

## Polygamy in some species of *Nepeta* (Lamiaceae)

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**Abstract.** Polygamy of monoecious type was established for the first time among the studied Bulgarian species of *Nepeta* and in *N. transcaucasica*. It was expressed in the distribution of all so far known sexual types of flowers in *Magnoliophyta*. This phenomenon, as well as the shrinking in number and size of the flowers and reduction of the number of layers in the anthers of structurally male flowers, show a high-degree evolution in the generative sphere of the investigated taxa.

**Key words:** embryology, evolution, gynodioecy, hermaphrodite flower, monodioecy, *Nepeta*, polygamy, reduction

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### Introduction

Gynodioecy is a broadly occurring phenomenon among *Magnoliophyta* (Kordym & Glustenکو 1976; Delannay 1978; Owens & Ubera-Jimenez 1992). Ample data have been collected so far concerning the reproductive capacity of polygamous flowers, but the origin and their evolution in the different groups of *Magnoliophyta* have not been clarified yet.

A number of hypotheses exist relating to the different sexual types of flowers within *Magnoliophyta*, based on the size of flowers, the growth and development of flower and fruit, on different phenological factors (Sakai 2000), the amount of auxins in flowers (Tsikov & Tsikova 1981), as well as the fact that they are controlled by nuclear or cytoplasmic genes or by both simultaneously (Frankel & Galun 1977). Major mathematical models have been created (Sakai 2000) and classification systems have been evolved (Poddubnaya-Arnoldi 1976; Kordym & Glustenکو 1976) of the existing polygamous flowers in *Magnoliophyta*.

Family *Lamiaceae* makes no exception along these lines and gynodioecy in a different degree has been recognized in over 124 of its species (Ubera & Valdes

1983; Garcia & Munoz 1988). It has been also found out that similarly to other plant families polygamy is controlled by nuclear genes, as well as by a combination of nuclear and of cytoplasmic genes (Owens & Ubera-Jimenez 1992). Male sterile forms (Daskalova 1993) have been identified among the Bulgarian representatives of family *Lamiaceae*, as well as functionally female flowers (Daskalova & Genova 1996a, b).

Gynodioecy was reported for the first time in the species of *Nepeta* already late in the 19<sup>th</sup> century (Knuth 1899), namely in *N. grandiflora*, *N. melissifolia*, *N. pannonica*, and *N. cataria*. In the latter species gynodioecy was also found later on, in the 20<sup>th</sup> century by Baker (1948) and Poyarkova (1954), who also reported it in *N. sibirica* and *N. parviflora*.

Subsequently, gynodioecious forms were referred too by Turner (1972) and Demyanova (1981) in *N. parviflora* and *N. sibirica*.

Along with gynodioecy, within the framework of *Nepeta* the less frequent phenomenon of dioecy was recognized too among the *Magnoliophyta* and *Lamiaceae*, chiefly in single sections such as *Oxynepea*, in which Poyarkova (1954) and Ubera & Valdes (1983) had found simultaneously dioecious and monoecious species.

In the *Flora of the People's Republic of Bulgaria* (Assenov 1989) gynodioecy was used as a basic criterion for determination of the species of *Nepeta*. Male sterile forms were established in *N. transcaucasica* (Peneva & al. 1987), an introduced species in Bulgaria.

The analysis of literary data has shown that the cytoembryological method of research has been seldom used (Kordym & Glustenko 1976; Tsikov & Tsikova 1981) to study the specificities of formation of the generative organs in the different sexual forms of flowers in *Magnoliophyta*. This method allows, on the one hand, to identify the common principles of formation of the flowers of different sex and, on the other, helps elucidate their taxonomically related specificity and the reasons for sterility of pistils and anthers. That is why, our purpose in this work was to establish cytoembryologically, along with the morphological and anatomical comparative methods, whether and to what degree gynodioecy and dioecy are distributed in the Bulgarian representatives of *Nepeta* and in the introduced in Bulgaria species *N. transcaucasica*

## Material and methods

The Bulgarian species of *Nepeta*, four altogether, with eight populations, and *N. transcaucasica*, an introduced species in Bulgaria, are subject to this study: *N. cataria* with two populations, the first one near Balchik town at the Northern Black Sea Coast, and the second from Mt Lozenska, Sofia district; *N. nuda* with two populations, the first from Beglika locality, Central Rhodopes, and the second from Mt Vitoshka, Sofia district; *N. parviflora* with two populations, the first from Vlas village, Southern Black Sea Coast, and the second from Shabla, Northern Black Sea Coast; and *N. transcaucasica* from the experimental field of the Institute of Botany in Gorni Lozen village, Sofia district.

Material collected during the 4<sup>th</sup>–8<sup>th</sup> months in the period 2001–2003, both from nature and from the collection of living plants at the experimental field of the Institute of Botany in Gorni Lozen village, was used in the study. The flowers, since the moment of their formation and until the moment of formation of mature seeds have been periodically fixed in Navashin's mixture.

The material was further treated according to the generally accepted cytological techniques for permanent microscope slides. Sections 6–18 µm thick, depending on the age of material, were cut with Minot

rotation microtome. The staining was made with Heidenhain's hematoxylin. The drawings were made both from living plants and from the permanent microscope slides with Abbe drawing device.

The improved classification of Kordym & Glustenko (1976) was applied for presentation in the article, based on the former classification of Rozanova (Poddubnaya-Arnoldi 1976), as it seemed to suit best the purposes of our study. In this classification the polygamous flowers are divided into hermaphrodite, structurally female and male flowers, with no rudiments of the opposite sex whatsoever, and potentially male and female flowers with rudiments of the opposite sex.

## Results

A comparative analysis of the flower organogenesis in the five species of *Nepeta* studied since the start of their development and until the formation of seeds has shown the following several types of polygamous flowers with various degree of distribution in the different investigated taxa: hermaphrodite in *N. transcaucasica* and *N. cataria*; functionally and structurally male and functionally and structurally female flowers in the two above-mentioned species, as well as in *N. parviflora* and *N. ucrainica*; and only structurally female in *N. nuda*. The simultaneous distribution of these types of flowers has been described so far only in *Plantago media*, as well as in family *Araliaceae* and family *Orchidaceae* (Poddubnaya-Arnoldi 1976) which include all so far known flowers in the *Magnoliophyta*.

We shall dwell in detail on the morphology of the above-mentioned types of polygamous flowers in the various investigated species of *Nepeta*, which also differ in size. Hermaphrodite flowers have been the largest, followed by the functionally female, functionally male and structurally female, while structurally male flowers were usually the smallest. The polygamy found by us was monoecious, because the different flowers were distributed simultaneously in various numbers and correlation in one and the same individual.

### Hermaphrodite flowers

This is the main type of flowers distributed in *Lamiaceae* that occurs only in *N. cataria* (Plate I, Fig. 1) and *N. transcaucasica* (Plate I, Figs 2, 3).

Hermaphrodite flowers are with 5-lobed calyx and 5-lobed corolla, four stamens inserted under the up-

per corolla lip in *N. cataria*, while in *N. transcaucasica* they are as long as the upper lip and the style, the central usually longer than the lateral. Other parts of the hermaphrodite flower are the 4-locular pistil, with one ovule set in each locule (Plate I, Fig. 6), with a style and bifid stigma (Plate I, Fig. 3).

We have frequently found in the different hermaphrodite flowers of the two studied species complete accretion of the corolla tube, so that morphologically the flowers looked as being composed of structurally male and structurally female flowers, inserted into each other.

The flower buds of hermaphrodite flowers emerge centripetally of the expanded axis of the inflorescens.

Their further differentiation begins with the setting of primordiums of the perianth consisting of 5-lobed calyx and 5-lobed corolla, of different length in the two investigated species. Differentiation of the elements of the stamens, pistil and gynobasic style is simultaneous until they reach the normal place and size for the different investigated species (Plate I, Figs 1, 2, 3).

We have traced out some embryological processes and structures in the male generative sphere of the flower, in order to compare them with those in the other sexual types of flowers. One such process was the setting in each stamen composed of two equal in size thecae of four microsporangia (Plate I, Fig. 4), each constituted of four layers and each undergoing further development until their distinct morphological differentiation during the development of the male gametophyte. Finally, prior to splitting up of the anther, only two layers remained: a fibrous endothecium and epidermis (Plate I, Fig. 5; Plate II, Fig. 3). Another process was the normal microsporogenesis and formation mainly of 6-colpate 3-celled pollen (Plate IV, Fig. 4).

In the female sphere of the flower we have found one anatropous, tenuinucellar unitegmic ovule set in each locule of the 4-locular sincarpous pistil (Plate I, Fig. 6); *Polygonum*-type development of the embryo sac and formation of an *Investing*-type embryo. The embryonal processes described above are typical for most investigated species of family *Lamiaceae* (Wunderlich 1967).

### Functionally male and female flowers

In the plant kingdom they have been recognized in *Rhamnus cathartica*, *Vitis vinifera*, *Sagittaria sagitifolia*, etc. (Kordym & Glustenko 1976).

We shall dwell simultaneously on two types of functional flowers distributed in *N. transcaucasica*, *N. cat-*

*aria*, *N. parviflora*, and *N. ucrainica*, because the initial stages of their organogenesis are the same, run similarly to those in the hermaphrodite (Plate I, Fig. 2), and both the stamens and pistils are set. No changes in the morphology of the perianth have been observed in the polygamous flowers. We found only shrinking in size as compared to the hermaphrodite.

During the initial development stages, the primordiums of the stamens, pistil, style and stigma of the functionally male and female flowers are equal in shape and size with those of the hermaphrodite. During the subsequent development phase, differentiation of the different elements of the stamens sets in the functionally male flowers, as well as increase in size, while the shape and size of the carpels remains almost unchanged and they linger as rudiments in the further formation of functionally male flowers.

Conversely, in the functionally female flowers differentiation and increase in size of the pistils is gradual, as well as the emergence and development of the style and stigma, while the stamens retain nearly their initial shape and size, without differentiation of the embryological structures and processes in them.

### Functionally female flowers

These flowers mostly have four normally developed locules of the pistil and a normally situated and developed style with bifid stigma.

In the different locules of the pistil we have observed normally set anatropous, tenuinucellate ovules. However, we have not witnessed any further development of the embryonal structures and thus were unable to determine this type of flowers as fertile, while in the functionally female flowers of other investigated species (Kordym & Glustenko 1974) development of the female gametophyte was observed expressed in the initial phases of the embryo sacs development. These flowers frequently remained closed. Quite often deviations from the normal development of pistils has been observed in them, chiefly expressed in the reduction of the number of locules from four to two and even to one, most frequently in *N. cataria*, as well as frequent emergence usually of a reduced in size style not in its normal place. Apparently, among the various species investigated the sterility of different generative parts of the flower was rather advanced and extended even to the style, for in *N. nuda* (Poyarkova 1954) the style was preserved and was twice longer than the corolla tube. Similar variation in the number of loc-

ules in the pistils has been established in the male sterile forms of *Nicotiana* (Tsikov & Tsikova 1981) and in *Salvia sclarea* (Daskalova 1993).

In the male generative sphere of the flower we have established the following major differences as compared to the hermaphrodite: lagging in the elongation of filaments so that the anthers were not situated as in the normal hermaphrodite flowers in the curve of the upper lip, but remained on the level of the corolla tube. Occasionally, insignificant remains of the stamens have been found, which did not contain any rudiments of set anthers (Plate I, Fig. 8); or a reduced number of stamens from four to two as a consequence of their underdevelopment; as well as stamens with abnormally developed thecae (Plate I, Fig. 7; Plate II, Fig. 1). In the different stamens with normally developed filaments we have often observed the setting and development of two strongly deformed locules (Plate II, Fig. 2), or setting of no locule at all, owing to the fact that in the place where the setting should have started degeneration of tissues had begun (Plate II, Fig. 5). This was a step forward in the reduction of functionally female flowers in the species of *Nepeta* investigated by us, because in *N. noraschenica* and *N. parviflora* (Poyarkova 1954) normally developed staminodia had been always found on thin filaments.

We have also observed in these flowers partial or full degeneration of the pollen (Plate II, Fig. 2).

### Functionally male flowers

These flowers were usually smaller in size than the functionally female ones. Only the four stamens of the flower normally formed and developed in them, while the female parts were set and degenerated in a different manner and at a different stage of their development. We have established certain deviations in the embryonal processes and the structures in them, as compared to the hermaphrodite flowers. These deviations were usually expressed in the number of layers forming the anther wall – usually three, without an middle layer, against the background of the normal four layers in the hermaphrodite flowers – as well as in the morphology of cells forming the different layers. All three layers were made of tangentially flattened cells that retained their initial shape and size as long as the stage of one-celled pollen (Plate II, Fig. 4). However, frequently in single flowers and mostly in *N. ucrainica* and *N. parviflora* we have observed an early degeneration of the tapetum, while prior to this in

its cells a large formed vacuole situated towards the internal part of the anther. The microsporogenesis generally ran normally. Usually, the one-celled pollen was without a cytoplasm and with a well-formed exine, and it degenerated massively at that stage: a phenomenon recognized in many male sterile plants (Tsikov & Tsikova 1981; Daskalova 1993)

In the female generative sphere of these flowers there was frequently only one locule formed in the pistil (Plate II, Fig. 6), instead of four and the normally set pistil tissue degenerated further (Plate II, Fig. 7) in *N. parviflora*, *N. cataria* and *N. ucrainica*. Similar phenomena have been described for the cytoplasmic male sterility in *Nicotiana* (Tsikov & Tsikova 1981). The style was preserved in a number of these flowers, but it was not situated and developed normally.

### Structurally female flowers

This was the only type of flowers distributed in *N. nuda*, while in the other investigated species they occurred along with the functionally female and male flowers, and with structurally male and hermaphrodite flowers in *N. cataria* and *N. transcaucasica*.

Structurally female flowers were usually situated in the inflorescens, where more distinct degeneration processes took place, affecting a great number of single flowers. Morphologically, they divided into two types: a broader one prevalent in *N. cataria* and *N. ucrainica*, and a narrower in *N. parviflora* (Plate III, Figs 4, 5, 6).

Four locules are normally set in the pistils and develop in them, without style and stigma, and no rudiments characteristic of the male sphere of the flowers (Plate III, Figs 1–5). On the epidermis of some pistils we have found glandular trichomes (Plate III, Fig. 6), similarly to those in the hermaphrodite flowers of *N. cataria* and *N. transcaucasica*.

In our opinion, these are fertile flowers that form autogamous seeds, because we have observed in them normal *Polygonum*-type development of the embryo sacs, usually in *N. cataria* and *N. transcaucasica* (Plate III, Fig. 3), and of *Investing*-type embryos in *N. nuda*.

As compared to the hermaphrodite flowers, certain differences have been observed in these flowers too, chiefly in the formation of various in size locules in the pistils of *N. parviflora*, *N. transcaucasica* and *N. ucrainica*; in the reduced number of locules to one in *N. cataria*; and in the emergence of an improperly situated style in some of them, as well as in the increased number of locules in the pistils of *N. nuda*

(Plate III, Fig. 6). Organogenesis of this type of flowers ran similarly to that described for *Vitis vinifera*, *Acer saccharinum*, *Gleditschia triacanthos*, etc. (Kordym & Glustenko 1976).

### Structurally male flowers

The structurally male flowers are widely distributed in the following families: *Aceraceae*, *Fagaceae*, *Moraceae*, *Oleaceae*, etc. (Kordym & Glustenko 1976). According to the available literary sources, so far they have not been described in *Nepeta*.

They are characteristically two to three times smaller than the hermaphrodite flowers and were fewest in number among all polygamous flowers found by us in the species of *Nepeta*.

Structurally male flowers in the investigated species of *Nepeta* are with 5-lobed calyx, 5-lobed corolla and four stamens, each developing normally four locules in the anthers (Plate IV, Figs 2, 3, 6). We have observed the different stages of organogenesis in these flowers (Plate IV, Fig. 1).

Mention deserves the fact that structurally male flowers were usually situated in close proximity to the hermaphrodite flowers in the different nodes of the inflorescens in *N. transcaucasica* and *N. cataria*. This situation, as well as the presence of one- and two-celled pollen in their anthers and of mature embryo sacs in the hermaphrodite flowers invited the conclusion that the pollen of the structurally male flowers has often pollinated the hermaphrodite, as in this case, and that geitonogamy occurred instead of self-pollination typical of most species of *Nepeta*.

The anther wall in this type of flowers was four-layered, occasionally three-layered, with equal in shape and size cells in the different layers throughout their existence, as in the functionally male flowers, which differentiates them from the hermaphrodite flowers. The tapetum here also degenerated often in the stage of prophase of the meiosis: a peculiarity established in other male sterile plants too (Daskalova 1993). The pollen lacked cellular content but had a well-shaped exine and the grains were often agglutinated. Such peculiarities have been found for *Salvia tomentosa* (Daskalova & Genova 1996a) and *S. sclarea* (Daskalova 1993). The observed pollen was nearly by half smaller than that in the hermaphrodite flowers, of the six-colpate one-celled and six-colpate two-celled type, contrary to the six-colpate three-celled type (Plate IV, Figs 4, 5) in the hermaphrodite flowers.

In comparison with the hermaphrodite flowers deviations occurred more seldom here and occasionally only two locules formed in the anther instead of four as in the functionally male flowers.

In the different development stages of the above-described flowers we have found a great percentage of degenerating flowers of all sexual types on the nodes of the racemes, which actually testifies to an evolutionary trend in family *Lamiaceae* towards reduction of the number of flowers in the different nodes of the inflorescens.

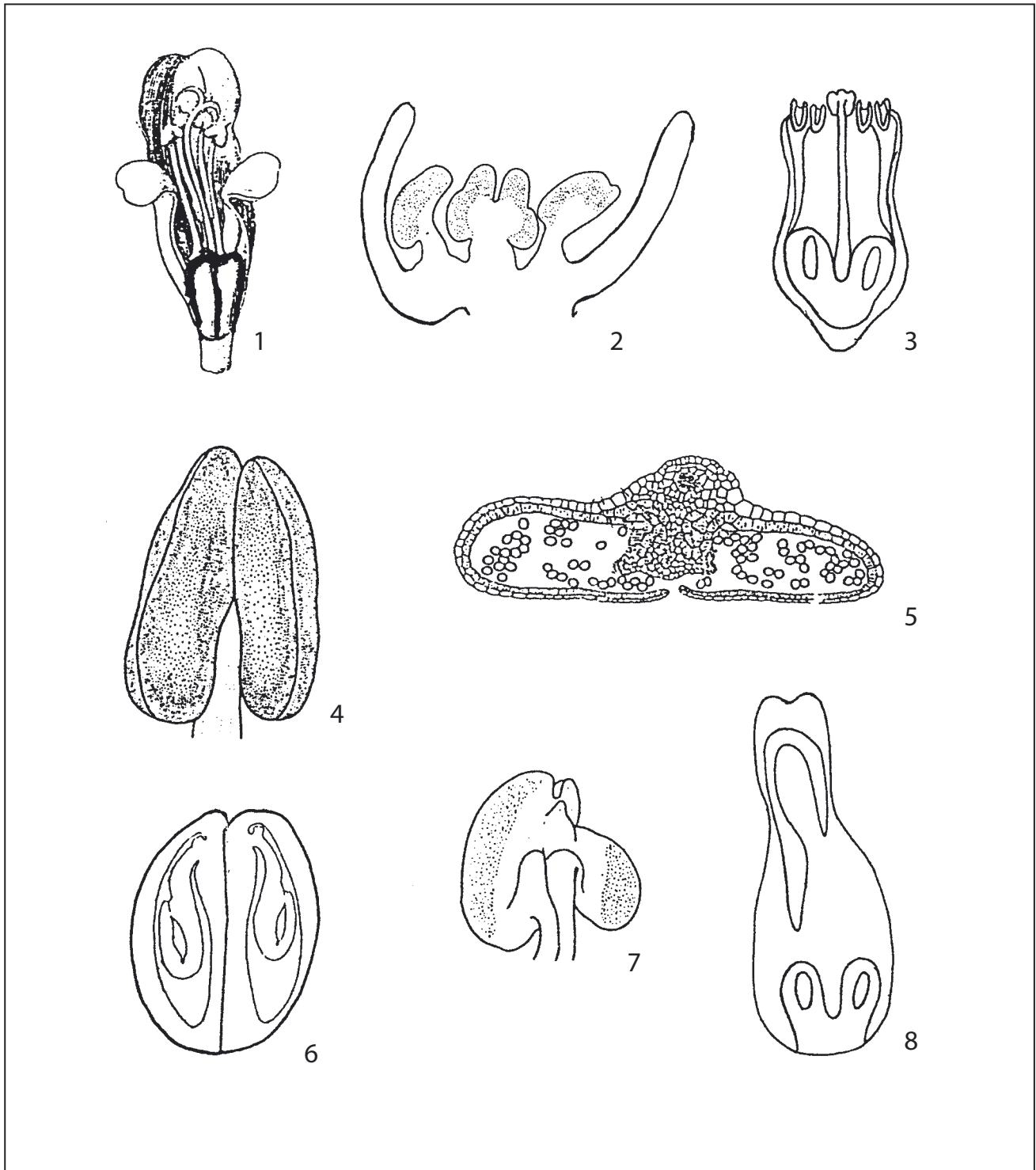
Besides the above-described polygamous flowers, in all investigated species of *Nepeta*, we have found flowers formed only of calyx and corolla, without any pistils, stamens and style. We decided to call conditionally these flowers empty (Plate IV, Fig. 7)

## Discussion

The comparative analysis of morphology, anatomy, histogenesis and organogenesis of the flowers in the investigated species of *Nepeta* has established the following sexual types of flowers: hermaphrodite in *N. cataria* and *N. transcaucasica*, functionally male and functionally female, as well as structurally male and structurally female in *N. cataria* and *N. transcaucasica*, *N. parviflora* and *N. ucrainica*, and only structurally female in *N. nuda*, as a comparatively rare phenomenon among the *Magnoliophyta*. We did not establish any particular regularity in the distribution of the different sexual types of flowers in the investigated species. Simultaneous distribution of all these types of polygamous flowers is reported for the first time for *Nepeta*, in which so far only hermaphrodite and functionally male and female flowers have been described (Poyarkova 1954), as well as hermaphrodite and female flowers and mono- and dioecious plants (Turner 1972).

Our research has shown a rather advanced reduction of the single generative structures in the polygamous flowers as compared to the other investigated species of the genus, supported by the so far unreported within the framework of the genus structurally male and female flowers found by us. Apparently, application of the so far seldom used comparative cytobryological method of research would lead to the establishment of new and yet unknown sexual types of flowers in *Nepeta*, *Lamiaceae* and *Magnoliophyta* and would show a higher degree of polygamy.

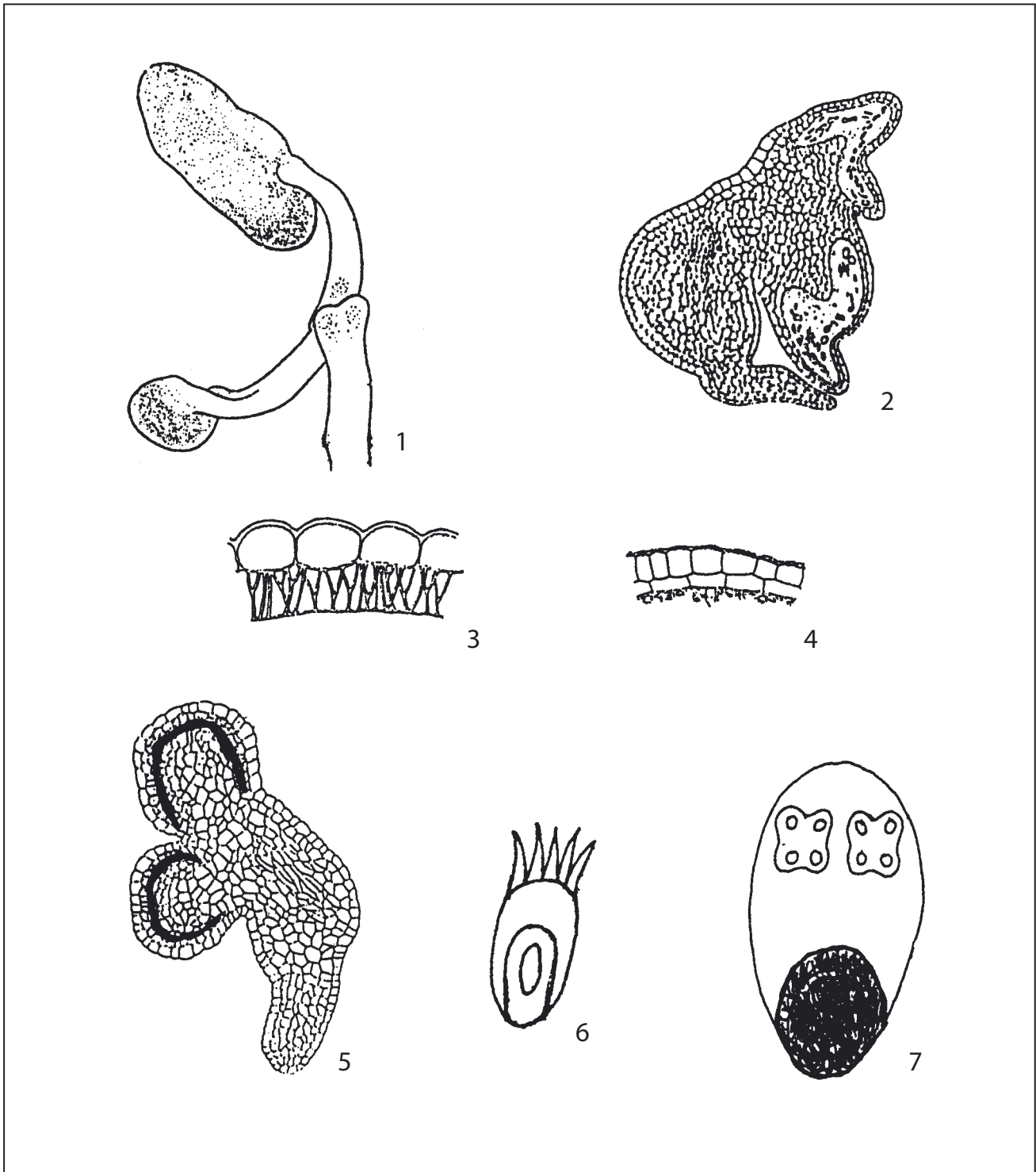
## Plate I



**Figs 1–8.** Polygamous flowers:

1, hermaphrodite flower in *N. cataria* ( $\times 600$ ); 2, initial stages of the organogenesis of a hermaphrodite flower in *N. transcaucasica* ( $\times 500$ ); 3, hermaphrodite flower in *N. transcaucasica* ( $\times 500$ ); 4, two normally developed thecae of a stamen in *N. cataria* ( $\times 1000$ ); 5, longitudinal section of the one half of the anther, with endothecium and epidermis in *N. transcaucasica* ( $\times 800$ ); 6, longitudinal section of a pistil, with two normally developed anatropous unitegmic ovules in *N. transcaucasica* ( $\times 800$ ); 7, stamen with one degenerating theca in *N. cataria* ( $\times 500$ ); 8, longitudinal section of a functionally female flower, with normally developed locules in the pistil; above: rudiments of stamens in *N. cataria* ( $\times 450$ ).

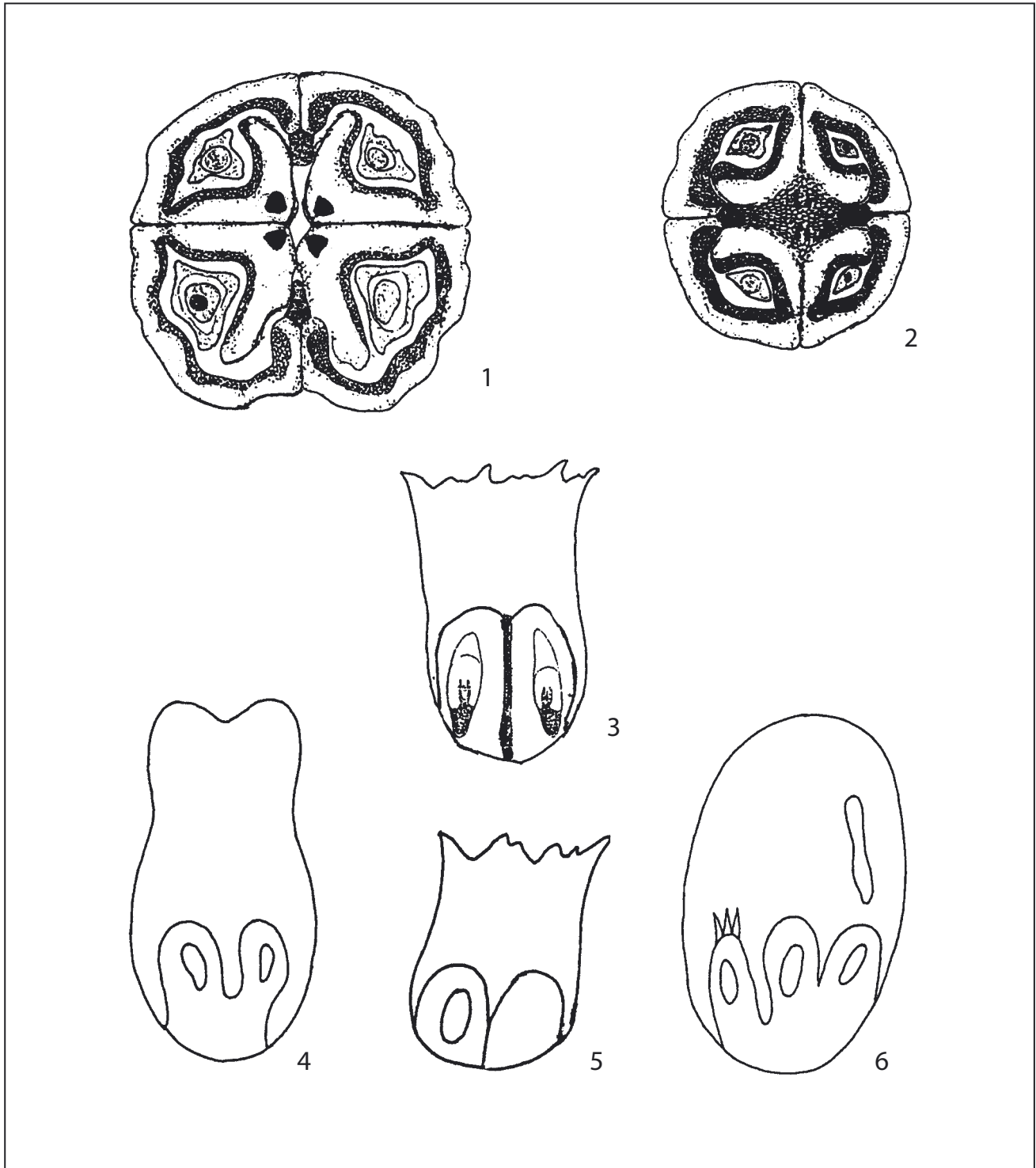
## Plate II



Figs 1–7. Polygamous flowers:

1, stamen with one normal and one degenerating theca in *N. parviflora* ( $\times 1000$ ); 2, section of an anther with only two set degenerating locules in *N. ukrainica* ( $\times 600$ ); 3, part of an anther wall, with preserved epidermis and fibrous endothecium in the hermaphrodite flowers of *N. cataria* ( $\times 550$ ); 4, part of an anther wall in the functionally female flowers in *N. ukrainica* ( $\times 550$ ); 5, stamen with a degenerating tissue in the place of differentiation of the two anther locules in *N. transcaucasica* ( $\times 600$ ); 6, functionally male flower, with only one developed pistil locule in *N. cataria* ( $\times 160$ ); 7, functionally male flower with normally developed locules of the anthers and degenerating pistil tissue in *N. parviflora* ( $\times 600$ ).

## Plate III

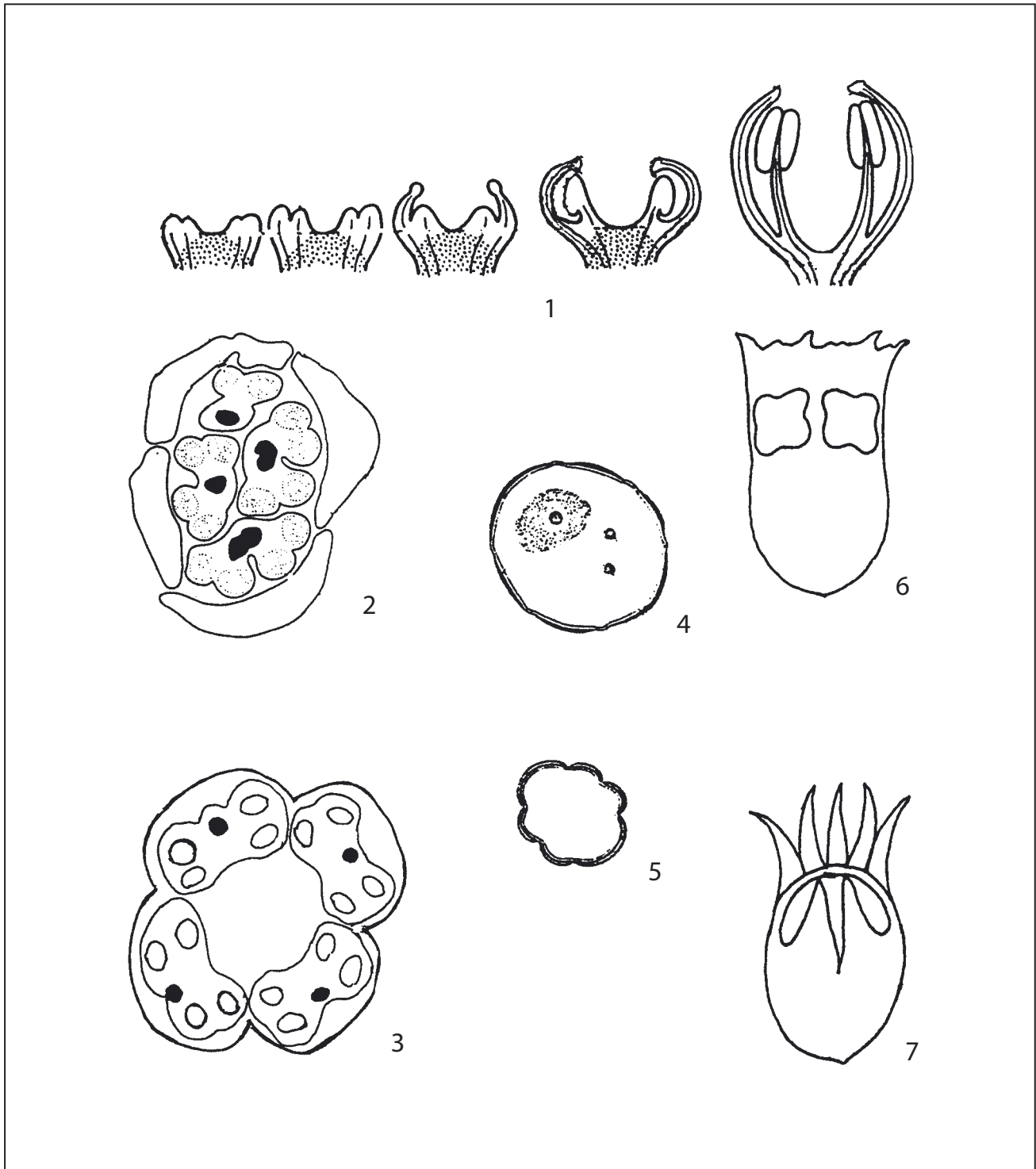


**Figs 1–6.** Structurally female flowers (SFF)

1, cross section of a pistil, with four normally developed locules with ovules in *N. nuda* ( $\times 850$ ); 2, cross section of a pistil, with four normally developed locules with ovules in *N. cataria* ( $\times 600$ ); 3, cross section of SFF, with set ovules in *N. parviflora* ( $\times 500$ ); 4, longitudinal section of SFF of the narrow type, with two unequal in size locules in the pistil of *N. parviflora* ( $\times 500$ ); 5, SFF of the broad type in *N. ucrainica* ( $\times 500$ ); 6, SFF with three improperly situated locules pistils, an improperly situated style, glandular trichomes on the epidermis of the left pistil in *N. nuda* ( $\times 550$ ).



## Plate IV



**Figs 1–7.** Structurally male (SMF) and “empty” flowers

1, scheme of some stages of the organogenesis of SMF in *N. nuda* ( $\times 450$ ); 2, cross section of an anther in *N. nuda* ( $\times 550$ ); 3, cross section of an anther in *N. transcaucasica* ( $\times 700$ ); 4, Six-colpate, three-celled pollen in *N. cataria* ( $\times 1000$ ); 5, six-colpate pollen in *N. cataria* ( $\times 1000$ ); 6, cross section of SMF in *N. ucrainica* ( $\times 450$ ); 7, “Empty” flower without differentiated generative organs ( $\times 450$ ).

The shape, size and number of the different generative organs in the polygamous flowers of the investigated species of *Nepeta* has not been genetically asserted yet. This was evidenced by the various degree of reduction in the setting and development of the different elements of andro- and gynodioecy in the two functional and structural types of flowers found by us. The highest degree was achieved in *N. nuda* in which only structurally female flowers were distributed.

The other types of polygamous flowers found besides the hermaphrodite flowers in *N. cataria* call for revision of the Determination key to the species of *Nepeta* (Assenov 1989) in an eventual edition of the *Flora of Bulgaria*.

Among the investigated species of *Nepeta* only monoecy has been established, contrary to the dioecy found by Poyarkova (1954) in *N. cataria* and by Turner (1972) in the species of *Nepeta*. This testifies once again that the distribution of monoecy and dioecy in *Magnoliophyta* depends on the conditions in their habitats.

Apparently, the evolution of reproductive sphere in *N. cataria* and *N. transcaucasica* has advanced and, along with proterandry, another compensational mechanism has evolved in order to avoid self-pollination and transfer to geitonogamy when the structurally male flowers appeared in close proximity to the hermaphrodite flowers.

Our comparative morphological analysis of the flowers in all Bulgarian species of *Nepeta*, as well as of *N. transcaucasica*, has shown a rather advanced evolution in the reproductive sphere that followed the evolution described in other species of *Lamiaceae* (Hedge 1961). It was expressed in the reduction of the number and size of flowers (the largest in the hermaphrodite flowers and the smallest in the structurally male flowers) and reduction of the number of layers building the anther, combined with actinomorphy, proterandry, monoecy and dioecy on a large scale.

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