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The development rhythm of the flower-bud in some *Papilionaceae* species

Part II. Microsporogenesis, macrosporogenesis and early gametogenesis in *Pisum* sp. forms against the background of bud development

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Abstract

The process of microsporogenesis and development of pollen grains was found to occur in an identical rhythm in 14 examined forms of *Pisum* sp. as compared with the development of the perianth. In the 3 forms studied in detail: *Pisum sativum* L. cultivar Folger, cultivar Peluszka Bordowa and *Pisum sativum* L. ssp. *transcaucasicum* Gov. an identical development rhythm of the bud was observed as compared with that of microsporogenesis, pollen grain formation and macrosporogenesis.

INTRODUCTION

The investigations were undertaken to answer the question whether, in the development of the flower-bud of monoecious angiosperms, there exist specific regularities in the particular taxonomical groups or within groups of some other type as for instance auto- and allogamous ones.

As mentioned in Part I, as a rule the processes of microspore, pollen grain and macrospore formation and embryo-sac development are described in the pertinent literature separately without reference to their mutual relations, with some exceptions (Davis, 1968, 1969; Charechko-Savicka, 1940; Kuperman 1963a,b, 1968, 1973; Rodkiewicz, 1961; B. Wojciechowska, 1972a,b; W. Wojciechowska, 1975, 1976, and the authors of Kuperman's group whose papers are published in "Biologicheskii kontrol v sel'skom khozyaistve" 1962; "Eksperimentalnyi morfogenez", 1963 and "Morfogenez ovoshchnykh ra-

stenii", 1971). The investigations of Kuperman and collaborators referred to by Poddubnaya-Arnoldi (1976, p. 55) concern plant organogenesis as a whole. Kuperman et al. established 12 stages of organogenesis in representatives of angiosperms from a dozen or so families including *Papilionaceae*.

The course of gamete formation in reference to perianth development is described in *Ornithopus pinnatus* (W. Wojciechowska, 1975) and in *Lupinus elegans* and *L. mutabilis* (W. Wojciechowska, 1976). The present paper presents the interrelations in the development of male and female organs of the flower and the perianth in the bud of various forms of pea.

MATERIAL AND METHODS

For study 14 forms of *Pisum* were used received from the Department of Plant Genetics, Polish Academy of Sciences from Dr Kurhańska, Prof. Przybylska and Dr Hurich.

Comparison of development of the particular stages of flower buds and flowers was based on the classification introduced by B. Wojciechowska (1972). This author divided bud and flower development in *Ornithopus* in to 8 stages, assuming as criterion for the division the sepals to petals ratio. In stage I buds the petals are not yet visible between the sepals, that is in the closed green bud (Fig. 1). It was ascertained that in the examined pea forms full macro- and microsporogenesis occur in the completely closed green bud. For following in detail the initial steps of development, it proved necessary to divide stage I into substages. As criterion for this was assumed the position of the petals, particularly the vexillum, in relation to the androecium. Four substages were distinguished in stage I:

I/1 — vexillum (V) below the apex or equal to the height of the apex of the lower androecium whorl (verticillus I), Fig. 1 — I/1;

I/2 — vexillum (V) above lower androecium whorl (verticillus I), but below apex of upper whorl (verticillus II), Fig. 1 — I/2 and Plate I, Photos 1 and 2;

I/3 — vexillum (V) at equal height with apex of upper androecium whorl (verticillus II) or standing out above it. Fig. 1 — I/3, Fig. 2 and Plate I, Photo 3);

I/4 — androecium (A) enclosed in overlapping petals (pet), Fig. 1 — I/4 and Plate I, Photo 4.

In the observations of the developmental rhythm of the bud the method of analysis of fresh buds was applied for all the 14 forms examined. The substage and the colour of the anthers were established and smears were prepared from the latter in acetocarmine. For 3 forms

the paraffin method was used, in the case of some buds both methods were combined: before embedding in paraffin the colour of the anthers was checked and the substage established in the fresh bud. In order to distinguish the substages, fresh buds were cut open delicately on the ventral side under the binocular. In pea buds the sepals are longer on the ventral than on the dorsal side. The buds were fixed before embedding in paraffin for 2 min in AA and then in FAA and deaerated. After embedding they were cut longitudinally into 4- to 15-μ sections and stained with iron haematoxylin and fast green. For easier distinction of the substage the sections representing the middle of the longitudinally cut bud were photographed.

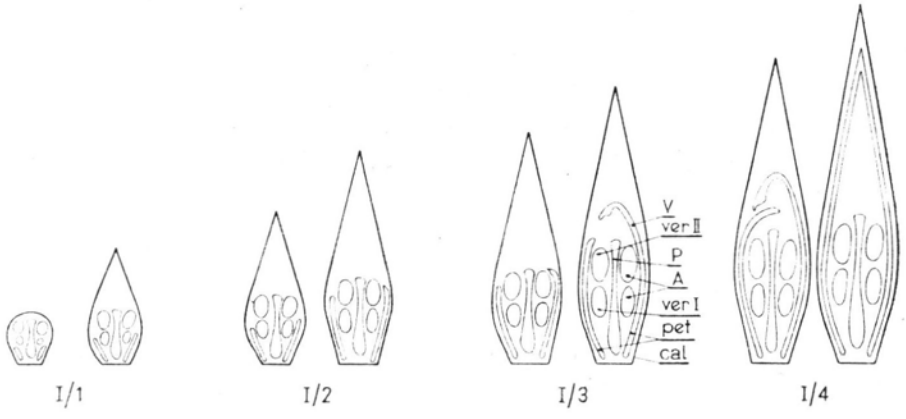


Fig. 1. Schematic diagrams of the substages (I/1 — I/4) of the Ist, closed green bud stage in pea, illustrated by early (left diagram) and late (right diagram) phases in each substage

Substage I/1 — the largest petals vexillum *(V)* below apex or equal with apex of lower androecium whorl *(ver I)*. Substage 1/2 — vexillum *(V)* above lower whorl *(ver I)*. Substage I/3 — vexillum *(V)* at the same height as apex of upper androecium whorl *(ver II)* or stading out above. Substage I/4 — androecium *(A)* closed in overlapping petals *(pet)*.

A — androecium; *cal* — calyx; *pet* — petals; *p* — pistil; *ver I* — verticillus I = lower whorl; *ver II* — verticillus II = upper whorl; *V* — vexillum

The nomenclature of species and subspecies was used afted Brower et al. (1975) who adopted the recommendations of the International Nomenclature Commission, according to which, cultivated forms distinguished so far as *Pisum sativum* with white flowers and *Pisum arvense* with many-coloured ones are considered as covarieties of *Pisum sativum* ssp. *sativum*. The white forms were denoted as convarietas *sativum* and those with coloured flowers, as convarietas *speciosum*. The following abbreviations are used for the names: *Pisum sativum* L. ssp. *sativum* conv. *sativum* = *P.* conv. *sativum* and *P. sativum* L. ssp. *sativum* conv. *speciosum* (Dierb.) Alef em. C. O. Lehm. = *P.* conv. *speciosum*. The following forms were investigated:

1. *P.* conv. *sativum*, cultivar Folger.
2. *P.* conv. *speciosum*, cultivar Peluszka Bordowa.
3. *Pisum sativum* L. ssp. *transcaucasicum* Gov.
4. *P.* conv. *speciosum*, cultivar Kormowoj.
5. *P.* conv. *speciosum* var. *centrali sibiricum* Gov. Svalöfs Nota Art × *P.* conv. *speciosum*, cultivar Peluszka Wąsata — generation F_4.
6. *Pisum syriacum* (Berger) C. O. Lehm. = *P. humile* (Boiss) et Noé non Mill.
7. *P.* conv. *sativum*, cultivar Kungsärt.
8. *Pisum* unclassified (*P. cinereum*).
9. *Pisum abyssinicum* A. Br.
10. *Pisum fulvum* Sibth. et Sm.
11. *P.* conv. *sativum*, cultivar Tordsdag.
12. *P.* conv. *sativum*, Institut de Gembloux.
13. *P.* conv. *sativum*, cultivar Regina.
14. (*P.* conv. *sativum*, cultivar Wiktoria × *P.* conv. *speciosium*, cultivar Peluszka Angielska), × *P.* conv. *sativum*, cultivar Akacjolistna — generation F_4.

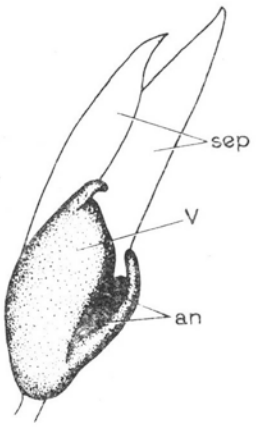
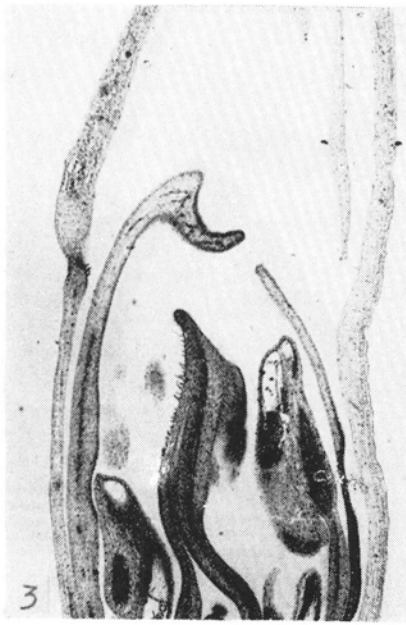


Fig. 2. Schematic diagram of the prepared bud of pea in the late phase of I/3 substage

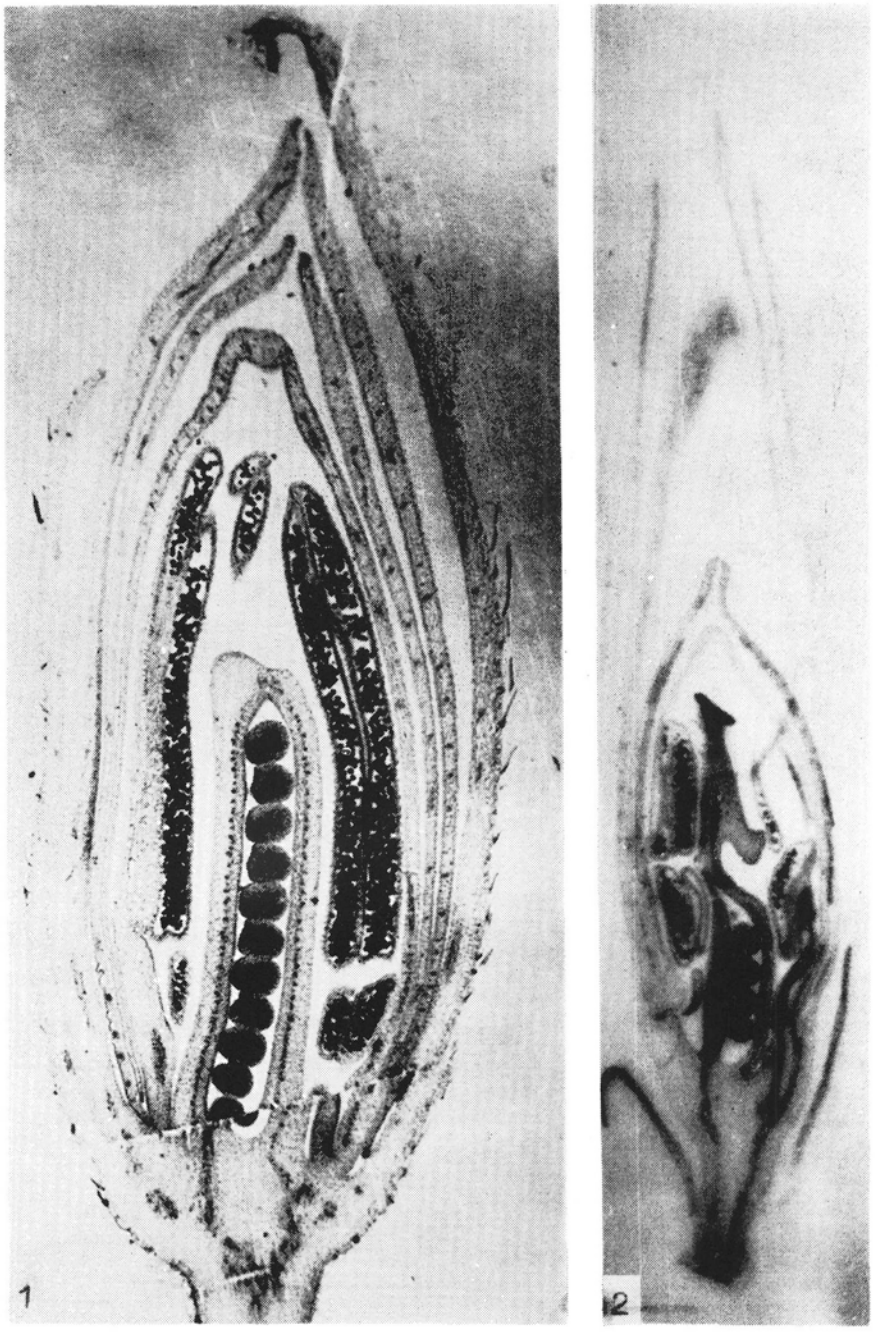
an — anthers; *sep* — sepals; *V* — vexillum

Pea seeds were sown in the springs of the years 1974—1977 in the glasshouse and in the field. Only a part of seeds of *P. transcaucasicum* were sown in a culture room in the winter of 1976/1977. These plants were artificially illuminated. The number of buds in the first 3 forms collected under various conditions and examined by various methods, is given in Table 1. Fresh buds from the forms listed as items 4-10 were analysed after collection in the glasshouse (10-45 specimens), and from the forms under items 11-14 several specimens of each.



Pisum sativum L. cultivar Folger — longitudinal sections of buds and theirs fragments in stage I of flower-bud development (× 16)

Photo 1 — a young bud in substage I/2, Photo 2 — an older bud in substage I/2, Photo 3 — fragment of bud in the late phase of I/3 substage, Photo 4 — fragment of bud in the substage I/4



Longitudinal sections of buds: *Lupinus elegans* H.B.K. Photo 1 (× 21) and *Pisum sativum* L. cultivar Folger Photo 2 (× 13) at the same phases of gametogenesis but at the different developmental stages:

Bud of lupin in stage II — corolla petals are already visible through sepals; bud of pea in stage I, substage I/4 — corolla petals are still deeply in the calyx

Table 1

Number of buds examined by various methods in three forms of *Pisum*

Pisum forms	Growth conditions	Number of buds			
		fresh	embedded in paraffin	analysed by both methods	total number
P. conv. *sativum* cultivar Folger	glasshouse	5	82	—	205
	field	97	—	21	
P. conv. *speciosum*, cultivar Peluszka Bordowa	glasshouse	18	—	—	82
	field	21	20	23	
P. sativum L. ssp. *transcaucasicum* (Gov.)	glasshouse	47	—	18	99
	culture room	19	—	15	

RESULTS

Table 2 shows the course of macro- and microsporogenesis in relation to the changing colour of the anthers in the substages of stage I of the cultivar Folger. The data of this table are based on analysis of pea buds collected in the period 1974-1976, fixed and cut with a microtome. The colour of the anthers was checked in 1976 by cutting open the buds before fixation. It results from Table 2 that the colour change of the anthers from green to yellow and later orange occurs in substage I/3 (Table 2 and Fig. 2). Similarly as for the cultivar Folger, observations were performed with the use of the paraffin method for the cultivar Peluszka Bordowa and *Pisum sativum* ssp. *transcaucasicum*. The results obtained with healthy buds do not differ from the data listed in Table 2. For illustration of this, the phases of gametogenesis in substage I/4 are given in Table 3 for all the above enumerated *Pisum* forms. In spite of the different conditions in which the plants grew and the morphological differences between the forms, the same gametogenesis phases were noted with but slight deviations which may be considered as negligible since their range does not exceed the deviations found among the ovules of one pistil and the stamina of one androecium. For instance, in the particular ovules of one and the same pistil, diads, tetrads and mononuclear ovaries were found. It should be mentioned that the repeatability of the results was established by comparing material collected during the entire vegetation period, both on cool and very hot days.

In supplementation of the data in Table 2 attention should be called to the relation between the process of integument growth, the course of meiosis and gametogenesis in the ovule: with the beginning of prophase I

there appear protuberances at the site where the integuments arise. The one from which the inner integument is formed is visible earlier. Towards the end of prophase I the outer integument outgrows the inner one In the late tetrad stage the outer integument reaches to the top of the ovule nucellus and the inner one half way up the nucellus. At the stage of binucleate embryo-sac ovary both integuments already form micropyles. It should be mentioned that in pea ovaries there often are two or three macrosporocytes, but a tetrad arises only from one of them.

Table 2

Course of gametogenesis in *Pisum* conv. *sativum*, cultivar Folger on the basis of observation of longitudinal sections of bud in period 1974—1976

Substage	Anther colour	Microsporogenesis and pollen grain formation	Macrosporogenesis and development of embryo-sac
I/1 vexillum below apex or equal with apex of lower androecium whorl	light green glassy	anthers with archesporial cells	from ovules in form of undifferentiated protuberances to ovules with archesporial cells
I/2 vexillum above lower whorl but below upper whorl	light green glassy	from archesporial cells to very young non vacuolized microspores	from ovules with archesporial cells to ovules with macrosporocytes in prophase I
I/3 vexillum at the same height as apex of upper androecium whorl or standing out above	light green glassy green mat light yellow orange	from tetrads to slightly vacuolized microspores from slightly vacuolized microspores to two celled pollen grains	from ovules with macrosporocytes in prophase I to ovules with macrosporocytes in metaphase I from ovules with macrosporocytes in prophase I* to those with 2-nucleate embryo sacs
I/4 androecium closed in overlapping petals	orange	most frequently two-celled pollen grains in younger buds, sometimes still vacuolized and dividing microspores	from ovules with tetrads or triads to those with 8 free nuclei, sporadically in some ovules earlier stages of meiotic division

*—in ovary of one pistil, beside scarce ovules at this stage of bud development in prophase I, ovules in later phases of meiosis

If we compare the longitudinal sections of *Lupinus elegans* and *Pisum sativum* cultivar Folger buds, in the phase of mononucleate embryo-sac in lupin and mono- and binucleate ones in pea, and in the phase of two-celled pollen grains in both species, a much more advanced development

Table 3

Course of gametogenesis in substage I/4 three different forms of *Pisum* in various years and conditions

Pisum forms		*P.* conv. *sativum*, cultivar Folger			*P.* conv. *speciosum* cultivar Peluszka Bordowa	*P. sativum* L. ssp. *transcaucasicum* (Gov.)
Floret length mm		19 mm			16 mm	14 mm
Date and growth conditions		Glasshouse 1974	Glasshouse 1975	Field 1976	Field 1974	Glasshouse 1977
Gametogenesis	♀	from macrospore tetrads to 8-nucleate free embryo-sacs	1—4 nucleate embryo-sacs	from tetrads or triads to 4-nucleate embryo-sacs. Sporadically earlier meiosis stage	1—4 nucleate embryo-sacs	1—4 nucleate embryo-sacs
	♂	two-celled pollen grains	two-celled pollen grains; sometimes vacuolized microspores	two-celled pollen grains; sometimes vacuolized microspores	two-celled pollen grains; sometimes vacuolized microspores	two-celled pollen grains; sometimes vacuolized microspores

of the corolla petals is seen in the lupin bud (W. Wojciechowska, 1976) as compared with the pea bud (Plate II).

Fresh buds of 14 pea forms were analysed — and the stages of bud development (substages) were recorded as well as the colour of the anthers and the phase of microsporogenesis. Most numerous closed green buds (as many as 123) of the variety Folger were examined. The colour of the anthers and the microsporogenesis phases in the particular substages were the same as in Table 2 with a single exception. The latter was a bud with anthers already turned orange and vacuolized microspores in the late substage I/2. Its vexillum was not typical for substage I/2 (lower than the androecium of the second whorl). This bud was taken in the very hot first half of July, 1976 from a plant growing in the field.

It results from Table 2 that, in the end phases of each younger substage, the same stages of gametogenesis occur as in the beginning of the later substage. This fact indicates that the stage of development of the gametes in relation to the corolla petals may change within certain definite limits in dependence on the environmental conditions. Fresh buds collected on very hot days in July, 1976 and on cool days in August, 1976 and at the beginning of June, 1977 were compared. In all these buds the vexillum was equal in height with the stamina of the second whorl. Buds collected during the heat wave usually already had yellow or orange anthers with vacoulized microspores inside, whereas those collected in cooler weather had green anthers with young unvacuolized microspores or even tetrads. Neither in the variety Folger or in any of the 14 forms examined, however, were green anthers found in substage I/4 in healthy and normally developed buds. Healthy anthers in this substage always had already changed their colour.

Of all the pea forms studied 569 buds were examined. In all anthers in the particular substages the same phases of microsporogenesis and pollen grain formation were observed as are shown in Table 2 for the variety Folger. In the first two substages the anthers were green, with the exception described in the variety Folger. As a rule in substage I/3 early phases of microsporogenesis were no more seen, in *P. cinereum*, however, in one of the 12 analysed buds metaphase I was noted.

DISCUSSION

Of the 12 stages of organogenesis of angiosperms established by Kuperman (1963a and b, 1968, 1973) five (V—IX) correspond to the 8 stages of bud and flower development classified by B. Wojciechowska (1972a,b). At present special attention was devoted to the development of the pea bud in stage I according to B. Wojciechowska's

classification (closed green bud, petals not visible through sepals). This stage comprises the end phase of stage V, the entire stage VI and in some plants the beginning of stage VII of organogenesis according to Kuperman. In stage V of organogenesis, according to this author, differentiation of the floret takes place and formation of archaespore cells, in stage VI anthers and ovaries form, micro- and macrosporogenesis takes place, and in stage VII elongation growth of vegetative organs of the flower and gametogenesis occur. Kuperman (1963b, 1968) reports that, according to numerous authors, stage VI is characterized by an enhanced growth of the sepals and weak growth of the petals, whereas in stage VII the corolla in most species has bypassed the sepals. Such a weak growth of the petals as compared with that of the sepals, characteristic for stage VI of organogenesis was also observed in the pea and is schematically illustrated in Figs 1 and 2.

It has been mentioned at the beginning that morphological and cytological investigations calling attention to the correlation in the development of male and female organs of the flower and perianths are scarce. Kendeler (1972) calls attention to the gap in physiological investigation of the further development of already formed flower organs. This author gives a brief account of some few experiments concerning this problem, he also mentions that in studies *in vitro* of the flower primordia of *Aquilegia*, the sepals inhibit development of the petals, stamina and carpels.

It results from the paper of Eremienko (1971) and of those available to the present author from Kuperman's group that they are concerned with plant organogenesis from germination to full maturity and that they take into account a number of additional factors affecting plant development such as daylength, the light spectrum, temperature, the seeding date, herbicides etc. In none of the available papers, however, did I find a list of the processes of microsporogenesis and macrosporogenesis analogous to the here included tabular presentation in reference to the development of the bud and the changing anther colour, nor any serial photographs of longitudinal section in the substages of stage I of the growing green bud. Earlier investigators who studied in detail gamete formation in pea elaborated separately the process of macrosporogenesis and the development of the embryo-sac and separately microsporogenesis and the development of pollen grains (Roy, 1933; G. O. Cooper, 1938). However, only a combined study of generative and vegetative organs of the flower, permits to find slower growth of the corolla petals in relation to the development of female and male gametes. This slow growth favours selfpollination. The growth of the corolla petals in pea (*Pisum*) is considerable slower than in the previously examined allogamous species: *Lupinus elegans* and *L. mutabilis*. The moment of selfpollination in pea was found by D. C. Cooper (1938) on 2 com-

mercial varieties, Little Marvel and Asgrow Pride to occur about 24 h before opening of the flower.

The course of integument growth in connection with meiosis and gametogenesis in *Trifolium repens* ovules has been well illustrated by R e m b e r t (1977). This author observed the ovule surface under a scanning electron microscope and clarified ovules under contrast phase and interference optics. His results agree well with those described here in *Pisum*. There is, however, a difference. According to R e m b e r t the integuments in *Trifolium* begin to form as early as the stage of the multicellular archaespore, whereas in *Pisum* the beginning of integument growth was observed as late as early prophase I.

Further investigations will decide whether the supposition is true that, in spite of slight differences, the time relation between the processes of meiosis and gametogenesis, and integument growth is similar in all *Papilionaceae*. Most representatives of this family have campylotropous ovules and the same monosporetype of ovule development (*Polygonum*). The causes of the slight differences in the rate of development may be: the different mode of producing sporogenous cells in the particular species and formation of different tetrads (R e m b e r t, 1969, 1971).

The influence of environmental factors like temperature, daylength, light intensity etc. may within certain limits accelerate or delay the course of microsporogenesis and pollen grain development in relation to the growth of petals. The precise establishment of the influence of these factors requires special studies.

CONCLUSIONS

Analysis of the rhythm of bud development allows — in the 3 pea forms examined in detail — to establish with a good approximation both the micro- and macrosporogenesis phase on the basis of the anther colour and position of the vexillum in relation to the androecium. In the remaining 11 forms the phases of microsporogenesis can also be determined. This may greatly facilitate pea micro- and macrospore culture *in vitro* and also prove useful in selection of material for electron microscopic investigations.

Comparison of the present results with earlier ones (W. W o j c i e c h o w s k a, 1975, 1976) shows distinct differences in the rate of growth of the petals as compared with the processes of micro- and macrosporogenesis in representatives of the genera *Ornithopus*, *Lupinus* and *Pisum*. Slow growth of petals, as compared with the processes of gametogenesis, has been noted in typically autogamous representatives of species of the

genus *Ornithopus* and *Pisum*, whereas allogamous species, which, though poorly, set seeds after selfpollinations, as for instance species of the genus *Lupinus*: *L. elegans* and *L. mutabilis* exhibit a much faster petal growth.

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Rytm rozwojowy pąka u wybranych gatunków z rodziny Papilionaceae
Część II. Mikrosporogeneza, makrosporogeneza i wczesna gametogeneza u form Pisum sp. na tle rozwoju pąka

Streszczenie

Stwierdzono u 14 form grochu, że mikrosporogeneza i rozwój ziarn pyłku na tle rozwoju okwiatu, przebiega w identycznym rytmie. U trzech form zbadanych najdokładniej (*Pisum sativum* cultivar Folger i cultivar Peluszka Bordowa oraz u *Pisum sativum* L. ssp. *transcaucasicum* Gov.) stwierdzono identyczny rytm rozwojowy pąka w odniesieniu do procesów tak mikrosporogenezy i tworzenia się ziarn pyłku jak i makrosporogenezy. Przeanalizowanie tego rytmu pozwala u wymienionych trzech form — na podstawie tylko zabarwienia pylników i ułożenia żagielka w stosunku do pręcikowia — z dużym przybliżeniem określać fazy zarówno mikrosporogenezy, jak i makrosporogenezy, a u pozostałych 11 form fazy mikrosporogenezy. Może to znacznie ułatwić pracę w hodowli *in vitro* mikrospor i makrospor grochu, a także może być przydatne przy wybieraniu materiału do badań w mikroskopie elektronowym.

Porównanie wyników w obecnie przedstawionej części badań i poprzednich (W. Wojciechowska 1975, 1976) wskazuje na wyraźne różnice w tempie wzrostu płatków korony w stosunku do procesów mikrosporogenezy i makrosporo-

genezy u przedstawicieli rodzajów *Ornithopus*, *Lupinus* i *Pisum*. Powolny wzrost płatków korony w stosunku do procesów gametogenezy obserwowano u typowo samopylnych przedstawicieli gatunków z rodzaju *Ornithopus* i *Pisum*, natomiast obcopylne, choć wiążące słabo nasiona po samozapyleniu, gatunki z rodzaju *Lupinus*: *L. elegans* i *L. mutabilis* odznaczają się znacznie szybszym wzrostem płatków. Jak zwrócono już uwagę w części I (W. Wojciechowska 1976), szybkie tempo wyrastania płatków korony z kielicha w stosunku do procesów gametogenezy jest jednym z wielu czynników utrudniających samozapylenie, podczas gdy powolne ich wyrastanie sprzyja samozapyleniu, o ile dany gatunek nie wytworzył innych mechanizmów utrudniających lub uniemożliwiających przyjęcie własnego pyłku.