and may lead to the short arms' removal after squash. Submetacentric chromosomes also bear a secondary constriction next to the primary, on the short arm, too, but it is not that obvious as appears in the metacentrics.

Regarding the hybrids, all cytotypes are found having the same secondary constriction next to the centromere of the metacentric chromosomes, just like the parental taxa. Moreover, it is important to note that they all come with fewer markers (two or three pairs) than the typical species (four pairs). *Fritillaria spetsiotica* × *F. rhodocanakis* has also two different ploidy levels. The diploids have six marker chromosomes: two m, two sm, two st with secondary constrictions (Figure 6D), while triploids that are observed here for the first time, have only three metacentric and three submetacentric marker chromosomes, as well as 0–2 B-chromosomes (Figure 6E). On the other hand, *F. spetsiotica* × *F. graeca* appears with the common m and sm chromosome pair, but also a characteristic double satellite st chromosome and 0–5 B-chromosomes with clear primary constrictions, sometimes secondary constrictions, too (Figure 6F).

According to our knowledge, this is the first time to describe the variability of marker chromosomes in hybrids and to report different levels of ploidy. Our chromosome counts are in agreement with the existent reference, although two B-chromosomes were observed by Zaharof (1987a, 1987b) for *F. rhodocanakis* from Idra, while Kamari (1986) and Kamari and Phitos (2009b) referred the existence of 0–3 B-chromosomes, often characterized by the presence of centromere and secondary constrictions, as well, for *F. spetsiotica*. Concerning *F. graeca*, our results agree with Kamari (1991a), who reported two satellite chromosome pairs, while up to six B-chromosomes have been reported from a population at Mt. Taigetos belonging to *F. graeca* var. *guicciardii* (Zaharof 1989). Kamari (1991a) reported 1–5 B-chromosomes in populations where *F. graeca* coexists with other taxa, leading her to the conclusion that the presence of accessory chromosomes in *Fritillaria* taxa is generally connected to hybridization.

Polyploidy

Polyploidy is found in most of the plant taxa (70% of angiosperms and 95% of pteridophytes), playing an important role in their evolution (Soltis and Soltis 1999). According to Peruzzi et al. (2009), the family Liliaceae is generally characterized by low percentage (16%) of polyploids. *Fritillaria* neither belongs to the exclusively diploid genera nor is it among the three genera with more than 50% of polyploids (*Amana* Honda, *Clintonia* Raf., *Gagea* Salisb.), but polyploidy is rare in the genus and only triploid individuals have been reported (Peruzzi et al. 2009; Ambrozova et al. 2011; Day et al. 2014). For example, triploidy in some taxa with $x = 12$ was reported and $2n = 3x = 36$ chromosomes were counted in *F. affinis* (Schult.) Sealy (Darlington 1936; Schweizer 1973; Marchant and Macfarlane 1980 under the name *F. lanceolata* Pursh; La Cour 1978 under the name *F. phaeanthera* Purdy), *F. bithynica* Baker (Rix 1971), *F. camschatcensis* (L.) Ker Gawl. (Matsuura 1934; Nishikawa 1986; Yamagishi et al. 2010), *F. elwesii* Boiss. (Rix 1971), *F. ionica* subsp. *ionica* Halácsy (Zaharof 1987b, 1989 under the name *F. graeca* subsp. *ionica* (Halácsy) Zaharof), *F. latifolia* Willd. (Rix 1971), *F. recurva* Benth. (Darlington 1936) and *F. uva-vulpis* Rix (Leitch et al. 2007). Furthermore, triploids with $x = 9$ ($2n = 3x = 27$) were also reported, such as *F.*

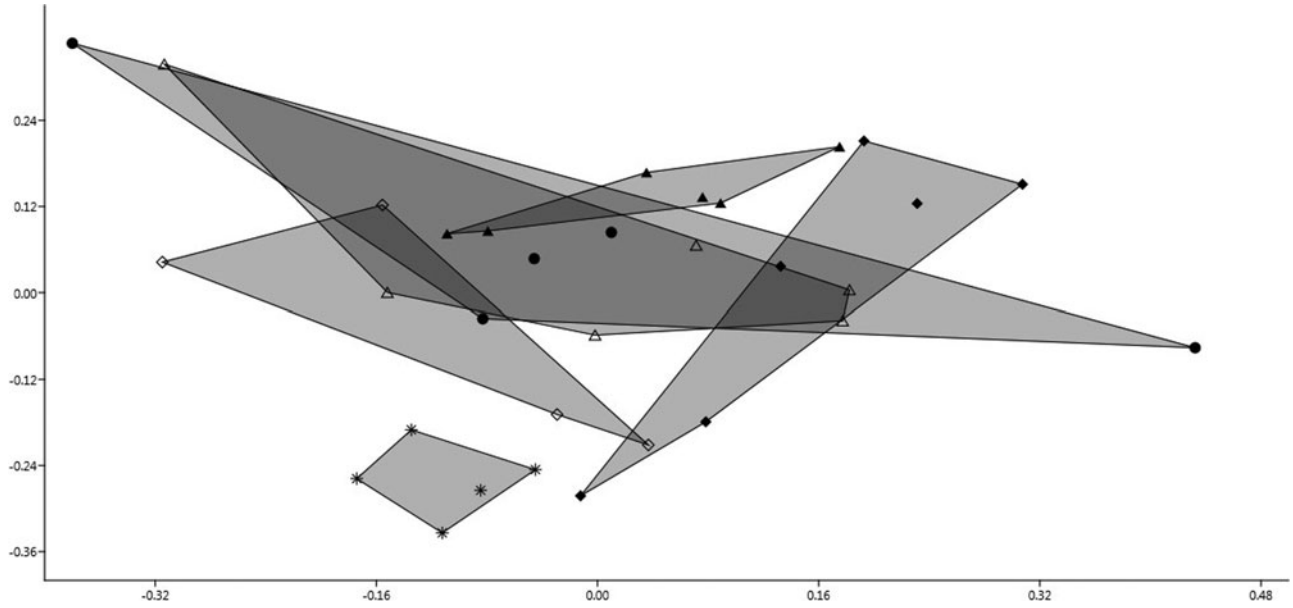

Figure 7. PCoA analysis based on six quantitative karyological parameters: (◆) *F. graeca*; (▲) *F. rhodocanakis*; (●) *F. spetsiotica*; (◇) *F. spetsiotica* × *F. graeca*; (△) *F. spetsiotica* × *F. rhodocanakis* ($2n = 2x$); (*) *F. spetsiotica* × *F. rhodocanakis* ($2n = 3x$).

montana Hoppe ex W.D.J. Koch (Cesca 1986 under the name *F. tenella* M. Bieb.; Kamari 1991a; Samaropoulou et al. 2016) and *F. legionensis* Llamas & J. Andrés (Fernández-Arias and Devesa 1991), as well as with $x = 13$ ($2n = 3x = 39$), such as *F. pudica* (Pursh) Spreng. (Darlington 1936). All above species are primarily diploid and the triploids occur as isolated individuals or clones within a species (Rix 1971, 1974). Even though Zonneveld (2010) referred to the measurement of the DNA amount of the tetraploid *F. assyriaca* made by McLeish and La Cour in 1971 (cited in Bennett and Smith 1976), he expressed his doubts and following Rix (1974) he assumed that McLeish and La Cour used *F. uva-vulpis* instead. Marchant and Macfarlane (1980) later stated that the only tetraploid chromosome count was obtained from pollen grain mitosis in *F. lanceolata* by Beetle (1944) and no tetraploid somatic cell had been observed by that time.

Even though several cases of triploidy have been mentioned for *Fritillaria* taxa, it is considered a rare phenomenon in Greece, and in the present study combined hybridization and triploidy are referred for the first time according to our knowledge.

B-chromosomes

B-chromosomes – otherwise called accessory, supernumerary or selfish chromosomes – have been described in several species of animals, fungi and plants, cultivated or wild (Camacho et al. 2000; Marques et al. 2013). Such fragments had been reported for *Fritillaria* species since 1944 by Beetle who studied taxa from North America. B-chromosomes are mostly considered to have originated from A-chromosomes through procedures of chromosome rearrangements and their number varies between populations, individuals or even cells of the same tissue. Their frequency depends both on the tolerance of the species and on selective, historical or transmission factors (Battaglia 1964; Camacho et al. 2000). B-chromosomes can include large amounts of repetitive DNA very similar between related species or ribosomal DNA (NOR region) which is usually located on secondary constrictions and can be easily removed from A-chromosomes. These karyotype rearrangements and B-chromosomes' formation are very frequent when hybridization occurs (Houben et al. 1997; Mitchell McGrath and Helgeson 1998). Indeed, in Greece, Kamari and Phitos (2006) mentioned that B-chromosomes are common in *Fritillaria* individuals from areas where distribution ranges of two or more taxa overlap. Examples of *Fritillaria* taxa with B-chromosomes in Greece were reported for *F. ehrhartii* Boiss. & Orph. (Kamari 1984a; Zaharof 1989), *F. epirotica* Turrill ex Rix (Zaharof 1987b; Kamari 1991a), *F. graeca* Boiss. & Sprun. var. *guicciardii* (Heldr. & Sart.) Boiss. (Zaharof 1989 as "*F. graeca* subsp. *guicciardii*"), *F. gussichiae* (Degen & Dorfler) Rix (Zaharof 1989), *F. ionica* subsp. *ionica* (Zaharof 1989 under the name "*F. graeca* subsp. *ionica*"), *F. ionica* Halácsy subsp. *thessala* (Boiss.) Kamari (Zaharof 1989 under the name "*F. graeca* subsp. *thessala*"), *F. messanensis* Raf. subsp. *messanensis* and subsp. *gracilis* (Ebel) Rix (Kamari and Phitos 2006), *F. montana* (Kamari 1991a; Samaropoulou et al. 2016), *F. obliqua* Ker Gawl. (Rix 1971; La Cour 1978; Kamari 1984a; Zaharof 1987b), *F. rhodocanakis* (La Cour 1953; 1978; Rix 1971; Kamari 1986; Zaharof 1987a), *F. spetsiotica* (Kamari 1986) and *F. mutabilis* Kamari (Kamari 1991b).

As a consequence, our finding of B-chromosomes in hybrids' karyotypes is not a surprise. According to Jones and Houben (2003), interspecific hybridization and allopolyploidization cause a plethora of genome rearrangements, and B-chromosomes arise because of errors during meiosis that generate A-chromosomes.

PCoA analysis of karyological parameters

Following the multivariate analysis (PCoA) of six karyological indexes (Figure 7), the values of all hybrids overlap with their

parental species, apart from triploid individuals grouping alone due to the different ploidy level. *Fritillaria spetsiotica*'s values overlap with those of *F. graeca*, *F. rhodocanakis* and all diploid hybrids. *F. spetsiotica* is proved to share a similar karyotype morphology with *F. rhodocanakis*, a fact that probably explains their ability to massive hybridization. However, the multivariate analysis is based on quantitative characters and does not take into account very important features for reconstructing relationships between species, such as satellites and secondary constrictions, which are used to characterize marker chromosomes, or B-chromosomes.

Accordingly, even though PCoA analysis presents values' overlapping, parental taxa and their hybrids differ significantly on marker chromosomes, while *F. spetsiotica*, *F. rhodocanakis* and *F. graeca* are morphologically distinct species based on features, which are considered taxonomically significant on the species level, such as the color and shape of the perianth segments and nectaries, the presence or not of a clear fascia on the segments, as well as the shape of their leaves (Table 1; Figure 2).

Concluding remarks

The morphological and karyological variety (different marker chromosomes, ploidy levels, hybridization and B-chromosomes) prove the genus is evolving (Johnson 2003). Hybridization is a very important key to evolution as it can lead to gene flow, and consequently to many possible genotypes, sometimes more adaptable to the environment than their parents (Barton 2001). In addition, B-chromosomes and polyploidy lead to important genome size variation, and thus to speciation (Siljak-Yakovlev et al. 2010). But what remains as a question is whether these procedures are responsible for the great number of *Fritillaria* taxa in Greece. Like Argolis, several other areas host these phenomena, while others are extremely isolated leading to evolution and speciation through a completely different way.

Disclosure statement

No potential conflict of interest was reported by the authors.

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Appendix of specimens karyologically examined

Fritillaria graeca Boiss. & Sprun

Greece: Sterea Ellas: Nomos Attikis: Ins Salamis, in collibus saxosis, 27 Mar 1965, *D. Phitos 2695* [Herb. Phitos & Kamari]; Ins. Salamis, ad Mavrovounion, ca. 200 m., in saxosis calcareis, 19 Apr 1973, *D. Phitos 19585* [Herb. Phitos & Kamari]; Porto Rafti, May 1977, *G. Kamari 946 b* [Herb. Phitos & Kamari]; Mt Imittos, rocky calcareous slopes, with short macchie around the summit, alt. 900–1026 m, 37°57′N, 23°49′E, 6 May 1990, *K. Athanasiou 1661* [Herb. Phitos & Kamari]; Eparchia Megaridos, Mt Pateras, ca. 1 km W of Palaeokundura, along the road driving to the summits, alt. ca. 400 m, 38°06′N, 23°24′E, 29 Apr 1994, *Th. Constantinidis s.n.* sub Kamari cult. no. F187 [Herb. Phitos & Kamari]; Ep. Megaridos, Mt Gerania, the summit Makriplagi, calcareous substrate, alt. ca. 1340–1351 m, 38°01′N, 23°08′E, 07 May 1995, *Th. Constantinidis & A. Iliadis 5509* [Herb. Phitos & Kamari]; Isl. Salamina: Ampelakia, Ep. Selinia, Mt Mavrovounio, slopes with phrygana, alt. ca. 160 m, 37°55′34″N, 23°30′34″E, 18 Mar 2015, *S. Samaropoulou & A. Samaropoulos SF1051* (ACA); Eparchia Spata, Hill Perati, alt. ca. 160 m, 37°54′48″N, 24°01′22″E, 01 Apr 2015, *S. Samaropoulou & A. Samaropoulos SF1056* (ACA); Eparchia Spata, Hill Palati, 01 Apr 2015, *S. Samaropoulou & A. Samaropoulos SF1057* (ACA); Mt Imittos, above Argiroupoli, alt. ca. 310 m, 37°54′N, 23°46′E, 15 Apr 2015, *S. Samaropoulou, A. Samaropoulos & I. Kofinas SF1062* (ACA); Mt Parnitha, shelter of Mpafi, alt. ca. 1198 m, 38°10′05″N, 23°43′35″E, 22 Apr 2015, *S. Samaropoulou & I. Patrikios SF1063* (ACA); Mt Kithaironas, at the top of the mountain Profitis Ilias, just before the entry of the old airport base, stony substrate, alt. ca. 1387 m, 38°10′58″N, 23°14′58″E, 29 Apr 2015, *S. Samaropoulou & A. Samaropoulos SF1066* (ACA); **Nomos Viotias**: Mt Parnassos, shelter opposite Ski-club, alpine meadows, alt. ca. 1650 m, 4 May 1985, *A. Tiniakou 1190* sub Kamari cult. no. F66 [Herb. Phitos & Kamari]; Mt Elikonas, alt. ca. 1500 m, 5 May 1996, *D. Vassiliades s.n.* sub Kamari cult. no. F25 [Herb. Phitos & Kamari]; **Aegean Islands: Evia:** Ep. Chalkidas, mons Skotini, supra pagum Metochi alt. 1200 m, 38°35′N, 23°59′E, in saxosis calc. 27 Apr 1989, *D. Phitos & G. Kamari, 20395* [Herb. Phitos & Kamari]; Mt Oxilithos, 17 Apr 2015, *N. Kalogiannis SF1000/1* (ACA); Kimi, Mt Mavrovouni, 2 May 2017, *S. Samaropoulou & N. Kalogiannis SF1124* (ACA); **Peloponnisos: Nomos Achaias:** Ep. Lakedemonos, mons Klokos, supra pagum Pteri, alt.

1350–1400 m, in apertis silvae Abietis cephalonicae, solo calcareo, 38°08′N, 22°03′E, 26 Apr 1987, *D. Phitos & G. Kamari 19943* [Herb. Phitos & Kamari]; Ep. Patron, mons Panachaikon, in declivibus meridio-occidentalibus, alt. 1450 m, 38°10′N, 21°52′E, 13 May 1987, *D. Phitos & G. Kamari 21774* [Herb. Phitos & Kamari]; Ep. Kalavriton, mons Chelmos, in declivibus borealibus, alt. ca. 1800 m, in saxosis calc. 38°03′N, 22°09′E, 18 May 1996, *G. Kamari 24687* [Herb. Phitos & Kamari]; Mt Chelmos, next to the shelter, 2080 m, 37°59.427′N, 22°11.534′E, 23 May 2015, *P. Trigas SF1078* (ACA); **Nomos Arcadias**: mons Parnon, in declivibus occidentalibus, alt. 1400–1500 m, in apertis silvae Abietis, 17 Apr 1979, *D. Phitos*, *G. Kamari*, *Gr. Iatrou & D. Tzanoudakis 16489* [Herb. Phitos & Kamari]; Ep. Mantinia, Mt Menalon, slopes E and SE of the plateau with the ski resort, toward Mt Ostrakina, alt. 1650–1850 m, 37°38′50″N, 22°15′20″E, sparse *Abies cephalonica* wood and bare slopes, on limestone, 4 Jun 1995, *G. Kamari*, *C. Beurton*, *Th. Constantinidis*, *M.A. Garcia Garcia*, *R. Jahn*, *N. Jogan*, *U. Mätthas*, *P. Mazzola*, *M. Popova*, *E. Rico*, *K. Siems*, *V. Stevanovic*, *W. Strasser*, *S. Savic & K. Sutory 1212* [Herb. Phitos & Kamari]; **Nomos Korinthias:** Mt Killini, Ziria, 10 May 2015, *G. Kofinas SF1073* (ACA).

Fritillaria rhodocanakis Orph. ex Baker

Greece: Sterea Ellas: Nomos Attikis: Isl. Dokos: facing Ermioni, 23 Apr 1994, *D. Phitos, G. Kamari, D. Christodoulakis & Th. Constantinidis s.n.* sub Kamari cult. no. F185 [Herb. Phitos & Kamari]; **Isl. Idra:** supra vicum Hydra, in saxosis calcareis, at the edges of vineyards, alt. ca. 30 m, 10 Mar 1972, *D. Phitos & G. Kamari 16748* [Herb. Phitos & Kamari]; along the road towards the summit Profitis Ilias, stony substrate, *Pinus* forest, 225 m, 37°20′31″N, 23°27′56″E, 21 Feb 2016, *S. Samaropoulou & I. Patrikios SF1104* (ACA); **Isl. Poros:** close to the monastery of Agios Efstathios ca. 100 m alt, 12 Mar 1972, *G. Kamari s.n.* sub Kamari cult. no. F34 [Herb. Phitos & Kamari].

Fritillaria spetsiotica Kamari

Greece: Sterea Ellas: Nomos Attikis: Isl. Spetses: Eparchia Trizinies, ad locum Zagoria, in apertis silvae *Pinus halepensis*, alt. ca. 50 m, 37°36′N, 23°24′E, 10 Mar 1972, *D. Phitos & G. Kamari 18942* [Herb. Phitos & Kamari]; **Peloponnisos: Nomos Argolidos:** Nafplio, beside the castle of Palamidi, slopes with phrygana, 195.5 m, 37°33′31″N, 22°48′30″E, 24 Feb 2016, *S. Samaropoulou & I. Patrikios SF1098* (ACA).

Fritillaria spetsiotica × *F. rhodocanakis*

Greece: Peloponnisos: Nomos Argolidos: in ditione pagi Nea Epidavros, in nanofruticetosis, alt. ca. 100 m, 13 Mar 1985, *G. Kamari & M. Tzini 19432* [Herb. Phitos & Kamari]; inter Moni Agnountos et pagum Nea Epidauros, in fruticetosis, alt. ca. 100 m, 13 Mar 1985, *G. Kamari & M. Tzini 19430* [Herb. Phitos & Kamari]; ad Iera Moni, 3 km ab urbem Navplion, in fruticetosis, alt. ca. 150 m, 13 Mar 1985, *G. Kamari & M. Tzini 19431* [Herb. Phitos & Kamari]; above the village Tolo, in fruticetosis, alt. ca. 50 m, 13 Mar 1985, *G. Kamari & M. Tzini 19433* [Herb. Phitos & Kamari]; Didima: along the road towards the village, cultivated fields with olive trees, along with *Tulipa* sp., ca. 170 m, 37°27′15″N, 23°10′16″E, 23 Feb 2016, *S. Samaropoulou & I. Patrikios SF1100* (ACA); Moni Agnountos, 500 m after the monastery, towards Epidavros, macchie with *Juniperus* sp., alt. ca. 190 m, 37°42′28″N, 23°7′43″E, 24 Feb 2016, *S. Samaropoulou & I. Patrikios SF1099* (ACA).

Fritillaria spetsiotica × *F. graeca*

Greece: Peloponnisos: Nomos Korinthias: Close to the village Sofiko, at the edges of olive groves, ca 150 m, 13 Mar 1985, *G. Kamari & M. Tzini 19434* [Herb. Phitos & Kamari]; between the villages Sofiko and Amoni, calcareous substrate, below *Pinus halepensis* forest, 420 m, 37°49′19″N, 23°06′11″E, 24 Feb 2016, S. *Samaropoulou & I. Patrikios SF1115* (ACA).