THE DIAGRAM FOR PHYLLOTACTIC SERIES

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ABSTRACT

Many authors studying phyllotaxis in various plant species have reported the occurrence of many different numbers of contact parastichy pairs that are members of different Fibonacci-like series. On the basis of these reports a diagram was constructed in which any theoretically possible series was represented by the two first members of a given series.

KEY WORDS: phyllotaxy, diagram, Fibonacci-like series.

INTRODUCTION

Phyllotaxy, that is an arrangement of leaves or their modifications (e.g. flower parts) on a plant stem, has been an object of study for many botanists for almost two centuries (Braun 1831; Schimper 1835, 1836; Schwendener 1878; Church 1904; Snow & Snow 1931, 1962; Fujita 1937, 1938, 1939; Richards 1948, 1951; Cutter 1963; Thomas 1975; Thornley 1975a, 1975b; Jean 1978, 1982, 1988, 1992; Endress 1987).

Two types of phyllotactic patterns were defined: the whorled and spiral (Wardlaw 1965; Williams 1975; Schwabe 1984; Endress 1987; Jean 1994). More extensive classification and description of different spiral phyllotaxes is presented in most of monographs concerning the development of the shoot meristem (Wardlaw 1965; Williams 1975; Schwabe 1984). Some authors study phyllotaxis on the growing apex with successively appearing primordia (Meicenheimer 1982; Lacroix & Posluszny 1989; Kirchoff & Rutishauser 1990; Battjes, Bachmann & Bouman 1992; Battjes, Vischer & Bachmann 1993; Zagórska-Marek 1994). Others deal with the arrangement of organs in a mature part of a stem (Brousseau 1968, 1969; Davis 1970; Davis & Bose 1971; Zagórska-Marek 1985; Stępień 1993; Szymanowska-Pułka 1994). In this case deformations of the stem during and after its growth can influence the final phyllotactic pattern.

In helical phyllotaxis, the so-called "genetic helix" connects successive primordia. The angle between radii of the two consecutive primordia, i.e. between the lines linking the centres of these primordia (or leaves) with the axis of a stem, is known as the divergence angle and in many cases it equals 137,5°, the so-called Fibonacci angle. This angle is related to the limit of the series of the ratios of the following numbers: 1, 2, 3, 5, 8, 13,... (Jean 1994). These numbers form a series called Fibonacci or the main series. They equal the numbers of parastichies, that is helices connecting every n-th leaf, for instance every second, every third, every fifth, etc. Parastichies can also be traced towards the most recently formed primordia on the shoot apex. There are usually two sets of parastichies oriented in two opposite directions (left-hand and right-hand) and they cross at an angle of about 90° (square to each other). They are called contact parastichies. The numbers of contact parastichies in each direction are members of a phyllotactic series and the type of the series can thus be established on this basis.

Any member of the Fibonacci series is a sum of two preceding, except the first and second numbers, which are 1 and 2, respectively. There are also other Fibonacci-like series describing phyllotaxes observed in nature. These series are formed under the same rules, but their initial numbers, e.g. the two smallest members of a given series, fulfil the following condition: the second number is greater than the first doubled.

It happens sometimes that, simultaneously, two or more equal primordia or leaves arise at the same level on a growing apex with the angle between them φ/n, where $\varphi \neq 180°$ and n is a number of the arising primordia. Then two or more genetic helices can be drawn, respectively. In such a case, on the apex there occur sets of contact parastichies, the numbers of which equal double or multiple numbers of the basic series, for example: sets of 6 and 10, that is 2(3,5) or sets of 15 and 24, that is 3(5,8). Obviously, such numbers also form series which are called multijugies (bijugy, trijugy, tetrajugy etc.), while basic series are called monojugies.

Many authors have reported upon different phyllotactic patterns. In 1831 Braun observed several Fibonacci-like series, other than the main one, beginning with numbers (2,5), (2,7), (2,9) and (3,8). Hofmeister (1868) presented the series (1,3) and (3,14) and Schwendener (1878) the series (3,7) and (12,26). In the subsequent years other researchers confirmed these observations and described many different series (Geyler 1867; Church 1904; Barthelemess 1935; Fujita 1938; Schoute 1938; Crafts 1943). Most authors studying phyllotaxis have even mentioned many other different series occurring within the same plant species (Weisse 1897; Fujita 1942; Sterling 1945; Voeller & Cutter 1959; Zagórska-Marek 1985, 1994). Recent observations on capitula of *Carlina acaulis* L.

(Stępień 1993; Szymanowska-Pułka 1994) provided information on many new series. Some authors who were engaged in theoretical problems of phyllotaxis had also anticipated a number of series different than the main one (Fujita 1937; Jean 1980, 1988, 1992). Williams & Brittain (1984) and Van der Linden (1990) even presented some graphic models for some series where the initial numbers were small [e.g. the series (1,2), (1,3) (2,4)].

The monojugy of the Fibonacci series has been observed in 91.3% of all studied plant species. The next most frequent series are the bijugy of the main series (in 5.2%) and the series (1,3) (in 1.5%). Other series make up the remaining 2% of the observed specimens (Jean 1992). In some plant species series other than the main one were observed exclusively or were in majority (Davis & Bose 1971). There are some plant families, that represent the bijugy of the Fibonacci series as the only series occurring on the apex, for example *Rhizophoraceae* (Tomlinson & Wheat 1979).

Zagórska-Marek (1987, 1994) proposed a diagram "from which any pattern of phyllotaxis can be generated". Patterns are represented by points in a grid with numbers of contact parastichy pairs (e.g. pattern expressions) specified for each point. A given phyllotactic series is represented in the grid many times by different expressions.

The aim of this paper is to summarise available information of the various types of spiral phyllotaxy found in nature and to present how they may be systematised.

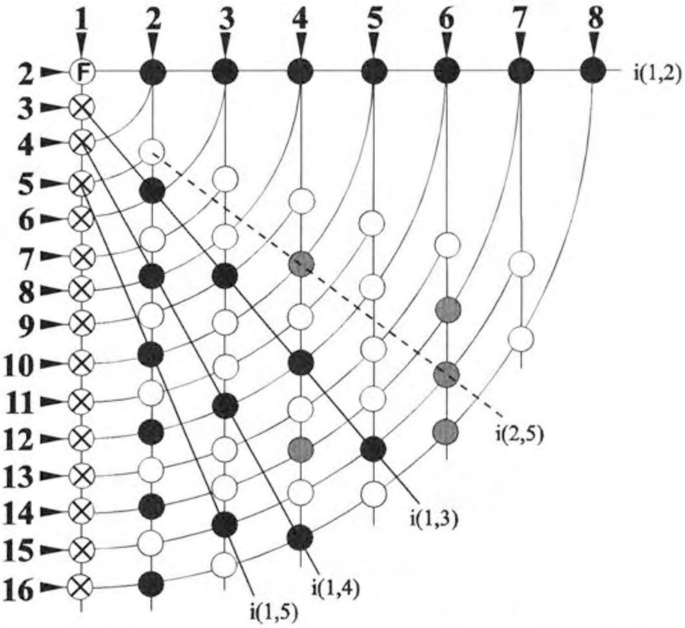

Fig. 1. The diagram for phyllotactic series. Series are marked with small circles. The type of each series is indicated by shading of circles in the following way:

Ⓕ – the Fibonacci series,
⊗ – accessory series,
● – multijugies of the Fibonacci series and of accessory series,
○ – lateral series,
● – multijugies of lateral series (detailed information in the text).

The numbers in the horizontal line at the top of the diagram represent first members of the series and are related to vertical lines (arrows indicate which number is related to a given line).
Numbers in a column on the left of the diagram represent the second members of the series and they correspond to the arcs of concentric circles (see: arrows). The horizontal line joins the main series (in the centre of the circles, indicated by F) with its multijugies. Slanting solid lines connect some accessory series with their multijugies (indicated below each line). A dashed line joins the series (2,5) (the first lateral series) with its multijugies (indicated below the line).

METHODS

A diagram has been proposed that contains all the observed series and embraces other, theoretically possible, series. The following assumptions were done to construct the diagram: a) each series is represented by its two smallest numbers – the initial numbers; b) each series has its only one strictly defined position in the diagram.

On the basis of phyllotactic series presented in the literature and the series observed by the authors, the following classification has been proposed:

1. the main series: (1,2) and accessory series: (1,n), for $n \geq 3$;
2. multijugies of the main series: i(1,2) and of accessory series: i(1,n), for $i \geq 2$ $n \geq 3$;
3. lateral series: (t, k), for $t \geq 2$, $k \geq 2t+1$, t and k having no common divisor;
4. multijugies of lateral series: i(t, k), for $i \geq 2$, $t \geq 2$, $k \geq 2t+1$, t and k having no common divisor.

It is easy to notice that the first group contains series with the initial number '1'. In this group the Fibonacci series (1,2), which is the most frequent in nature, is distinguished. Multiples of all series with the first number 1 belong to the second group. The third group contains all the monojugies not mentioned in the first group, i.e. the ones where the first number is not 1, and the fourth group – their multijugies.

RESULTS AND DISCUSSION

The series have been arranged in such a manner that, in the graphic diagram (Fig. 1), they are represented by their two first members, which are the smallest possible numbers of a given series. The series are marked with circles that are shaded according to the classification of the series (see: Fig. 1). Vertical lines correspond to the first numbers of the respective series. These numbers are situated on the horizontal line at the top of the diagram: each number over its own line. Arcs of the concentric circles represent the second component of the series whose numbers are situated in the vertical column on the left side of the diagram. In order to have regular arcs of circles (representing the second numbers), distances between the first numbers of series (at the top of the diagram) are twice as long as distances between the second numbers (in the column). At the point of crossing of any vertical line with any arc, one and only one series is represented, determined by its two first members: the first indicated by a vertical line and the second by an arc. For instance, the circle which is situated at the crossing point of a line coming from number 4 and of the arc coming from number 12 (in the vertical column) represents the series (4,12), e.g. the tetrajugy of the accessory series (1,3). The point at the left top corner of the diagram is the centre of all big circles, of which arcs represent second numbers of series. At that point the main series occur (signed with F in Fig. 1). The multijugies of the main series are situated on the horizontal radius. Multijugies of any monojugy can be connected by a direct line in the diagram.

The slanting solid lines connect points representing multijugies of the three accessory series [i(1, n), for i≥2; n=3, 4, 5]. Points that represent multijugies of the lateral series with the least possible initial numbers, i.e. of the series (2,5), are connected by a dashed line in Fig. 1. Multijugies of the following lateral series starting with number 2, that is of the series (2,7), (2,9), (2,11) etc., can be joined with slanting lines under the dashed line connecting points i(2,5), i=1,2,3,..; in the diagram. The following lines joining multijugies of the lateral series (3,7), (4,9), (5,11), (6,13) etc. can be drawn higher and higher over the dashed line.

A given series is a multijugy of another series (of a monojugy) if both numbers representing that given one have the same divisor. The biggest common divisor of these numbers is a product of that monojugy. Arcs corresponding to these second numbers of series, which are odd, are shorter than arcs representing second even numbers of the series, i.e. they do not reach the horizontal radius at the top of the diagram, because on this radius multijugies of the main series are placed, and their second numbers are always even. Any series, observed or theoretically possible, has its own place in the diagram.

In Fig. 2 a developed diagram is presented. Series that have been described in literature are distinguished with circles, and series that have not been observed with dots. Frequency of different observed series is not indicated because only a few such series have been reported very often [e.g. (1,2), (2,4), (1,3)] while a great majority of them have been described as single cases (Zagórska-Marek 1985, 1994; Stępień 1993; Szymanowska-Pułka 1994). In this figure the lines connecting multijugies of the series (1,3), (1,4), (1,5), (1,6), (1,7) and (2,5) are drawn. Some of the known series are real phyllotactic series discernible at the top of the stem. These are the series of small initial numbers, for which divergence angles have been determined (Fujita 1942; Richards 1951; Zagórska-Marek 1985; Jean 1992). The other series are presented on the basis of the pairs of contact parastichy numbers (which means on the basis of an expression of a given series), that have been observed in the plant apices and mature inflorescences.

A specification shown in Fig. 2 indicates that most of the known series are those of rather small initial numbers. These series are situated in the upper part of the diagram. Many accessory series have been observed: (1,3) up to (1,18) and the series (1,41). This suggests that the first number of the series is very important: the smaller it is the bigger is the chance of the series' occurrence. For example the known series with the first number 2 are: (2,4), (2,5), (2,6), (2,7), (2,9), (2,10), (2,12), (2,16) and (2,17). Among the series with the initial number 3, for which expressions have been described are the following: (3,6), (3,7), (3,8), (3,9), (3,12), (3,14) and (3,27). The series (3,27) is interesting because it is the trijugy of another series (1,9).

Some series starting with number 4 and 5 have also been observed. A group of the series with the first number 6 is special. This number is divisible by 2, 3 and 6, which means that it belongs to many multijugies in which these numbers occur [for instance (6,12), that is 6(1,2), or (6,14) which can be written as 2(3,7), etc.]. Expressions of not less than eight series of that group have been observed; only one of them, (6,13), is not a multijugy of another series. Number 8 is divisible by 2, 4 and 8 and this is why it seems that the series starting with it should occur as in the case of the series with the first number 6. Nevertheless, only one such series has been observed, that is the octajugy of the Fibonacci series (8,16) or 8(1,2).

Nine series which are the multijugies of the main series have been described. They can be presented in the following way: i(1,2) for i=2,3,4,5,6,8,11,14,17. The series (2,4), i.e. 2(1,2), which is the bijugy of the Fibonacci series, has been reported by many authors (Weisse 1897; Church 1904; Fujita 1938, 1939; Schoute 1938; Sterling 1945; Namboodiri & Beck 1968; Gregory & Romberger 1972; Tomlinson & Wheat 1979; Zagórska-Marek 1985, 1994; Szymanowska-Pułka 1994). The trijugy (3,6) is less frequent (Barthelemess 1935; Zagórska-Marek 1985), and the tetrajugy (4,8) has been mentioned by three authors (Church 1904; Zagórska-Marek 1985; Szymanowska-Pułka 1994). Other multijugies of the main series have been described on the basis of parastichy numbers in capitula of *Carlina acaulis* (Stępień 1993; Szymanowska-Pułka 1994).

Four multijugies of the first accessory series (1,3) have been observed: 2(1,3), 3(1,3), 5(1,3) and 6(1,3) but only two of the series (1,4): 3(1,4), 9(1,4). The following accessory series have only single described multijugies: 2(1,5), 2(1,6), 2(1,8) and 3(1,9). There are several known multijugies of the lateral series: the bijugy and trijugy of the series (2,5) and eight series of which every one is the multijugy of another lateral series: 3(2,17), 2(3,7), 2(3,8), 2(3,19), 2(5,11), 2(6,13), 3(7,16) and 2(8,17).

Single series starting with large numbers have been reported. Expressions of most of them have been observed in inflorescences of *Carlina acaulis* L. It seems impossible that the series for which at least one of the two initial numbers is large could appear on the small area in the distal part of the growing apex. However, in the outer part of a quite big capitulum, an arrangement of flowers displaying large numbers of parastichies is likely to happen. A possible influence of growth deformations, like fasciations or connations (Gorter, 1964), on the ultimate phyllotactic pattern, cannot be excluded. Expressions of several series starting with large numbers have been observed even in two different inflorescences of *Carlina*; these are: (4,11), (8,16), (10,22), (11,22) and (21,48). The series (6,14) is an interesting example: its expressions have occurred even in four different disks. Some of these series have occurred as the only series in a given capitulum, for instance: (3,27), (6,51), (7,54), (9,36), (21,48), others in apices with the discontinuous transformation of the pattern (Zagórska-Marek 1987; Szymanowska-Pułka 1994). In the last case, the series that transform one into another are usually localised very close to one another in the diagram (Fig. 2). Such characteristic pairs of series are: (1,41) and (4,41), (6,38) and (7,37), (13,44) and (13,45), (16,34) and (17,34). In all capitula with these pairs of series the transformation occurs in higher parastichy groups, that is rather in the outer part of the disk (Stępień 1993; Szymanowska-Pułka 1994). Another situation occurs in the capitulum with the series (2,17) which transforms into the series (17,38), relatively far from it in the diagram, and the pattern transformation takes place near the centre of the disk. Both the transformations and numerous deviations from the parastichy group number observed in the central part of some *Carlina* disks (Szymanowska-Pułka 1994) suggest that the phyllotactic pattern in the capitulum is not stable, especially in the case of series with great initial numbers. Such patterns can be determined as transient. Yet, on the other hand, transformations from the main series (which seems to be the most stable) often happen (Stępień 1993; Szymanowska-Pułka 1994).

In Fig. 2 certain series, that have been reported, are gathered in some groups. In the case of the group (9,20), (9,22), (10,21), (10,22), (11,22), (11,23), (11,24) and (12,26) only

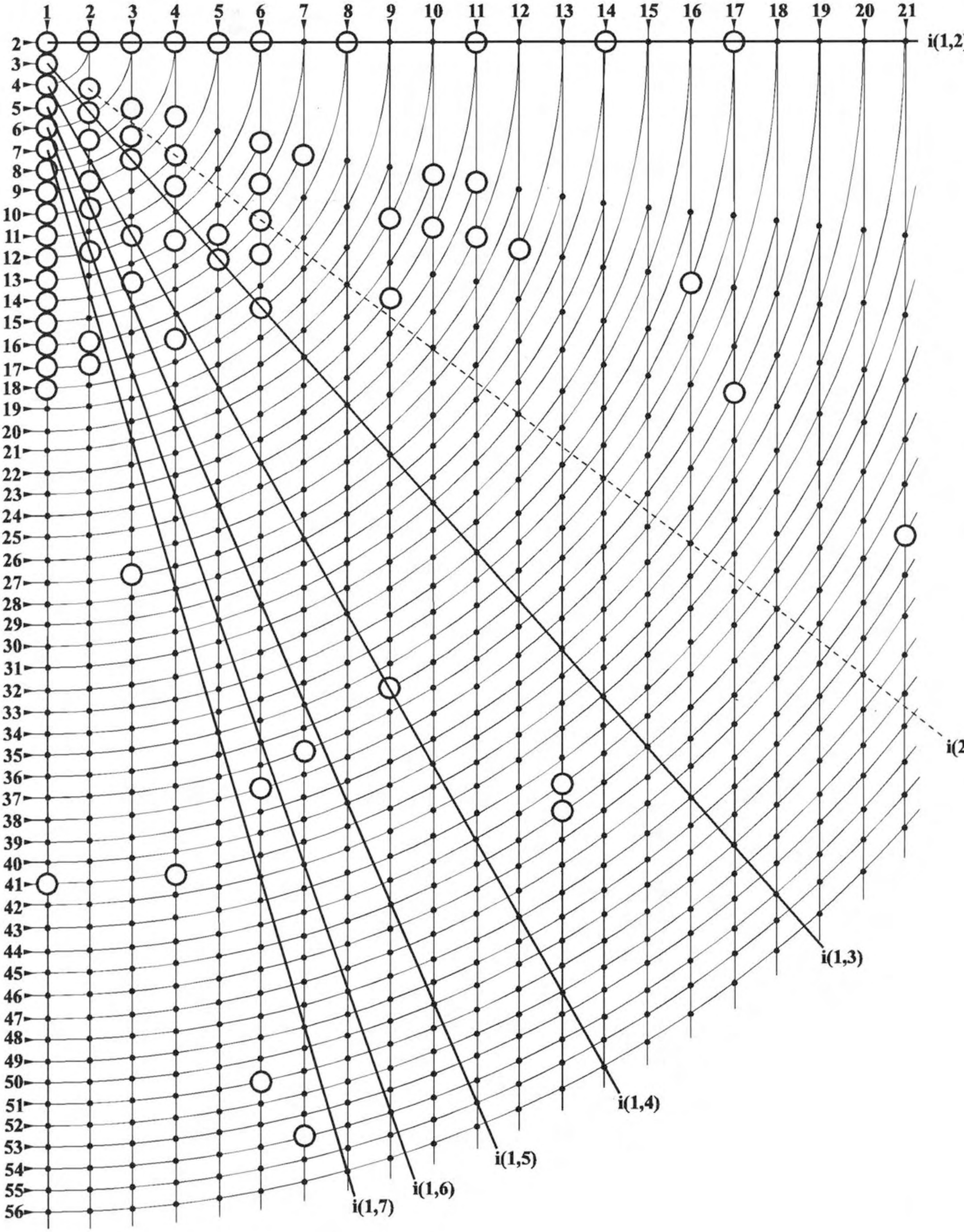

Fig. 2. The developed diagram. The observed series (presented in literature) are indicated by circles. The lines joining some series with their multijugies are drawn (indicated below each line).

three series [(9,22), (10,21), (11,22)] have been observed in the capitula with transformation. Yet it is very characteristic that initial numbers of these series 'fluctuate' around certain numbers of the main series, that is around 8, 13 and 21. This fact seems to be more noticeable as far as the second numbers of these series are concerned, which are mostly very close to number 21. The series (1,41), (4,41) and (6,38), (7,37) gathered in another group occurred in capitula of *Carlina acaulis* with the discontinuous transformation of the pattern (Szymanowska-Pułka 1994).

As mentioned above, a phyllotactic series present in a given specimen can be determined on the basis of numbers of contact parastichy pairs. Basing on their observations of spadices of some aroids species (family *Araceae*) Davis & Bose (1971) described 'clear spirals that are discernible on the arrangement of the flowers'. Numbers of these spirals generally equal Fibonacci numbers, but in many cases (within the same species) some spadices show different numbers of spirals. The authors called such cases 'variations'. According to the figures and photographs in the cited paper the clear spirals are contact parastichies, so the phyllotactic series occurring in each specimen can be determined. In this way we established and arranged the series which in all probability occur in the searched spadices of aroids and which had not been defined

TABLE 1. The unequal contact parastichy pair numbers observed in spadices of some aroids according to the results by Davis & Bose (1971). The presumable series (*) indicated on the basis of the pairs are proposed by the authors of this paper. All these series have been observed as real series by other authors.

No.	Species	Left-handed spirals	Right-handed spirals	Presumable series *
1	*Dieffenbachia picta*	3	4	(1,3)
2	*Anthurium crassinervum*	11	18	
3	*Aglaonema sp.* *Syngonium sp.* *Alocasia sp.* *Dieffenbachia picta*	5	6	(1,5)
4	*Spathyphyllum sp.* *Dieffenbachia picta* *Aglaonema sp.* *Syngonium sp.*	6	5	
5	*Spathyphyllum sp.* *Alocasia sp.*	6	7	(1,6)
6	*Dieffenbachia picta* *Syngonium sp.* *Alocasia sp.*	7	6	
7	*Dieffenbachia picta viridis* *Alocasia sp.*	7	8	(1,7)
8	*Dieffenbachia picta viridis* *Alocasia sp.*	8	7	
9	*Alocasia idica mettalica*	9	8	(1,8)
10	*Alocasia idica mettalica*	9	10	(1,9)
11	*Alocasia idica mettalica*	10	11	(1,10)
12	*Alocasia idica mettalica*	12	11	(1,11)
13	*Philodendron sp.*	12	13	(1,12)
14	*Philodendron sp.*	14	13	(1,13)
15	*Philodendron sp.*	14	15	(1,14)
16	*Philodendron sp.*	15	14	
17	*Syngonium sp.*	5	7	(2,5)
18	*Aglaonema sp.*	7	5	
19	*Spathyphyllum sp.* *Alocasia sp.*	6	8	(2,6)
20	*Alocasia idica mettalica*	11	9	(2,9)

by the authors. They are presented in Tab. 1. All the presumable series in this table have been described in literature by other researches. In some specimens showed in the mentioned paper, the numbers of the right-handed and left-handed parastichies are equal. Tab. 2 contains these cases. They can be interpreted as either helical (Tab. 2, a) or whorled patterns (Tab. 2, b) which could be determined on the basis of the divergence angle. The presumable multijugies of the main series: (7,14), (9,18), (12,24), (13,36) and (15,30) have not been observed, except in the cited paper. They are not presented as known series in Fig. 2 because we cannot say with certainty that these are real series.

Zagórska-Marek (1987) suggested that a sectorial change in the apex circumference causes a discontinuous transformation of phyllotactic pattern. The diagram presented by her (1987, 1994) illustrates this interesting hypothesis in such a manner that different patterns expressions of similar numbers are closely situated in the grid and the distance of points representing contact parastichy pairs from the point specified as the first in a grid is identified with the apex circumference. Thus phyllotactic series are represented there many times: each time by a different pair of the series' numbers. A diagram proposed in this paper is an attempt to classify and systematise different phyllotactic series and that is why each series has its own, only one position in it: a point characterised by two initial numbers of a given series. The developed diagram in Fig. 2 contains circles representing known series and dots wchich are empty positions for potentialy existing series.

In 1937 Fujita presented an interesting classification of the observed and theoretically possible phyllotactic series and described seven series other than the main one. He introduced three systems of series with a distribution to subsystems. Jean (1980) proposed the so-called interpretative model that allowed only some types of series. None of these classifications (Fujita 1937; Jean 1980) takes into account the possibility of the occurrence of all kinds of observed series. Fujita's classification neglects some of lateral series like the ones observed in *Carlina acaulis* (Stępień 1993; Szymanowska-Pułka 1994): (7,37), (7,54), (9,20), (9,22) or (21,48). Jean (1992) does not consider the existence of certain series with great initial numbers. It seems that Jean's model concerns steady states that can occur in a distal part of the apex, i.e. series of small initial numbers. Nevertheless, Jean does not exclude the possibility of a formation of series with large initial numbers, but he suggests that they can be formed as a result of the pattern transformation (Jean 1992). Some of the series not mentioned in Jeans classification have been reported by many authors. For instance series 2(6,13), (3,14), (3,8), (3,7) were described by Fujita (1937) on the basis of other studies (Braun 1831; Hofmeister 1868; Schwendener 1878). The series (3,8) has also been observed by Zagórska-Marek first on elongated shoots of *Abies balsamea* (1985) and then on the apex of *Magnolia acuminata* where it had been documented on SEM microphotography (1994). Its presence in nature has been also confirmed by Szymanowska-Pułka (1994) in the mature capitulum of *Carlina acaulis*. The series (3,7) has been reported by Fujita (1938) in *Salix viminalis* var. yezoensis, by Zagórska-Marek in *Abies balsamea* (1985) and *Magnolia acuminata* (1994) and by Szymanowska-Pułka (1994) in *Carlina acaulis*. It is worth mentioning that the patterns in the capitula of *Carlina acaulis* (Stępień 1993; Szymanowska-Pułka 1994) and floral patterns in other species could be formed as a result of stem deformations during the plant growth.

Roberts (1987) presented three series other than the main one, i.e. 2(1,2), (1,3), (1,4) and called them 'anomalous'. Richards (1951) indicated two more: (1,5) and (2,5); Zagórska-Marek (1985, 1994) other three: (2,7), (3,7) and (3,8). All these authors applied different terms for different series. In this paper the terminology used by Jean (1992) has been adopted. He called the series starting with number 1 'accessory' (except the Fibonacci series), i.e. (1,n) for n≥3, and the series with the first number larger than 1 'lateral'.

TABLE 2. Equal contact parastichy pair numbers observed in spadices of some aroids according to the results by Davis & Bose (1971). The authors of this paper propose that on the basis of the pairs the phyllotactic patterns can be indicated as *a* spiral (multijugies of the main series) or *b* whorled. Presumable series that have not been observed, except in the cited paper are marked with asterisks and they are not specified as known in Fig. 2.

No.	Species	Left-handed spirals	Right-handed spirals	a Presumable series	*b* Presumable number of members in whorl
1	*Aglaonema sp.* *Syngonium sp.* *Alocasia sp.*	5	5	(5,10)	5
2	*Alocasia sp.* *Syngonium sp.* *Dieffenbachia picta*	6	6	(6,12)	6
3	*Syngonium sp.* *Alocasia sp.* *Dieffenbachia picta*	7	7	(7,14)*	7
4	*Alocasia idica mettalica*	9	9	(9,18)*	9
5	*Alocasia idica mettalica*	11	11	(11,22)	11
6	*Philodendron sp.*	12	12	(12,24)*	12
7	*Philodendron sp.*	13	13	(13,26)*	13
8	*Philodendron sp.*	15	15	(15,30)*	15

CONCLUSIONS

1. A classification of series was proposed regarding the first number of a given series; any series is represented by its two initial numbers.
2. A diagram of phyllotactic series was constructed in which any series has only one and strictly defined position. The diagram enables a systematic arrangement of all series and an occurrence of series that have not been observed so far.
3. Only a few of all possible series have been observed in Nature.

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DIAGRAM CIĄGÓW FILOTAKTYCZNYCH

STRESZCZENIE

Wielu autorów, badających filotaksję u różnych gatunków roślin, opisało występowanie różnorodnych liczb par parastych kontaktowych, które są elementami ciągów typu Fibonacciego. Na podstawie tych doniesień skonstruowano diagram, w którym każdy teoretycznie możliwy ciąg filotaktyczny jest reprezentowany przez jego dwie liczby początkowe.

SŁOWA KLUCZOWE: filotaksja, diagram, ciągi typu Fibonacciego.