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**ЭКОЛОГО-МОРФОЛОГИЧЕСКИЕ ОСОБЕННОСТИ
ПОДЗЕМНЫХ ОРГАНОВ У ПРЕДСТАВИТЕЛЕЙ
РОДА *FRITILLARIA* (*LILIACEAE*)**

M. V. BARANOVA

THE ECOLOGO-MORPHOLOGICAL PECULIARITIES OF THE UNDERGROUND ORGANS
OF THE REPRESENTATIVES OF THE GENUS *FRITILLARIA* (*LILIACEAE*)

ENGLISH TRANSLATION
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THE ECOLOGICAL-MORPHOLOGICAL PARTICULARITIES OF THE UNDERGROUND ORGANS OF REPRESENTATIVES OF THE GENUS *FRITILLARIA* (*LILIACEAE*)

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Foreword to the translation

In the last twenty years DNA techniques have fundamentally changed our understanding of plant evolution such that many plant classifications have had to be re-written and the value placed on flower part reduced as they have been shown to evolve rapidly. However, traditional morphological systematic classification has not been replaced by these new techniques but enhanced as the true systematic value of a plants physical characteristic can be better understood.

The Russian botanist Marina Baranova made meticulous observations of the underground structure of the bulbs of *Liliaceae* with particular emphasis on *Lilium*. In 1981 she published a detailed account of the ontogeny and annual bulb renewal of *Fritillaria* and made important recommendation on the taxonomy of the genus.

An account of the phylogenetic relationships within *Fritillaria* was published by Nina Rønsted et al. in 2005 in which the close relationship of *F. imperialis*, *F. pallidiflora*, *F. persica* (*F. libanotica*) and *F. sewerzowii* was confirmed. Other work at Kew by Ilia Leitch on genome size fits closely with the findings of Baranova.

The following is an English translation of Baranova's 1981 paper. Images of the underground structures of *Fritillaria* can be found at www.fritillariaicones.com

Introduction

The structure of the underground organs and the particularities of their formation in ontogeny are studied. Within the genus *Fritillaria* are differentiated three basic types of bulb each with its own distinctive development and structure. The significant features of each type of bulb are determined and their significance for the taxonomy of the genus is demonstrated. A correlation between the types of structure of the underground organs and ecological conditions

is established. Among the representatives of the genus are differentiated bulbs of mesomorphic and xeromorphic structure. It is made clear that this genus and the closest genus *Lilium* have similar features of adaptation of the underground organs to similar conditions of growth.

The study of living forms in concrete taxonomical groups has a many-sided significance; in particular it enables one to make a more well-founded judgement regarding the ways and means of transformation of living forms in the course of

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evolution against the background of changes over time in ecological conditions. It shows that a number of features of the living forms have a high taxonomical value and can be used for systematic classification. All this is particularly relevant to the taxonomical groupings of bulbous plants, which have not been fully enough understood in this aspect.

The bulb is the single constant organ throughout the calendar year of bulbous plants. The features of its structure are constant within a species and often serve to characterise even larger taxonomical units. They may play a large role in the diagnostic of bulbous plants. This is confirmed by a series of works in which the features of the structure of the bulb are used for taxonomy (Chouard, 1931; Vassilievskaya, 1939; Baranova, 1962, 1965; Zahariadi, 1962; Artyushenko, 1963, 1970; Mordak, 1970; Davliyanidze, 1976). The number of such works is still not very great owing to a lack of data on the structure and formation of bulbs in various systematic groups.

Of particular interest is the connection between the structure of plants with bulbs with ecological conditions, including climate, soil, light, moisture, photosynthesis factor etc. Although this connection is very complex, it is possible to trace the ways in which the structure of the plants has been established in the course of evolution on the basis of the influence of a few environmental factors, such as temperature and moisture.

The object of the present study is the genus *Fritillaria* L.,¹ all types of which, and there are

¹ We used a wide definitions of the genus which included the sub-genera. *Fritillaria*, *Petilium* (L.) Baker, *Theresia* (C. Koch) Baker, *Rhinopetalum* (Fisch.) Baker, *Korolkowia* (Regal) Baker, *Liliorhiza* (Kellogg) Baker (Baker, 1874; Turrill, 1948; Beck, 1953; Rix, 1977).

nearly 100, are bulbous plants growing in temperate and subtropical zones of the northern hemisphere. Within the bounds of the genus, the bulb structures are quite varied. Many researchers have paid attention to this, emphasizing the particular significance of the bulb structure for the taxonomy of the genus *Fritillaria* (Stapf 1925; Beetle, 1944; Turrill 1948, 1959, 1952; Beck 1948, 1953; MacFarlane 1975). W. Turrill wrote (1952: 119) "In the family Liliaceae as a whole and in particular in the genus *Fritillaria* the underground organs have an exceptionally important significance both for the correct determination of species and for scientific generic classification." Nonetheless right up until the present time only a few species of the genus *Fritillaria* have been submitted to morphological study (Beck 1948; Bochantseva, 1963; Popova, 1965; V. Skripchinskii, Vl. Skripchinskii, 1965; Golovkin, 1967; Dvorakovskaya, 1973; Gomozova, 1974).

Before us stood the task of studying the structure of the shoots of various representatives of the genus *Fritillaria* and their formation in ontogeny; of distinguishing the features of the structure of the bulbs which could be used as diagnostic for generic classification; of outlining the course of transformation of the underground organs in the course of taxonomical evolution.

The work was based on the material in the collection of the family Liliaceae held in the Botanical Institute in the name of V.L. Komarova AN USSR. The plants in the collection were gathered from the wild (the Caucasus, Middle Asia, the Far East) or grown from seeds, many of which were collected or received from the natural habitats of the species.

The structure and formation of the shoots in species of the genus *Fritillaria*

All species of the genus *Fritillaria* are sympodially branching semi-rosulate plants. The bulb of a Fritillary is the rosulate part of the monocarpic shoot with shortened internodes and lower leaves metamorphosed into scales. The underground part of the shoot has more or less elongated internodes. In this way the monocarpic shoot of specimens of the genus *Fritillaria* – their basic structural singularity – consists of two parts: the underground (rosette) part with the lower leaves storage (scales) (fig. 1, II, a²) and the above-ground (elongated) part, consisting of the assimilating leaves and flowers (fig. 1, II, a¹). A system of shortened parts of the shoots of a single year or a number of years (orders) makes up the bulb of the fritillary. Its structure is determined not only by the number of shoots, their age and the character of their branching, but also by the type and number of scales on their axes. Fritillary bulbs renew themselves every year and do not have the shoots of past years in their structure.

The shoots of the specimens of the genus *Fritillaria* studied here branch sympodially at the expense of the development of lateral (side) buds, located in the axil of the upper storage leaf of the bulb.

I General view

II Schematic view of plant's structure

- a Monocarpic shoot (shoot of order I)
- a¹ Above-ground part of monocarpic shoot (flower bearing shoot)
- a² Underground part of monocarpic shoot (bulb)
- 6 Next year's shoot (shoot of order II)
- 1 the storage scales of the bulb
- 2 papery scales
- 3 The leaves of the flower bearing shoot
- 4 Supplementary roots
- 5 Flower

It is quite a complex matter to define the type of branching in bulbous plants, since the nodes in the bulb are closely packed and it is difficult to establish the arrangement of the buds of renewal. In some cases the uppermost bud is displaced to one side by the peduncle and then occupies the lateral position, whilst the lateral bud, as it grows, can be displaced towards the top. In such cases it is essential to pay attention to the position of the first scale of the bud in relation to the peduncle. In the lateral bud, this must be located on the spinal (adaxial) side in relation to the peduncle (Artyushenko, 1970). This is indeed the location occupied by the first scale of the bud of renewal in species of the genus *Fritillaria*.

We studied specimens of the species with bulbs of various structures. We investigated the formation of the plants in ontogeny and studied the annual cycle, i.e. the development of mature plants over the course of a calendar year. As a result of this study, all species were split into three groups, each of which is characterised by a particular type of bulb structure and the particularities of its formation.

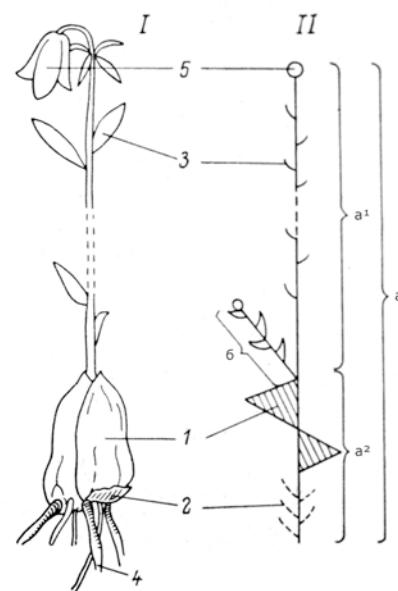


Figure 1: *Fritillaria pallidiflora* during the flowering period

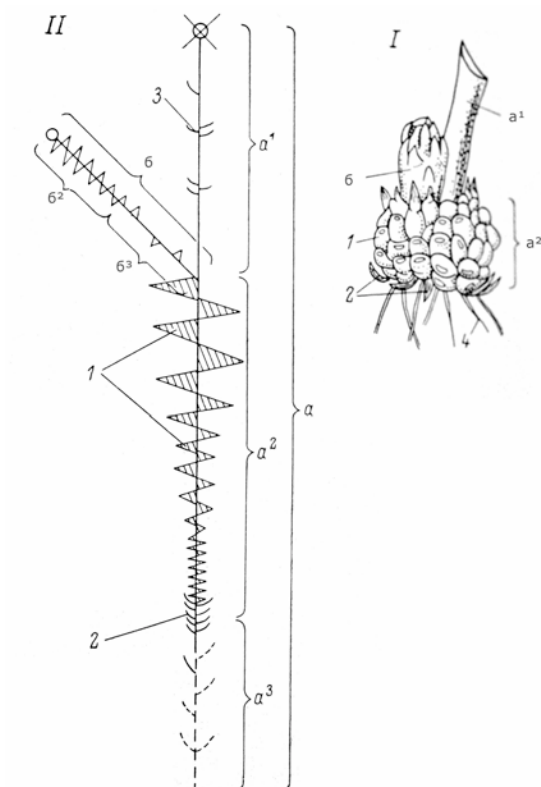


Figure 2: *Fritillaria camshatchensis* after completion of flowering (June)
 a³ – withered stolon of the monocarpic shoot of the first order I, 6² - shortened part of the monocarpic shoot of order II, 6³ – stolon of the monocarpic shoot of order II. The remaining items are as figure 1.

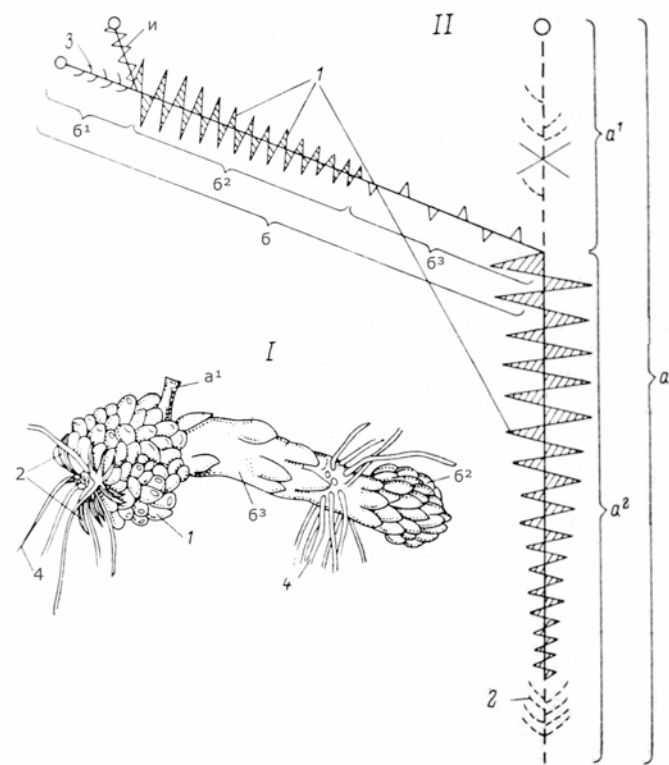


Figure 3 *Fritillaria camshatchensis* after the end of vegetation (September).
 6¹ – flower-bearing shoot (above-ground part of the shoot of order II). и – Shoot of the next, second year (also embryo of the shoot of order III). The remaining items are as for figure 1.

First Type The bulb is tiled, formed on a stolon and made up of many (up to 50) small, narrow, loosely-packed scales. *Fritillaria camshatchensis* (L.) Ker-Gawl., *F. maximowiczii* Freyn, *F. dagana* Turcz ex Trauv all have bulbs like these.

We can see the particular structure of the shoots with bulbs of the first type in the example of *Fritillaria camshatchensis*, after following through the annual cycle of its development and formation from seed.

The flower-bearing shoot of *Fritillaria camshatchensis* reaches 30-50 cm in height and bears 10-20 widely lanceolate leaves, gathered into 2-4 "whorls". The flowers are of a wide bell shape and dark brown. The bulb is white with many scales. The plant flowers in May.

At the time of flowering of the plant a bud can be seen in the bulb at the base of the flower-bearing shoot (above-ground shoot of order I) amongst the upper storage scales. This is next year's shoot (shoot of order II). At this time, the process of laying down new embryos is actively going on within the bud. The capacity of the bud is 15-20 embryos. Immediately following the completion of flowering, the internodes of the first 6-10 embryos of the scales of the bud begin to grow, forming the stolon, which carries the bud outside the boundaries of the mother bulb (fig 2, 6). From this time the monocarpic shoot (bud) forms outside it. The further development of next year's shoot, i.e. of the young replacement bulb, goes on at the top of the stolon (fig 3, 6²).

Towards the end of June, after the completion of vegetation, all the vegetative organs of next year's shoot (the shoot of order II) are laid down in the bud. However, it is still

difficult to determine the borderline between the shortened underground and elongated above-ground parts of the future shoot; there is no distinction between the embryos of the lower storage leaves and the future assimilating leaves. This borderline only becomes noticeable during the period of formation of the flowers at the tip of the shoot in August, when the lower internodal future flower-bearing shoot begins to stretch itself out. In this period, it is possible to see the number of embryonic metamers of the shortened part of the shoot is greater than the number of metamers of the elongated part. At the same time, at the base of next year's flower-bearing shoot, in the shelter of its topmost storage scale, is found a new bud – the embryo of the shoot of the order III (fig. 3, II, и), while at the base of the young bulb on the intersection with the stolon, a ring of fine supplementary roots is forming (fig. 3, I, 4). *Fritillaria camshatchensis* does not have contractile roots.

The full differentiation of flowers on the shoot of order II is completed in September-October, and with this concludes the formation within the bud of the monocarpic shoot, which takes about a year. Around this time in the new bud (the shoot of order III) are laid down up to 15 embryonic lower leaves. In the autumn, the underground organ of *Fritillaria camshatchensis* presents as two bulbs of different ages – the mother and daughter bulb, joined together by the stolon (fig. 3, I).

In the spring of the following year, around the start of vegetation, the mother bulb and the stolon die. The bulb of *Fritillaria camshatchensis* does not conserve the shoots of previous years in its structure. Only the daughter bulb remains. The lower leaves which make up the bulb are still fine. Only at

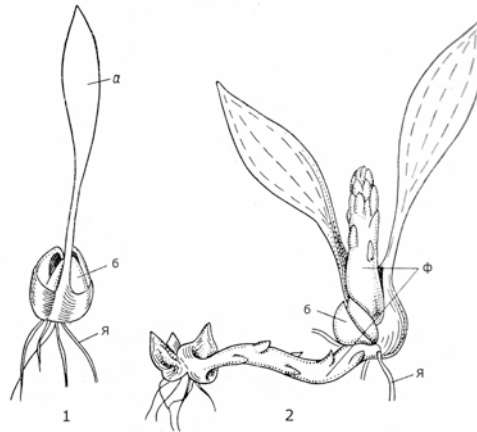


Figure 4: seedlings of *Fritillaria camschatchensis*

1 – A two year-old seedling 2 – a four-year old seedling ; a- first leaf; б – lower leaves; φ – the young stolon; Я - the supplementary roots

the start of vegetation does the process of collecting up a supply of nutrients become activated and even then not in all the lower leaves. At the same time only the bases of the lower leaves grows strongly, turning into scales, and the tips, corresponding to the leaf blades, soon dry out and fall away, leaving a scar on top. The lower leaves of the bulb (scales) are metamorphosed rosulate leaves, in which the vagina grows strongly, becoming fatter, while the leaf blades reduce in size. The origins of the lower and the assimilating leaves are the same. Their laying down and development in the early stages is similar. Only once the leaf primordia reach 1-2 mm does their differentiation proceed. The activation of cell division in the base of the primordial – in the zone of the future vagina – leads to the formation of the lower leaf. At the same time, the leaf blade in such an embryo either develops weakly or does not develop at all. If active cell division takes place in the upper part of the primordial, then an assimilating leaf is formed (Denne, 1960). The reasons for the localisation of active cell division in one or other part of the primordia are not yet clear.

In *Fritillaria camshatchensis* there are small white scales, similar in appearance to grains of rice loosely distributed around the bottom

of the bulb. These will separate from the bulb at a light touch. They serve for vegetative reproduction.

We will trace the formation of the plant of *Fritillaria camshatchensis* from seed.

The germination of seeds of this type is above-ground, accompanied by the development of a green lanceolate cotyledon and 1-2 lower leaves, in which is laid down the whole supply of nutrients of the one year old bulb. In this way, on the first year's shoot of the plant scale-like leaves follow the green ones. The vagina of the cotyledon grows weakly and at the end of the first year of vegetation it dies. In the second year the second year shoot develops, continuing growth along the main axis. It carries one assimilating leaf and two lower leaves (fig 4, 1). Nutrients are laid down both in the vagina of the green leaf and in the lower leaves. In the third/fourth year the main shoot of the seedling continues to grow, but the lower part of the annual growth has the form of a stolon (fig 4, 2). The stolon in formation takes the form of a continuation of the main axis. On the tip of the stolon on closely packed nodes are distributed assimilating leaves with hundreds of vaginum and lower leaves, which together form the bulb.

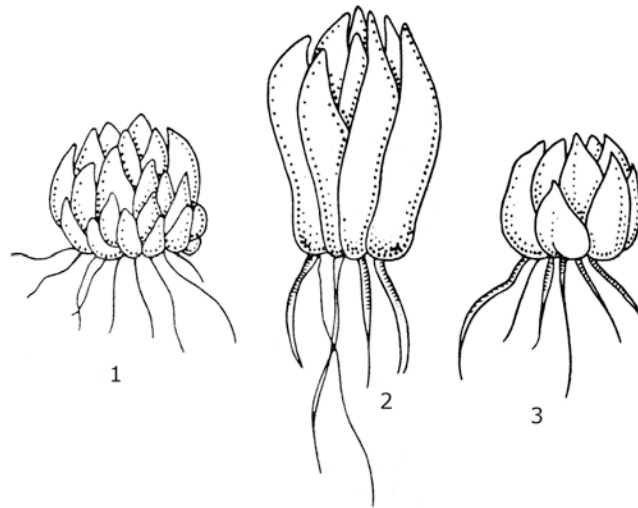


Figure 5: bulbs of North American species of the genus *Fritillaria*

1. - *F. lanceolata*; 2. - *F. agrestis* ; 3. - *F. biflora*

With the appearance of the stolon the rosulate, monopodially growing annual shoot, characteristic of the one and two-year old seedling is transformed into a unique semi-rosulate shoot which continues to grow monopodially. In this case the stolon represents the non-rosulate part of the annual shoot and the young bulb at its tip is the rosulate part.

In the next years, the number of lower leaves in the annual shoot increases. Some of these are located on the stolon. However, the lower leaves of the stolon do not collect nutrients and wither together with the stolon at the end of vegetation. Only the lower leaves located on the top of the stolon and the vaginum of the assimilating leaves become storage leaves.

The first elongated underground annual shoot appears in *Fritillaria camshatchensis* in the fifth to seventh year. It bears only leaves. Once it has died the growth pattern of the shoot system switches from monopodial to sympodial. Thus the “culmination” in *Fritillaria camshatchensis* is marked not by a

change in the structure of the shoot, but the appearance of the first underground shoot and passes into a pregenerative period. The plant flowers in the sixth to eighth year. The first flowers appear on the underground shoot of order II or III.

Thus for the stoloniferous species the following particularities of structure and formation of shoots are characteristic: 1. the monocarpic shoot of the mature plant forms outside the mother bulb; it is formed from the underground shortened part (the bulb), from the underground elongated part (stolon) and the above-ground elongated part (flower-bearing shoot). The duration of the life of each of these parts of the shoot is not the same: the flower-bearing (above ground) shoot and the stolon live for one year, the shortened part up to 2.5 years. 2. The number of metamers on the above ground part of the shoot is greater than the number of metamers of the flower-bearing shoot. 3. There are no contractile roots among the supplementary roots. The bulb is anchored by

the stolon – the underground plagiotropic shoot. Its length is directed so that the supplying bulb is set at the optimal depth. 4. The annual shoot of the first or second year seedling is rosulate, growing monopodially. The appearance of the stolon converts the structure of the shoot into semi-rosulate, without changing the type of its growth. In juvenile plants nutrients are laid down in the lower leaves and in the vaginum of the assimilating leaves (except the lower leaves of the stolon). 5. The pregenerative period lasts 5-7 years. 6. The switch from monopodial growth to sympodial growth happens in the pregenerative period, after the formation of the first above-ground shoot.

Stoloniferous species of the genus *Fritillaria* have a unique structure of the underground organs. One of them - *Fritillaria camshatchensis*- occupies a wide habitat. It is the only species of the genus which can be found both in North America (the west coast of Alaska, Canada and the USA down to the river Columbus) and in Asia (Kamchatka, Sakhalin Island, Hokkaido, Honshu, the Aleutian and Kurile Islands, the coastal regions). It grows in woods, in boggy places, amongst dense grass and bushes. In the moist parts of the deciduous and birch forests of Eastern Siberia and the Far East also grow two other stoloniferous species, *F. dagana* and *F. maximowiczii*. Stoloniferous, many-scaled bulbs lie almost at the surface of the soil – at a depth of not more than 4 cm. As a result of this, if washed away, the bulb can only anchor itself again in the soil with the help of the stolon; it has no contractile roots.

Stolon-forming species and particularly *F. camshatchensis* are distinguished by the high intensity of vegetative reproduction based on

loosely distributed scales of the bulb. The scales easily detach themselves from the bulb and take root, each representing a separate organ of vegetative reproduction. This is why it is not uncommon in writings to find an incorrect reference to descendant-bulbs. This type of reproduction allows the species to take over a large territory, even though reproduction by seed is almost entirely suppressed in the plants.

Type 2

Tiled bulbs with no stolon, consisting of a few (up to 20) rounded or lanceolate scales with narrow bases, more or less loosely distributed at the bottom. North American species of the genus have bulbs of this type (fig 5).

Among the North American species of the genus *Fritillaria* can be distinguished two groups according to the number and size of the scales in the bulb. In the species of the first group there are more than 10 narrow scales in the bulb, up to 0.5 cm long; the outer scales are often rounded and fine (*F. lanceolata* Pursh, *F. phacantha* Eastwood, *F. recurva* Benth. and others). The species of the second group have 5-10 lanceolate scales up to 1 cm in length, they have no fine scales (*F. agrestis*, Greene, *F. biflora* Lindl., *F. liliacea* Lindl, *F. pluiflora* Torr. ex Benth.).

The structure of the plant can be seen in *F. biflora*. The height of the plant is 25-45 cm. The flower-bearing shoot carries 3-7 closely-spaced leaves and 2-4 dark purple, bell-shaped flowers. The bulb is up to 2.5 cm in diameter and consists of 6-9 lanceolate scales. The species grows on open grassy slopes of the Californian hills. In its native land the

plants start the vegetative period after the autumn rains, in October-November, and they flower in February-March.

In the flowering period, at the base of the flower-bearing shoot (the shoot of order I) there is visible the bud of renewal (the shoot of order II) which contains all or almost all of the lower leaves of next year's shoot. The formation of the shoot happens within the mother bulb and is completed in the summer months. About 20-27 embryos form within the bud of renewal. 15-18 of these are lower leaves and the rest are the future assimilating leaves of the underground shoot. In *F. biflora* the number of lower leaves contained in the bud is usually greater than the number of assimilating leaves. However, not all of the lower leaves become storage scales: only the inner (last) lower leaves of the shoot grow and become storage scales (6-9 lower leaves in *F. biflora*) whilst the outer (first) lower leaves wither and die together with the part of the bottom of the bulb where they are situated. This feature is also a characteristic of stoloniferous species. At the time of the completion of the formation of the shoot of order II there is laid down a new bud – the shoot of order III. In the autumn, at the start of the plant's vegetative period, numerous supplementary roots appear with a noticeable zone of adherence at the base.

Limitations on available material for the North American species of *Fritillaria* prevented the study of a larger number of species and a more detailed investigation into the annual cycle of development of the plants. However, the data which was gathered revealed a series of particularities of their structure in comparison with the stoloniferous species.

These particularities appeared even more marked when studying the development of the plants from seed, which we did with the species *F. biflora*, *F. agrestis*, *F. roderickii* Knight, *F. lanceolata* Pursh, *F. liliacea*, *F. Pluriflora*. The seeds of the North American species, like other species of the genus, germinate above-ground.

A distinction from the Eurasian species appears in the very first year and consists of the fact that the function of supply in the North American species is fulfilled only by the assimilating organs (the cotyledon and leaves); the stock of nutrients is laid down only in the base of the cotyledon or in the bases of the assimilating leaves and their green blades wither and die. The lower leaves, which form from the second year, remain papery and wither at the end of the vegetation of the seedlings. The germinating and juvenile plants of the American fritillaries have a type of "tuber", made up of the growing bases of the cotyledon or leaves (fig 6). The scar from the fallen-away green blade can be seen on their surfaces, while to the side, at the base, is located the topmost bud of renewal. As the plant gets older the number of lower leaves laid down gets larger, but only the bases of the assimilating leaves fulfil the roles of storage leaves. Only after the formation of the first above-ground shoot do the inner lower leaves take on the role of nutrient supply and the outside ones remain thin and papery. During the process of gathering nutrients only the bases of the lower leaves grow and the papery tips wither.

Up until the appearance of the first overground shoot the annual shoot of the seedlings of North American species have a monopodially growing rosulate structure.

With the appearance of the first overground shoot, the structure of the shoot changes to semi-rosulate. After this, the further growth of the shoot is realised via the axillary bud, located on the base of the aboveground shoot, i.e. it proceeds sympodially. The first above-ground shoot appears in the 4th to 6th year and does not bear flowers. It forms on the above-ground shoot of order II or III. Thus the transformation is not connected with the switch of the plant into flowering mode and takes place in the pregenerative period. The first flowering in North American species occurs usually in the 5th to 7th year after the seed is sown.

In the formation of the bulbs the fritillaries adhere closely to their rosulate nature. They take the form of a metamorphosed rosette, whose scales are nothing other than metamorphosed rosulate leaves. In the bulbs of the north American species and the species of the first type all the traces of origination from the rosette are preserved: they consist of small, numerous scales, narrow with papery tips, spread freely around the bottom of the bulb.

And thus the representatives of the North American species of the genus, having bulbs of the second type, are characterised by the following particularities: 1. The monocarpic shoot of the mature plant forms inside the

mother bulb. It consists of the underground shortened part (the bulb) and the above-ground elongated part (flower-bearing shoot). The length of life of the peduncle is about one year and of the bulb, about two years. 2. The number of metamers of the underground part exceeds the number of metamers of the flower-bearing shoot (usually in the species of the first group) or is equal to these (usually in species of the second group). 3. The supplementary roots have a clearly defined zone of adherence. 4. The annual shoot of juvenile plants is rosulate with monopodial growth; the functions of the leaves of the annual shoot are distinct: the store of nutrients is laid down only in the bases of the assimilating leaves, and the lower leaves remain flat and fulfil the function of protecting the bud of renewal. 5. The pregenerative period occurs in plants in the 4th to 6th year. 6. The switch from monopodial to sympodial growth occurs after the switch of the structure of the annual shoot in the pregenerative period.

Species of the genus *Fritillaria* with bulbs of the second type grow in North America, in the west of the USA, in the main in the state of California, in regions with a temperate maritime type of climate. The habitats of the North American species are quite varied, despite the relatively small area occupied by the state of California and the high concentration there (17 species) of fritillaries.

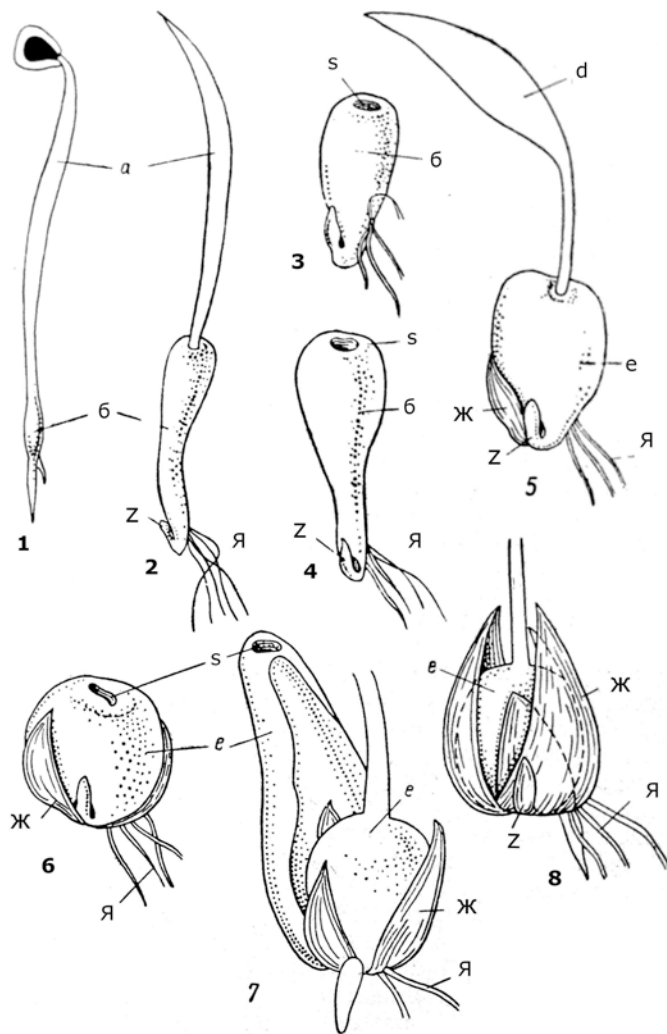


Figure 6 – Seedlings of North American species of the genus *Fritillaria*.

- 1 Adolescent *F. glauca*, 2 – one year old seedling of *F. agrestis*, 3 – one year old seedling of *F. glauca*,
 4 - one year old seedling of *F. liliacea*, two year old seedling of *F. liliacea*,
 5 – two year old seedling of *F. liliacea* 6- two year old seedling of *F. roderickii*
 7 – three year old seedling of *F. biflora* 8- three year old seedling of *F. agrestis*

a-the leaf-blade of the cotyledon; б- vagina of the cotyledon s – scar where the leaf blade of the cotyledon (leaf) falls away;
 z – bud of renewal; d – leaf blade ; e- vagina of the leaf, ж – lower leaves; Я – supplementary roots

Some of them can be found in forests, in the shade of the trees, on crumbly, waterlogged soil. Species growing in these conditions are of the first group with bulbs of the second type – *F. multiflora* Kellogg, *F. mutica* Lindl., *F. lanceolata*, *F. phaenthera*, *F. brandegei* Eastwood and others. Their bulbs settle in the soil at a depth of 8-10cm. The anchoring

of the bulbs occurs with help from the supplementary roots, at whose bases there is a zone of adherence. The outer small scales of the bulbs serve as organs of vegetative reproduction. The development of the plants from such scales proceeds slowly and they do not flower for several years. Quite often in nature it is possible to see a whole colony of

plants among which only a very few individuals are flowering (Macfarlane, 1975.) The species of this group are noted for a high rate of sterility. In a population of *F. phaeanthera* Eastwood, for example, over 60% of flowers had imperfectly -formed pistils and 30% had sterile pollen (Beetle, 1947).

The native habitats of the North American species are of notably small area, closely connected with areas where the remains of tertiary forests can be found. This applies both to the woodland North American species and the stoloniferous species growing in Asia in similarly damp conditions. A similar type of structure of the bulb and of the whole plant is linked to damp growing conditions and evidently is a more ancient type within the genus (bulbs of mesomorphic structure). It is indeed in the bulbs of mesomorphic structure that the traces of originating from a rosette are most apparent.

The species of the second type of the genus *Fritillaria* are found in drier habitats; on open plains, in meadows and scree slopes on clay or gravel soils. The species native to these habitats – *F. biflora*, *F. agrestis*, *F. liliacea*, *F. pluriflora* etc – have more thick-set bulbs with quite large lanceolate scales, the number of which does not exceed 7-10. The traces of rosulateness are not as marked in these as in species of the first group. The open and drier conditions of growth allow for the formation of broader and larger scales, guaranteeing better protection for the bud of renewal. The development of contractile roots leads to the attachment of the bulb in the soil at a

sufficient depth (15-25 cm) to prevent it from drying out in a long hot summer. The bulbs of meadow species do not have on the outside small, lightly attached scales and have only a weak rate of vegetative reproduction. In the given conditions these scales could not serve as organs of vegetative reproduction because of the depth at which the bulb settles in the soil. However, usually all these plants fruit abundantly. It is not without interest to remark here upon the variety of pollinators for North American meadow species of fritillary – from flies to hummingbirds (Macfarlane, 1975).

Third type The bulbs consist of 1-3(4) very fleshy, broad scales. Within this type two groups can be distinguished.

First group: Species in which the bulbs consist of 2-3 fleshy scales which have not fused, or have barely fused, above the base. Such “semi-tunicate” bulbs are characteristic for the majority of species of the the genus (*F. meleagris* L., *F. caucasia* Adam, *F. lutea* Mill., *F. crassifolia* Boiss. et Huet., *F. karelini* Baker, *F. pallidiflora* Schrenk et al.) (Fig 7, I).

Second Group: Species in which the bulbs consist of 1-4 fleshy fully grown or half-grown scales – “tunicate” bulbs (*F. raddeana* Regel, *F. imperialis* L., *F. sewerzowii* Regel) (Fig 7, II, III).

In the first group we studied the structure of the bulb based on *F. pallidiflora* (Fig 1). Its flower-bearing shoot reaches up to 40 cm and sometimes 70 cm and carries 20-30 bluish-grey broad-lanceolate leaves and 1-5 pendant greenish-yellow flowers. The plant flowers in May.

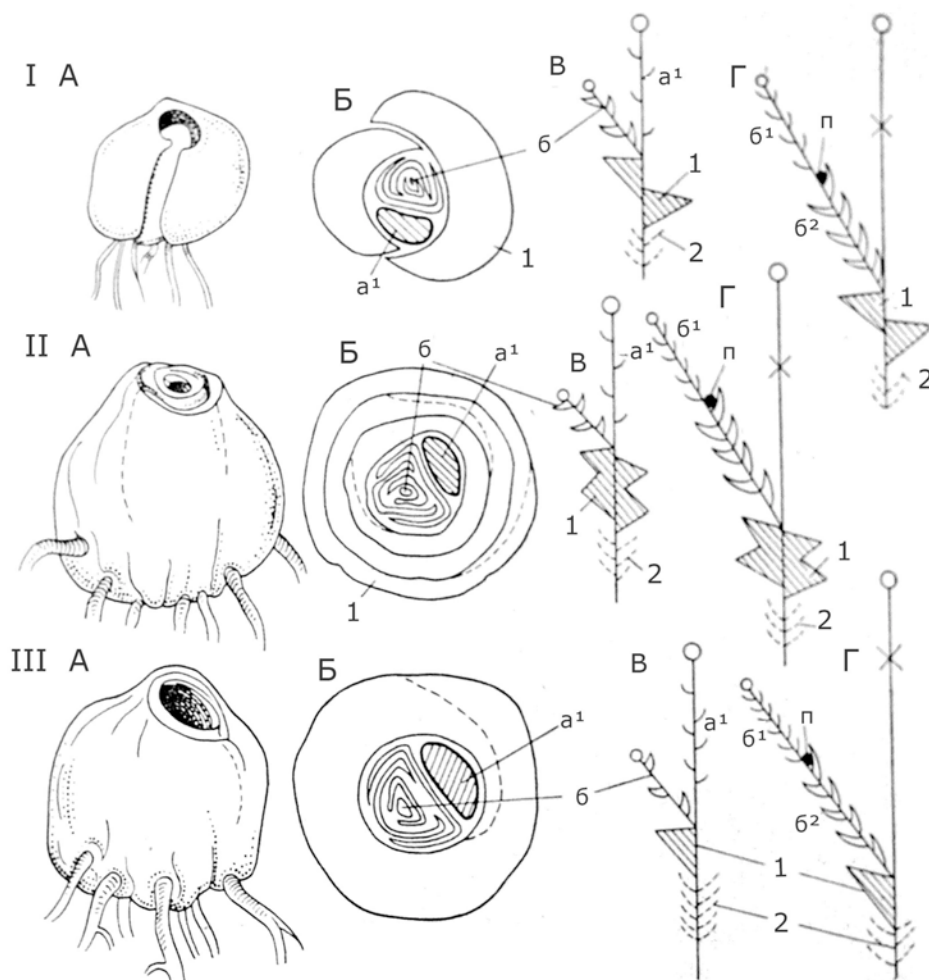


Figure 7 – species of the genus *Fritillaria* with bulbs of the third type

I - *F. meleagris*; II – *F. imperialis*; III – *F. sewerzowii*; A- general view of the bulb; Б – section across the bulb (May); B - Diagram of the structure of the plant in the period of vegetation (May); Γ – scheme of the structure of the plant after vegetation (September).

The remaining labels are as for figures 1-3.

The bulb of the flowering plant reaches 3 cm in diameter and consists of 2-3 very fleshy broad separate scales, closely wrapped around one another and growing into each other at the base. (Fig 7, I). At the time of flowering of the plant, a bud is visible at the base of the flower bearing shoot (shoot of order I); this is the embryo of next year's shoot (the shoot of order II), in which is laid down 3-5 embryo lower leaves. Towards the end of vegetation, at the beginning of July, next year's shoot reaches 2.5 cm and carries up to 10 embryo leaves; in another month

there are already 20-24 of these. The first 5-9 embryo leaves are the lower leaves, the rest are the future assimilating leaves of the flower-bearing part of the shoot. In August, in the period of formation of the flowers, a new bud forms at the base of the shoot of second order; this is the shoot of order III. Before the onset of the winter months 2-3 embryo leaves will form in this bud. Thus the formation of the monocarpic shoot for next year (shoot of order II) is completed in September. Throughout the period of its formation the shoot remains in the bud inside the bulb.

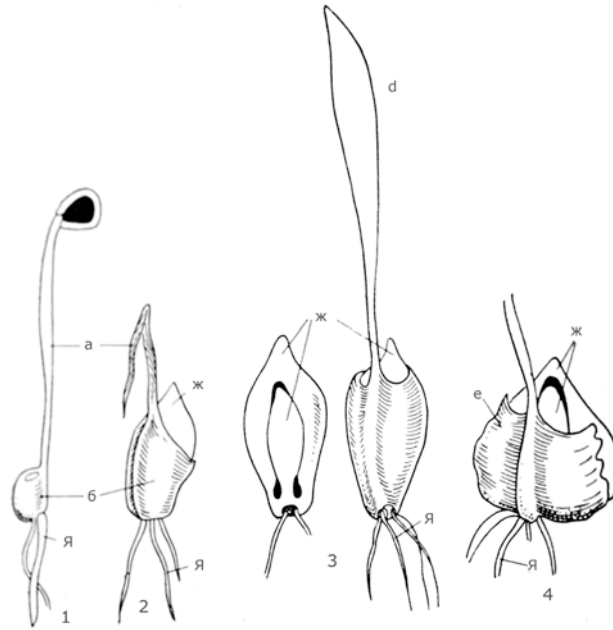


Figure 8 – seedlings of *Fritillaria pallidiflora*

1.- adolescent; 2- bulb of a one-year-old seedling; 3- two year old seedling; 4 – three year old seedling. Remaining labels are as for figure 6.

In the spring, at the start of vegetation, the laying down of nutrients begins in the lower leaves. Out of the 5-9 already-formed lower leaves only the 2-3 inner (last) ones become storage leaves, the outer ones remain papery and soon dry out, together with the bottom of the bulb on which they are located. As a result at the end of vegetation the bulb of *F. pallidiflora* consists of 2-3 very fleshy, broad scales.

The study of the development of plants of *F. pallidiflora* from seed allows us to determine their particularities in the early stages of life. The seeds of *F. pallidiflora* germinate above ground. The green, lanceolate, flat cotyledon represents the only organ of assimilation of the seedling in the first year of life (fig 8, 1). Apart from the cotyledon, the seedling forms a lower leaf, in which is laid down the entire stock of nutrients. The cotyledon has no storage function and dies at the end of vegetation.

In the second year the seedling forms an assimilating leaf and two lower leaves. The entire store of nutrients is concentrated in the latter, while the assimilating leaf withers at the end of vegetation. The size of the bulb doubles in comparison with the first year and reaches 7-8 mm in diameter. During its first years, the rosulate annual shoot grows monopodially.

In the third year it is usual for the first above-ground shoot to appear, consisting only of leaves (3-6 leaves). As in species of the second type, the appearance of the above-ground shoot signifies the switch in the structure of the above-ground shoot from rosulate to semi-rosulate. The change from monopodial growth to sympodial growth occurs in the period of formation of the first above-ground shoot. The plant flowers in the fourth year. The flowers usually form when the number of leaves on the above-ground shoot reaches a specific minimum (no fewer than 8 leaves in the case of *F. pallidiflora*).

In the first year of development the root system consists of a main root, which within 2-3 months becomes supplementary. In the second and subsequent years thick roots with a developed zone of adherence appear amongst the fine supplementary roots; these are the contractile roots. During the course of a year it is possible to observe two periods of root formation – in the autumn and in the winter. The length of life of a root is a year or more.

In the second group of the third type are included species with tunicate bulbs. Their development was followed based on *F. imperialis* (*F. eduardii* Regel) and *F. sewerzowii*. *F. imperialis* grows in Central Asia and Afghanistan in the mountains on scree slopes at heights of up to 2300m above sea level; its bulbs settle in the ground to a depth of up to 25 cm. The flower-bearing shoot reaches a height of 40-60cm. It is thickly-leaved and carries 3-7 bright-orangey or lemon-yellow pendulous flowers. The bulb is 4-6 cm in diameter and consists of 2-4 half grown-together scales. The plant flowers at the end of April-May. During the period of flowering a bud is visible at the centre of the bulb by the base of the flower-bearing shoot; this is next year's shoot (shoot of order II) with 4-6 embryo lower leaves. Towards the beginning of September, as with most species of the genus, the formation of next year's monocarpic shoot takes place within the bud (fig 7, II). It is possible to distinguish in this shoot the future flower-bearing shoot part and the shortened underground part with the lower leaves. 5-9 lower leaves form in the bud. They are not fused together and wrap themselves freely around each other.

During the course of the autumn months the growth of each part of the shoot proceeds unevenly. Out of the 5-9 established lower leaves the first 3-5 (the outer ones) remain fine, their size barely increases, but in

comparison in the spring the size of the last (inner) 2-4 lower leaves noticeably increases. They grow fatter, close up at the edges and fuse together at the base, sometimes up to $\frac{1}{3}$ or $\frac{1}{2}$ of the height of the bulb, so that the lower half forms into a single scale. The upper fleshy part of the scales and their papery tips are usually not fused together. In the spring, at the start of vegetation, the papery tips of the bulb surround the base of the flower-bearing shoot and sometimes turn green. They protect the young shoot from mechanical damage at the beginning of its growth. Towards the end of vegetation, a dividing layer forms between the papery tip and the fleshy base of the scales, similar to that observable in an autumn leaf on the branch, the papery tips of the scales wither and fall leaving a scar at the top of the bulb. Towards the end of vegetation the bulb reaches its maximum weight and size and consists of 2-3(4) scales fused at their base. The lower leaves which were the first to be formed on the shoot do not grow further and soon wither.

The root system of *F. Imperialis* consists of numerous supplementary roots, amongst which can be distinguished vigorous attaching roots. The supplementary roots of the young replacement bulb begin their growth at the end of the summer/start of the autumn. They grow through the outer old scales of the mother bulb, creating the impression of roots appearing directly out of the scales of the bulb.

Another representative of the second group is *F. sewerzowii*, whose bulb is made up of a single, fused scale. *F. sewerzowii* grows in the foothills of mountains on stony or clay slopes, in the forests of the western regions of the Tian-Shan mountains and in the northern regions of the Pamira-Alaya mountains. The

bulbs reach 4-7 cm in diameter. The height of the flower-bearing shoot is 40-60 cm; it carries up to 30 leaves and 15-20 yellowish-brown bell-shaped flowers.

The cycle of development of *F. sewerzowii* is in many ways the same as that of *F. imperialis*. The differences are that out of 5-9 lower leaves laid down in the bud usually only one, the last, grows on and becomes a storage scale. The base of the scale is broad and almost completely surrounds the flower-bearing shoot. Its edges overlap each other and fuse together as they grow. As a result a tunicate bulb develops (fig7, III). In *F. sewerzowii*, instances have been observed when not just one but two or three of the scales grow on (Lapteva, 1972). These fuse with each other and also form a tunicate bulb, similar in its structure to that of a bulb of *F. imperialis*.

In this way the process of formation of tunicate and semi-tunicate bulbs of the third type is similar in species of the genus *Fritillaria*. The same may be said also about the particularities of the ontogenetic development of bulbous plants of the third type. The basic particularities of their development from seeds is similar to that of *F. pallidiflora*.

In tunicate and semi-tunicate bulbs the metamorphosis of the rosette is so advanced that the traces of the rosette have almost disappeared. However in the early stages of ontogenesis their annual shoots have a rosulate structure.

It is clearly possible to associate species with bulbs of the third type with *F. libanotica* (Boiss.) Baker, which grows in the mountainous regions of the Lebanon on dry, stony soil. The plant reaches 80 cm in height and bears up to 25 lanceolate leaves and from

7 to 20 bell-shaped brownish-yellow flowers. The bulb of *F. libanotica* is spindly, 5-6 cm high and 3-4 cm in diameter and consists of a single, fleshy scale. The uniqueness of the structure of this bulb has drawn the attention of researchers to it. As commented O. Stapf (1925) "the bulb of *F. libanotica* appears to occupy an intermediate position between those of *F. meleagris* and *F. imperialis*." Lack of material has prevented us from making a more detailed study of plants of this species.

Thus, plants with bulbs of the third type are distinguished by the following features: 1. The monocarpic shoot of the mature plant is formed inside the mother bulb and consists of above-ground and underground parts. 2. The number of metamers of the underground part of the shoot is significantly fewer than the number of metamers of the above-ground part. 3. The contractile roots are numerous and well-developed. 4. The annual shoot of the juvenile plant is rosulate and grows monopodially; the function of the leaves arranged around the annual shoot is clearly separated: the organs for the storage of nutrients are the lower leaves, the green leaves perform only the function of assimilation. 5. The pregenerative period is no more than 3 years. 6. The switch from monopodial growth to sympodial growth is connected to the switch in the structure of the annual shoot and takes place in the pregenerative period.

A striking number of species of the genus *Fritillaria* have bulbs of the third type, i.e. they consist of 2-3(4) broad, fused or unfused scales. If you analyse the conditions of growth of the plants then it is possible to note that the majority of them grow on open mountain slopes, in the steppes, in gravelly soil.

Species of the first group of the third type tend to be found in moister habitats and can

be found in meadows and forest clearings (*F. meleagris*, *F. montana* Hoppe, *F. ruthenica* Wikstr.). The habitats of these species occupy significant territories and the conditions of growth within each habitat can vary. Thus, for example, within a single population of *F. ruthenica* were distinguished plants growing in settled meadows and bushy thickets (Rotov, 1976). Their bulbs consisted of two or three unfused or barely-fused, broad scales. The well-developed contractile roots held the bulbs at a depth of 10-15 cm. The basic means of reproduction was by seed. Vegetative reproduction was weak and took place thanks to the formation of baby bulbs, which sometimes develop in the shelter of the papery outer scales or the fleshy storage scales of the bulbs. In the latter case, the baby bulbs sometimes form on slender, thread-like stolons, which carry them upwards towards the surface of the soil. This is characteristic of some species of the eastern Mediterranean – *F. assyriaca* Baker, *F. hermonis* ssp *amana* Rix, (Rix 1974).

Species of the second group (*F. raddeana*, *F. imperialis*, *F. sewerzowii*) grow in arid conditions in the hills of Central Asia. Their bulbs have semi-fused or fused scales and well-developed contractile roots, which anchor the bulbs at a depth of up to 25cm (Rodionenko, 1955). Among these is *F. sewerzowii*, whose bulb gives a clear example of extreme adaptation to arid conditions: a single broad, fleshy scale protects the bud of renewal and the withered scales from previous years cover the outside of the bulb with a thick layer which protects it from drying out.

The significant depth of the bulb in the soil markedly suppresses the formation of axil buds in the bulb, which leads to a weakening of vegetative reproduction. The main means of reproduction of these plants is by seed.

As a result of the study of the structure of the underground organs in specimens of the genus *Fritillaria* and their formation in ontogenesis, we have established three basic types of bulb, which are distinguished by a number of particularities. The basic features of each type are: 1. The number of storage scales of the bulb, in other words, the number of storage scales of the shortened underground part of the monocarpic shoot. 2. The presence of free-standing or fused (to various degrees) scales (tiled bulbs, semi-tunicate bulbs and tunicate bulbs). 3. The presence or absence of a stolon and, connected with this, the structure of the underground shoot. 4. The relationship between the number of metamers of the underground shoot to the number of metamers of the flower-bearing shoot.

A series of particularities correlates with each of these basic features: the length of the pregenerative (virgin) period, the functional particularities of the vegetative organs in the early stages of development, the character of the root system etc.

As well as these distinguishing features, it is impossible to ignore the general features of the underground organs which are common to all species of the genus *Fritillaria*. 1. The bulb renews itself every year and does not retain in its structure the shoots of past years. 2. There are no specialised protective scales. 3. The bulbs of mature plants (at the end of the vegetative period) contain elements of the shoots of three orders: the shortened part of the shoot of the current year and two embryonic shoots of future years. 4. The number of lower leaves laid down in the bud of renewal is greater than the number of storage scales formed from them; the first lower leaves of the bud die. The storage scales are distinguished by their significant thickness.

Many of the common features of species of the genus *Fritillaria* can be observed in the early stages of the development of the plant. Among them are the following: 1. The above-ground germination of the seed. 2. The formation of a rosulate, monopodially growing annual shoot in the first years of life. The rosulate stage lasts for different lengths of time in different species, ranging from the first two to the first six years of life. 3. A switch from monopodial growth to sympodial growth associated with the appearance of the first overground shoot (in species of the second and third type this coincides with a switch in the structure of the annual shoot) and observed in the pregenerative period.

The arising of a bulb in species of the genus *Fritillaria* is associated with the gradual reduction of the rosette. Research has shown that for all species of the genus a rosulate structure of the annual shoot is characteristic in the early stages of ontogenesis. The length of this stage varies from species to species. The more prolonged this stage (in the North American species it reaches six years) the more the signs of the rosulate form are preserved in the bulb of the mature plant. And in plants whose rosulate stage lasts no longer than one or two years the traces of the rosette almost disappear in the mature plant.

In the process of evolution the leaves of the rosette have metamorphosed into specialised storage scales. Further metamorphosis of the scales tends towards a change in their form, a reduction in their number, the fusing of their edges and fusing with one another. The development of the tunicate bulb in specimens of the genus *Fritillaria* demonstrates an example of the most profound metamorphosis of the rosette.

The structural particularities of the bulbs are a very good diagnostic feature in the genus *Fritillaria* and should be more widely used for

interspecies classifications. The first monograph of the genus by J Baker (1874) used the type of structure of the bulb for dividing the genus into subgenera (“bulbus tunicatus”, “bulbous squamosus”). However, he produced a series of inaccuracies in the way he distinguished the bulb types of various species. Thus he defined as “bulbus squamosus” the bulbs of representatives of the genus *Petilium*, in particular the bulbs of *F. imperialis* and other species; he defined the bulb of *F. sewerzowii* as “bulbus tunicatus stoliniferous” and the bulb of *F. pudica* as “bulbus tunicatus” (Baker, 1874: 252-253). In “Flora of the USSR” when setting out the characteristics of different groupings of *Fritillaria* it distinguishes different numbers of scales in the bulb: 2, 4, many. But on its own this is not a sufficient indication of the type of bulb. Thus, for example, in the grouping *Liliorhiza* are included species with many-scaled bulbs both with stolons and without. Our researches have indicated that bulbs with stolons and those without stolons differ significantly not only in their structure but, most importantly, in the particularities of their development in ontogeny. They belong, as has been explained, to at least two different basic types – the first and the second. Moreover, species with bulbs of the first and second type have clear-cut geographical delimitations. All of this gives a basis for the re-examination of the entire *Liliorhiza* grouping against the background of the particularities of the reproductive organs.

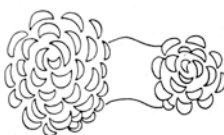
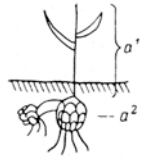

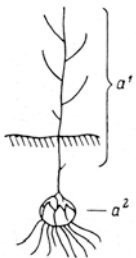



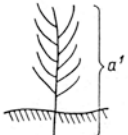


On the other hand, the Eurasian species of the genus, belonging to various sub-genera – *Fritillaria*, *Theresia*, *Rhinopetalum*, *Petilium*, *Korelkowia*, have bulbs with the structure of a single type (the third type). The separating-out of *Petilium* and *Korelkowia* into separate genera, mainly based on differences in the bulb structure (the bulbs of *Petilium* have four half-fused scales and those of *Korelkowia*

have one or three fused scales) cannot be justified. The study of the annual cycle and the process of formation of the bulb in ontogenesis in species of the third type has shown that their development proceeds in an identical way. The fusing of the scales happens at the last stages of development. This feature is expressed in the majority of species of the third type and is nothing new when encountered in species of the sub-genus *Petilium* or *Korelkowia*. Only the stage at which this feature expresses itself varies in species of the third type.

The results of the study of the annual cycle of the plants showed that the structure of the underground organs can vary in different periods of the year (*F. camschatchensis*, *F. imperialis* etc). This explains the plethora of sometimes contradictory data in the description of the structure of the bulbs. The reason for it is not mistakes by the authors, but the fact that the plants were described at differing periods of their lives. Thus it is essential when describing the structure of underground organs to indicate the life phase of the plant.

When examining the particularities of the structure of the underground organs of differing types in representatives of the genus *Fritillaria* in the context of ecological conditions it is impossible not to notice that species with similar structures to their underground organs often also coincide with more or less similar conditions. Overall, the conditions in which fritillaries grow are very diverse – from the damp forests of regions of the far east of the USSR and North America to the dry, arid mountains of far and middle Asia. However, even in arid conditions representatives of these species continue to be mesophyte. Their overground shoots do not have any indication of xeromorphism and the adaptation to the arid climate is

expressed in a variation to the rhythm of development of the plant. The plants “flee from the dryness” as memorably expressed by A. Schimper (1935), making sure that vegetation coincides with the very short and damp spring or, occasionally (North American species of the genus), the winter. With the advent of the hot, dry summer months the leafy overground shoots wither. In contrast to the overground organs, the underground organs of the plants remain in place throughout the year and are subject to the harmful influence of their milieu. Under the influence of arid conditions the bulbs take on in the course of evolution a series of adaptive features which distinguish them from the bulbs of species of the damp, forested habitats. The transformation of the structure of bulbs of the genus *Fritillaria* under the influence of increasingly arid climates was expressed in the reduction in the number of scales, which allowed for greater protection of the bud of renewal; in the end this tendency led to the transformation of tiled bulbs into tunicate bulbs. Species with tiled bulbs are associated with damp regions and present with bulbs of mesomorphic type, which can be sorted into many-scaled and few-scaled, loosely attached around the axis, sometimes forming a stolon, lacking contractile roots and the associated formation of the bulb at the surface of the soil, a depressed level of reproduction by seed and a high intensity of vegetative reproduction. Bulbs of the first type and of the first group of the second type can be described as mesomorphic. Species with tunicate bulbs, on the other hand, are connected with dry habitats and represent the xeromorphic type of bulbs in the genus. Bulbs of the second group of the third type belong to the xeromorphics. Between these two extremes of ecological type there exist a series of intermediate forms (see table).

type of structure	group	Section through the bulb (schematic)	Depth of settling of the bulb in the soil	Relationship between the number of metamers (n) of the overground shoot (a ¹) to the number of metamers of the underground shoot (a ²).
I	1			$na^1 < na^2$
				$na^1 < na^2$
II	2			$na^1 = na^2$
	1			$na^1 > na^2$
III	2			$na^1 > na^2$

Similar features of adaptation of the underground organs to similar conditions of growth were observed in representatives of the nearest genus to the genus *Fritillaria*, the genus *Lilium* L. (Baranova 1978). This fact is a manifestation of the law of homological series. Analysing the bulbs of representatives of both species, one can note that species with mesomorphic bulbs predominate in the genus *Lilium*, whereas in the genus *Fritillaria* most species have xeromorphic bulbs. However, the degree to which the bulbs are mesomorphic or xeromorphic varies between species in both genera. Among the mesomorphic lily bulbs we noted generally much more ancient forms of the bulb. They were characterised by the plagiotropic

direction of growth of the underground shoot, by a larger number of annual cycles (up to 6) and connected with this a larger number of scales (up to 120), the long length of the virginal period and so on. Not one of the representatives of the genus *Fritillaria* has bulbs with such an extensive collection of ancient features. Among the species of genus *Fritillaria* those which are most mesomorphic in character are the stoloniferous species with bulbs with many scales and a single annual cycle.

As for the adaptation of bulbs to arid conditions of growth, in this species of the genus *Fritillaria* have made more progress than those of the genus *Lilium*, having formed tunicate bulbs. There are no such bulbs in any

species of lily; the tendency towards fusion of the scales is generally not expressed. The spread of the genus *Fritillaria* extends into the steppes and semi-deserts, where lilies are not found. The range of habitat conditions in the genus *Fritillaria* is wider than in the genus *Lilium*. This finds its expression in the greater range of adaptive features in species of the genus *Fritillaria*.

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Summary

The structure of the underground organs and peculiarities of their formation in ontogeny have been studied. Within the limits of the genus three basic types of bulbs with the peculiar features of their structure and development have been established. The main characters of the bulbs and their significance for the taxonomy of the genus have been shown. The correlation of the structural types of the underground organs and ecological conditions were determined. Among the representatives of the genus *Fritillaria* the bulbs of the mesomorphic and xeromorphic structure have been determined. Similar characters of adaptation of the underground organs to the adequate growth conditions have been found in this species and the species of the closely related genus *Lilium*.

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Notes and References to the translation

Synonyms used in this paper:

<i>F. lanceolata</i> Pursh	=	<i>F. affinis</i> (Schult. & Schult. f.) Sealy
<i>F. libanotica</i> (Boiss.) Baker	=	<i>F. persica</i> L.
<i>F. lutea</i> Mill.	=	<i>F. collina</i> Adam
<i>F. multiflora</i> Kellogg	=	<i>F. affinis</i> (Schult. & Schult. f.) Sealy
<i>F. mutica</i> Lindl.	=	<i>F. affinis</i> (Schult. & Schult. f.) Sealy
<i>F. phaenothera</i> Eastw.	=	<i>F. eastwoodiae</i> Macfarlane

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