

The life cycle of *Ficaria verna* HUDS.

Životný cyklus *Ficaria verna* HUDS.

Milan Križo and Marta Korínková

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This paper deals with the morphogenesis of vegetative and reproductive organs of *Ficaria verna* HUDS. subsp. *bulbifera* (ALBERT) Á. et D. LÖVE. Facts about disorders in microsporogenesis and about disorganization of embryo sacs were confirmed. On the other hand the information about generally low viability of pollen grains was not confirmed. This work brings new findings about morphogenesis of vegetative organs: feeding roots, root tubers, renewal buds and axillary bulbils.

University of Forestry and Wood Technology, Maršova 24, 960 53 Zvolen, Czechoslovakia.

INTRODUCTION

Among the plant life forms, which were divided by Raunkiär (1934) into six basic groups according to the protection of renewal buds (buds producing new shoots the next season) in unfavourable seasons of the year, geophytes have some interesting and at the same time conspicuous life demonstrations. The renewal buds are buried in the ground surface soil on metamorph stems such as tubers, bulbs and rhizomes during unfavourable period. Shoots growing from renewal buds early in the spring have usually only a short existence and dry up very soon, in June or July, after having formed their reproductive organs — flowers and fruits. With regard to the short existence of their shoots, these plants are called ephemeroïds. Taking into consideration the two mentioned characteristics, they are called geoephemeroïds. In the geoephemeroïds life growth cycle short periods which are significant with visible growth and actions of monocarpic shoot and also roots are alternated with longer periods when no growth processes are shown. Two periods of dormancy can be recognized — winter and summer rest (GORYŠINA 1973, ŠULA 1976), when morphogenic activity of the vegetative apices are of various intensity. Generally, it can be said that the rest does not in fact exist, but different grades of morphogenic activity alternate during the year (SKRIPČINSKIĀ V. V. et SKRIPČINSKIĀ VL. V. 1976).

Ephemeroïds common either in deciduous leaf woods, or in open places without trees, begin to blossom very early in spring. Such as *Ficaria verna*, *Isopyrum thalictroides*, *Anemone nemorosa*, *A. ranunculoides*, the genera *Gagea*, *Arum*, *Scilla*, *Corydalis*, *Galanthus*, *Leucojum*, *Crocus*. There are also species from the genera *Tulipa* and *Hyacinthus* in this plant group. Many regularities of morphogenesis and life cycle were investigated by studying the latter two genera. Methods were worked out to speed up the alternation of life cycle periods and the forming of stems with flowers in other seasons of the year, as in natural conditions.

The present investigation deals with some aspects of the morphogenesis of *Ficaria verna* HUDS. (*Ranunculaceae*). This species is interesting from the point of view of the cytotaxonomy and the morphology with regard to an interesting phenomenon such as pseudomonocotily (WINKLER 1926), vegetative reproduction and mainly from the point of view of a generative one. The original aim of our research was to investigate the floral initiation and the course of the floral differentiation with special reference to processes of generative organs. Through this we had occasion to study some specific morphogenic processes.

According to DOSTÁL (1982) there are two subspecies of *Ficaria verna* HUDS. in Czechoslovakia: subsp. *verna* [Syn.: *Ranunculus ficaria* L. subsp. *fertilis* (Clapham) Lawalrée] and subsp. *bulbifera* (MARS.-JONES) Á. et D. LÖVE [Bas.: *Ranunculus ficaria* L. var. *bulbifer* MARS.-JONES, Syn.: *Ficaria bulbifera* (MARS.-JONES) HOLUB]. *Ficaria calthaeifolia* REICHENB. [Syn.: *Ranunculus ficaria* L. subsp. *nudicaulis* (A. J. KERNER) HEGI; *R. f.* subsp. *calthaeifolius* (REICHENB.) ARCANG.; *Ficaria verna* HUDS. subsp. *calthaeifolia* (REICHENB.) VELEN.] is regarded to be a different species.

The characteristic vegetative reproduction by way of bearing small bulbils in the axils of the caulines is mentioned for tetraploid type subsp. *bulbifera* ($2n=32$). This tetraploid type is highly sterile (MARSDEN-JONES 1935, METCALFE 1939, NEVES 1942, MARSDEN-JONES et TURRILL 1952, PERJE 1952, GILL et al. 1972, POGAN et WCISLO 1981). The reason of bad fructification may be according to these authors either abnormalities in the microsporogenesis and lack of germinating pollen grains and disorganization of embryo sac, or may be connected with nutrition qualities of the habitat (DOSTÁL R. 1923, METCALFE l.c.). The two other types (*F. calthaeifolia* and *F. verna* subsp. *verna*) are diploids ($2n=16$) (POGAN et WCISLO 1973, 1974, 1975).

Májovský (MÁJOVSKÝ et al. 1974, 1978) and FUTÁK (1982) mention two subspecies of *Ficaria verna* Huds. in Slovakia: subsp. *bulbifera* (ALBERT) Á. et D. LÖVE ($2n=32$) and subsp. *calthifolia* (REICHENB.) VELEN. ($2n=16$). We can suppose the taxonomic situation in our country is similarly complicated as in Poland and Hungary, where triploids and hexaploids were discovered (NEVES l.c., POGAN et WCISLO l.c.). The chromosome number $2n=20, 21$ and the presence of B chromosomes were published from western Europe (MARSDEN-JONES et TURRILL 1952., GILL et al. 1972).

All taxa from *F. verna* HUDS. bear underground root tubers. The initiation, the morphogenesis, the life cycle with its phases of varied activity of these tubers, their significance for the life of an individual and for the establishment of filial monocarpic shoot was the subject of more research works (DOSTÁL R. 1923., ŠULA 1976 etc.).

MATERIAL AND METHODS

Plant material for investigation was obtained from 17 populations from various parts of Slovakia (The Považský Inovec mountains, The Zvolenská kotlina valley, The Low Tatras, The Krupinská vrchovina mountains, The Podunajská nížina lowland). *Ficaria verna* HUDS. subsp. *bulbifera* (MARSDEN-JONES) Á. et D. LÖVE is common in all these localities. The population of *Ficaria calthaeifolia* REICHENB. and mixed populations of both mentioned taxa are in the locality of the castle park Palárikovo (The Podunajská nížina lowland).

The plant material was collected once a month during dormancy, once and twice a week in the time of more intensive development and growth processes during the period of three years (1981–1983). Navashin fixative was used. Then common methods of dehydration, infiltration and embedding were used. Sections were cut between 10 and 15 μm . Delafield and Heindenhein's haematoxylin and anilin blue were used for staining.

The germinability of pollen grains was examined by cultivation in vitro in laboratory conditions on 1 % agar with various percents of saccharose and glucose. The percentage of germinated pollen grains was counted of 50 pollen grains. The average length of pollen tube was obtained from measurement of 30 pollen tube lengths after 48 hours from the beginning of cultivation.

RESULTS

Towards the beginning of September, when the summer dormancy of root tubers was finished, the activity of all living processes resumes. Basal part

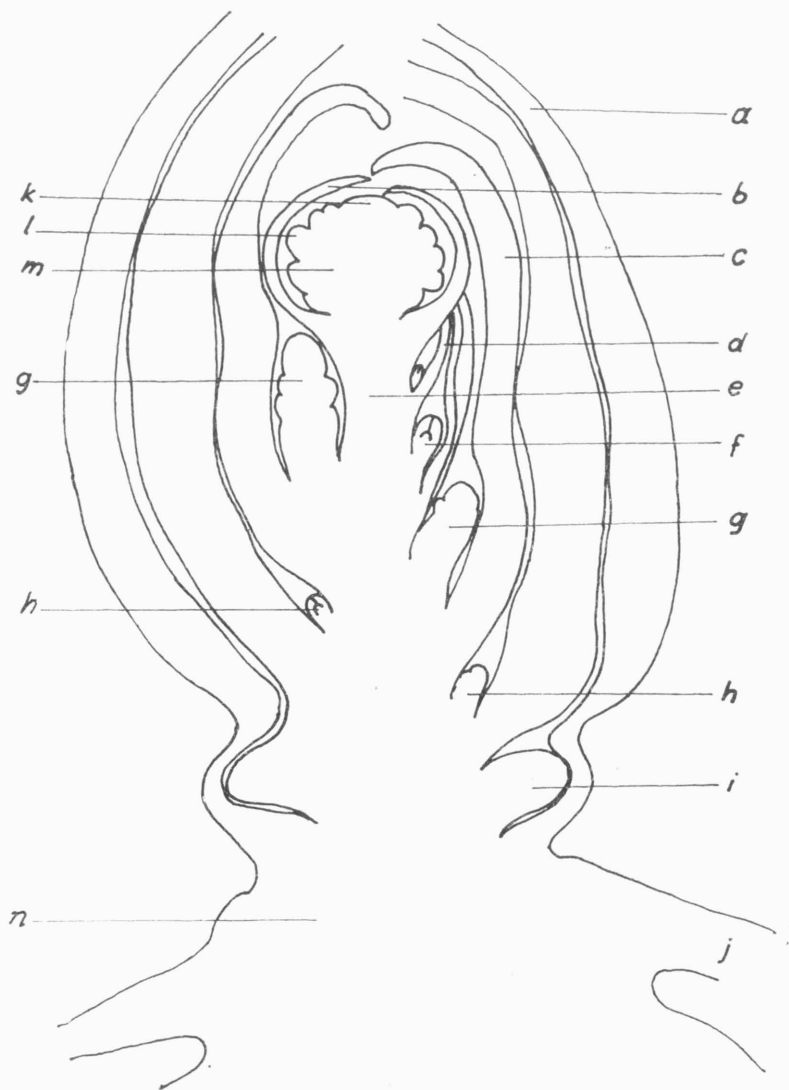


Fig. 1. Schematic longitudinal section of the renewal bud: a — scale leaf, b — perianth, c — rosette leaf, d — cauline, e — caulone, f — axillary bulb primordium, g — lateral shoot, h — bud primordium for the next vegetative period, i — root tuber, j — feeding root, k — primordium of pistils, l — stamen primordium, m — floral primordium, n — residue of the shoot from the last vegetative period.

of sister root tubers is connected by a residue of the monocarpic shoot, which has the appearance of a disc-like formation with many scars from squamae similar to rhizomes of other geophytes. A few renewal buds (1—6) formed a year ago in that part of disc-like formation, which remains connected with bases of root tubers. Only one of these buds usually gives the origin of new monocarpic shoot. The first demonstration of morphogenic activity is the feeding root formation at the base of the renewal bud. A few weeks later several new root tubers arise in the axils of its outer scale leaves. These root tubers develop and in the same vegetative period grow out through the scale leaves of the mother bud. At about that time the growth apex of the monocarpic shoot prolongates and the rosette primordia form and later on cauline ones, too. The caulines (2—4) alternate on the young stem. In the axils on rosettes a few stems are formed (2—3), which are of ascendent axis character.

In the beginning of October the rich system of feeding roots is produced at the base of one renewal bud. In the axils of the bud outer scale leaves root tubers are established and in different degrees differentiated. Bud primordia for the new vegetative period originate into axils of bud inner scale leaves.

The qualitative transformation of the growth apex from vegetative structure to the generative — reproductive one takes place in November. At that time bud primordia are recognized in the axils of young caulines. After winter dormancy, a single root tuber arises at the base of each bud. This formation is usually called the axillary bulbil (Fig. 1, 3).

High regenerative ability of each root tuber was observed. After the amputation of the basal part of root tuber and its cultivation *in vitro* a callus is formed round the cutting part. In suitable conditions (high humidity, temperature about 0 °C) a few (1—3) new buds originate into the callus during three or four weeks. The tuber tissue has this regenerative ability only up to a certain distance from its base. Several days before growth apex prolongation in these buds new root tubers are initiated in axils of outer scale leaves without feeding roots being formed at the base of the bud. In the first vegetative period the growth apex does not transform into generative structure. It can be said, that morphogenesis into these buds differs from that into intact individuals (Fig. 6).

Petals are originated from the base of the floral primordium first and sepals follow. Androeceum originates from the peripheral fundament of the floral primordium at about beginning of November. Sepals grow up over the floral primordium and cover it.

Soon after the stamen initiation the anther wall is differentiated. The subepidermal layer of the stamen primordium, primary archesporium is divided into the outer parietal layer and the inner layer of secondary archesporium. The wall of a mature anther is formed from three rows of cells: epidermis and two cell rows of the fibrous layer. The tapetum is secretitious. Before and during winter dormancy the tapetum cells are two — nuclear. Secondary archesporium is composed from large cells (ca. $20 \times 20 \mu\text{m}$) with a distinct nucleus (ca. $10 \times 10 \mu\text{m}$) with nucleolus. The mitotic division of the archesporial tissue lasts till the end of November. Winter dormancy takes from eight to ten weeks.

Futher facts concern the flower of the main stem. The activity of the male

archesporium is renewed in February, when the sporogenous cells are enlarged. They become round, have denser cytoplasm with a larger nucleus and nucleolus than the other anther cells have. The cells of secondary archesporium are transformed into microsporocytes in spring. Meiosis in microsporocytes takes place in March. During the meiosis tapetal cells are polygonal with three to five nuclei. Their size is about $30 \times 40 \mu\text{m}$. Meiocytes are round, large in average $30 \times 30 \mu\text{m}$. Duration of meiosis is in different anthers asynchronic. Microspores are placed in a tetradic shape. Tetradsogenesis takes place simultaneously. The course of meiosis is relatively quick. The heterotypic and homeotypic phases of meiosis take place during two or three days, respectively. The microspores stay in tetrads about four or five days. Development of pollen grains takes about two weeks. The exine is formed immediately which makes observation of the first mitotic division of the pollen grain nucleus very difficult. The mature pollen grain is two-nuclear. Division of the generative nucleus follows the entrance of the nucleus into the pollen tube.

Anomalies in tetradsogenesis were observed in some microsporocytes. Instead of tetrads, pentads up to polyads were originated. Due to these anomalies, microspores of different diameters and also pollen grains of various shapes and diameters were formed.

The tapetal cells do not keep their diameter until anthesis. In stages of tetrads tapetal cells keep their diameter, as was mentioned, by the stage of meiocytes, but during the pollen grain formation they change their shape and diameter. The shedding of pollen grains starts in April and in various individuals continues slowly for about a month.

There were many germinating pollen grains and growing pollen tubes (1—15) found on the longitudinal sections of stigma. The viability of pollen grains *in vivo* seems to be sufficient.

It was experimentally found that the most suitable medium for the germination of pollen grains *in vitro* is 1 % agar with 10 % saccharose. The viability of pollen grains was observed in ten populations. It varied from 25 % (The Zvolenská kotlina valley, The Low Tatras) to 90 % (The Podunajská nížina lowland). The pollen tube lengths varied from 150 to 1450 μm .

The female reproductive organs originate on the apical part of the floral primordium in autumn (the second half of November). These organs are formed as an apocarpous gynoeceium. The ovule primordium arises in autumn as a small group of meristematic cells on the adaxial side of the forming carpellary cavity. The single integument is developed from the outer part of the meristematic initial and the nucellus from its central part in February. The mature ovule is anatropous, unitegminal and crassinucellar and completely fills the carpellary cavity (Fig. 2,5).

The hypodermal archesporial initial enlarges and functions directly as a mother cell of megaspores. The meiotic division in the megasporocytes takes place a few days later than it does in microsporocytes in the same flower. Tetrads of megaspores are not formed the same way in all ovules neither of the same floral bud. Megaspores are placed in tetrads in a tetradic, linear or T shape.

The development of megaprothallium has not been observed in all details due to anomalies in its various developing stages. It was observed two, four,

eight and seven — cellular stages of the embryo sac and stage of the free nucleate endosperm.

The size of the four cellular embryo sac is approximately $100 \times 90 \mu\text{m}$. During development up to ripeness its size does not change. The size of the ripe embryo sac is $110 \times 90 \mu\text{m}$. Antipods are round cells, easily stainable, their size is about $30 \times 30 \mu\text{m}$ with a large nucleus ($20 \times 25 \mu\text{m}$). Synergids have a tear shape and their nucleus is about $8 \times 8 \mu\text{m}$. This nucleus is pressed to the micropylar end of the embryo sac by a large vacuole. The egg cell is small (about $15 \times 15 \mu\text{m}$) with the nucleus (about $8 \times 8 \mu\text{m}$) in its centre. The size of the polar nuclei is about $20 \times 20 \mu\text{m}$ with a small nucleus ($8 \times 8 \mu\text{m}$). The fusion of the polar nuclei takes place before fertilization.

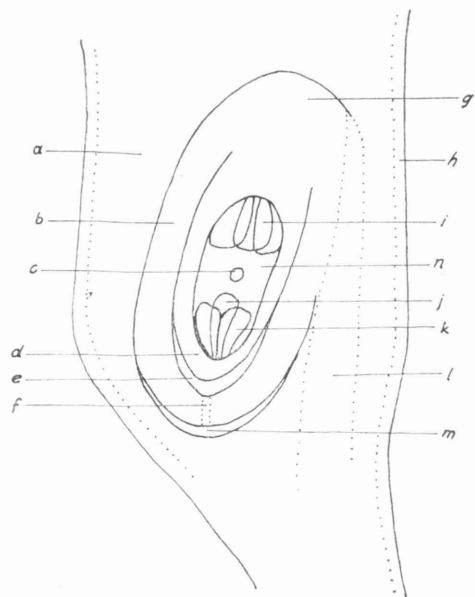


Fig. 2. Schematic longitudinal section of the ovary: a — ovary, b — integument, c — nucleus of the central cell, d — nucellus, e — cavity between the top of the nucellus and the integument, f — micropyle, g — chalaza, h — epidermis, i — antipods, j — egg cell, k — synergid, l — vascular bundle, m — cavity of the ovary, n — embryo sac

The development of the female gametophyte is quite variable. In many cases anomalies in tetradogenesis caused the degeneration of all four megaspores were observed. In some ovules a disorganization of the embryo sac takes place in its two or four cellular stage. In many section of pistils such embryo sacs were observed, which have neither any nuclei nor cytoplasm on its micropylar end. Either in these or in normal developed embryo sacs into their eight cellular stage and in the stage of free nuclear endosperm three large antipods were found into the chalazal and of embryo sacs. The size of these embryo sacs has not been changed in comparison with the ripe embryo sac stage. The cavity of this embryo sac is about $200 \times 120 \mu\text{m}$. In later stages after the abortion of embryo sac a disorganization of nucellar cells begins.

Pollen tubes growing through the tissue of stigmas were found either in normal or in abnormal developing megaprothalliums. The growth of the pollen tubes through a tissue of the ovule has never been observed not even in these ovules, where free nuclear endosperm has been found (Fig. 4).

DISCUSSION

There are two subspecies of the genus *Ficaria* in the territory of Slovakia according to our present knowledge. A different taxonomical value — species or subspecies is given to these taxons by different authors (MÁJOVSKÝ 1974, 1978, FŮTÁK 1982).

Ficaria verna HUDS. subsp. *bulbifera* (MARSDEN-JONES) Á. et D. LÖVE rank among those spring geophytes which were given attention from various points of view. The reason of this interest is certainly the great changeability of different populations. Also some of the other characteristics of this taxon have attracted attention of investigators: at first there are axillar bulb formation and a very striking reduction of the sexual reproduction, it means the limited production of viable seeds. These two characteristics mentioned above have been given to a coherence by many authors. The other investigators explained the reduction of the sexual reproduction above all by nutritious conditions, by quality of environment (DOSTÁL R. 1923).

Many authors have given attention to the cytotaxonomic research but more to the morphogenesis of male and female generative organs, to the processes of the fertilization and the production of viable seeds respectively to reasons and processes of their disorganization.

Our observations confirm the reduction of generative organs in a various stages of development, which were previously observed. An unambiguous answer of reasons of the frequent sterility of *Ficaria bulbifera* has not yet been given and it is hardly expected in future. The most acceptable opinion seems to be Loschnigg's one (l.c.), who mentioned that the disorganization of reproductive organs of *Ficaria bulbifera* is hereditary fixed.

Some authors believed, that a failure of the pollen to germinate is partly responsible for the lack of viable seed. Our results do not confirm these suggestions.

Some authors have brought new and interesting views about the initiation and further morphogenesis of vegetative and reproductive organs. ŠULA (1976) evidently gave the most attention on this problem. Some of our results agree with his information. From some points of view we bring additional and new observations mainly in the initiation of underground tubers and axillary bulbils, monocarpic stem of a different order, in the morphogenesis of leaves and generative organs.

In the main renewal bud formed a year ago, a rich system of feeding roots is developed in September. In the axils of the outer bud scale leaves are based and in different degrees differentiated root tubers. Some of them grow through the scale leaves of the mother bud in the same vegetative period. In axils of inner bud scale leaves originate bud primordia for the next vegetative period. The growth apex prolongates during October and the rosette primordia and later cauline ones are formed. In the axils of young caulines there are based axillary bulbils. The initiation and differentiation of floral parts take place in November.

There are not any conclusive arguments about a way of the embryo

initiation. Neither LOSCHNIGG (l.c.) nor the other authors observed any apomixis. On the other hand no authors have been able to demonstrate amphimixis yet, in spite of that fact that a presence of pollen tubes were observed on the stigma.

From the results of our research, we can conclude that there are two obvious reasons of this condition. The first being based on internal hindrances, which are genetically fixed. The second being based on environmental conditions.

SÚHRN

Štúdium morfogénézy reprodukčných orgánov *Ficaria verna* Huds. subsp. *bulbifera* (ALBERT) Á. et D. LÖVE potvrdilo údaje starších autorov o poruchách v mikrosporogénéze a megasporogénéze, ako aj disorganizáciu zárodočného mieška v rôznom štádiu vývoja. Ako príčinu sterility druhu uvádzajú niektorí autori nedostatok životaschopného peľu. Na rozdiel od týchto údajov sme pozorovali v pletivách blizny niekoľko (1–15) kľúčiacich peľových zŕn resp. rastúcich peľových vrecúšok. Skúška kľúčivosti in vitro ukázala, že kľúčivosť peľových zŕn kolíše pri rôznych populáciách medzi 25 % až 90 %. Dĺžky peľových vrecúšok in vitro boli od 150 μ m do 1450 μ m.

V bazálnych častiach obnovovacieho púčika, založeného pred rokom, sa v septembri vytvorí bohatý koreňový systém. V pazuchách vonkajších obalových šupín púčika sa zakladajú a ďalej diferencujú koreňové hlúžky. Niektoré z nich ešte v tom istom vegetačnom období prerastú cez obalové šupiny materského púčika. V pazuchách mladších obalových šupín púčika sa zakladajú primordiá nových obnovovacích púčikov.

Rastový vrchol púčika sa predlžuje. V októbri sa zakladajú listy prízemnej listovej ružice a neskôršie aj listy striedavo postavené na stonke. Začiatkom novembra sa rastový vrchol premení na kvetný základ. V pazuchách listov na stonke sa zakladajú primordiá púčikov, ktoré v budúcom vegetačnom období dajú vznik pazušným hlúžkam.

Zimná dormancia trvá u *Ficaria verna* subsp. *bulbifera* v sledovaných populáciách 8–10 týždňov. V mikrosporangiách prebieha mitotické delenie buniek sekundárneho archesporu do konca novembra, v tom istom čase sa vo formujúcej dutine semenníka zakladá primordium vajčka.

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See also Plate X (figs. 3—6) in the Appendix

F. Boerner:

Blüengehölze für Garten und Park

3. vydání, přepracoval H. Scheller. Verlag Eugen Ulmer, Stuttgart 1985, 272 str., 94 barevných fotografií, cena váz. 88,— DM. (Kniha je v knihovně ČSBS.)

Nedostatek populárně vědeckých dendrologických příruček má u nás bohužel již dlouholetou tradici, kterou nenarušilo ani poměrně nedávné vydání Praktické dendrologie K. Hiekeho (1978). V tomto směru bychom se měli poučit od německých kolegů; Boernerova kniha vychází již ve třetím vydání, upraveném po smrti autora H. Schellerem.

F. Boerner patřil k nejvýznamnějším praktickým dendrologům. Pro jeho práci je příznačná snaha o pochopení života rostlin, která již od zahradnických začátků určovala i celý běh jeho života. Rozsáhlé znalosti a zahradnická praxe získané v různých oblastech světa ho přivedly až do botanické zahrady v Darmstadtu, kde se stal ředitelem na mnoho let. Z jeho publikací, významných pro popularizaci dendrologie, jmenujme alespoň knihu *Nadelgehölze für Garten und Park* (1969).

Prvé kapitoly recenzovaného díla (asi 20 stran) podávají ve zkrácené formě informace o historii introdukce dřevin, o pravidlech pojmenování, vysvětlují základní ekologické pojmy, uvádějí příklady v odných druhů pro některá stanoviště (vřesoviště, „stepi“), možnosti nákupu a praktické rady pro přesazování a řez. Těžiště publikace spočívá ve výčtu dekorativně nejvýznamnějších listnatých dřevin parků a zahrad, tříděných podle zahradnického použití do několika skupin: keře, pěníšníky a jiné vřesovcovité, stálezelené listnáče, stromy a vysoké keře, dřeviny zvláštních tvarů, stromy a keře ozdobné plody, podzemním zbarvením listů, liány a dřeviny zakrslé. Autor uvádí jejich nápadné morfologické znaky, vybrané kultivary, péstitelské požadavky a způsob použití. Úsporná forma textu nedovolila zařazení většího počtu druhů a kultivarů, jmenovaných v rozsáhlejších dendrologických příručkách. Přesto je výčet rodů rozsáhlý a sadovnický významný vypadlo jen nemnoho (např. *Aristolochia*, *Carya*, *Diervilla*, *Gymnocladus*, *Platanus*). Publikaci uzavírá kombinovaný rejstřík latinských a českých jmen druhů.

Taxonomovi poněkud vadí, že nejsou uvedena jména čeledí jmenovaných rodů, což má často význam i pro pochopení stanovištních nároků. Rozdělení rostlin do skupin podle praktického použití má v zahradnické příručce své oprávnění, ale většina čtenářů dává přednost abecednímu řazení. Publikace je ilustrována 94 barevnými fotografiemi vesměs vynikající kvality. Lze ji doporučit všem, kteří mají zájem o bližší poznání a pěstování okrasných dřevin.

V. Zelený