

Occurrence of abnormalities in the ovary and ovule structure and their effect on fruit production in *Chaerophyllum cicutaria* Vill. (*Umbelliferae*)

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Abstract

Chaerophyllum cicutaria is an andromonoecious member of the *Umbelliferae* family. Apart from male flowers it also produces numerous hermaphrodite flowers the ovaries of which fail to transform into fruits. Almost one quarter of such non-fruitle hermaphrodites reveal an abnormal structure of their ovaries and/or ovules while the development of others is arrested without visible structural changes. Twelve abnormalities are distinguished and their distribution among plants from various populations of the species is described. Presumed consequences of the abnormalities are discussed.

Key words: *Chaerophyllum cicutaria*, plant embryology, fruit production

INTRODUCTION

Chaerophyllum cicutaria Vill. occurs mainly in the mountains of Central Europe and is regarded as a montane species, though it also grows in some lowland localities (Hegi 1926). In Poland it is quite common in the south, rare in the north and does not occur in the central part of the country (Koczwarra 1960). Previous investigations concerning megasporogenesis and embryo sac development in *Ch. cicutaria* (Chojnacki 1979) revealed that in plants from both mountain and lowland localities numerous flowers showed some structural abnormalities. It also appeared that production of ripe, healthy fruits was rather low as compared with the large number of produced flowers.

The present study was undertaken to describe the abnormalities taking place during ovary and ovule development in *Ch. cicutaria* and to find

out what, if any, correlation existed between their occurrence and low fruit production. Moreover, the study was aimed at checking whether there were any differences between lowland and mountain populations in the above respect.

MATERIAL AND METHODS

The plants used in this study came from five natural lowland populations in the Kashubian Lake District in northern Poland (L-1 Babi Dół, L-2 Kolbudy, L-3 Kartuzy, L-4 Stryśza Buda, L-5 Wejherowo) as well as from five southern Polish populations occurring in various mountain ranges like the Sudetes (M-1 Bierutówice), the western Carpathians (M-2 Szczyrk, M-3 Chochołowska Valley, M-4 Sromowce) and the eastern Carpathians (M-5 Ustrzyki Górne). In 1974, 3-5 specimens were transplanted from each population to the departmental garden in Gdynia, so that they might grow under the same soil and microclimatic conditions.

The material for embryological studies was collected from the cultivated specimens during three consecutive years, 1975-1977. Flower buds, flowers and fruits were fixed either in Farmer's fluid or in CrAF II fixative. After dehydration in the alcohol-xylene series they were embedded in paraffin and cut into sections of 8, 10 or 15 μm . The majority of sections were stained with Newton's gentian violet; staining with Mayer's alum haematoxylin and staining with thionine and orange G were also applied.

The observations concerning flower and fruit production were carried out in the natural localities in 1976. They required several visits to each locality during the vegetative season. Initially, five shoots bearing inflorescences were labelled at each locality. Unfortunately, it appeared during the next visits that some labelled shoots had perished, so, with the exception of the L-1 locality, the observations were completed on a smaller amount of material (Table 1). An estimation of the percentage fruit set was also made on the material collected for embryological studies.

RESULTS

An inflorescence of *Ch. cicutaria* is usually composed of a primary umbel, which terminates the main shoot and 1-3 secondary umbels. Sometimes, a few small tertiary umbels may also occur. The inflorescence always consists of both hermaphrodite and staminate flowers. The percentage of staminate flowers, which constitute approximately half of all the flowers

produced by a plant (Table 1), is low in primary umbels (5-20%) whereas it tends to increase in secondary ones (65-100%). Tertiary umbels, when present, comprise solely staminate flowers. There were no significant differences in the percentage and the distribution of staminate flowers between plants sampled from various mountain and lowland localities (Table 1).

The flowers of *Ch. cicutaria* are epigynous, incomplete (sepals are lacking), actinomorphic and pentamerous, and have a bicarpellary, syncarpous gynoecium. Ovarian development is completed only in hermaphrodite flowers. One of the two ovules which arise in each chamber of the inferior, bilocular ovary grows downward and occupies the lower, larger part of the chamber while the other ovule remains in its upper part. Usually, only the lower ovule is functional and the upper one is arrested before or soon after the differentiation of the archesporial cell in its nucellus (Fig. 1). Rudimentary ovaries of staminate flowers remain small and either contain the shrivelled remnants of ovular primordia or reveal no traces of ovules at all.

Functional ovules of *Ch. cicutaria* are pendulous, anatropous, unitegmic and tenuinucellate. The single archesporial cell functions directly as the megaspore mother cell and the development of the embryo sac follows the bisporic, *Allium* type (Fig. 2). The structure of the ovules and embryo sacs of *Ch. cicutaria* at successive stages of their development has already been described (Chojnacki 1979).

The endosperm is of the nuclear type (Fig. 3). The majority of endosperm nuclei and later cells are triploid, though some cells containing apparently larger nuclei or multinucleate cells may also occur, especially in the chalazal part of the endosperm tissue. The embryogeny conforms to the *Sherardia* variation of the *Solanad* type. The fruit is a schizocarp which dehisces into two mericarps comprising one seed each. At shedding, the seed contains an incompletely organized embryo arrested at the globular stage. Further development of the embryo is continued after a period of dormancy, during germination.

Ripe, healthy mericarps are produced by a rather small number of hermaphrodite flowers. According to the observations carried out in the natural localities of *Ch. cicutaria*, the production of fruits seems to be connected neither with the number of umbels in an inflorescence nor with the total number of hermaphrodite flowers borne by a plant. The percentage of fruit set varies considerably, from less than 10 per cent up to almost 50 per cent, even in plants belonging to the same population (Table 1). Very similar rates of fruit set have been estimated by counting the shrivelled ovules occurring in the material investigated embryologically (Table 2).

The development of ovules can be arrested at any stage (Fig. 1). The percentage of shrivelled ovules, which is comparatively low at premeiotic

Table 1

Production of flowers and fruits by plants of *Chaerophyllum cicutaria* growing in their natural localities

Symbol of locality	Plant number	Number of umbels	Number of flowers (t)	Number of hermaphrodite flowers (h)	Percentage of hermaphrodite flowers $\left(\frac{h}{t} 100\right)$	Total fruit set (f)	Percentage of fruit set $\left(\frac{t}{h} 100\right)$
L-1	1	6	2077	987	47.5	299	30.3
	2	5	1737	694	39.9	108	15.6
	3	3	1537	662	43.1	76	11.5
	4	4	1186	573	48.3	124	21.6
	5	3	854	502	58.8	113	22.5
L-2	1	3	1772	958	54.1	97	10.1
	2	3	1402	761	54.3	211	27.7
L-3	1	5	1381	766	55.5	243	31.7
	2	3	1283	514	40.1	61	11.9
	3	4	734	406	55.3	47	11.6
L-4	1	3	781	452	57.9	135	29.9
L-5	1	5	1824	920	50.4	203	22.1
	2	3	1675	746	44.5	80	10.7
	3	3	1267	597	47.1	64	10.7
M-1	no data						
M-2	1	3	1788	895	50.1	163	18.2
	2	4	1263	712	56.4	108	15.2
	3	3	1132	643	56.8	61	9.5
	4	4	1079	492	45.6	91	18.4
M-3	1	2	983	442	45.0	96	21.7
M-4	1	5	2736	1455	53.1	247	17.0
	2	3	1417	754	53.2	368	48.8
M-5	1	3	1502	627	41.7	98	15.6
	2	3	878	523	59.6	121	23.1

Table 2

Numbers of shrivelled functional ovules as compared with the total number of investigated functional ovules (figures in brackets)

Developmental stages	Lowland populations						Mountain populations						Percentage of ovules	
	L-1	L-2	L-3	L-4	L-5	Σ	M-1	M-2	M-3	M-4	M-5	Σ	arrested at this stage*	starting the next stage**
Premeiosis	4 (65)	3 (23)	4 (6)	5 (7)	— (20)	16 (121)	3 (28)	— (—)	— (28)	2 (9)	1 (21)	6 (86)	10.6	89.4
First meiotic division	— (128)	3 (20)	— (7)	— (—)	— (31)	3 (186)	5 (82)	— (16)	2 (46)	1 (16)	1 (32)	9 (192)	3.2	86.5
Second meiotic division	— (12)	6 (14)	8 (18)	5 (5)	2 (18)	21 (67)	2 (53)	5 (19)	1 (18)	8 (41)	3 (22)	19 (153)	18.2	70.8
Two-nucleate embryo sac	16 (169)	5 (52)	4 (13)	17 (53)	8 (44)	50 (331)	4 (25)	14 (52)	7 (37)	11 (44)	8 (42)	44 (200)	17.7	58.3
Four-nucleate embryo sac	47 (163)	— (25)	— (43)	8 (70)	2 (24)	57 (325)	16 (54)	19 (83)	6 (54)	23 (115)	23 (111)	87 (417)	19.4	47.0
Eight-nucleate embryo sac	17 (158)	4 (33)	30 (44)	11 (51)	7 (60)	69 (346)	31 (141)	6 (35)	35 (164)	38 (121)	28 (115)	138 (576)	22.4	36.5
Mature embryo sac	7 (228)	31 (127)	40 (132)	19 (78)	14 (46)	111 (611)	25 (72)	47 (64)	23 (109)	8 (51)	24 (95)	127 (391)	23.7	27.9
Zygote	1 (124)	— (32)	3 (54)	— (43)	— (65)	4 (318)	— (29)	13 (27)	1 (35)	— (7)	— (34)	14 (132)	4.0	26.8
Proembryo	— (20)	— (5)	— (5)	— (2)	1 (7)	1 (39)	— (—)	1 (52)	— (8)	— (—)	— (4)	1 (64)	1.9	26.3
Globular embryo proper	4 (73)	1 (32)	— (13)	1 (18)	— (34)	6 (170)	7 (19)	3 (63)	2 (22)	— (8)	4 (28)	16 (140)	7.1	24.4
Total	96 (1140)	53 (363)	89 (335)	66 (327)	34 (349)	338 (2514)	93 (503)	108 (411)	77 (521)	91 (412)	92 (504)	461 (2351)		

* Calculated in respect to the total number of ovules observed at the same stage of development.

** Calculated in respect to the theoretical, initial number of functional ovules.

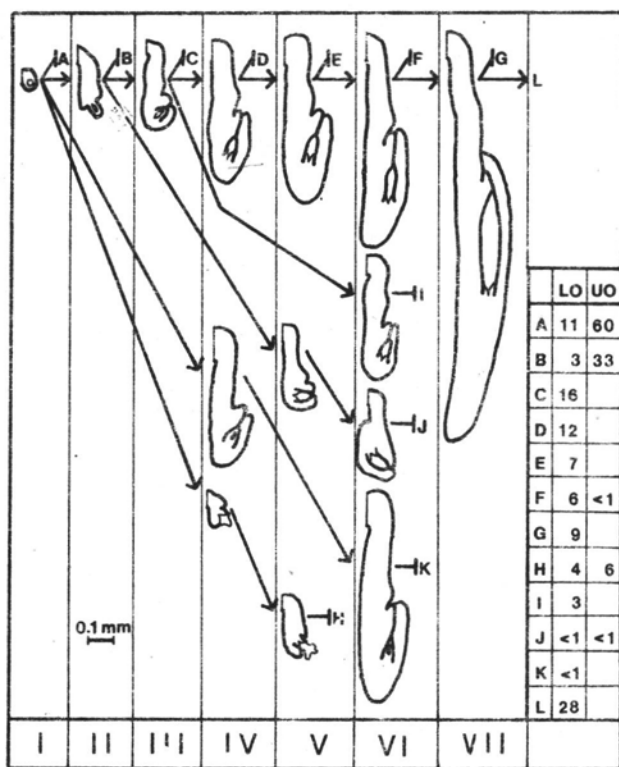


Fig. 1. Structure of normal ovules of *Ch. cicutaria* and of ovules revealing various disturbances of their development. Roman numerals denote successive stages of ovule development: I — premeiotic stage, II — first meiotic division, III — second meiotic division, IV — two-nucleate embryo sac stage, V — four-nucleate embryo sac stage, VI — eight-nucleate embryo sac stage, VII — mature embryo sac stage. Letters A, B, C, D, E, F and G denote ovules arrested at particular stages of their development which do not exhibit any visible abnormalities while letters H, I, J and K denote arrested ovules revealing various structural abnormalities. The letter L denotes ovules capable of strating further, postfertilization development. The figures in the columns on the right hand side represent the percentage occurrence of the distinguished groups with reference to lower ovules (LO column) and upper ovules (UO column)

and meiotic stages, increases markedly during the successive stages of embryo sac development. Therefore only about 36 per cent of potentially functional ovules can reach the mature embryo sac stage (Table 2). The process of fertilization does not take place in about one quarter of the ovules containing mature embryo sacs, so the percentage of healthy young seeds decreases to less than 30 per cent. Taking into account the seeds arrested during the postfertilization development, only about 24 per cent of functional ovules formed at the beginning give ripe, normally developed seeds (Table 2).

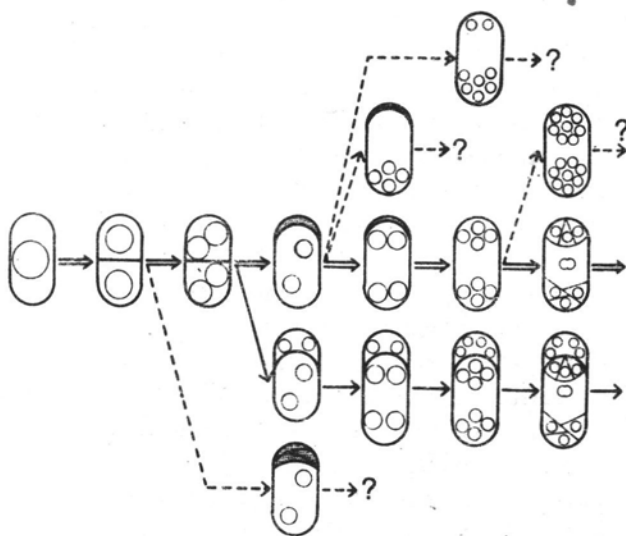


Fig. 2. Schematic diagram showing normal course of megasporogenesis and embryo sac development in *Ch. cicutaria* (double-line arrows) and development of twin embryo sacs (single-line arrows). Possible ways in which monosporic embryo sacs and embryo sacs with an abnormal position or number of their nuclei might arise are indicated by dotted-line arrows

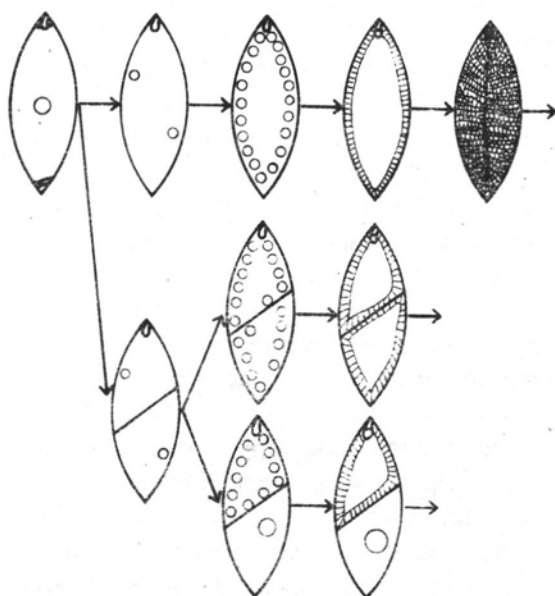


Fig. 3. Normal (nuclear) and Helobial-like types of endosperm development in *Ch. cicutaria*

One or both of the lower ovules formed in an ovary may fail to develop. The latter possibility is more frequent at earlier stages while the former is mainly observed at older stages of ovule development. Flowers, the ovaries of which contain two arrested lower ovules do not develop any further and are soon shed. On the other hand, when only one ovule is arrested or unfertilized, half of the ovary becomes shrivelled while the other half remains unaffected and may transform into healthy mericarp.

The same rules apply to disturbances which lead to structural alterations. The disturbances that take place at early stages usually affect the structure of the whole ovary, while effects of those that occur at later stages are more confined. Although in the latter case only one ovule or even a particular part of it has an abnormal structure, the abnormality may cause further disturbances which may eventually end in failure.

Among the various abnormalities found in flowers of *Ch. cicutaria* (Table 3), there are at least three which may be attributed to disturbances occurring at the very beginning of the pistil's ontogenesis. One of them is represented by flowers with a tricarpellary gynoecium which were found in plants from the M-1 population. The appearance of three carpels instead of two causes the formation of a trilocular ovary which contains three functional ovules (two instances), and gives rise to a fruit splitting into three mericarps (one instance). The second abnormality occurs sporadically in plants of all the investigated populations. It is the presence of ovules placed outside the ovary (Table 3). These extra-ovarian ovules are usually situated between the bases of the styles. They can be observed only in younger stages, so they probably degenerate later and vanish.

The third disturbance gives rise to flowers with shrunken, defective ovaries containing four atypically developed ovules. Such flowers were observed only in plants belonging to the lowland populations (Table 3). The structural patterns of upper and lower ovules are similar here. They have very short funiculi and no integuments, so their embryo sacs, after crushing the nucellar epidermis, grow straight into the ovary chamber (Figs. 1H, 4A), often becoming irregular in shape. The ovules may develop up to the stage of eight-nucleate embryo sac before degenerating.

Apart from the cases described above, in plants of all the populations there may occur ovaries containing upper ovules in which megaspores or young embryo sacs are present, even though the structures of both the lower ovules and the whole ovary are normal (Table 3). Since its development is normally arrested at the premeiotic stage, the upper ovule in whose nucellus an embryo sac appears must be regarded as abnormal. The prolonged development of the nucellus is usually unaccompanied by the growth of the funiculus and integument, which remain undeveloped.

Table 3
Types of abnormalities and their occurrence

Type of abnormality	Number of flowers showing abnormalities										Σ
	lowland populations					mountain populations					
	L-1	L-2	L-3	L-4	L-5	M-1	M-2	M-3	M-4	M-5	
Tricarpellary gynoecium						3					3
Extra-ovarian ovules	7	4	3	2	4	5	1	5	3	3	37
Defective ovaries with ovules lacking integuments	43	10	8	15	10						86
Embryo sacs in upper ovules	8	3	2	5	1	4	1	6	2	5	37
Two functional ovules in one locule						2					2
Incompletely inverted functional ovules			3						5		8
Functional ovules with underdeveloped integuments	8	7	1	5	7	4	2	3	10	7	54
Functional ovules with shrivelled nucelli						4		1	5	2	12
Twin embryo sacs in a functional ovule	18	2	4	4	1	1	5	3	4	3	45
Three degenerating megaspores (a monosporic embryo sac?)				1		1					2
Embryo sacs with abnormal structure	1		1			1					3
"Helobial" endosperm					3						3

In the M-1 population, however, ovaries were observed to contain two functional ovules in one locule (Table 3). It can be assumed that one of them represents an upper ovule, which is formed like a lower one as a result of its downwardly directed growth.

The disturbances which are confined to lower ovules may retard the development of a nucellus or an integument. Sometimes, they also hinder the process of ovule inversion. Incompletely inverted ovules (Figs. 1J, 4B) were found in the material from one lowland and one mountain population (Table 3). Functional ovules with somewhat underdeveloped integuments occurred occasionally in plants of all ten populations (Table 3, Fig. 1I), while ovules with normally developed integuments containing shrivelled nucelli were observed only in plants from the mountain populations (Table 3, Fig. 1K).

Further abnormalities of the nucellus structure appear in the course of megasporogenesis and embryo sac development. Since bisporic embryo sacs of *Ch. cicutaria* derive from the chalazal coenomegaspore, the micropylar coenomegaspore usually degenerates very quickly and is soon crushed by the growing embryo sac. Sometimes, however, it may remain intact for a longer time, or it may even develop into an additional embryo sac (Figs. 2, 4C), which can reach the four-nucleate stage before it eventually degenerates. Functional ovules containing twin embryo sacs were found in plants of all the populations (Table 3).

The embryo sac development seems to be quite uniform in the majority of the investigated functional ovules. Apart from two cases, where three degenerating cells instead of one were visible between the nucellar epidermis and the micropylar pole of a young embryo sac (Fig. 2), it always follows the bisporic, *Allium* type, though some embryo sacs showing abnormal structure may sometimes appear (Table 3). In the material investigated embryologically a four-nucleate embryo sac all of whose nuclei were gathered at its chalazal pole, an eight-nucleate embryo sac with two nuclei at its micropylar pole and six nuclei at its chalazal pole and an embryo sac containing sixteen nuclei (Fig. 2) were observed.

Finally, an interesting variation of endosperm development was observed, which resembles to some extent the *Helobial* type (Fig. 3). It was found in three functional ovules from plants of the L-5 population (Table 3). Unlike the other cases, division of the primary endosperm nucleus seems to be followed by cytokinesis in these ovules. This gives rise to a transverse cell wall dividing the central cell of the embryo sac into two chambers containing one endosperm nucleus each. Further development of the endosperm can take place either in both chambers (one instance) or only in the micropylar chamber (two instances). In the latter case the nucleus of the chalazal chamber enlarges (Fig. 4D) and persists at least up to the time

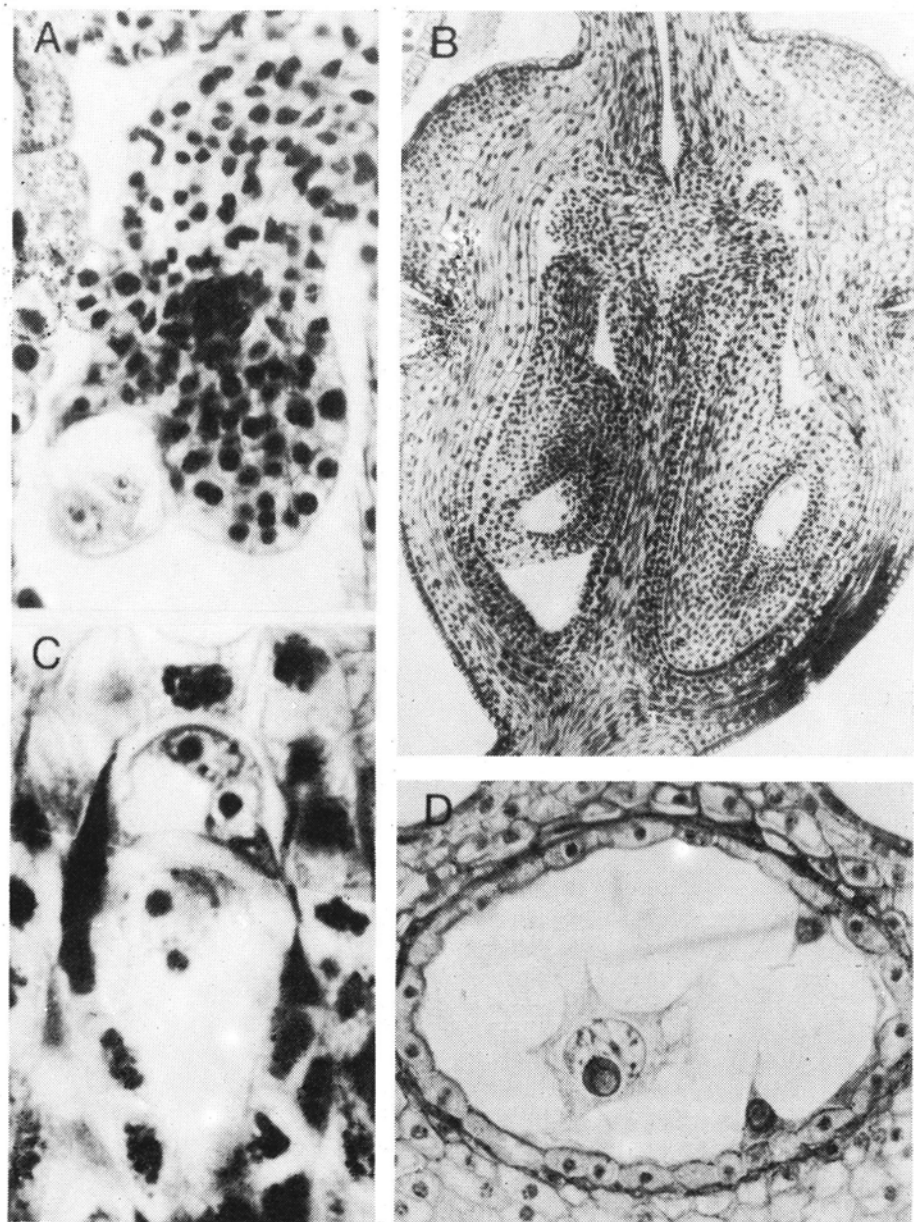


Fig. 4. Microphotographs showing the abnormal structure of *Ch. cicutaria* ovules: A — longitudinal section of a functional ovule at two-nucleate embryo sac stage with a very short funiculus and no integument (500 x), B — longitudinal section of an ovary containing one normal and one incompletely inverted functional ovule, both at the eight-nucleate embryo sac stage; remnants of two abortive, upper ovules are also visible (100 x), C — longitudinal section of a functional ovule containing twin embryo sacs; the upper, additional embryo sac derives from the micropylar coenomegaspore (2000 x), D — cross-section of a functional ovule where the endosperm reveals a Helobial-like type of development; two small endosperm nuclei from the micropylar chamber and a large nucleus from the chalazal chamber are visible (400 x)

when the endosperm derived from the micropylar chamber reaches the cellular stage (Fig. 3).

As regards the total number of flowers that reveal structural abnormalities, no significant differences were observed between plants growing in the centre of the distribution area of *Ch. cicutaria* (mountain populations) and those from isolated localities (lowland populations). Some differences, however, are seen when a particular type of abnormality is considered, even though only six types out of twelve are frequent enough to be taken into account (Table 3). Defective ovaries containing four ovules similar to each other, i.e. which have very short funiculi and no integuments, were found only in plants from the lowland populations while functional ovules with shrivelled nucelli surrounded by well-developed integuments were found only in plants collected in the mountains. The frequencies of the remaining four abnormalities are similar in plants of both groups.

DISCUSSION

Some abnormalities described in *Ch. cicutaria* have already been reported in other members of *Umbelliferae*. It must be added, however, that they were usually found by chance, during routine embryological investigations, and have never been the subject of any detailed studies. A tricarpellary gynoecium was reported in *Hydrocotyle vulgaris* and *Meum athamanticum* (Håkansson 1923) and in *Aethusa cynapium*, *Coriandrum sativum*, *Daucus carota*, *Eryngium maritimum*, *Foeniculum vulgare* and *Psammogeton biternatum* (Gupta 1964). Extra-ovarian ovules were observed in a species of the *Hydrocotyle* genus (Håkansson 1923), while locules containing two functional ovules were found by Penzig (1921) in *Astrantia maior* and *Eryngium maritimum* and by Kordyum (1967) in *Chaerophyllum aromaticum*, *Foeniculum vulgare* and *Pimpinella anisum*.

The occurrence of ovules containing two embryo sacs was reported in *Seseli gracile* (Håkansson 1923), *Foeniculum vulgare* (Gupta 1964), *Muretia lutea* (Kordyum 1967) and in *Bupleurum longifolium* (Chojnacki in press). All the same, the origin of the additive embryo sac is different in all these species except *B. longifolium*, because their embryo sacs do not follow the bisporic type of development as in *Ch. cicutaria* but a monosporic one. Actually, it is the monosporic, *Polygonum* type which characterizes the bulk of the umbellifers. Other, bisporic and tetrasporic types have been reported so far only in a few species (Håkansson 1923, 1927, 1952, Chojnacki 1979, in press). Although it was affirmed in the previous paper (Chojnacki 1979) that only the bisporic, *Allium* type of embryo sac development takes place in *Ch. cicutaria*, the present study shows that a monosporic development is sometimes possible too.

More than one type of embryo sac development may also occur in *Bupleurum rotundifolium* and in *Sanicula europaea* (Kordyum 1967).

The other abnormalities observed in *Ch. cicutaria* are described here for the first time in *Umbelliferae*, though it is quite possible that they also occur in other members of the family. Since these abnormalities are generally less conspicuous, the previous workers might have either overlooked them or considered them to be insufficiently interesting to mention. Nevertheless, they often cause more important consequences than more conspicuous ones. For instance, ovules containing twin embryo sacs or those that have arisen in a tricarpeillary gynoeceium usually succeed in their development, while an ovule that remains incompletely inverted or has an underdeveloped integument is bound to fail. In the latter case, the abnormal structure or position of the micropylar part of the integument prevents pollen tubes from entering the micropyle, this resulting in non-fertilization.

Whatever the consequences of the abnormalities, their effect on fruit production depends mainly on how frequently they occur. Among almost five thousand functional ovules of *Ch. cicutaria* examined during the present study, barely two hundred (3.5 per cent) ovules revealing structural abnormalities considered to end in failure were observed. At the same time, there were eight hundred (18.6 per cent) ovules the development of which was arrested at various stages. Therefore the structural abnormalities may be reckoned to be the cause, or at least the accompanying phenomenon, of less than one quarter of all failures.

The notably low fruit production rate in *Ch. cicutaria* is due to the abundance of both male flowers and such hermaphrodite flowers whose ovaries fail to transform themselves into fruits, also called "non-fruiting hermaphrodites" (Lovett Doust 1980). Without giving rise to any fruits, both categories of flowers usually develop stamens producing viable pollen grains, so their place in the breeding system of *Ch. cicutaria* is quite similar. On the other hand, their structure as well as occurrence and distribution within an inflorescence exhibit considerable differences.

According to Håkansson (1923), the gynoeceium development is arrested so early in male flowers of andromonoecious umbellifers that they reveal no ovaries but have cup-like hollows in their centres instead. In male flowers of *Ch. cicutaria*, however, gynecium development must be arrested a little later than in the plants investigated by Håkansson (1923), because flowers devoid of ovaries are lacking here. On the other hand, numerous flowers are present with small, closed ovaries containing either no ovules or shrivelled remnants of ovular primordia. As long as their stamens have developed normally, they have been regarded as male flowers. The other flowers with defective ovaries, which have revealed

ovules arrested at various stages of development, have been assigned to non-fruiting hermaphrodites. They are the ones in which the bulk of the described abnormalities occurs.

The percentage of male flowers is remarkably constant in all the investigated specimens of *Ch. cicutaria* and usually amounts to about 50 per cent of the total number of flowers. A constant floral sex ratio has also been reported in many other andromonoecious umbellifers; in *Smyrniololus*, *Pastinaca sativa* and *Anthriscus silvestris*, for example, the number of male flowers has always remained close to about 80 per cent (Lovett Doust 1980). The ratio of male to hermaphrodite flowers is considered to be genetically determined and not modified by environmental factors (Håkansson 1923, Kordyum 1967, Cruden 1976, Lovett Doust and Harper 1980). The distribution of male and hermaphrodite flowers within the inflorescences of *Ch. cicutaria* follows the same general trends that have been described in other andromonoecious umbellifers (Kordyum 1967, Bell 1971, Froebe 1964, Lovett Doust 1980).

On the contrary, the proportion of non-fruiting hermaphrodites varies markedly among individual specimens of *Ch. cicutaria*, ranging from 9.5 to 48.8 per cent of all hermaphrodite flowers. In other members of the family it also tends to be variable and, as has been shown in *Smyrniololus* (Lovett Doust 1980), it apparently depends on the soil conditions. Moreover, the number of non-fruiting hermaphrodites and their distribution within the inflorescence seem to be connected not only with the quantity of nutrient resources available to the plant, but also with their patterns of allocation among particular umbels, umbellets and flowers (Håkansson 1923, Kordyum 1967, Lovett Doust and Harper 1980).

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Występowanie nienormalności budowy zalążni i zalążków oraz ich wpływ na produkcję owoców u Chaerophyllum cicutaria Vill. (Umbelliferae)

Streszczenie

Chaerophyllum cicutaria, podobnie jak wiele innych roślin z rodziny Umbelliferae, wytwarza dwa rodzaje kwiatów: męskie i obupłciowe. Owoce i nasiona tworzone są jedynie przez niewielką część kwiatów obupłciowych, gdyż większość ich zamiera w trakcie rozwoju. U blisko jednej czwartej nieowocujących kwiatów obupłciowych obumieraniu towarzyszą zmiany normalnej struktury zalążni, a szczególnie zalążków; u pozostałych nie obserwowano takich zmian. Wyróżniono dwanaście typów nienormalnej budowy zalążków i zalążni i określono częstość ich występowania u roślin pochodzących z różnych populacji gatunku.