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PHYLLOTACTIC PATTERNS IN CAPITULA OF *CARLINA ACAULIS* L.

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ABSTRACT

Phyllotaxis of inflorescences in *Carlina acaulis* L. is spiral. In the majority of capitula it is represented by the main Fibonacci series. From the one thousand of specimens, that were examined, thirty five new phyllotactic series were found: eighteen monojugies, for instance (2,17), (4,11), (7,37) and seventeen multijugies, such as 2(8,9), 2(5,11), 8(2,3). The patterns had been identified on the basic of two or more consecutive numbers of phyllotactic series. Both, the continuous and discontinous transformations of phyllotactic patterns, as well as 'deviations' from the parastichy group numbers were observed. The deviations were distinguished as the probable cases of the discontinuous transformations in which the sectorial change in the parastichy number occured, but the ultimate phyllotactic series could not be determined.

KEY WORDS: *Carlina acaulis* L., phyllotactic pattern, parastichies, transformations

INTRODUCTION

Phyllotaxis is an arrangement of leaves, flowers or other organs on the plant stem. Depending on the way the organs are set on the stem, a number of different phyllotactic patterns occurs in nature. They have been described by several authors (Williams 1975, Hejnowicz 1980, Schwabe 1984, Zagórska-Marek 1985, 1994). The 'whorled' phyllotaxis develops when several organs are inserted at each node on the stem, however, it is not necessary to assume that the initiation of these organs must occur simultaneously (Schwabe 1984). In 'distichous' phyllotaxis a single organ is inserted in each node and the circumferential distance between two consecutive organs, known as 'divergence angle', is 180°. The same sequence of organs, i.e. one organ in one node, occurs typically in 'spiral' phyllotaxis, where the divergence angle is less than 180°. In most of the cases it approximates 137.5°, i.e. the Fibonacci angle. In spiral pattern the spiral taking the shortest way of connecting succesive organs, starting with the oldest one, is called 'the genetic spiral' (Hejnowicz 1967). It winds clockwise or anticlockwise, which determines the chirality of the pattern as S or Z, respectively. Steeper spirals connecting not all consecutive organs but every second or third one are called 'parastichies'. Their number is equal to one of the numbers of the phyllotactic series associated with the particular pattern. The one which is most common in many plants is the main Fibonacci series. It starts with the numbers 1 and 2. Every number of the series, except the first and the second, is the sum of the two preceeding numbers. The same principle is observed for other series, where the first numbers and the divergence angle are different than in the main series. Sometimes it happens that in a spiral pattern two or three organs are initiated at the same level, in the first case opposing each other, in the second – with the circum ferential interval of 120°. In these cases two or three genetic spirals can be drawn and the angle between succesive pairs or groups of three organs is Θ/2 or Θ/3, where Θ is the divergence angle associated with the specific series. Such spiral systems are called bijugy and trijugy respectively.

A number of theories explaining a proces of phyllotactic pattern formation have been proposed. The most significant are: Schwendener's (1878) contact pressure model developed by Adler (1975, 1977), the reaction-diffusion theory by Schoute (1913) and Richards (1951) and the first available space theory by Snow and Snow (1962). They all have been reviewed and shortly described by Schwabe (1984).

It is not obvious why the main Fibonacci series is favoured by nature as a basic pattern of the arrangement of organs on the stem. Jean (1980) suggested the possibility of occuring Fibonacci-type phyllotactic series based on his concept of minimal entropy. According to this model the main Fibonacci series has to be most frequent in nature; nevertheless, other series may also occur.

Among different categories of patterns various monojugies have been reported in plants by many authors (Weisse 1897; Fujita 1937, 1938, 1939, 1942; Schoute 1938; Sterling 1945; Cutter 1964; Davis and Bose 1971; Gregory and Romberger 1972; Zagórska-Marek 1985, 1994; Jean 1992). Some multijugies of the main and accessory series have been observed. Among these bijugate condition of the main series is the most frequent (Weisse 1897; Fujita 1938, 1939; Shoute 1938; Sterling 1945; Gregory and Romberger 1972; Zagórska-Marek 1985, 1994). Other series such as main trijugy and tetrajugy are rare (Zagórska-Marek 1985). Occasionaly the bijugy of the Lucas series (of the first accessory series) occurs (Davis and Bose 1971; Zagórska-Marek 1985).

Two types of ontogenetic transformation of the phyllotactic pattern were defined by Zagórska-Marek (1987): the continuous and discontinuous. A continuous transformation it is a change in order of phyllotaxis within the same pattern with no change of the series, .whereas discontinuous transition means the ontogenetic change from one phyllotactic series to another. The latter, associated with assymetric dislocations of the phyllotactic grid was observed in vegetative shoots of *Abies balsamea* Mill. and in the carpel arrangement of some *Magnolia* species (Zagórska-Marek 1985, 1987, 1994).

From preliminary studies on capitula of *Carlina acaulis* it appeared that they represent an excellent material to study the phenomenon of spiral phyllotaxis. On one hand there is a great variety of phyllotactic series and both, the continuous and discontinuous transformations are present. There are even indications of not only unknown, but also uncommon series. On the other hand the patterns are relatively easy to study. Capitula have been very often examined both theoretically (Vogel 1979, Ridley 1982, Williams and Brittain 1984, van der Linden 1990) and empirically (Battjes, Vischer and Bachman 1993) but usually in *Heliantus* – the model object. The aim of this paper is to provide detailed information on phyllotactic pattern occuring in capitula of *Carlina acaulis* and point out how useful this species is for more general studies referring to the transitions of phyllotactic patterns.

MATERIAL AND METHODS

Capitula of *Carlina acaulis* were collected in a springtime after the fruits had been dispersed. The scales of tubular flowers were cut off and the receptacle was polished and wetted. Capitula were then placed between two sheets of blotting paper and pressed in order to obtain the disks as flat as possible. The flattened disks were photographed with use of convertible photography. The type of phyllotactic series, the shape and size of floral bases and the chirality of the genetic spiral were determined in each disk. Parallel parastichies similarly curved were termed as 'parastichy group'. Their number in a group always belonged to the phyllotactic series. Several groups of opposite parastichies were conspicuous in each capitulum and the pattern was always determined on the basis of more than one number from the phyllotactic series.

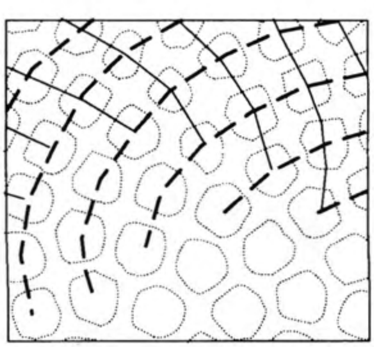
One thousand of capitula had been examined. In the majority of them contact parastichies (Sinnot 1960) were easily recognizable (Fig. 1a). They were marked as well as other parastichy groups possible to identify. All parastichies passed trough the centres of flowers. Parastichies of two consecutive groups created a set of 'rhombs'. The diagonals of these rhombs appeared to be fragments of parastichies belonging to the group either of a bigger number (shorter diagonals) or of a smaller number (longer diagonals) (Fig. 1b). In cases where it was difficult to find contact parastichies, centres of four neighbouring flowers were connected. In the grid that subsequently appeared, parallel segments were considered to belong to parastichies. Special attention was paid to the presence of dislocations indicating phyllotactic transitions.

A deviation from the parastichy groups numbers was defined as a reduction or an addition of one or more parastichies within a group with no obvious change of the series. It was always observed in the group or groups representing the smallest identifiable number of the series occuring in the capitulum and this is why it was impossible to determine the ultimate series. The notation used in Tables for describing the deviations is F_n-k or F_n+k, where F_n is a number of the series, k is a number of parastichies reduced or added to the group; for instance the notation 8-1 means that one parastichy was reduced in the group of eight. In Tables 3-8 theoretical series are underlined and the series observed in capitula are written beneath. The series that had been observed earlier by other authors are marked with an asterisk.

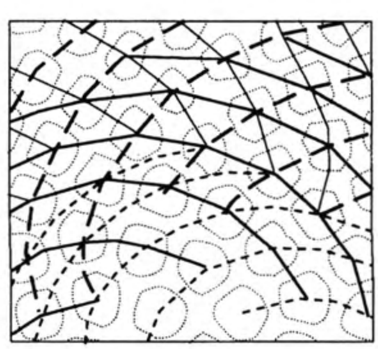
Some patterns were diffcult to interpret because of many local disturbances. In such cases the most probable, in the author's opinion, interpretation had been adopted.

RESULTS

In capitula of *Carlina acaulis* L. phyllotactic pattern is spiral. The frequency of series found in capitula is presented in Tables 1 and 2. Table 1 shows pure patterns, patterns with deviations and these to which not known phyllotactic series could be attributed. All these were present in 865 capitula, i.e. constituted 86.5% of the total. In Table 2 the patterns, associated with the discontinuous transformations are presented. There were 135 capitula with such transformation, which makes 13.5% of all specimens. In 134 of them the transition took place only once thus two different series ocurred. In one case there were two consecutive transitions thus three series were observed. This is why in the Table 2 there are 271 series



a



b

Fig. 1. Fragment of capitulum with contact parastichies which form a system of 'rhombs' (a). Their diagonals are parastichies from another, consecutive group (b). Parastichies belonging to the same group are drawn with the same line.

TABLE 1. The percentage comparison of the phyllotactic series occuring in capitula, in which pure patterns, patterns with deviation and unknown patterns were present.

Fibonacci series	pure patterns	63,2%
	patterns with deviations	18,2%
Other monojugies	pure patterns	1,1%
	patterns with deviations	0,9%
Multijugies of the Fibonacci series	pure patterns	0,5%
	patterns with deviations	0,4%
Multijugies of other series	pure patterns	0,6%
	patterns with deviations	0,5%
Unknown		1,1%
		Total 86,5% of the series in 865 capitula

TABLE 2. The percentage comparison of the series found in capitula, in which discontinuous transformations occurred.

Fibonacci series	11,6%
Other monojugies	7,1%
Multijugies of the Fibonacci series	0,6%
Multijugies of other series	7,8%
	Total 27,1% of the series in 135 capitula

listed (2·134 + 3·1). The total of data presented in Tables 1 and 2 covers all patterns found in one thousand of examined inflorescences.

The main Fibonacci series

In 93.0% of the capitula the main Fibonacci series occurred. The 63.2% of these constituted 'pure' patterns, i.e. patterns without sectorial dislocations indicating discontinuous transformations or deviations (Table 1). Fig. 2 shows such case with the pure Fibonacci series, where four groups of parastichies are marked: 34_S, 21_Z, 13_S, 8_Z. In 18.2% of capitula with this series deviations were observed (Table 1). In 11.6% the discontinuous transformation occurred (Table 2), meaning that the Fibonacci series was not the only one in these capitula.

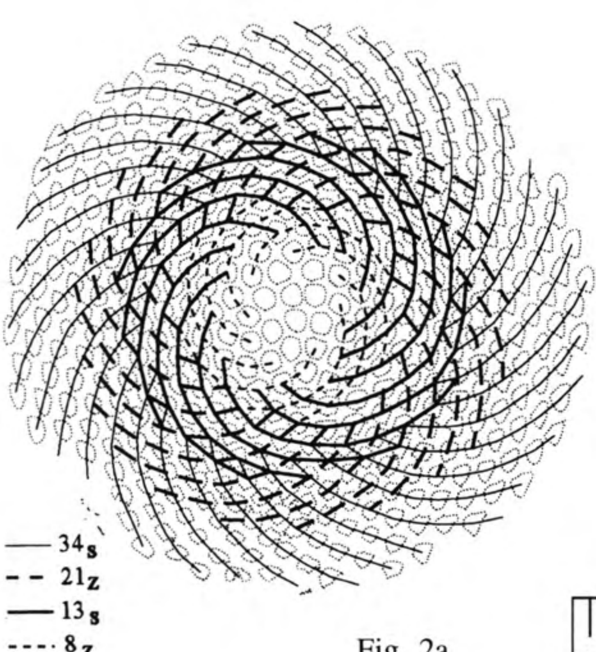
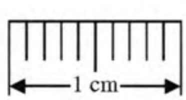


Fig. 2a



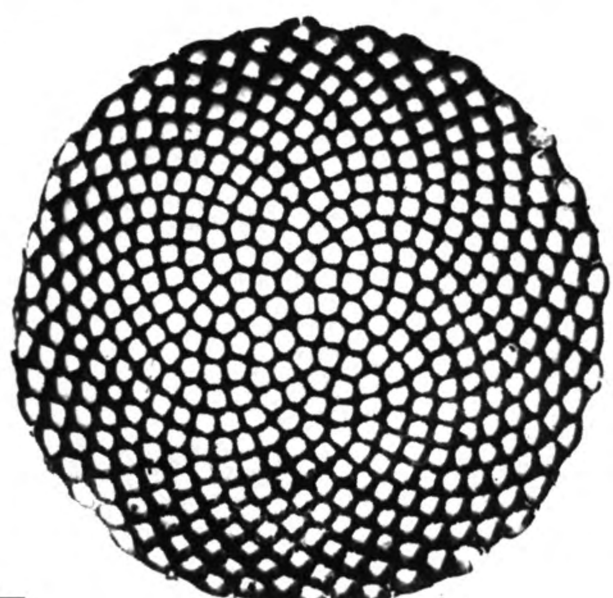


Fig. 2b

Figures 2a-17a and 19a are drawings of capitula with not all but some parastichies marked, while figures 2b-17b and 19b are photographs of these capitula, respectively. Legends to the drawings contain numbers of parastichy groups marked in such a way, that the greater numbers occuring in the outer, i.e. the older part of the capitula, are written first. Changes of the parastichy groups numbers, leading to the discontinuous transformation or deviation, are indicated by arrows. Magnification of each picture is indicated by the bar shown at the bottom.

Fig. 2. The main Fibonacci series.

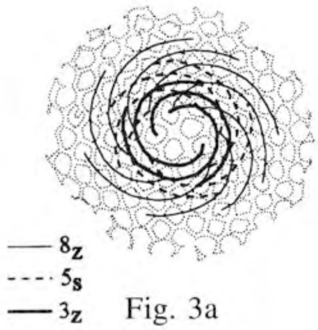


Fig. 3a

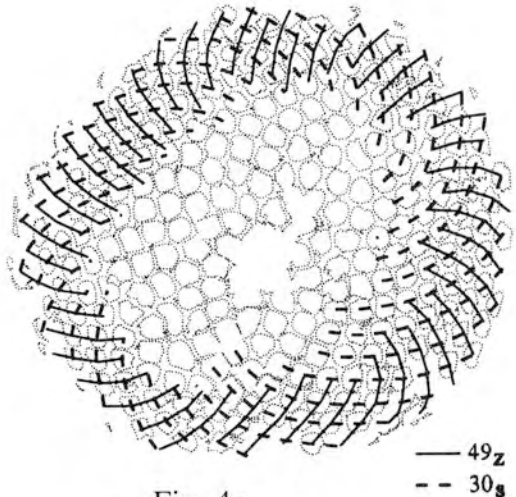


Fig. 4a

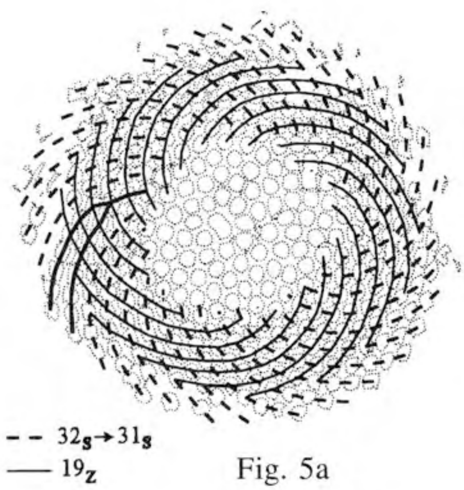


Fig. 5a

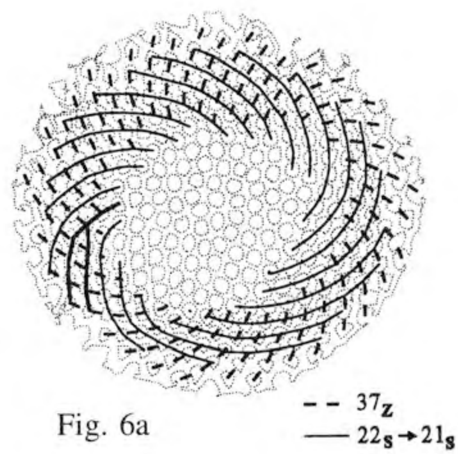


Fig. 6a

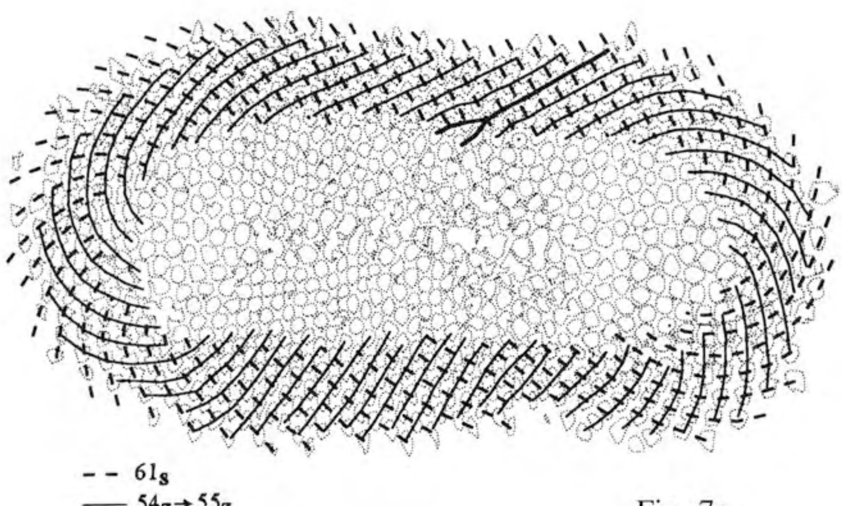


Fig. 7a

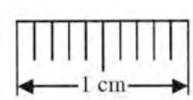


Fig. 3. The main Fibonacci series in a very small capitulum.
Fig. 4. The (3,8) series in the outer part.
Fig. 5. The (6,13) series in the outer part. A reduction of one parastichy of thirty two (marked with the thicker line).
Fig. 6. The (7,15) series in the outer part. A reduction of one parastichy of twenty two (marked with the thicker line).
Fig. 7. The (7,54) series in the outer part. An addition of one parastichy to the group of fifty four (marked with the thicker line).

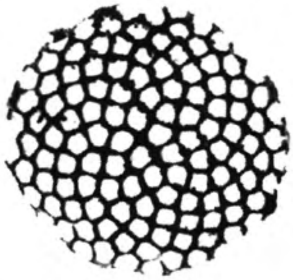


Fig. 3b

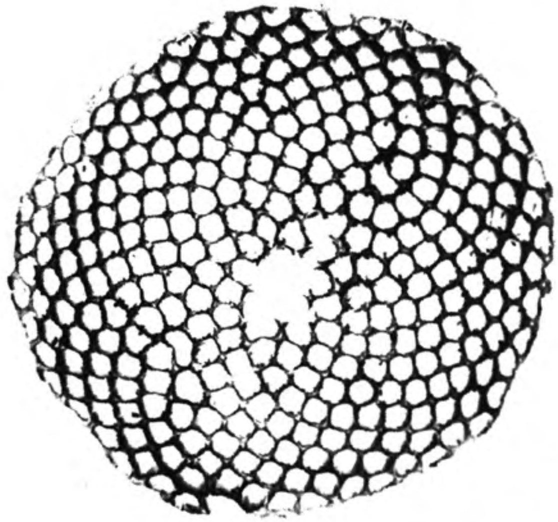


Fig. 4b

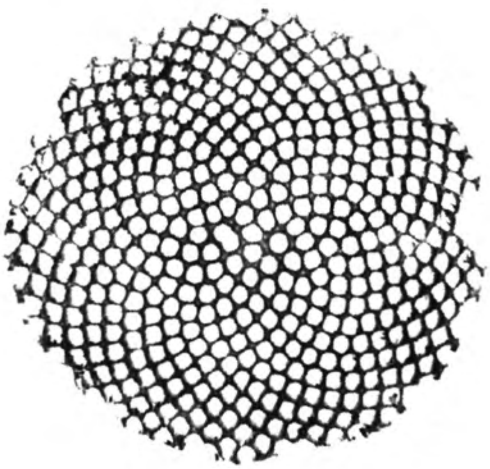


Fig. 5b

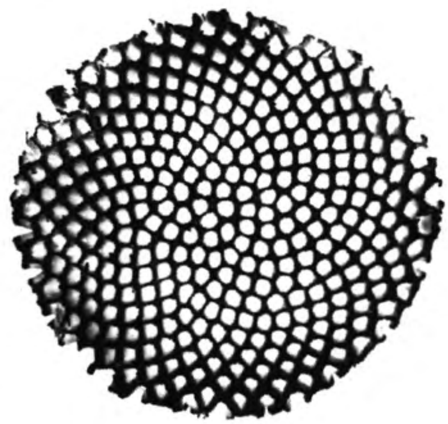


Fig. 6b

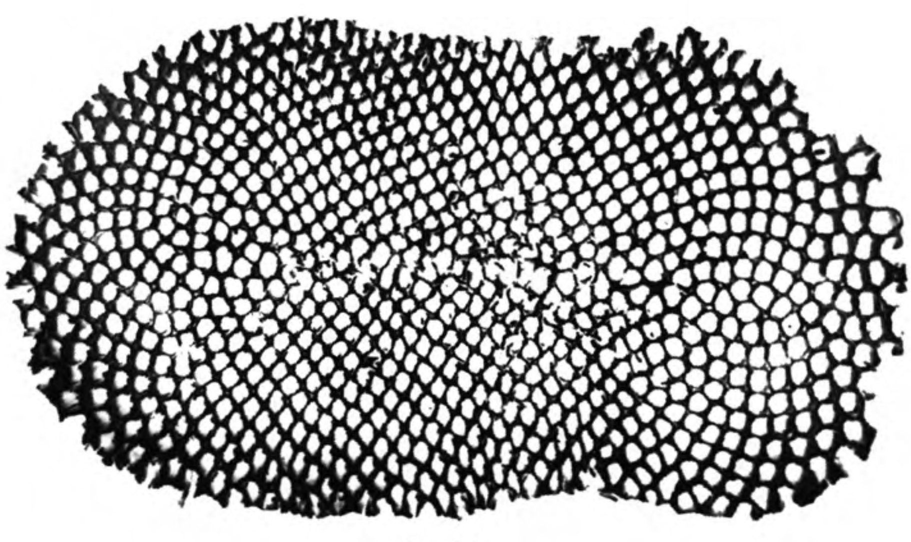


Fig. 7b

The inflorescences which were very small usually had a very regular parastichy course with neither deviations nor discontinuous transformations. Fig. 3 shows such capitulum with the main Fibonacci series in which the smallest conspicuous parastichy group is three.

Monojugies of the Fibonacci type

The 9.1% of capitula had other monojugies of the Fibonacci type: 1.1% of them were pure patterns (Table 1), in 0.9% there were deviations (Table 1), and in 7.1% discontinuous transformations occured (Table 2). Among them, eighteen new monojugies in nineteen capitula were found. Fig. 4 shows the capitulum with the rare series (3,8). Another series (6,13) with the change $32_s \rightarrow 31_s$ in the outer part of the capitulum is shown in Fig. 5. New series (7,15) and (7,54) observed in the outer parts of capitula are shown in Fig. 6 and Fig. 7, respectively. Localized changes in the parastichy numbers in these patterns mark discontinuous transformations. Table 3 presents the Fibonacci type monojugies which occured in capitula as the only series in each disk. The pure patterns and the patterns with deviations are listed together. Monojugies associated with the discontinuous transition, thus occurring with other series, are presented in Table 4.

TABLE 3. Fibonacci type monojugies in capitula of *Carlina acaulis*. The series occuring as the only one pattern in each capitulum are presented here.

* (3, 4)	3,	4,	7,	11,	18,	29,	47,	76,	123,	...
			7,	11,	18,	29,	47,	76		
				11,	18,	29,	47,	76		
				11-3,	18,	29,	47,	76,	123	
					18-1,	29,	47,	76,	123	
* (4, 5)	4,	5,	9,	14,	23,	37,	60,	97,	... .	
		5,	9,	14,	23,	37,	60			
* (5, 6)	5,	6,	11,	17,	28,	45,	73,	118,	...	
			11,	17,	28,	45,	73,			
				17-1,	28,	45,	73,	118		
				17-2,	28+1,	45,	73,	118		
* (6, 7)	6,	7,	13,	20,	33,	53,	86,	139,	...	
		7,	13,	20,	33,	53,				
		7+1,	13,	20,	33,	53,	86			
			13,	20,	33,	53,	86			
			13,	20,	33,	53,	86,	139		
* (2, 5)	2,	5,	7,	12,	19,	31,	50,	81,	131,	...
				12,	19,	31,	50,	81,	131	
* (3, 7)	3,	7,	10,	17,	27,	44,	71,	115,	...	
				17-3,	27,	44,	71,	115		
* (3, 8)	3,	8,	11,	19,	30,	49,	79,	...		
			11-2	19,	30,	49				
(6, 51)	6,	51,	57,	108,	165,	...				
		51-1	57-3,	108						
(7, 15)	7,	15,	22,	37,	59,	96,	155,	...		
		15,	22,	37,	59,	96				
((7, 54)	7,	54,	61,	115,	176,	...				
		54+1,	61,	115						
(9, 20)	9,	20,	29,	49,	78,	127,	...			
		20,	29,	49,	78					
(11, 23)	11,	23,	34,	57,	91,	...				
	11,	23	34,	57						

* (18, 19)	18,	19,	37,	56,	93,	149,	...	
		19,	37,	56,	93			
(41, 42)	41,	42,	83,	125,	208,	...		
	41,	42,	83					
(2, 17)	2,	17,	19,	36,	55,	91,	146,	...
			19,	36,	55,	91		
(4, 11)	4,	11,	15,	26,	41,	67,	108,	...
		11,	15,	26				
				26,	41,	67		
(4, 13)	4,	13,	17,	30,	47,	77,	124,	...
			17,	30,	47,	77		
(4, 17)	4,	17,	21,	38,	59,	97,	156,	...
		17,	21,	38				
(4, 41)	4,	41,	45,	86,	131,	217,	...	
		41,	45,	86				
(6, 13)	6,	13,	19,	32,	51,	83,	134,	...
		13,	19,	32,	51,	83		
(6, 15)	6,	15,	21,	36,	57,	93,	150,	...
				36,	57	93		
(7, 37)	7,	37,	44,	81,	125,	206,	...	
		37,	44,	81				
(10, 21)	10,	21,	31,	52,	83,	135,	218,	...
	10,	21,	31,	52				
(13, 44)	13,	44,	57,	101,	158,	259,	...	
		44,	57					

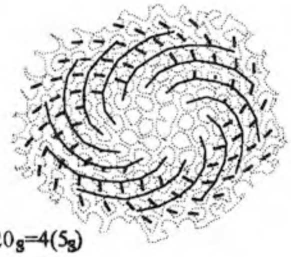


Fig. 8a

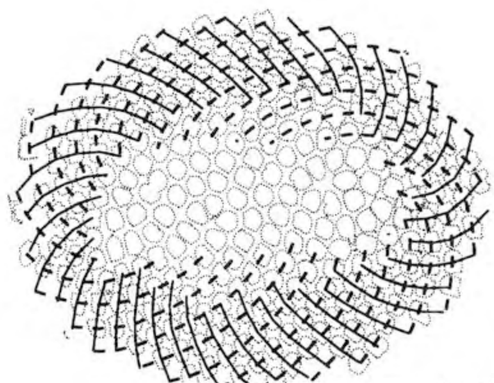


Fig. 9a

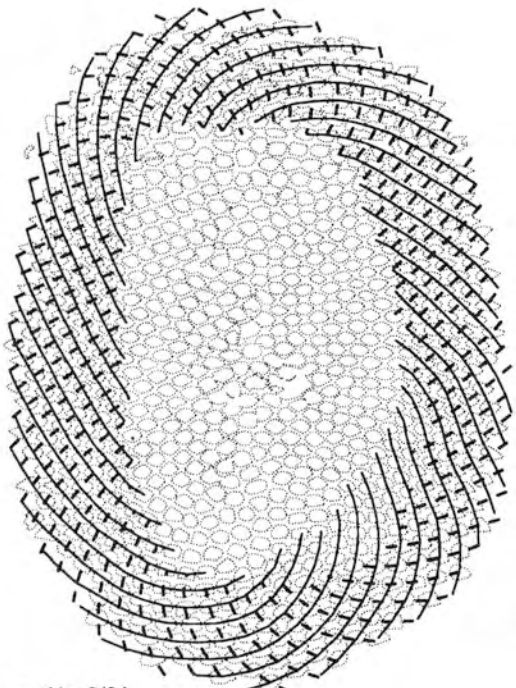


Fig. 10a

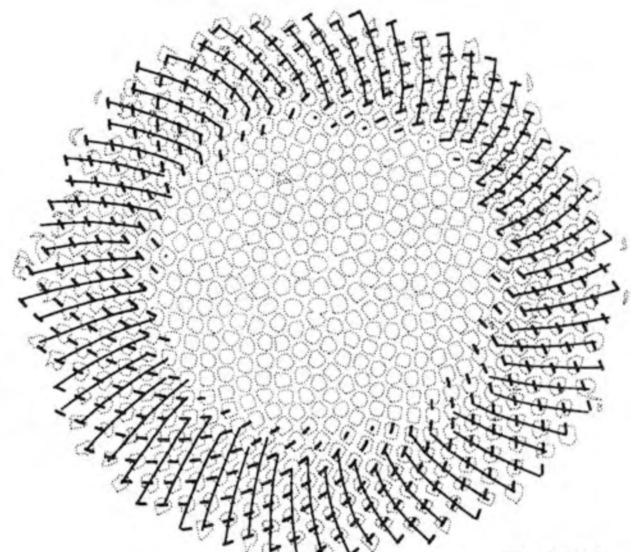


Fig. 11a

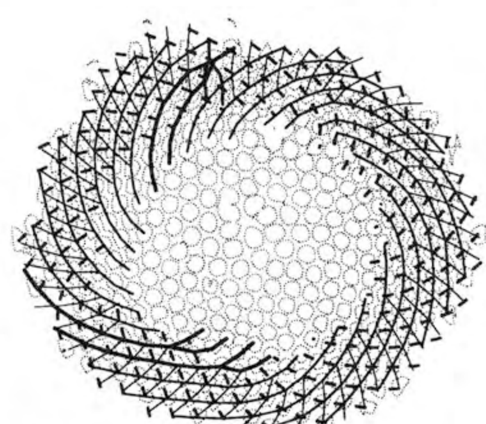


Fig. 12a

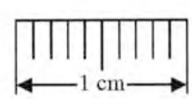


Fig. 8. The tetrajugy of the main Fibonacci series [4(2,3)].
Fig. 9. The pentajugy of the main Fibonacci series [5(2,3)].
Fig. 10. The octajugy of the main Fibonacci series [(8(2,3)].
Fig. 11. The 3(4,5) series.
Fig. 12. The 2(2,5) series in the outer part. All changes in parastichy groups are marked with the thicker line.

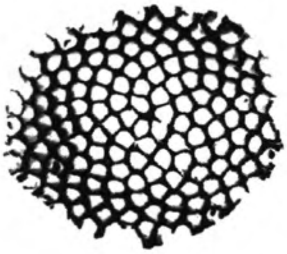


Fig. 8b

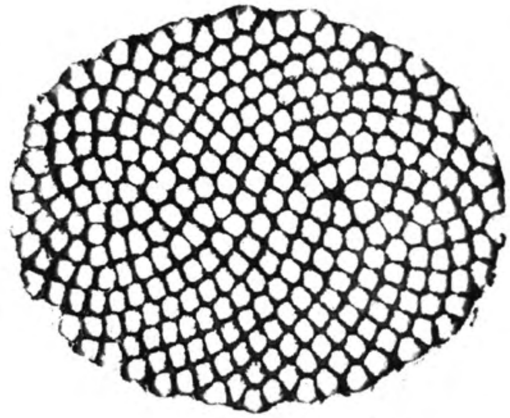


Fig. 9b

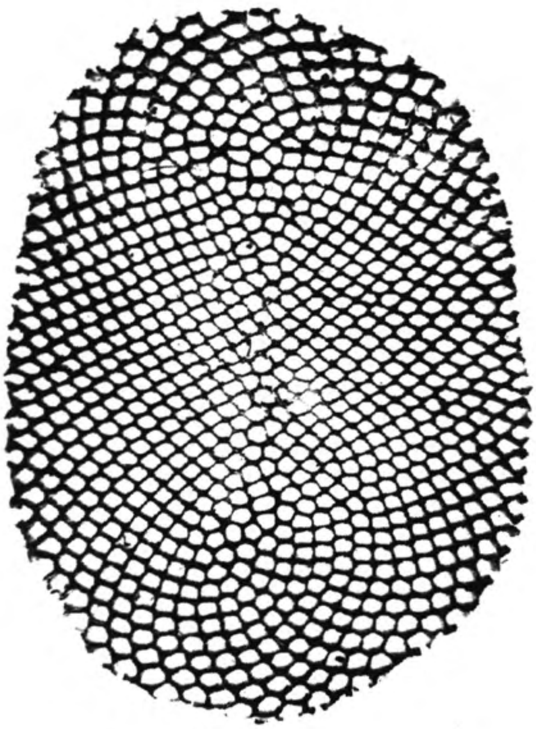


Fig. 10b

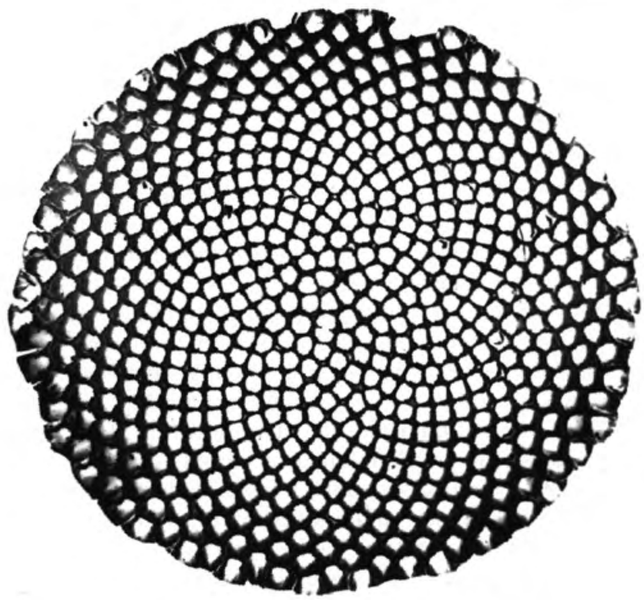


Fig. 11b

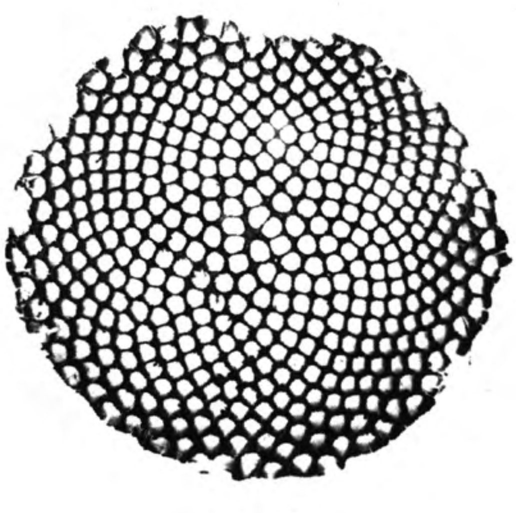


Fig. 12b

TABLE 5. Multijugies of the main Fibonacci series occuring in capitula as the only series.

* 2(2, 3)	4,	6,	10,	16,	26,	42,	68,	110,	178,	...
		6,	10,	16,	26,	42,	68			
		6,	10,	16,	26,	42,	68,	110		
* 4(2, 3)	8,	12,	20,	32,	52,	84,	136,	...		
	8,	12,	20,	32,	52					
		12-1,	20,	32,	52,	84				
		12,	20+1,	32,	52,	84,	136			
5(2, 3)	10,	15,	25,	40,	65,	105,	...			
		15,	25,	40,	65					
		15-1,	25,	40,	65					
8(2, 3)	16,	24,	40,	64,	104,	168,	272,	...		
		24,	40,	64,	104,	168				
		24-2	40,	64,	104					

Multijugies of the main Fibonacci series

In 1.5% of the cases the multijugies of the Fibonacci series occurred. The 0.5% of them were pure patterns (Table 1) exemplified by the tetrajugy 4(2,3) – Fig. 8, the pentajugy 5(2,3) – Fig. 9 and the octajugy 8(2,3) – Fig. 10. Despite the different shapes and sizes of these disks no disturbances in the phyllotactic patterns were observed. In Fig. 10 the course of some parastichies on the right side is slightly disturbed, which does not visibly affect the phyllotactic pattern. In 0.4% of inflorescences with multijugies of the main series the deviations from the parastichy groups numbers occurred (Table 1), whereas in 0.7% of them discontinuous transformations were observed (Table 2). Four new multijugies of the Fibonacci series were found in seven capitula. Table 5 presents all cases of the multijugies of the main series that occur in the inflorescence as the only series, including pure patterns and the patterns in which deviations are present. Table 6 shows the cases with the discontinuous transformations.

TABLE 6. Multijugies of the main Fibonacci series occuring in capitula, in which the transformation of the pattern was observed. The series which occurred as the only ones in capitula are not shown

6(2, 3)	12,	18,	30,	48,	78,	126,	204,	...
	12,	18,	30					
11(2, 3)	22,	33,	55,	88,	143,	231,	...	
	22,	33,	55,	88				
	22,	33,	55,	88				

Multijugies of the Fibonacci type series

In 8.9% of the capitula the multijugies other than of the main series were encountered. In 0.6% of them there were pure patterns (Table 1), in 0.5% the deviations were observed (Table 1), but the majority of these cases, that is 7.8%, occured in capitula with discontinuous transformation of the pattern (Table 2). Fig. 11 shows the disk in which the pure 3(4,5) pattern occurs. In Fig. 12 the specimen is shown in which both, the pattern transformation and the deviation, were found. In the outer part of this capitulum the 2(2,5) series is present. The dislocation near the top edge of the capitulum transforms the pattern into the one characterized by the series (12, 13). Another dislocation visible at the bottom of the picture represents the deviation. In seventeen capitula thirteen new multijugies of the accessory series were observed. Table 7 presents pure patterns and the ones in which deviations occur. The cases with the discontinuous transformation of the pattern are listed in Table 8.

Discontinuous transformations

In 13.5% of the capitula discontinuous transformations were observed. The 0.7% of them had also deviations. Figs 13, 14 and 15 show the disks in which such transformations were present. There can be two or more different series in the capitulum with the discontinuous transformation. Usually the one parastichy group, in which no changes are observed, belongs to both patterns – the initial from the outer part of the disk and the new one – result of the transformation. This is exemplified by the capitulum shown in Fig. 13, where the number fifty five belongs to the main series occuring in the outer part as well as to the pentajugy of the (3,4) series near the centre. The inflorescence shown in Fig. 15 contains the group of thirty four parastichies and this number also belongs to two series: 2(3,7) and (2,3), both present in the disk. Yet another example represents the capitulum shown in Fig. 14, where the change of parastichy numbers occurs in the groups of forty seven and seventeen, both of the same chirality, while the number of the group of thirty parastichies is unchanged. Only parastichies crossing the flower positioned at the site of transformation are marked. The transitions occured both in the small and in the big capitula, although they were more likely to be found in the big ones. In Table 9 all the types of transitions encountered are listed. In 1.1% of the cases it was impossible to define any Fibonacci type series.

Deviations

The deviations from the parastichy group numbers were observed in 20.7% of the phyllotactic patterns in all investigated capitula. The 18,2% of them occured in the inflorescences with the Fibonacci series. It is significant that deviations occurred in the groups with rather small parastichy number. For the main series they were five or eight up until thirteen, rarely

TABLE 7. Multijugies of additional phyllotactic series occuring in capitula as the only series.

2(5, 6)	2(5,	6,	11,	17,	28,	45,	73,	...)
	10,	12,	22,	34,	56,	90,	146,	...
	10,	12,	22,	34,	56,	90		
		12+1,	22,	34,	56,	90		
2(8, 9)	2(8,	9,	17,	26,	43,	69,	112,	...)
	16,	18,	34,	52,	86,	138,	224,	...
		18-1,	34,	52,	86			
2(3, 7)	2(3,	7,	10,	17,	27,	44,	71,	...)
	6,	14,	20,	34,	54,	88,	142,	...
		14-1,	20,	34,	54,	88		
		14-1,	20,	34,	54,	88		
			20,	34,	54,	88		
2(5, 11)	2(5,	11,	16,	27,	43,	70,	...)	
	10,	22,	32,	54,	86,	140,	...	
		22,	32,	54,	86,	140		
3(3, 4)	3(3,	4,	7,	11,	18,	29,	47,	...)
	9,	12,	21,	33,	54,	87,	141,	...
	9-1,	12,	21,	33,	54,	87		
		12,	21,	33,	54,	87		
3(4, 5)	3(4,	5,	9,	14,	23,	37,	60,	...)
	12,	15,	27,	42,	69,	111,	180,	...
	12,	15,	27,	42,	69,	111		
3(7, 16)	3(7,	16,	23,	39,	62,	...)		
	21,	48,	69,	117,	186,	...		
	21,	48,	69,	117				

TABLE 8. Multijugies of accessory phyllotactic series in capitula, in which the transformation of the pattern was observed. Series which occur as the only ones in capitula are not shown here.

2(6, 7)	2(6,	7,	13,	20,	33,	53,	86,	...)
	12,	14,	26,	40,	66,	106,	172,	...
			26,	40,	66			
2(7, 8)	2(7,	8,	15,	23,	38,	61,	99,	...)
	14,	16,	30,	46,	76,	122,	198,	...
	14,	16,	30,	46,	76			
2(2, 5)	2(2,	5,	7,	12,	19,	31,	50,	...)
	4,	10,	14,	24,	38,	62,	100,	...
			14,	24,	38,	62		
2(3, 8)	2(3,	8,	11,	19,	30,	49,	79,	...)
	6,	16,	22,	38,	60,	98,	158,	...
				38,	60,	98		
2(3, 19)	2(3,	19,	22,	41,	63,	104,	...)	
	6,	38,	44,	82,	126,	208,	...	
		38,	44,	82				
5(3, 4)	5(3,	4,	7,	11,	18,	29,	47,	...)
	15,	20,	35,	55,	90,	145,	235,	...
	15,	20,	35,	55				

TABLE 9. Types of discontinuous transformation of the pattern in capitula of *Carlina acaulis*. In the second column the number of capitula in which such transformation occured is written. The changes of parastichy group numbers, which caused the transformations, are given beneath the numbers of the series occurring in capitula in the third column.

(2, 3) → (6, 7)	30	89, 55, 34, 21, 13, 8 → 13, 7, 6 (8 → 7)
(2, 3) → (10, 11)	16	89, 55, 34, 21, 13 → 21, 11, 10 (13 → 11)
(2, 3) → (11, 23)	1	89, 55, 34, 21 → 34, 23, 11, 21 → 23)
(2, 3) → 2(5, 6)	7	89, 55, 34, 21 → 34, 22, 11 21 → 22
(2, 3) → 2(3, 7)	6	89, 55, 34, 21 → 34, 20, 14 (21 → 20)
(2, 3) → 3(3, 4)	52	89, 55, 34, 21, 13 → 21, 12, 9 (13 → 12)
(2, 3) → 5(3, 4)	1	89, 55, 34 → 55, 35, 20, 15 (34 → 35)
(10, 11) → (10, 21)	1	53, 32, 21 → 52, 31, 21, 10 (53 → 52)
(10, 11) → 4(2, 3)	1	138, 85, 53, 32, 21 → 32, 20, 12 (21 → 20)
(2, 17) → (17, 38)	1	91, 55, 36, 19 → 55, 38, 17 (36 → 38)
(3, 8) → 6(2, 3)	1	79, 49, 30, 19 → 30, 18, 12 (19 → 18)
(4, 11) → 2(6, 7)	1	67, 41, 26 → 66, 40, 26 (67 → 66)
(4, 13) → 2(7, 8)	1	77, 47, 30, 17 → 76, 46, 30, 16, 14 (77 → 76)
(4, 41) → (41, 42)	1	86, 45, 41 → 83, 42, 41 (86 → 83)
(6, 13) → (2, 5)	1	83, 51, 32, 19, 13 → 31, 19, 12 (32 → 31)
(6, 15) → (18, 19)	1	93, 57, 36 → 93, 56, 37, 19 (57 → 56)
(13, 45) → (13, 44)	1	103, 58, 45 → 57, 44 (58 → 57)
2(2, 3) → (13, 14)	1	68, 42, 26, 16 → 41, 27, 14 26 → 27
2(2, 3) → (4, 11)	1	110, 86, 42, 26, 16 → 26, 15, 11 (16 → 15)
2(2, 5) → (12, 13)	1	62, 38, 24, 14 → 63, 38, 25, 13 (62 → 63)
2(3, 7) → (2, 3)	2	88, 54, 34, 20 → 34, 21, 13 (20 → 21)
2(3, 8) → (4, 17)	1	98, 60, 38, 22 → 38, 21, 17 (22 → 21)
2(3, 19) → (7, 37)	1	82, 44, 38 →81, 44, 37 (82 →81)
3(3, 4) → (6, 7) → (10, 11)	1	87, 54, 33 →53, 33, 20 → 53, 32, 21 (54 →53) (33 → 32)
3(3, 4) → (10, 11)	1	87, 54, 33, 21, 12 → 21, 11, 10 12 →11
3(3, 4) → 2(3, 7)	1	87, 54, 33, 21 → 54, 34, 20 (33 → 34)
11(2, 3) → (2, 3)	1	88, 55, 33, 22 → 34, 21, 13 (33 → 34)
11(2, 3) → 3(3, 4)	1	88, 55, 33, 22 → 33, 21, 12, 9, 3 (22 → 21)

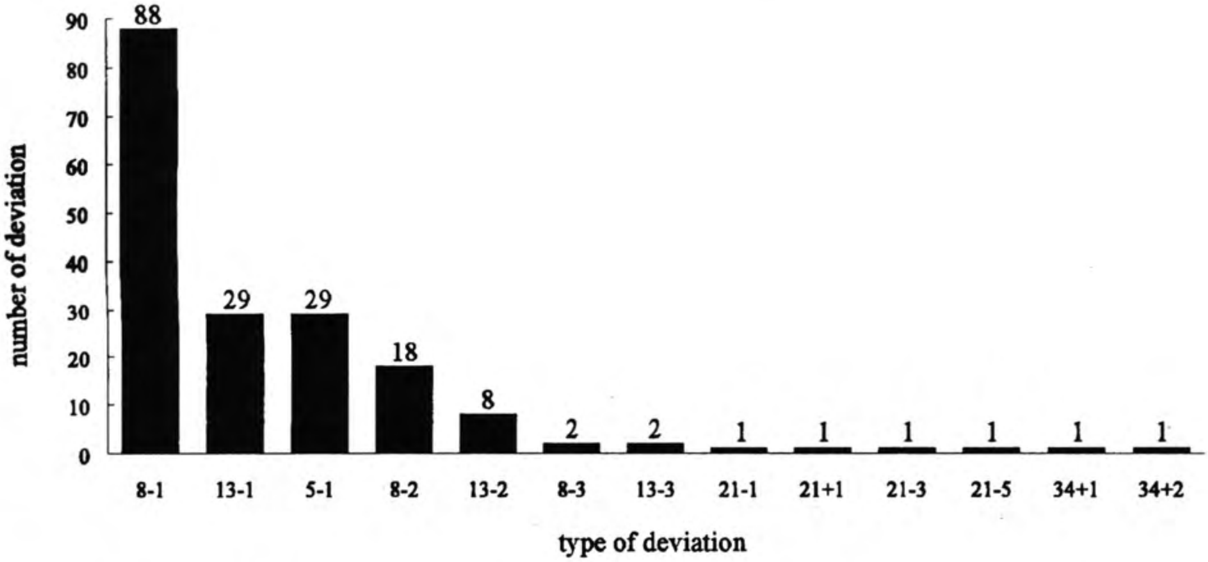


Fig. 18. Frequency of the deviations from the parastichy group numbers in the main Fibonacci series.

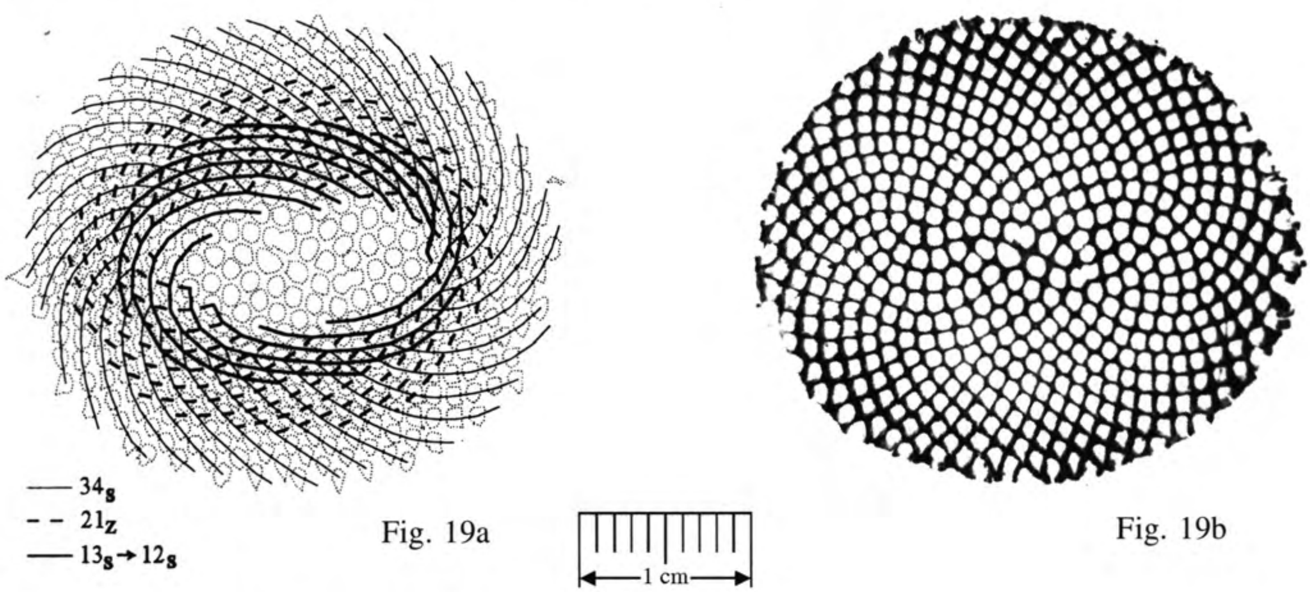


Fig. 19. The oval-shaped capitulum with the main Fibonacci series.

in the groups of twenty one or thirty four. This phenomenon is illustrated in Fig. 16. It shows the capitulum where one parastichy in the group of thirteen is reduced. Another example is given in Fig. 17 where one parastichy of eight is reduced. Only parastichies crossing the flower, located at the site of deviation are marked. Another interesting observation is that parastichies are more frequently reduced than added, which is probably due to the diminishing circumference of the parastichy system. Fig. 18 shows deviations quantitatively in the consecutive parastichy groups in all cases with the main series, where deviations occurred.

Most of the disks were circular in shape, however, some of them had a characteristic oval shape. Fig. 19 shows the example of such oval capitulum with the main series, where the deviation from the thirteen parastichy group number occurs. Because such deviations were observed in capitula of different shapes, the shape itself can not be considered as the obvious cause of the deviation. In oval disks there were usually two centres; the parastichies ran towards these centers, like in Fig. 9. It is not obvious if there is any relationship between the shape and the occurence of discontinuous transformations or deviations, because in some oval shaped inflorescences they happen and in some they do not.

Among the capitula studied 45.4% patterns were of the Z chirality of the genetic spiral and 44.5% of the S chirality. In 9% of the cases the change of the chirality of the pattern resulting from discontinuous transformation was noted. In 4.4% of them the change from S to Z chirality occurred and in 4.5% from Z to S. In one inflorescence the chirality changed twice: S $\rightarrow$ Z $\rightarrow$ S. In other cases the discontinuous transformation of the phyllotactic pattern occurred with no change in the chirality of the genetic spiral. In 1.1% of capitula it was impossible to attribute any phyllotactic series to the pattern although the same methods of pattern identification were applied. In these cases with the irregular phyllotaxis the chirality of the genetic spiral was not determined.

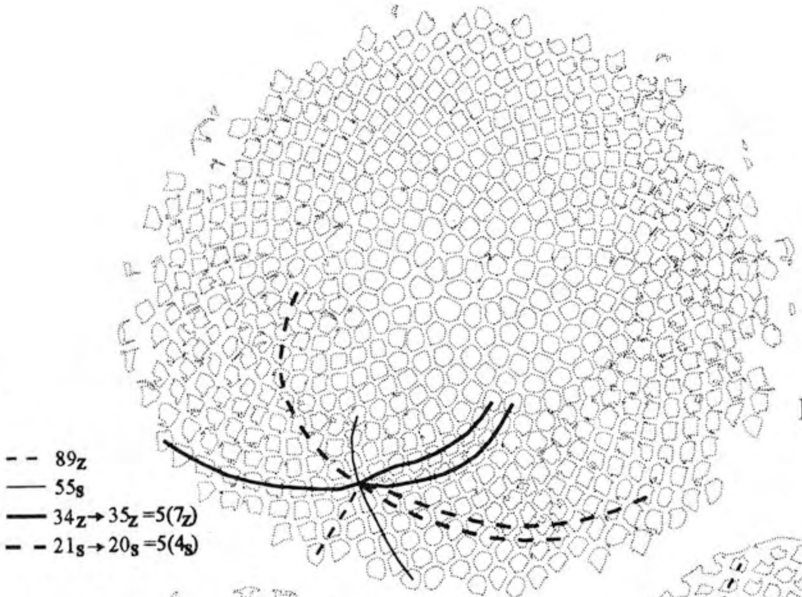


Fig. 13a

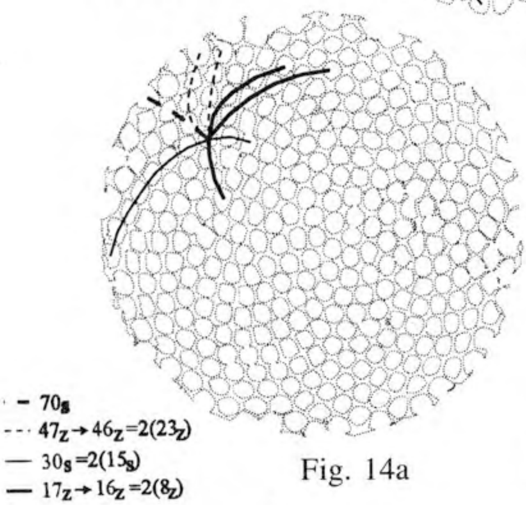


Fig. 14a

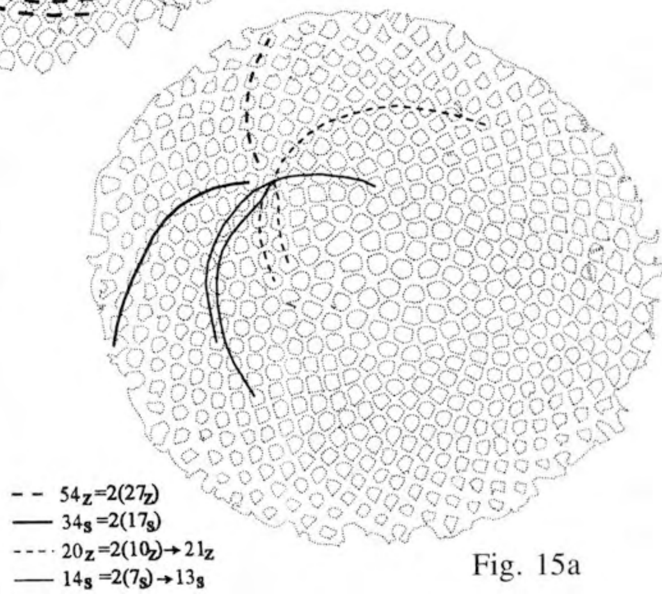


Fig. 15a

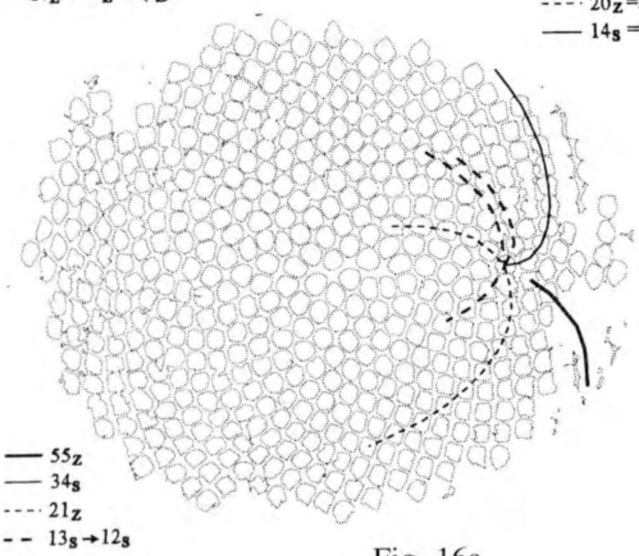


Fig. 16a

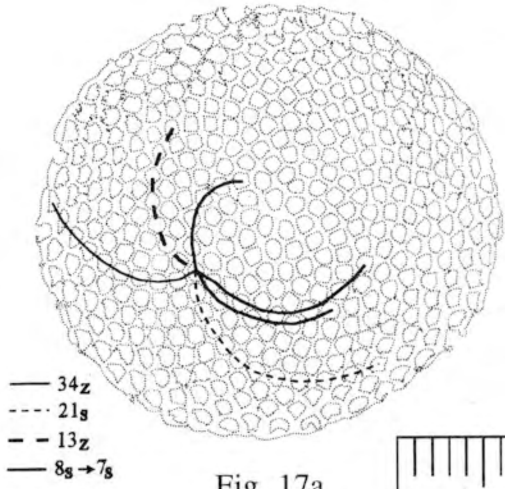


Fig. 17a

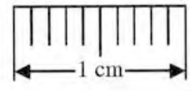


Fig. 13. The discontinuous transformation of the pattern [(2,3)-5(3,4)].

Fig. 14. The discontinuous transformation of the pattern [(4,13)-2(7,8)].

Fig. 15. The discontinuous transformation of the pattern from 2(3,7) in the outer part to (2,3) near the center.

Fig. 16. The deviation from the parastichy group number. One of thirteen parastichies is reduced. There is no confirmation of the dicontinuous transformation of the pattern.

Fig. 17. The deviation from parastichy group number. One parastichy of eight is reduced, but is does not cause the discontinuous transformation of the pattern or such transformation can not be confirmed.

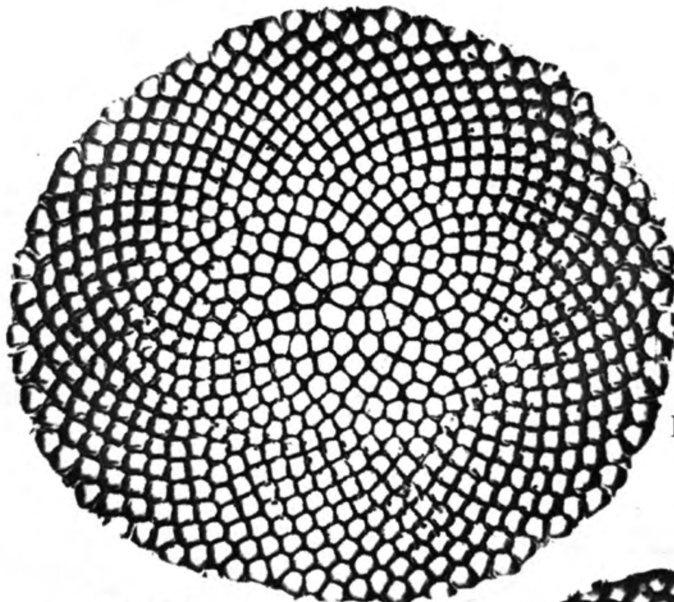


Fig. 13b

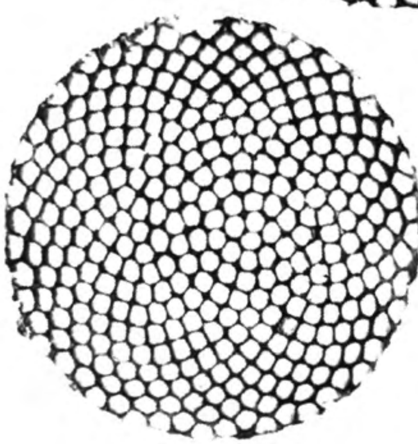


Fig. 14b

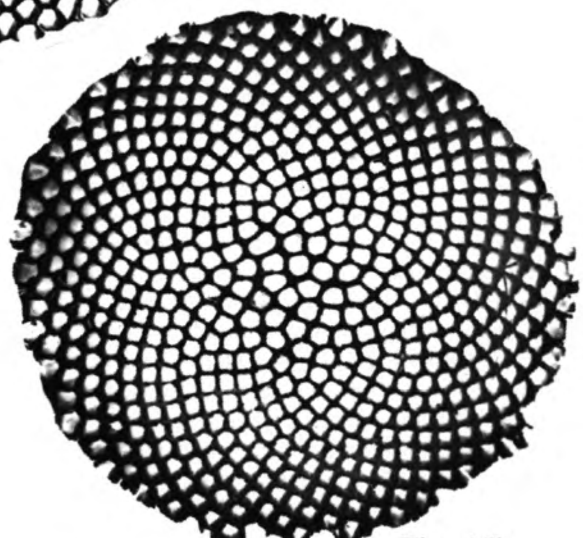


Fig. 15b

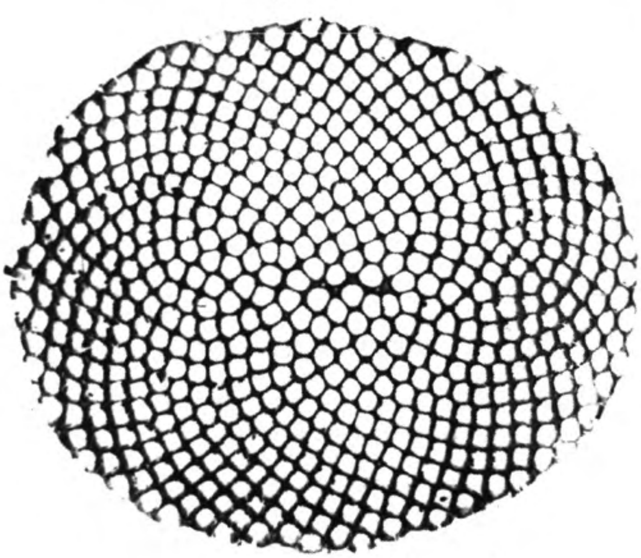


Fig. 16b

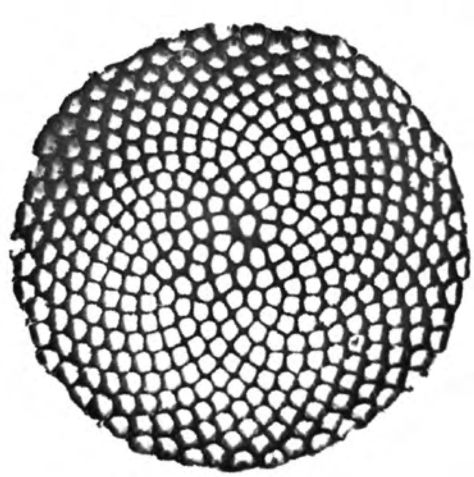


Fig. 17b

DISCUSSION

Until now it has been known that there are a few different phyllotactic series in nature. Their existence has been reported by many authors (Weisse 1897; Fujita 1937, 1938, 1939, 1942; Schoute 1938; Sterling 1945; Cutter 1964; Davis and Bose 1971; Gregory and Romberger 1972; Zagórska-Marek 1985, 1994; Jean 1992). Zagórska-Marek (1987) suggested that the patterns which had not been found so far could possibly exist, while Jean (1987, 1992) allowed only some types of series which he called the normal or abnormal ones. It is necessary to mention that Jean does not exclude the possibility of occurence of the series 'which according to the interpretative model should not be found in nature as primitive primordial patterns' (Jean 1992). The interpretative model was presented by Jean in 1980 and in 1988. This means that according to Jean such series can be observed in cases of discontinuous transformations of the pattern.

In this paper a number of different series, observed in capitula of *Carlina acaulis*, were presented, monojugies as well as multijugies (Tables 3, 4, 5, 6, 7, 8). They occur either as the only patterns in capitula or as the patterns involved in discontinuous transformations. Some of them satisfy Jean's terms, some do not. The latter are probably variations of normal and abnormal phylotaxis defined by Jean.

The variety of patterns and discontinuous transformations observed in capitula suggests that the phyllotactic pattern is not always stable there. The discontinuous transformation is caused by sectorial addition or reduction of parastichies. According to Zagórska-Marek (1987) the reason of such transformations is the local change in the circumference of the apex which causes either addition or the reduction of a certain number of parastichies in the existing pattern. Consequently the pattern changes, which means the change of the divergence and often, though not always, the change in the chirality of the genetic spiral. The local modification of the circumference may be caused by the displacement of the initial cells in the apical meristem. This could result in uneven growth on the oposite sides of the meristem (Zagórska-Marek 1987, 1992, 1994, Nakielski and Zagórska-Marek, in press).

There are capitula, in which the changes in the courses of the parastichies or disturbances in the arrangement of flowers occur near the center of the capitulum. This could be due to the similar sizes of the floral areas in a given disk. In such case the least possible parastichy group number to be marked for the main Fibonacci series is thirteen (like in Fig. 19) or even twenty one. In some capitula with the main series the greatest parastichy group number which could be marked is eighty nine or even one hundred and forty four. Different shapes of inflorescences might also be responsible for the variety of phyllotactic patterns, because the deviation from the standard circular shape can influence deformations of the parastichy courses (Müller 1991).

The cases shown in Figs 16 and 17 demonstrate patterns with deviations from the parastichy groups numbers. These deviations were found in the groups of the smallest number of the series occuring in the capitulum. In the majority of the cases with the deviation it was localized near the centre of the disk, what indicates that they could be connected with the rapidly diminishing circumference. This could cause the local irregular growth. The deviations are likely to be the cases of discontinuous transformations of the pattern, because they are associated, like the latter, with dislocations. The change of the number of the series occurs here in one parastichy group and the consecutive group of the smaller number cannot be marked, which means that it is not possible to determine the ultimate pattern. If the deviation occurs in two parastichy groups in one capitulum, the new numbers of groups, that appear as the result of the addition or reduction of the parastichies, do not form any phyllotactic series.

In capitula studied the parastichy groups become inconspicuous towards the centre of capitulum, what means the continuous transformation of the pattern (Zagórska-Marek 1987). It is connected with the continuous, i.e. even decrease of the circumference of the disk and causes the constant change of the pattern's expression, represented by the pair of contact parastichies. What does not change in such case is the series, the divergence and the chirality of the genetic spiral. The continuous transformation allows the occurrence of several (five to eight) parastichy groups of the series in one inflorescence. For example, in the pattern shown in Fig. 2 four groups are marked, however, it is possible to mark at least two groups more: fifty five and eighty-nine. Sinnot (1960, after Richards 1948) presents a diagram showing a spiral phyllotaxis in a capitulum. The continuous transformations are visible there as reduction of parastichies. However, they are regularly distributed on the circumference of the system. The continuous transformation is obvious in studied capitula of *Carlina* also because the areas occupied by flowers of the same inflorescence are almost of the same size regardless the distance from the centre of the capitulum. In a mature inflorescence of *Heliantus annuus* L. the areas occupied by flowers diminish towards the center of the capitulum (Schwabe, 1984). This might be the reason why the continuous transformations are infrequent there.

It is also possible that the variety of the patterns observed in capitula *Carlina acaulis* L. is related to the environmental conditions. This hypothesis will be tested in future investigations.

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WZORY FILOTAKTYCZNE W KWIATOSTANACH *CARLINA ACAULIS* L.

STRESZCZENIE

W koszyczkach kwiatowych *Carlina acaulis* L. występuje filotaksja spiralna. W większości kwiatostanów zaobserwowano główny ciąg Fibonacciego. Pośród tysiąca badanych przypadków znaleziono trzydzieści pięć nowych ciągów: osiemnaście monojugalnych, na przykład (2,17), (4,11), (7,37) oraz siedemnaście multijugalnych, jak 2(8,9), 2(5,11), 8(2,3). Wzory oznaczono na podstawie dwóch lub więcej kolejnych liczb ciągu filotaktycznego. Zaobserwowano zarówno ciągłe, jak i nieciągłe transformacje wzoru, a także odchylenia od liczby grupy parastych. Odchylenia zdefiniowano jako prawdopodobne przypadki nieciągłych transformacji, w których występują sektorialne zmiany w liczbie parastych, ale ostatecznego ciągu filotaktycznego nie da się określić.

SŁOWA KLUCZOWE: *Carlina acaulis*, wzory filotaktyczne, parastychy, transformacje.