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The development rhythm of the flower-bud in some *Papilionaceae* species. III. Macrosporogenesis, microsporogenesis and early gametogenesis in several species of the *Vicieae* tribe

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Abstract

Each of the examined species of the tribe *Vicieae* (*Vicia faba, V. sativa, V. villosa, Lathyrus silvester, L. pratensis* and *Pisum sativum*) has its peculiar characteristic development rhythm of the bud. A similarity has been demonstrated between the development rhythms of flower buds of *Vicia faba* and *Pisum sativum*. It was found that mature flowers of autogamous species had long calyces, whereas those of the allogamous species were short as compared with the petals of the corolla.

INTRODUCTION

The aim of earlier and of the present investigations was to find an answer to the question whether within definite plant groups such as for instance species, genus, family, class or else within autogamous of allogamous plants there exist specific regularities in the development of the flower bud. In the present study the development rhythms of flower buds were compared in six species of the *Vicieae* tribe. For this purpose the relations were investigated between generative and vegetative parts development in the flower, between the course of female and male sporogenesis and gametogenesis and between the development of the petals and sepals.

MATERIAL AND METHODS

The buds of the following autogamous species were studied: *Vicia sativa* cv. Jaga, and *Vicia faba* cvs. Nadwiślański and Major and of the allogamous species: *V. villosa* cv. Rea, *Lathyrus silvester* var. *platyphyllus* (Retz.) Aschers and *L. pratensis* L. with disregard in the last

of the enumerated species of female sporogenesis and gametogenesis. As starting material for comparison served the previously studied pea, *Pisum sativum* cv. Folger (W. Wojciechowska 1978, W. Wojciechowska and Mackiewicz 1981). The material was collected in the period 1976-1980. Fresh buds were analysed and those fixed in FAA, embedded in paraffin, sectioned longitudinally, stained with Heidenhein haematoxylin and additionally with Fast Green. Similarly as in *Ornithopus*, stages (B. Wojciechowska 1972) and in *Pisum*, substages (W. Wojciechowska 1978) were distinguished in bud development.

For ascertaining the way of pollination of both species of the genus *Lathyrus*, their flowers were isolated and the literature data were verified (Hegi 1924). One half of the isolated flowers were left without pollination until overblowing and the other half were artificially selfpollinated within the inflorescence. The number of pods and seeds set after selfpollination and free pollination served as index of the degree of selfcompatibility.

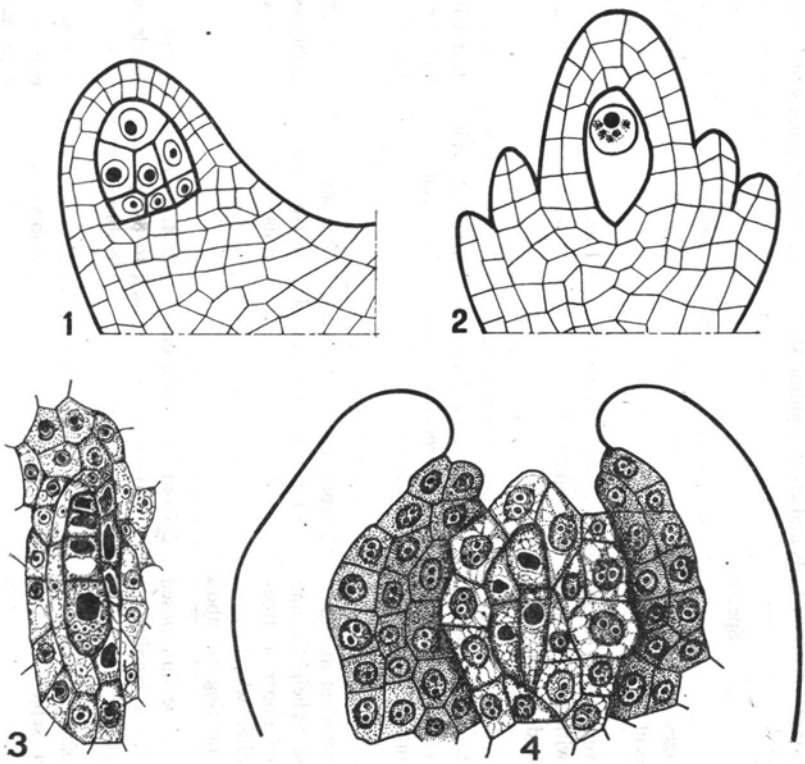
The drawings were prepared by means of a drafting machine.

RESULTS AND DISCUSSION

Most of the results are listed in Tables 1-3. The literature to date describes macrosporogenesis in three of the five here compared species: in *Pisum sativum* by Cooper (1938), in *Vicia faba* by Mitchel (1975) and in *Vicia villosa* by Rembert (1969). These authors found in the above named species linear tetrads and observed the development of the chalazal macrospore. Rembert (1969) reports also sporadic T-tetrads in *Pisum sativum* and triads in *Vicia villosa*. The results of these authors agree with those obtained in the present study. In the latter macrosporogenesis was for the first time analysed in *Lathyrus silvester* and *Vicia sativa*. A multi--celled archaespore (Fig. 1) was noted in the latter, in which one (Fig. 2) or more macrosporocytes arose. As the result of meiosis a linear tetrad was formed. The chalazal macrospore developed into a monospore sac of *Pologonum* type. Two tetrads were also observed in the ovules, one of which degenerated completely (Fig. 3). The appearance of two linear tetrads was observed by Rembert (1969) in *Vicia villosa*. Their formation in this species is confirmed by the present results. Neither in *V. sativa* nor in *V. villosa* were however, two mature embryo sacs observed in one ovule, this indicating degeneration of one tetrad or one of the two developing young sacs. In *Lathyrus silvester* anisobilateral and linear tetrads were observed (Fig. 4). Anisobilateral tetrads have been described in *L. latifolius* (Rembert 1969) and, a species closely related to

L. silvester. In this case the further developing macrospore is one of the two larger chalazal ones. It results from the foregoing descriptions that all the studied species are characterised by the development of a monospore embryo sac. Therefore, comparison of the rate of their macrosporogenesis with that of the remaining parts of the bud is possible. Macrosporogenesis was found to occur most rapidly in relation to the developing petals in *Vicia villosa* and *V. sativa*, slower in *V. faba* and slowest in *Lathyrus silvester* and *Pisum sativum* (Table 1). Later, however, in substage I/4 when the androecium is enclosed in the overlapping petals of the corolla, there begin to appear in all these species eight-nucleate embryo sacs. This indicates that the initial differences in the rate of female sporogenesis as compared with that of petal growth are obliterated in the course of gametogenesis.

As compared with petals growth, the steps of advancement of microsporogenesis and pollen grain formation (Table 2) are very similar in *Lathyrus pratensis, L. silvester* and *Pisum sativum*. In both *Vicia faba*



Figs. 1-3. Macrosporogenesis in *Vicia sativa*. Fig. 1 — young ovule with archaesporial cells, × 600. Fig. 2 — ovule with macrosporocyte in prophase I, × 600. Fig. 3 — two twin tetrads in one ovule; the one on the right degenerates completely, × 550

Fig. 4. Anisobilateral tetrad in *Lathyrus silvester*, × 550

Table 1

Development stages of flower buds and corresponding stages of megasporogenesis and embryo-sac development in some species of *Vicieae* tribe

Stages and substages of bud development \ Species		*Vicia faba* L. ssp. *minor* cv. Nadwiślański	*Vicia sativa* L. cv. Jaga	*Vicia villosa* Roth. cv. Rea	*Lathyrus silvester* var. *platyphyllus* (Retz.) Aschers	*Pisum sativum* L. cv. Folger
Stage I — closed green bud petals are not visible between the sepals	I/1 — vexillum ± equal with apex of lower androecium whorl	4 macrosporocytes in prophase I	1 archaesporial cells	—	—	13 from pistils without ovules to pistils with ovules with archaesporial cells
	I/2 — vexillum above lower androecium whorl but below upper whorl	2 from macrosporocytes in prophase I to macrosporocytes in metaphase I	22 from archaesporial cells to tetrads	8 from macrosporocytes in prophase I to 1-nucleate embryo-sacs	—	95 from ovules in form of undifferentiated protuberances to ovules with macrosporocytes in prophase I
	I/3 — vexillum at the same height as apex of upper androecium whorl or standing out above	2 from macrosporocytes in prophase I to tetrads	10 from tetrads to 1-nucleate embryo-sacs	4 from 1-nucleate embryo-sacs to 2--nucleate ones	8 from macrosporocytes in prophase I to 2-nucleate embryo-sacs	33 from macrosporocytes in prophase I to 1-nucleate embryo-sacs
	I/4 — androecium closed in overlapping petals	5 from 1-nucleate embryo-sacs to 8-nucleate ones	25 from tetrads to 8-nucleate embryo-sacs	3 from 4- to 8--nucleate embryo-sacs	3 from 2- to 8-nucleate embryo-sacs	31 from tetrads to 8-nucleate embryo-sacs
Stage II	petals slightly visible through sepals	4 from 2- to 8-nucleate embryo-sacs	11 8-nucleate embryo-sacs	10 from 4-nucleate embryo-sacs to 8-nucleate ones	—	3 from 4- to 8-nucleate embryo-sacs

Arabic numerals indicate the number of investigated buds

Table 2

Course of microsporogenesis, pollen grain formation in relation to the changing colour of anthers in some species of *Vicieae* tribe in reference to flower-bud development

Stages and substages		Course of microsporogenesis	*Vicia faba* L. ssp. *minor* cultivar Nadwiślański	*Vicia faba* L. ssp. *minor* cultivar Major	*Vicia sativa* L. cultivar Jaga	*Vicia villosa* Roth. cultivar Rea	*Lathyrus pratensis* L.	*Lathyrus silvester* var. *platyphyllus* (Retz.) Aschers	*Pisum sativum* L. cultivar Folger
Stage I Closed green bud — petals are not yet visible between the sepals	I/1 vexillum± equal with apex of lower androecium whorl	microsporogenesis and pollen grain development	3 microsporocytes in prophase I	2 archaesporial cells	7 from archaesporial cells to tetrads	0 —	3 archaesporial cells, microsporocytes in prophase I	0 —	18 from stamens at very early stages of differentiation to microsporocytes in prophase I
		anther colour	light green glassy	light green glassy	light green glassy	—	light green glassy	—	light green glassy
	I/2 vexillum between lower androecium whorl and upper whorl	microsporogenesis and pollen grain development	31 from archaesporial cells to slightly vacuolized microspores	6 from archaesporial cells to vacuolized microspores	46 from microsporocytes in prophase I to 2-celled pollen grains	14 from microsporocytes in prophase I to vacuolized microspores	29 from archaesporial cells to very young non-vacuolized microspores	18 from archaesporial cells to very young non vacuolized microspores	91 from archaesporial cells to very young non-vacuolized microspores; in one case slightly vacuolized microspores
		anther colour	light green glassy; green-white	light green glassy; green-white	light green glassy; green-mat	light green glassy; green mat	light green glassy	light green glassy; green	light green glassy
	I/3 vexillum at the same height as apex of upper androecium whorl or standing out above it	microsporogenesis and pollen grain development	51 from tetrads to 2-celled pollen grains	10 from very young nonvacuolized microspores to 2-celled pollen grains	31 from vacuolized microspores to 2-celled pollen grains	13 from very young non vacuolized microspores to 2-celled pollen grains	21 from tetrads to 2-celled pollen grains	24 from tetrads to 2-celled pollen grains	106 from tetrads to 2-celled pollen grains
		anther colour	green, green-white, white mat	green, green-white, white mat	light green glassy, green-white, white	green mat, green-yellow	green, green mat, light yellow	light green glassy, green, green-yellow	light green glassy, green mat, light yellow, orange
	I/4 androecium enclosed in overlapping petals	microsporogenesis and pollen grain development	49 from vacuolized microspores to 2-celled pollen grains	7 2-celled pollen grains	66 2-celled pollen grains	10 from vacuolized microspores to 2-celled pollen grains	16 from vacuolized microspores to 2-celled pollen grains	9 from slightly vacuolized microspores to 2-celled pollen grains	89 from vacuolized microspores to 2-celled pollen grains
		anther colour	green-white, white mat	green-white, white mat	green-white, white mat	green mat, green-yellow mat	green mat, light yellow mat	green, green--yellow	orange
Stage II	petals slightly visible throught sepals	microsporogenesis and pollen grain development	11 2-celled pollen grains	0 —	11 2-celled pollen grains	15 2-celled pollen grains	15 2-celled pollen grains	9 2-celled pollen grains	7 2-celled pollen grains
		anther colour	white mat	—	white mat	yellow--green mat	light yellow	yellow-green light yellow	orange

Arabic numerals indicate the number of investigated flower-buds

varieties the microsporogenesis rate in relation to the rate of growth of the petals is slightly faster than in the above mentioned species, whereas in *Vicia villosa*, and particularly in *V. sativa* the rate of microsporogenesis in relation to petal growth is fastest as compared with the rate in the above mentioned species. In the later stage of growth, when the petals are slightly visible between the sepals (stage II of bud development) only two-celled pollen grains are noted in all the species examined. In all these species the first distinct change in the anther colour occurs in the period of microspore vacuolisation (Table 2).

It results from Tables 1 and 2 that in the species in which a rapid rate of macrosporogenesis was observed as compared with that of the petals, microsporogenesis also has a faster course. It may, therefore, be supposed that the identical or closely similar rate of microsporogenesis in *Pisum, Lathyrus pratensis* and *L. silvester* may be an indication that in these species the rate of macrosporogenesis in relation to petal growth is also identical or very similar. The easiness with which the successive stages of microsporogenesis can be determined in the particular stages of bud development is very tempting as compared with the complicated methods of macrosporogenesis investigation. In order to check the above mentioned supposition, the corresponding in time stages of macrosporogenesis and ovule development in the studied species (Table 3) were confronted with the stages of microsporogenesis and pollen development. It does not, however, result from this comparison that the similarity appearing in various species in the rate of microsporogenesis in reference to petal growth indicates in the same species a similarity in macrosporogenesis. For instance in *Lathyrus silvester* the tetrad stage in the anthers is accompanied by a still young mononucleate embryo sac, whereas in *Pisum* at the same stage old vacoulised microspores are visible or two-celled pollen grains. It also results from Table 3 that there is agreement between the rhythms of micro- and megasporogenesis in *Vicia faba* and *Pisum sativum.* In these species sporogenesis in the anthers and ovules has in reference to petal growth a similar course, the course of male and female sporogenesis being slightly faster in *Vicia faba.* Identical or very similar rhythms of flower bud development are mostly observed in the species capable of forming hybrids or hybrid embryos. For instance castrated pea flowers after polination with *Vicia faba* pollen set hybrid embryos which degenerate (Gritton and Wierzbicka 1975). An identical bud development rhythm in *Ornithopus sativus* and *O. compressus* was found by B. Wojciechowska (1972). According to Griesinger and Klinkowski (1939) hybrids of these species occur spontaneously in natural conditions. The bud development rhythm in *Ornithopus pinnatus* is the same as in *O. compressus* (W. Wojciechowska 1975), hitherto, however, no trials have been made to obtain hybrids between

Table 3

Course of microsporogenesis and pollen grain formation in relation to macrosporogenesis and development of embryo-sac in some species of *Vicieae* tribe

Macrosporogenesis and embryo-sac formation	*Vicia faba* L. ssp. *minor* cv. Nadwiślański	*Vicia sativa* L. cv. Jaga	*Vicia villosa* Roth. cv. Rea	*Lathyrus silvester* var. *platyphyllus* (Retz.) Aschers	*Pisum sativum* L. cv. Folger
	microsporogenesis and pollen grain formation				
Archaesporial cells	1 microsporocytes in prophase I	1 microsporocytes in prophase I	—	—	43 archaesporial cells and microsporocytes in prophase I
Macrosporocytes in prophase I	2 from microsporocytes in prophase I to very young nonvacuolized microspores	15 from microsporocytes in prophase I to slightly vacuolized microspores	3 from microsporocytes in prophase I to tetrads	2 tetrads	68 from microsporocytes in prophase I to vacuolized microspores
From macrosporocytes in metaphase I to telophase II	2 from very young nonvacuolized microspores to vacuolized ones	2 slightly vacuolized microspores	—	3 tetrads	15 from very young nonvacuolized microspores to old and vacuolized ones
Tetrads	1 vacuolized and dividing microspores	15 from slightly vacuolized microspores to 2-celled pollen grains	3 from tetrads to very young nonvacuolized microspores	4 from tetrads to slightly vacuolized microspores	9 from old vacuolized microspores to 2-celled pollen grains
1-nucleate embryo-sac	1 2-celled pollen grains	10 from vacuolized microspores to 2-celled pollen grains	3 tetrads to vacuolized microspores	1 slightly vacuolized microspores	9 from vacuolized microspores to 2-celled pollen grains
2-, 4-, and 8-nucleate embryo-sac	8 2-celled pollen grains	20 2-celled pollen grains	14 from vacuolized microspores to 2-celled pollen grains	4 from slightly vacuolized microspores to 2-celled pollen grains	23 2-celled pollen grains

Arabic numerals indicate the number of investigated buds

these species. In *Lupinus mutabilis* and *L. elegans* similarity was noted in the development rhythm of buds (W. Wojciechowska 1976). As the result of crossing of these species mature hybrid pods are formed without seeds (Kazimierski 1963). It would seem that the ovaries persisting up to the period of maturity develop owing to suc-

Table 4

Pod setting as compared with number of flowers in inflorescence and number of seeds in reference to the number of ovules in the ovaries of *Lathyrus pratensis*, L. *silvester* and V. *villosa*

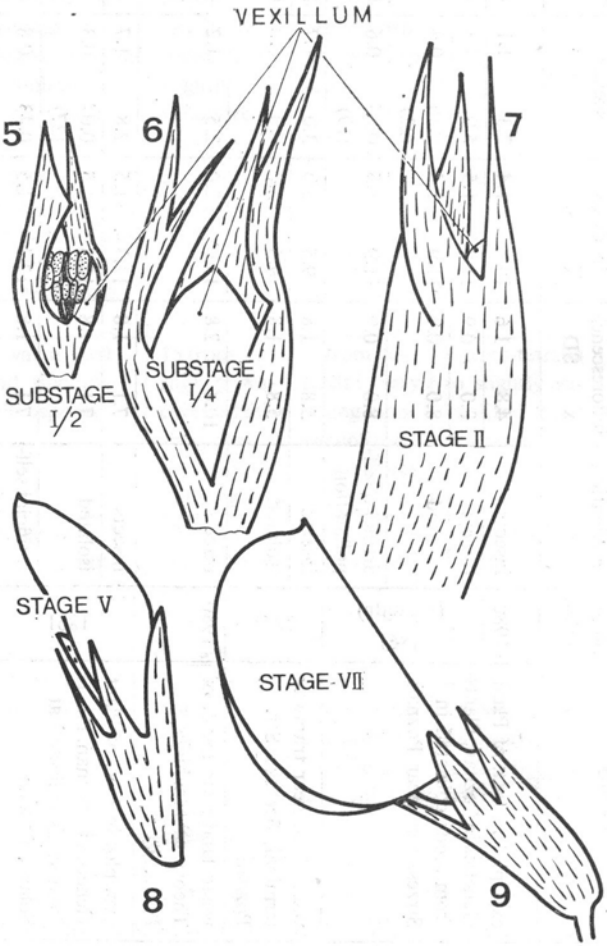
Species	Locality	Year of observation	Mode of pollination	No. of flowers in inflorescence $\bar{x}$	SD	No. of ovules in ovary $\bar{x}$	SD	No. of pods in infructescence $\bar{x}$	SD	No. of seeds in pod $\bar{x}$	SD	Percentage of pods set in infructescence	Percentage of seeds set in pod	Percentage of seeds set in infructescence
Lathyrus pratensis L.	exp. plot in Inst. of Plant Genetics in Poznań. Plants from seeds collected in Strzeszynek near Poznań	1980	insects	4.8	1.6	10.2	1.4	2.3	1.1	4.3	2.1	45.8	42.8	19.3
		1981 (aphides)	insects	8.0	0.9	11.9	1.5	5.0	1.8	4.1	2.0	62.5	34.5	21.5
			isolated	8.0	0.9	11.9	1.5	0.36 (22)	0.4	—	—	5.0	—	—
			artificial self-pollination	8.0	0.9	11.9	1.5	0.26 (19)	0.6	0.6	0.5	3.3	5.0	0.2
	waste land near tramway terminal, Serbska Str. Poznań	1981	insects	5.8	1.8	9.5	2.0	3.0	1.7	3.9	2.2	51.7	41.1	21.2
			isolated	5.8	1.8	9.5	2.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Lathyrus silvester var. *platyphyllus* (Retz.) Aschers	waste land near Dept. of Theory of Machines, Poznań	1980	insects	10.4	2.8	13.0	2.0	2.5	1.2	5.6	2.0	24.0	43.1	10.4
	exp. plot in Inst. of Plant Genetics in Poznań. Plants from seeds collected at Sołacz, Poznań	1981	insects	7.1	1.8	12.3	1.5	2.8	1.7	4.7	2.1	39.4	38.2	15.1
			isolated	7.1	1.8	12.3	1.5	0.07 (27)	0.3	5.0 (2)	—	0.8	44.2	0.4
			artificial self-pollination	7.1	1.8	12.3	1.5	0.43	0.8	4.6 (13)	2.4	6.1	37.4	2.3
Vicia villosa Roth.	exp. plot in Inst. of Plant Genetics in Poznań	1981	insects	17.4	4.8	6.7	0.9	3.1	1.2	3.5	1.4	17.8	52.2	9.3

$\bar{x}$ — mean, SD — standart deviation, means calculated from 30 observations, exceptionally from a smaller number given in parentheses under mean.

cessful allogamous fertilisation. This supposition, however, can only be confirmed by embryological studies.

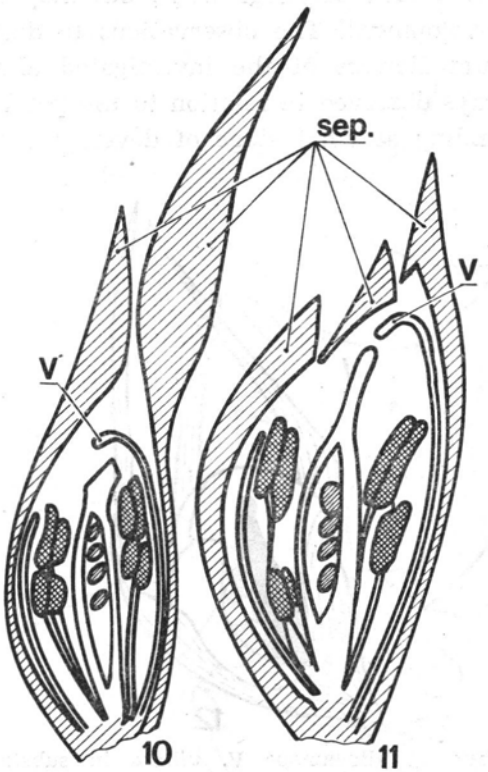
It results from Tables 1-3 that, in spite of similarities in bud development between related species each of the six investigated species of the *Vicieae* tribe has its specific development rhythm.

Analysis of pods and seeds setting after different ways of pollination confirmed the allogamy of both species of the genus *Lathyrus*, indicating at the same time their selfincompatibility (Table 4). Since pods setting in *Vicia villosa* has been exhaustively elaborated by Młyniec (1962), flowers of this species were not isolated. In the study of the interrelations in the development of the perianth the earlier advanced supposition (W. Wojciechowska 1976, 1978) that allogamous plants are characterised by a rapid growth of petals from the calyx,



Figs. 5-9. Buds and flower with long calyx from autogamous *Vicia sativa*. The buds show the slow growth of the petals in relation to the calyx: Figs. 5-7 — × 12.5; Figs. 8 and 9 — × 5

whereas in autogamous ones petal growth is slow was supplemented. Kuperman (1963, 1968) reports that, according to numerous authors, during flower development in angiosperms there is a stage of enhanced calyx growth with weak petal development. In autogamous species such as *Ornithopus pinnatus* (W. Wojciechowska 1975) and *Pisum sativum* (W. Wojciechowska 1978) the stage of enhanced calyx growth is very pronounced and the petals are hidden deeply in the calyx for a long time. In the allogamous species, *Lupinus elegans* and



Figs. 10 and 11. Longitudinal sections through bud in substage I/3. Fig. 10 — bud of autogamous *Vicia sativa*, × 15. Fig. 11 — bud of allogamous *Lathyrus silvester*, × 15. In *V. sativa* at this stage of development the sepals (sep.) are almost twice the length of the vexillum (V), whereas in *L. silvester* they hardly stand out beyond the vexillum

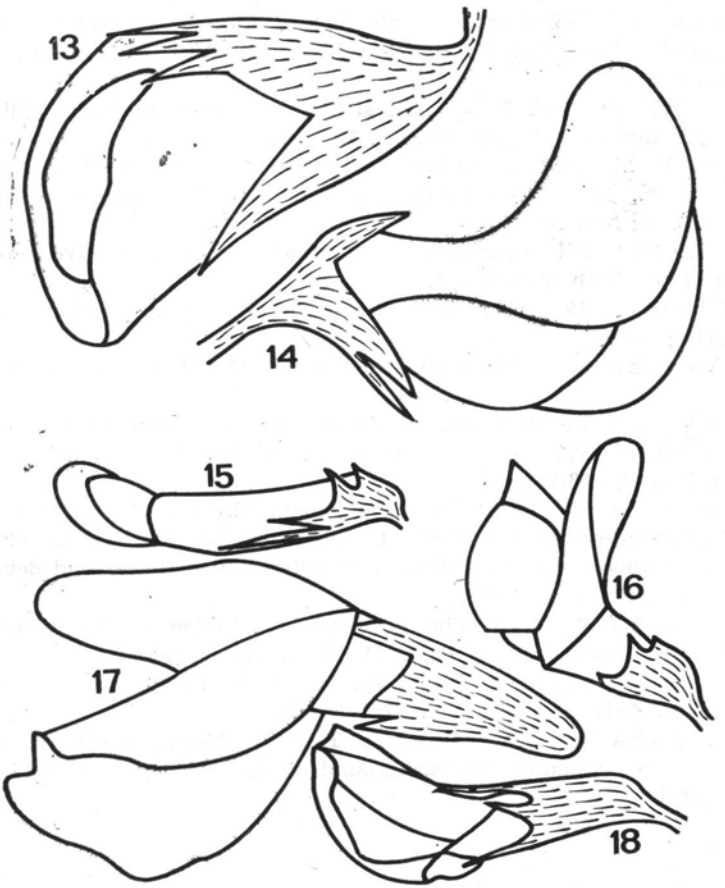
L. mutabilis, however, in the early stage of bud development the delay in petal growth in relation to calyx growth is not so distinct (W. Wojciechowska 1976). At present a similar slow growth of petals out of the calyx in two autogamous species, *Vicia faba* and *V. sativa* (Figs. 5-10) and the much quicker growth of petals from the calyx of the allogamous *Lathyrus silvester* (Fig. 11) was observed. The rhythm of

petal growth in the corolla of the allogamous *Vicia villosa* is somewhat different. In the early stage of bud development (Fig. 12), at the stage of "enhanced calyx growth" the petals grow slowly like in the examined autogamous plants, however, at a later stage, after their emergence from the calyx an enhanced growth of petals is observed so that mature flowers of *Vicia villosa* have short calyces as compared with petals (Fig. 15). It results from these studies that the beginning of enhanced petal growth in allogamous plants does not always occur as early as the stage of "enhanced calyx growth", but may appear at a later time of flower development. The observations to date indicate, however, that in mature flowers of the investigated allogamous plants a short calyx is always observed in relation to the petal dimensions (Figs. 14-16), notwithstanding at what stage of development the petals grow

Fig. 12. Dissected bud of allogamous *V. villosa* in substage I/4: sepals still markedly stand out beyond vexillum like in autogamous species, they are, however, narrow, × 13.5, V — vexillum

intensively. In autogamous plants, on the contrary, a relatively large calyx was observed as compared with the petals (Figs. 9, 13, 17, 18). Insect-pollinated flowers must allure insects; the petals of the corolla which rapidly emerge from the calyx form a larger colourful patch increasing the attractiveness of the flowers. The long petals and short calyx in allogamous plants may be explained by the fact that in the course of evolution the mechanism of natural selection singled out allogamous and day-insect pollinated plants with petals growing rapidly and giving, therefore, flowers with a short calyx. If the study of

a greater number of species confirms this supposition, the trait of short or long calyx may be used as rapid preliminary way of distinguishing the way of pollination of plants. However, when aggregation of flowers into inflorescence is a biological equivalent to a single flower we can not consider the calyx of a single flower.



Figs. 13-18. Flowers of species from the *Vicieae tribe*, × 3.3. Figs. 13, 17, 18 — autogamous species with large calyces: *Pisum sativum* (13), *Vicia faba* (17), *Vicia angustifolia* (18). Figs. 14, 15, 16 — allogamous species with short calyces: *Lathyrus silvester* (14), *Vicia villosa* (15), *Lathyrus pratensis* (16)

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Rytm rozwojowy pąka u niektórych gatunków z rodziny Papilionaceae. III. Makrosporogeneza, mikrosporogeneza i wczesna gametogeneza u kilku gatunków plemienia Vicieae

Streszczenie

Porównano przebieg żeńskiej i męskiej sporogenezy i gametogenezy oraz odbywający się równolegle rozwój wegetatywnych części pąka kwiatowego u sześciu gatunków plemienia *Vicieae: Vicia faba* L. cvs. Nadwiślański i Major, *Pisum sativum* cv. Folger, *Lathyrus pratensis* L. z pominięciem żeńskiej sporogenezy i gametogenezy, *L. silvester* var. *platyphyllus* (Retz.) Aschers, *V. villosa* Roth. cv. Rea i *V. sativa* cv. Jaga. Po raz pierwszy zbadano makrosporogenezę u *Vi-*

cia sativa i *Lathyrus silvester*. Stwierdzono, że woreczek zalążkowy rozwija się z reguły z makrospory chalazalnej. U *V. sativa* obserwowano w zalążkach jedną albo dwie tetrady, z których jedna degenerowała. U *L. silvester* obserwowano tetrady anizobilateralne i linearne. Każdy ze zbadanych gatunków ma charakterystyczny rytm rozwojowy pąka kwiatowego. Podobieństwo w tempie mikrosporogenezy w stosunku do wzrostu płatków korony, występujące u różnych gatunków nie wskazuje, że u tych gatunków w podobnym tempie przebiega makrosporogeneza. Stwierdzono, że u *V. faba* i *P. sativum* występują identyczne zależności między mikrosporogenezą i makrosporogenezą z tym, że u *V. faba* w stosunku do rozwoju płatków korony oba te procesy przebiegają nieco szybciej. U obecnie i uprzednio zbadanych gatunków zaobserwowano, że dojrzałe kwiaty gatunków samopylnych mają długie kielichy w stosunku do płatków korony a gatunków obcopylnych, zapylanych przez owady dzienne kielichy krótkie w stosunku do płatków korony. Ta obserwacja będzie przedmiotem dalszych badań na większej liczbie gatunków.