Title : Changing rounds into squares or combining stripes: Diversity and formation of checkerboard patterns in Eukaryotes

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Abstract

Important in many human artistic cultures, checkerboard patterns are rare in nature like many motifs based on squared geometry. Nevertheless, they are expected to be very detectable by the visual networks due to their periodic geometry, and diverse plant and animal species bear them, suggesting specific biological functions. Here, thanks to a biological survey, we first draw the diversity of species bearing checkerboard patterns. Then, we selected two genera,* Sarcophaga *flies and* Fritillaria *flowers to perform simulations and functional studies to decipher the mechanisms producing these very peculiar patterns. Although they share a similar geometry, these two genera appear to produce checkered patterns through two very different ways, showing a convergence of shape but not of mechanism. Together, this shows the extent of the mechanisms selected during evolution to generate complex forms, and confirms the importance of describing color patterns through the species diversity

Introduction

Contrary to hexagons and circles, squares patterns are much more uncommon in nature. Many studies have proven the difficulty to produce squares and the instability of such patterns. Nevertheless, square lattices (to which checkerboard patterns belong) have been described in some eukaryotic tissues, like the mouse auditory epithelium or the oviduct epithelium of the Japanese quail. Concerning color patterning, checkerboard patterns are the combination of two characteristics: a square lattice, and an alternation of coloration. The latter is very common in color patterning, and many processes are able to produce them, like the ubiquitous Turing-like mechanism. Two possibilities coexist, either squares and color alternation are directly produced by the same processus, (in the same way that in a Turing-like pattern the dots and their hexagonal arrangement are produced by the same mechanism), or produced by two separated mechanisms, simultaneously or not, which combine.

If some species are quite famously known for their checkerboard color patterns like the *Fritillaria* flower (Liliaceae) which bear them on their tepals, few species have been formerly described for those peculiar shapes, and no work has already presented them combined in a single study. We then chose to describe as many checkerboard patterns as possible, using multiple data sources, taking care to cover the maximum of eukaryotic biodiversity.

After the species survey, a large range of potential species to study was available and we decided to choose and compare an animal and an angiosperm species (and their genera):

Sarcophaga flies and *Fritillaria* flowers. They presented the patterns closest to a perfect checkerboard motif, and were accessible to functional studies, although not genetically. Simulations, microscopy observations and species comparison allowed us to propose two distinct mechanisms of formations, thanks to a cluster of clues.

Results

Checkerboard color patterns are rare but present in many diverse taxa of Eukaryotes, notably plant and animal species

To perform a survey of species bearing checkerboard patterns, we first had to define them properly. We chose to consider two separate characteristics of checkerboard patterns: square shaped-motifs and an alternation of two colors. Perfect checkerboard patterns are never reached by real patterns so we chose to extend the definition and include species with slightly diverging characteristics, like not perfect squares or partly irregular color alternation. Since no exhaustive survey was possible, we chose to use keywords to find the species (‘checkerboard’, ‘checkered’, ‘square’ and ‘*fritillaria’*, the latin word for ‘dice cornet’, a object exhibiting a checkerboard pattern and then used in species names to pinpoint the presence of this particular pattern, or one close to it).
Thanks to this, we described several species and genera, summarized in Figure 1, and qualitatively represented in a diagram thanks to the more or less perfectness of their characteristics. Both angiosperms and animals were found to exhibit checkerboard-like patterns, but we were not able to find any species belonging to Fungi. Very diverse animal species (vertebrates, insects, echinoderms, cephalopods) were found, but few plant species seem to bear such patterns. The two most perfect checkerboard-like patterns were found in *Sarcophaga* flies genus, exhibited on their abdomens, and *Fritillaria* genus, with *Fritillaria meleagris*. We then chose these two groups to explore pattern formation.

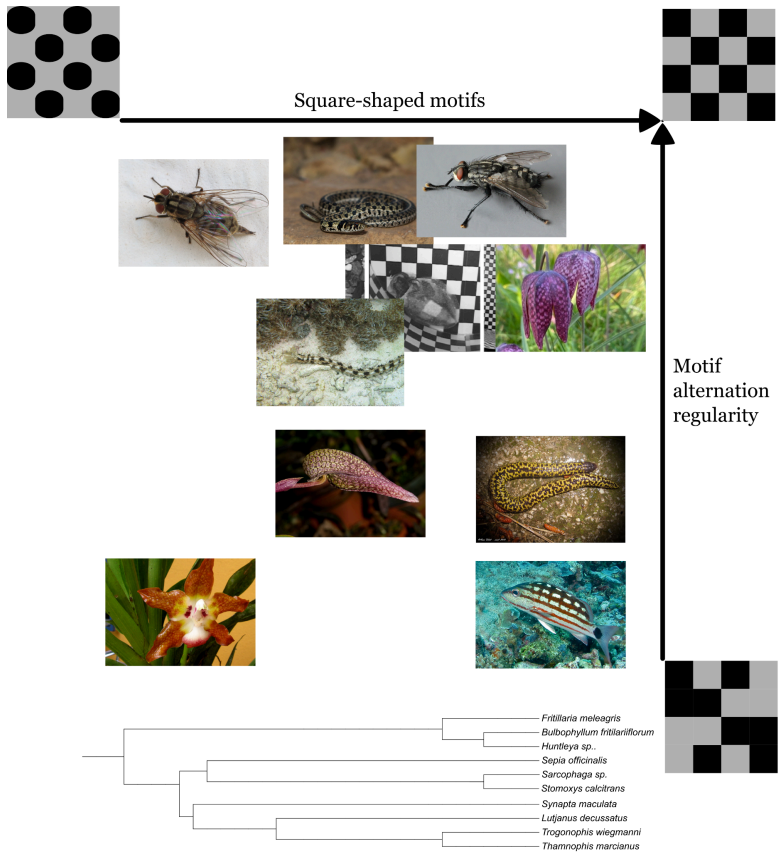

Figure 1: Diversity and variability of Eukaryotes checkerboard patterns

Fritillaria *checkerboard patterns are compatible with a Turing-like mechanism constrained by a parallel nervure frame*

To extract clues of *Fritillaria* mechanisms producing their checkerboard-like patterns, we performed microscopy on fresh individuals (Figure 2.A and B) and also from museum specimens presenting interesting features on their tepals, such as slight deviation from the classical patterns. We found that depending on the species, colored shaped go from squares (notably in *F. meleagris*) to sponge shapes for the pigmented areas (i.e. straight on the sides touching the nervures and with a negative curvature on the other two sides), and round shapes for the unpigmented areas. In the most distal part of the tepals, sponge colored shapes tend to break into two parts (Figure 1.B, left panels). In some individuals, especially in the *Fritillaria meleagris* museum specimens, we observed a very interesting feature in the places where the nervures are the widest: instead of alternations, several motifs were side by side, suggesting that nervures act as constraining barriers, but when the patterning mechanisms has sufficiently space, a spot pattern is produced. Given the periodicity of this pattern, and the round geometry of the motifs, this strongly suggests a Turing-like mechanism for its production. Indeed, at that time, it is the only mechanism demonstrated to produce periodic color dots patterning in angiosperms. Turing pattern relies classically on reaction and diffusion, and it seems that nervures could act as constraining semi-permeable barriers, which therefore shape the pattern into square-like shapes. Two clues suggest that nervures are semi-permeables to the diffusing agent (whatever its nature). First, no motif overlaps two nervures, indicating an impeded diffusion (REF Milinkovitch). But if nervures were totally impermeable, there is no reason that motifs perfectly alternate from one ‘line’ to

motif ↓ background ->	Brown	Purplish-brown	Purple	Pink	Red	Reddish-brown	Green	Yellowish-green	Greenish-Yellowish	Greenish-yellow	Yellow	Orange	Blue	White
Brown	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Purplish-brown	1	0	1	1	0	0	8	14	7	1	6	0	0	8
Purple	0	0	3	1	0	0	7	5	4	2	4	0	0	6
Pink	0	0	0	0	0	0	0	0	0	0	0	0	1	3
Red	0	0	0	0	0	0	0	0	0	1	3	0	0	2
Reddish-brown	0	0	1	1	1	1	8	23	1	3	5	0	0	0
Green	0	1	0	1	0	0	1	0	1	5	5	0	0	4
Yellowish-green	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Greenish-Yellowish	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Greenish-yellow	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Yellow	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Orange	0	0	0	0	0	0	0	0	0	0	2	1	0	0
Blue	0	0	0	0	0	0	0	0	0	0	0	0	0	0
White	1	0	0	0	0	0	0	0	0	0	0	0	0	0

Table 1: Color combinations counting for all Fritillaria *accepted species (rows: motif color, columns: background color)*

the next one, which is what we observe in every *Fritillaria* species. The most reasonable hypothesis is the possibility for a signal to diffuse to a long range, across nervures.

To sum up, to produce a final checkerboard-like pattern, several mechanisms need to interact: first, the lateral sides of the squares are produced by the straightness and parallelism of the tepal nervations. Secondly, the two other sides are more or less straight, depending on the species, and might depend on the Turing parameters of the system. Finally, the same Turing-like mechanism seems to be involved to produce an alternation of colored and uncolored zones, characteristics of the checkerboard-like patterns. This is summarized into a flowchart (Figure 4.A).

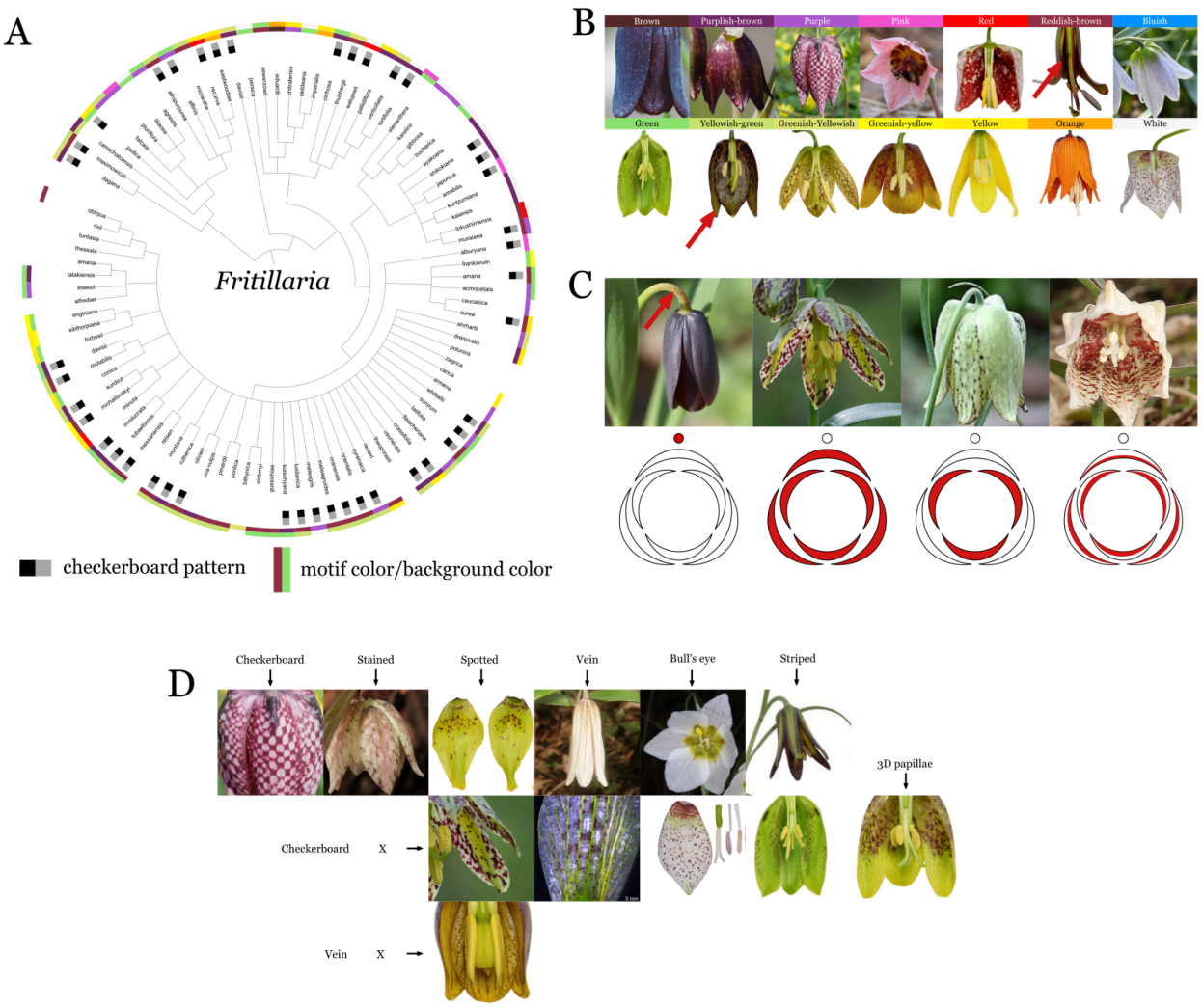

Figure 2: Diversity of Fritillaria *tepals color patterns. A: Presence of checkerboard patterns and motif/backgrounds colors mapped on* Fritillaria *genus phylogeny. B: The 14 color types defined in this study for motifs and background, with examples. C: Diversity of checkerboard patterns locations on tepals (and other organs) with examples. D: The seven categories of patterns defined in this study: checkerboard, stained, spotted, vein, bull's eye/nectary, striped and 3d papillae, with examples of flowers bearing a unique type of motif (1st row) or a combination (2nd and 3rd row).*

Sarcophaga checkerboard patterns are relying on a structural coloration generated by planar polarity of hair, compatible with the interference between two stripe patterns.

To explore *Sarcophaga* checkerboard-like patterns, we use several museum specimens of several species in the *Sarcophaga* genus. First of all, we observe the very peculiarity of these patterns. While it may appear as a black and white squares alternation, the reality is more complex. First, between two consecutive squares, there are tiny black zones, whatever the lighting. Then, under directional lighting, the black squares become light and vice versa depending on the angle of illumination and observation (Figure 3.A). These color changing patterns might then rely at least partially on structural coloration instead of only classical pigments. This was even more strongly suggested when specimens were

recovered by a thin layer of platinum for SEM microscopy. Most of the time, this is sufficient to cover and hide pigment-based patterns. On the contrary, checkerboard-like patterns were still visible, so the thin layer of platinum that molded the structure underneath seems to have taken a role of structural coloration. Under the SEM, we observed that the external tissues of the abdomen were covered by two types of hair, a big and sparse one, and small and coarse one. Only the latter is compatible with structural coloration, because of its micrometric scale. By qualitatively describing in a first part the mean direction and length of the hair (Figure 3.B, third panel), we observe a perfect correlation between the characteristics of the hair and the colors. The small black gaps between two squares are made up of tiny hairs, with not strong preferential direction, which give a glimpse of the structure underneath. On the contrary, color-changing areas correlate with dense hair with a strong preferential direction. Furthermore, if we compare two areas with opposite coloration behavior, (i.e. one is light when the other is black under a particular illumination angle), the hair length is similar but their direction is symmetrical in relation to the right-left axis of the abdomen. Together, this strongly suggests that hair is responsible for the color behavior of the abdomen.

Then, to explain the organizing into squares, we involved two observations: first, if we look at the thorax of the *Sarcophaga* flies, it is characterized by a striped pattern, parallel to the left-right axis. If we hypothesized that this mechanism of stripe patterning is also present in the abdomen, it could explain alternations of the checkerboard-like pattern parallel to the antero-posterior axis. In the perpendicular direction, we observed that there are exactly two alternations per abdomen segments. Many insect species including many flies possess a bicolor coloration in each abdomen segment, one color on the anterior side, and the other on the posterior side. If we assume that this is also the case for Sarcophaga flies, this could explain the alternations perpendicular to the antero-posterior axis. Finally, as coloration seems to be coded by the preferential direction of the hair, the combination of two perpendicular signals may explain this checkerboard-pattern. This is summarized into a flowchart (Figure 4.B).

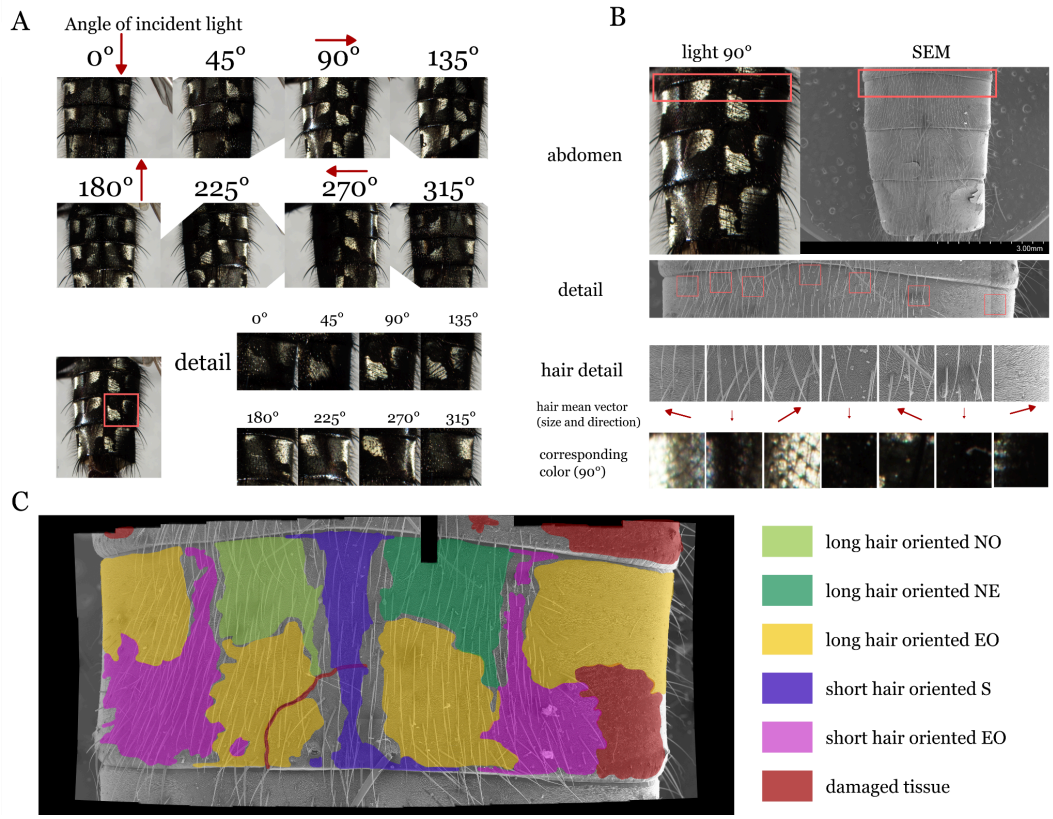

Figure 3: Sarcophaga checkerboard patterns are relying on a structural coloration generated by planar polarity of hair, compatible with the interference between two stripe patterns. A: checkerboard pattern color is depending on light orientation and observation. B, C: Pattern delimitations correlate with hair phenotype.

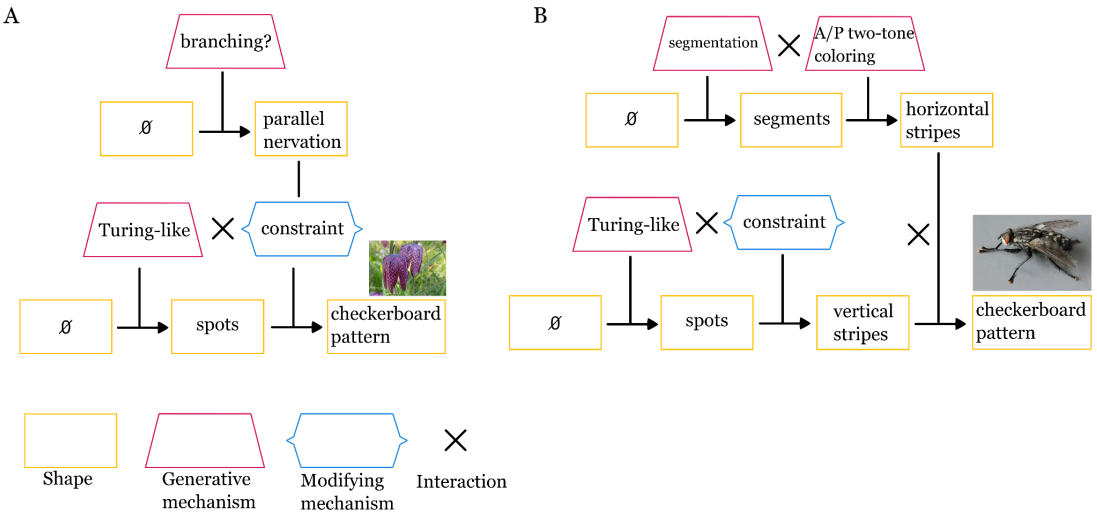

Figure 4: Logical diagrams of Fritillaria *and* Sarcophaga *checkerboard pattern formation*

Material and methods

Species survey and phylogenetic tree

The sources of photography were multiple, scientific literature was preferred, then online encyclopedias, Wikipedia (https://en.wikipedia.org/) and Wikimedia Commons (https://commons.wikimedia.org), eventually alternative sources (through search engines) with keywords such as "checkerboard", "checkered", "squares", “fritillaria”.

Phylogenetic relationships between species were built with phyloT (V2, https://phylot.biobyte.de/) based on NCBI taxonomy. Phylogenetic trees were plotted and annotated in iTOL (Interactive Tree Of Life, version 6.8.1, https://itol.embl.de/).

Scanning Electron Microscopy

A total of three abdomens were sampled from *Sarcophaga* sp. museum specimens (National Museum of Natural History, Paris, France). Samples were mounted on the aluminum stubs with colloidal graphite, sputter-coated with platinum using an EM ACE600 fine coater (Leica, Wetzlar, Germany), and observed using a SU3500 scanning electron microscope (SEM, Hitachi, Tokyo, Japan).

Light Microscopy

A total of 20 tepals were sampled from 8 specimens of *Fritillaria thunbergii*, harvested in the botanical gardens of the University of Tokyo (Koishikawa Botanical Gardens, Tokyo, Japan). Tepals gas were extracted by a vacuum pump to make the tissues more transparent and suitable for observation. Abaxial and adaxial sides were mounted in water and observed under light microscopy.

A total of 8 tepals were sampled from 3 specimens of *Fritillaria meleagris*, from museum specimens (National Museum of Natural History, Paris, France), after a survey of hundreds of museum specimens. They were rehydrated and observed under light microscopy.

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Supplementary tables

Genus	Species		Distribution area	Pattern	Organ and s	Other or	Geometrical descripti	Pattern variability (	Motif color	Background color	Source 1	2	3
Fritillaria	acmopetala		SW. & S. Türkiye to Is	O	SE+SI+PE		Green sepals with purple l	low	Purple	Green	https://powo.sc		
Fritillaria	affinis		W. Canada to W. U.S.	Y+O	All		Check-ish laterally, spottis	high	Purple	Green	https://upload.		
Fritillaria	agrestis	stin	W. & Central Californi	O	se+SI+PE+PI		Spottish pattern, scarce la	medium	Purple	Green	https://www.ca		
Fritillaria	alburyana		E. Türkiye	Y	All		Uniformly checkered	low	Pink	Pinkish white	https://www.pa	https://	http://
Fritillaria	alfredae		S. Türkiye to Lebanor	N			Glaucous outside, yellowis				https://journals		
Fritillaria	amabilis		S. Central & S. Japan	O	All		White with pink or purple-t	low	Pink or purple-t	White	http://wildplant	https://	http://
Fritillaria	amana		S. Central Türkiye	Y	se+si+PE+PI		Green, reddish-brown tess	medium	Reddish-brown	Green	https://journals		
Fritillaria	anhuiensis		China (Henan, Anhui)	O	SE+SI?+PE+PI?		Yellowish white or yellowi	N/A	Purple	Yellowish white or yellc	https://www.fri		
Fritillaria	ariana		E. Iran to Afghanistar	O	SI(bull's eye)+PI		Pink or reddish, unspotted		Reddish-brown	Pink or reddish (outsid	http://encyclop	https://	http://
Fritillaria	armena		E. Central & E. Türkiy	N		Pedicel[2]	Outside and inside purple		Purple		https://journals	https://	https:/
Fritillaria	arsusiana		Türkiye	Y	SI+PI		Purple, purplish-brown, ou	N/A	Purplish-brown	Yellowish-green	https://phytota	https:/	
Fritillaria	assyriaca		E. Türkiye to W. Iran	O(sometim	SE+PE		Sometimes striped. Usuall	high	Purplish brown	Yellowish	https://en.wikip	https:/	http://
Fritillaria	asumaniae		SW. Türkiye	O(sometim	SE+PE		Fritillaria asumaniae show	medium	White	Dark Brown	https://www.re		
Fritillaria	atrolineata		Iran	O(sometim			Perianth segments usually	N/A	Reddish-brown	Yellowish-green to gree	https://www.re		
Fritillaria	atropurpurea		W. & W. Central U.S.A	Y	All		Disordered checkerboard	high	Reddish-brown	Yellowish-green to gree	https://calscap		
Fritillaria	aurea		Central & S. Türkiye	Y	All		Characteristic brown tess	medium	Reddish-brown	Yellowish	https://www.m	https:/	
Fritillaria	avromanica		Iran	O	All		Purple with green or yellov	low	Reddish-brown	Yellowish-green	https://www.re		
Fritillaria	ayakoana		Japan (SW. Honshu)	O	All		Rare spots mostly located	medium	Purple-brown	White	http://wildplant	https:/	
Fritillaria	baisunensis		Uzbekistan	Y	All		Disordered checkerboard	medium	Purple-brown	White	https://uk.inatu		
Fritillaria	baskilensis		E. Türkiye	N			Dark purplish brown inner	N/A	Purple-brown	Yellowish-green	https://www.he	https:/	
Fritillaria	biflora		W. California to Mexi	O	All		Sometimes green patches		Green or Purple	Purple-brown or Green	https://upload.		
Fritillaria	bithynica		E. Aegean Islands to	N			Outside glaucous, inside g	low	Yellowish or gre		https://journals		
Fritillaria	brandegeei		S. Central California	O	SI+PI		Purple-brown tear-shaped	low	Purple-brown	Yellowish-green	https://www.ca		
Fritillaria	bucharica		Central Asia to NE. A	O	SI+PI		Diamond-shaped green pa	low	Green	White	https://powo.sc		
Fritillaria	byfieldii		Türkiye (Denizli)	N			Outside and inside orange	medium	Orange-pink or		https://dergipar		
Fritillaria	camschatce		Russian Far East to N	O(sometim	SE+PE		Sometimes green patches		Yellowish-green	Purple-brown	https://powo.sc		
Fritillaria	carica		E. Aegean Islands to	N			Yellow, greenish-yellow, sc		Yellow		https://journals		

Fritillaria	caucasica		N. & NE. Türkiye to N	N			perianth purple outside an		Dark purple		https://dergipa	
Fritillaria	chitralensis		NE. Afghanistan to N	O	All		Venation purple (or green)		Purple (or gree	Yellow	https://powo.s	
Fritillaria	chlorantha		W. Iran	N			Big tubular flowers; green[		Green		https://www.sc	
Fritillaria	chlororhabd		Iran	O	All?		Mostly purple-brown outsi	N/A	Dark purple	Greenish-Yellowish	https://www.fri	https:/
Fritillaria	cirrhosa		Pakistan to Central C	Y	All		Checkerboard patterns, wi	high	Purple-brown	Green	https://powo.s	
Fritillaria	collina		E. Türkiye to Caucas	Y	All		Checkerboard-like with re		Reddish-brown	Yellow	https://www.fri	
Fritillaria	conica		SW. Greece	O	All		Light green veins in yellow	N/A	Light green	Yellow	http://www.herl	
Fritillaria	crassicaulis		W. Nepal, China (SW.	Y	All		Greenish flower with sligh	N/A	Dark purple	Greenish-Yellowish	https://www.fri	https:/
Fritillaria	crassifolia		Türkiye to Iran	Y+O	All		Yellowish or green, usually	high	Purple or brow	Yellowish or Green	http://www.friti	https:/
Fritillaria	dagana		S. Siberia to N. Mong	Y+O	All		Checkerboard-like pattern	high	Purple or brow	Greenish-Yellowish	https://www.re	https:/
Fritillaria	dajinensis		China (NW. Sichuan)	O	SE+PE		Tepals yellowish green, sp	N/A	Purple	Greenish-Yellowish	http://www.efl	
Fritillaria	davidii		China (W. Sichuan)	Y+O	All		Checkerboard pattern in th	medium	Purple-brown	Greenish-Yellowish	http://www.fri	
Fritillaria	davisii		S. Greece	Y	All		Checkerboard pattern	medium	Purple-brown	Greenish	http://www.friti	https:/
Fritillaria	delavayi		Sikkim to S. Central C	Y	All	pedicel and l	Checkerboard pattern	high, camouflaged due	Purple-brown	Greenish-Yellow	https://www.fri	https:/
Fritillaria	drenovskii		NE. Greece to SW. Bu	O	SI+PI		The flower is normally bro		Purple-brown	Purple-ish-Yellow	https://www.fri	
Fritillaria	dzhabavae		Caucasus	Y	All		Holotype shows checkerb	N/A	N/A	N/A	https://www.eu	
Fritillaria	eastwoodiae		S. Oregon to N. Calif	Y	All	pedicel[2]	It is quite variable and can	high	Orange-pink	Yellow	https://www.fri	https:/
Fritillaria	ebeiensis		China (Hubei)	Y	SI+PI		tepals of F. ebeiensis are u	high	Purple	Yellow or Yellowish-gre	https://www.re	
Fritillaria	eceri		Türkiye	O	All		striped perigone[1]	N/A	Purple-brown	Greenish-Yellowish	https://bioone.	
Fritillaria	eduardii		Central Asia	O	All		Dark orange vein pattern c	low	Dark orange	Orange	https://powo.s	
Fritillaria	ehrhartii		Greece (Aegean Islar	O	SI+PI		Dark purple vein pattern o	low	Dark purple	Greenish-Yellowish	http://encyclop	
Fritillaria	elwesii		E. Aegean Islands to	O	All	pedicel[1]	Striped pattern with some	medium	Dark purple	Greenish	https://powo.s	
Fritillaria	enginiana		SW. Türkiye	O	All		perigon greenish-yellow[1]	low	Green	Greenish-Yellow	https://www.fri	
Fritillaria	epirotica		NW. Greece	Y	All		dark brownish-purple, not	medium	Purple-brown	Yellowish	http://encyclop	
Fritillaria	euboeica		Greece (Euboea)	O	All		Greenish vein pattern on y	low	Greenish	Yellow	https://www.fri	
Fritillaria	falcata		W. California (San Be	O	All		Spot-like pattern	low	Purple	Light yellowish green	https://www.ca	
Fritillaria	ferganensis		Central Asia	Y	All		Checkerboard-like pattern	N/A	Purple	Light Green	https://www.fri	
Fritillaria	fleischeriana		W. & Central Türkiye	O	All	pedicel[1]	Striped pattern or homoge	high	Dark-purple	Yellowish-Green	https://www.fri	
Fritillaria	forbesii		SW. Türkiye (Muğla)	O	All	pedicel[1]	greenish-yellow becoming	low	Greenish	Yellow	http://www.herl	https:/
Fritillaria	frankiorum		CS. Türkiye to Syria	O	All		It is a remarkably constant	very low	Greenish	Greenish Yellow	https://www.fri	
Fritillaria	fusca		S. Tibet	Y	All		Tepals yellowish, heavily te	N/A	Purple-brown	Yellowish	http://www.efl	
Fritillaria	gencensis		E. Central Türkiye	O	All		Green or dark purple vein	medium	Dark purple or	Light purple or white	https://www.re	https:/
Fritillaria	gentneri	Ger	S. Oregon	Y	All		Checkerboard-like pattern	low	Red	Yellow or Greenish yell	https://oregonf	
Fritillaria	gibbosa		S. Transcaucasus to	O	All		Spotted or even rosettes (	high	Purple	White or light purple	https://powo.s	
Fritillaria	glauca		S. Oregon to N. Calif	Y/O	All		*+/- purple or +- green mar	high	Red	Greenish yellow	https://wildflow	https:/ https:
Fritillaria	graeca		S. Balkan Peninsula t	Y+O	All		Checkerboard pattern + st	high	Purple-brown	Yellowish green	https://powo.s	
Fritillaria	grandiflora		SE. Transcaucasus	Y	All		dark purplish or green, obs	N/A	Purple-brown	Light green	https://www.sc	
Fritillaria	gussichiae		N. Balkan Peninsula	O	All		Striped pattern	medium	Reddish-brown	Light green	https://www.fri	
Fritillaria	hakkarensis		SE. Türkiye to N. Iraq	Y	All		Checkerboard pattern	N/A	Purple	Light green	https://www.fri	
Fritillaria	hermonis		Lebanon to SW. Syria	Y+O	All		Checkerboard pattern + st	high	Purple-brown	Light green	https://powo.s	
Fritillaria	imperialis		E. Central & SE. Türki	O	All		Venation pattern	medium	Dark orange or	Orange or Yellow	https://www.fri	http://
Fritillaria	involucrata		SE. France to NW	Y (+O some	All		Checkerboard pattern + st	high	Purple-brown	Light green	https://www.fri	
Fritillaria	japonica		Japan (C. Honshu)	Y	SI+PI		Checkerboard pattern (sp	high	Purple-brown	White	https://commo	https:/
Fritillaria	kaiensis		Japan (S. Central Ho	O	All		Stained pattern	N/A	Purple-brown	White	https://commo	
Fritillaria	karakocanen		Türkiye	O	All		Yellow tip outside, vein pa	N/A	Reddish-brown	Yellow	https://nsojour	https:/
Fritillaria	karelinii		Central Asia to Xinjia	O	All		Spotted or even rosettes (	high	Purple	White or light purple	https://www.fri	
Fritillaria	kittaniae		Türkiye (Antalya)	O	All		Outside and inside pale pu	high	Reddish-brown	Yellow	https://journals	
Fritillaria	kiusiana		Japan (Kyushu)	O	All		Venation pattern	N/A	Red-purple	White or light purple	http://www.friti	
Fritillaria	koidzumiana		Japan (N. Central Ho	O	All		fimbriate margins to the n	medium	Purple-brown	Light green or white	http://www.friti	https:/
Fritillaria	kolbintsevii		Kazakhstan	Y	All		Checkerboard pattern	N/A	Reddish-brown	Light green	https://www.sr	
Fritillaria	kordestanica		Iran	O	All		Outside purplish grey, rare	high	Purple-brown	Yellowish green	https://www.re	

Fritillaria	kotschyana	N. & N. Central Iran	Y/O	All		Checkerboard pattern or s	high	Purple-brown	Green	http://www.friti		
Fritillaria	kurdica	SE. Türkiye to W. Iran	Y+O	All		Checkerboard like-pattern	high	Purple-brown	Yellowish Green	http://www.friti		
Fritillaria	lagodechian	Caucasus	Y+O	All		Checkerboard like-pattern	N/A	Purple-brown	Yellowish Green	https://powo.sc		
Fritillaria	latakiensis	CS. Türkiye (Hatay) t	O	All		vein pattern	low	Purple-brown	Green	http://www.friti		
Fritillaria	latifolia	NE. Türkiye to Cauca	Y	All		Checkerboard pattern	low	Reddish-brown	Light reddish-brown (o	https://powo.sc	https://	http://
Fritillaria	legionensis	NW. Spain	Y	All		Checkerboard pattern	medium	Reddish-brown	Yellowish green	https://powo.sc		
Fritillaria	liliacea	W. California	O	All		vein pattern	low	Green	Greenish white	http://www.friti		
Fritillaria	lusitanica	Iberian Peninsula	Y+O	All		Checkerboard pattern + st	medium	Reddish-brown	Yellowish-greenish	http://www.friti		
Fritillaria	macedonica	E. Central Albania to	Y	All		Checkerboard pattern	low	Reddish-brown	Yellowish green	https://www.fri		
Fritillaria	macrocarpa	Morocco	Y+O	All		Checkerboard pattern + st	N/A	Reddish-brown	Yellowish green	https://www.tel		
Fritillaria	maximowicz	Siberia to N. China	Y/O	All		Checkerboard pattern or s	high	Reddish-brown	Yellowish green	http://www.friti		
Fritillaria	melananther	SSW. Türkiye	O	All		Striped pattern	N/A	Purple-brown	Green	http://www.friti	https://	
Fritillaria	meleagris	Europe to W. Siberia	Y	All		Checkerboard pattern	medium (pattern), high	Purple, Purple-b	White, Light Purple or l	https://powo.sc		
Fritillaria	meleagroide	W. Central Bulgaria to	Y	All		Checkerboard-like pattern	medium	Reddish-brown	Yellowish green	http://www.friti		
Fritillaria	messanensis	SE. Europe	Y+O	All		Checkerboard pattern + st	high	Reddish-brown	Light green	https://www.fri		
Fritillaria	michailovsky	E. Türkiye	Y+O	All		Checkerboard-like pattern	high	Reddish-brown	Greenish yellow	https://powo.sc	http://	https:/
Fritillaria	micrantha	Central California	O	SI+PI		Stained pattern	high	Reddish-brown	Yellowish green	https://www.ca		
Fritillaria	milasensis	Türkiye (Muğla)	O	All		usually has striped flower	medium	Reddish-brown	Greenish yellow	https://www.fri		
Fritillaria	minima	SE. Türkiye	O	All		Vein pattern	low	Green or orangi	yellow or orange-yellov	https://www.fri		
Fritillaria	minuta	E. & SE. Türkiye to N\	O	All		Vein pattern	low	Red-orange	Red-orange-yellow	https://www.fri		
Fritillaria	monantha	S. China	Y/O	All		It can be recognised by its	high	Dark Purple or	White to pale purple or	https://www.fri		
Fritillaria	montana	France to Ukraine	Y	All		Checkerboard pattern	medium	Reddish-brown	Yellowish green	http://www.friti	http://	http://
Fritillaria	mughlae	SW. Türkiye (Muğla)	O	All		Vein pattern	low	Green	Greenish-yellow	https://www.fri		
Fritillaria	muraiana	Japan (Shikoku)	Y/O	All	leaves	Checkerboard pattern and	high	Reddish-brown	Purplish white	http://www.friti	http://	
Fritillaria	mutabilis	Greece	Y+O	All		Checkerboard + striped	high	Reddish-brown	Yellowish green	http://www.friti	https://	
Fritillaria	obliqua	S. Greece	N					Reddish-brown		http://www.friti		
Fritillaria	ojaiensis	SW. California	O	SI+PI		Stained/spotted pattern	medium	Reddish-brown	Yellowish green	http://www.friti	https://	
Fritillaria	olgae	Central Asia	Y	SI+PI		Checkerboard pattern	medium	Reddish-brown	Yellowish green	https://www.fri		
Fritillaria	olivieri	W. Iran	Y+O	All		Checkerboard pattern + st	high	Reddish-brown	Yellowish green	http://www.friti		
Fritillaria	oranensis	N. Africa	Y?	SI+PI		Checkerboard pattern + st	N/A	Reddish-brown	Yellowish green	https://efloram	https://	
Fritillaria	orientalis	Caucasus	Y	All		Checkerboard pattern	medium	Reddish-brown	Yellowish green	http://www.friti		
Fritillaria	ozdemir-elm	SW. Türkiye	O	All		Vein pattern	N/A	Purple or green	Purple or Light green	https://www.re		
Fritillaria	pallidiflora	Central Asia to Xinjia	O	All		"large greeny-yellow flowe	medium	Purple-brown	Pale Yellow or Greenisi	https://www.fri	http://	
Fritillaria	persica	S. Türkiye to Iran and	O	All		Vein pattern	Medium	Green	Greenish white	http://www.friti		
Fritillaria	phitosia	E. Greece	O	All		Vein pattern	low	Green	Greenish yellow	https://www.re		
Fritillaria	pinardii	Türkiye to Iran and Le	O	All		Vein pattern "In most indiv	high	Reddish-brown	Yellowish green	https://www.fri	http://	
Fritillaria	pinetorum	N. Central & SW. Cali	O	All		Spotted/Stained pattern	low	Reddish-brown	Yellowish green	https://www.fri		
Fritillaria	pluriflora	N. California	O	All		Vein pattern	medium	Dark purple	Pink	http://www.friti		
Fritillaria	pontica	SE. Europe to NW. Tü	O	All		Vein pattern + striped + tip	medium	Reddish-brown	Yellowish green	http://www.friti		
Fritillaria	przewalskii	E. Qinghai to China (S	Y	All		Checkerboard pattern	N/A	Light purple?	Greenish yellow	https://www.fri		
Fritillaria	pudica	W. Canada to W. U.S.	Y	All		Vein pattern (very low colo	low	Green	Yellow	http://www.friti		
Fritillaria	purdyi	SW. Oregon to NW. C	Y/O	All		Checkerboard pattern to s	high	Purple to purple	White to Greenish Whit	https://www.ca		
Fritillaria	pyrenaica	S. Central France to N	Y+O	All		Checkerboard pattern + st	high	Dark purple	Yellowish green	http://www.friti		
Fritillaria	raddeana	NE. Iran to S. Turkme	O	All		Vein pattern	low	Green to Light p	Greenish white to purp	http://www.friti		
Fritillaria	recurva	S. Oregon to NW. Nev	Y	All		Checkerboard pattern	medium	Red	Yellow	https://www.fri		
Fritillaria	regelii	Central Asia	Y?	All?		Checkerboard pattern	N/A	Reddish-brown	Greenish-yellow	https://www.ina		
Fritillaria	reuteri	SE. Türkiye to W. Iran	O	All		Vein pattern + striped (sor	medium	Reddish-brown	Yellow	https://www.fri		
Fritillaria	rhodia	E. Aegean Islands (R	O	All		Vein pattern	medium	Green	Greenish-Yellowish	https://powo.sc		
Fritillaria	rhodocanaki	S. Greece (Idhra Islar	Y	All		Checkerboard pattern	high	Purple-brown	Greenish-Yellowish	https://www.fri	http://	
Fritillaria	rugillosa	Kirgizstan	O	All		Vein pattern + bull's eye	medium	Pink	Light pink	https://www.sn		
Fritillaria	ruthenica	E. Europe to Central A	Y	All		Checkerboard pattern	medium	Purple-brown	Yellowish green to Pur	https://powo.sc		

Fritillaria	sajanensis	Central Siberia	Y	All	Checkerboard pattern	N/A	Reddish-brown	Yellowish green	https://www.pl		
Fritillaria	selenica	Iran	O	All	Striped pattern	N/A	Purple-brown	Yellowish green	https://nsojour		
Fritillaria	serpenticola	Türkiye (Eskisehir, Ar	O	All	Vein pattern (low color co	low	Green	Greenish yellow	http://www.frit		
Fritillaria	sewerzowii	Central Asia	O	All	numerous brown to green	medium	Reddish-brown	Green to reddish-brow	https://www.fri	http://v	
Fritillaria	shehbazii	Iran	O	SI+PI	Striped pattern	N/A	Purple-brown	Yellowish green	https://nsojour		
Fritillaria	shikokiana	Japan (Shikoku. Cen	Y	All	Checkerboard pattern	low	Pink to purple b	White to pinkish white	http://www.frit	http://v	http://
Fritillaria	sibthorpiana	E. Aegean Islands (Si	O	All	Vein pattern	low	Greenish yellow	Yellow	http://www.frit		
Fritillaria	sichuanica	S. Qinghai to China (1	Y/O	SI+PI	"Tepals yellowish green, s	medium	Purple	Yellowish green	http://www.efl	https://	
Fritillaria	sinica	China (W. Sichuan)	Y/O+O	All?	striped, The flowers are si	N/A	Purple	Pale yellow	https://www.fri	http://e	https:
Fritillaria	skorpili	S. Bulgaria	N/A	N/A		N/A	N/A	N/A			
Fritillaria	sonnikovae	Krasnoyarsk	Y	All	These specimens have the	low	purplish yellow	Greenish yellow	https://www.m	https://	http://
Fritillaria	sororum	S. Türkiye	Y	All		medium	Purple	Glaucous	http://www.frit	https://	
Fritillaria	× spetsiotica	Greece	Y+O	All	Checkerboard-like pattern	N/A	Reddish-brown	Yellowish green	https://www.re		
Fritillaria	stenanthera	Central Asia	O	All	Vein pattern + proximal re	low	Green	Pinkish white	https://www.fri	http://v	
Fritillaria	straussii	SE. Türkiye to W. Iran	Y	All, sometimes l	This can have either green	medium	Reddish-brown	Green	https://www.fri	http://v	
Fritillaria	striata	California (C. Tulare (	O	All	Vein and sometimes spott	high	Purple	White	https://www.fri	https://	https:
Fritillaria	stribrnyi	S. Bulgaria to Türkiye	O	All	Striped pattern	low	Reddish-brown	Green	https://www.fri	http://v	
Fritillaria	taipaiensis	Central China	O	All	Spotted pattern sometime	medium	Reddish-brown	Yellowish green	https://web.arc	http://v	
Fritillaria	thunbergii	Central Asia (Tar Bag	Y	All	Checkerboard pattern	medium	Green or reddis	Greenish-Yellowish	https://powo.s	http://v	
Fritillaria	× tokushime	Japan (Shikoku)	Y	All	Checkerboard pattern	high	Reddish-brown	Reddish-white	http://www.frit		
Fritillaria	tortifolia	NW. Xinjiang	Y	SI+PI	Checkerboard or stained p	medium	Purple-brown	White	https://www.fri	http://v	
Fritillaria	tubaeformis	als SW. & S. Alps	Y	All	Checkerboard pattern	high	Purple to reddi	Yellowish Green	https://en.m.wi		
Fritillaria	tunievii	S. Transcaucasus	N				Purple-brown	Purple-Pink	https://cyberle		
Fritillaria	umitkaplanii	Türkiye	O	SI+PI	Vein pattern	Medium	Purple-brown	Purplish Yellow	https://nsojour	http://r	
Fritillaria	unibracteata	SE. Qinghai to China	Y	se+pe+SI+PI	Tepals blackish purple, tes	high	Purple-brown	Brownish yellow	http://www.efl	http://e	https:
Fritillaria	usuriensis	Primorye to N. Korea	Y	All	Checkerboard pattern	Medium	Purple-brown	Yellowish Green	http://www.frit		
Fritillaria	uva-vulpis	SE. Türkiye to NW. Ira	O	SI+PI	Vein pattern x Spot patter	Medium	Purple-brown	Yellowish-Greenish	http://www.frit		
Fritillaria	verticillata	S. Siberia to Japan	Y/O	SI+PI	Checkerboard-like to stain	high	Purple-brown	Yellowish-Greenish Wh	https://powo.s		
Fritillaria	viridea	California (San Benit	O	(SE+PE)+(SI+PI pedicel[1]	Vein pattern (inside) + spo	low	Purple-brown	Yellowish-Greenish Wh	https://www.ca		
Fritillaria	viridiflora	S. Türkiye (Kurd Da.)	N/A	N/A	N/A	N/A	N/A	N/A	https://powo.s		
Fritillaria	walujewii	Central Asia to Xinjia	Y/O	SI+PI	Tesselated to densely tes	low	Dark Red	White	http://www.frit		
Fritillaria	wendelboi	SSW. Türkiye	O	All	Veined pattern	low	Purple	Yellowish green	https://www.fri		
Fritillaria	whittallii	SW. Türkiye	Y	All (sometimes	Checkerboard-like pattern	medium	Purple-brown	Yellowish Green	http://www.frit	https://	
Fritillaria	yuminensis	NW. Xinjiang	O	All	Veined pattern	medium	Pink	Bluish-White	https://www.fri	https://	https:
Fritillaria	yuzhongensi	N. China	Y/O + O	All	Tesselated + sometimes v	N/A	Purple-brown	Yellowish Green			

Table 1: Color and pattern data for all accepted species of *Fritillaria*