PHYLLOTAXIS DIVERSITY IN *LYCOPODIUM CLAVATUM* L. AND *LYCOPODIUM ANNOTINUM* L.

EDYTA GOLA

Institute of Botany, Wrocław University,
Kanonia 6/8, 50-328 Wrocław, Poland

(Received: January 17, 1996. Accepted: May 18, 1996)

ABSTRACT

In shoots of *Lycopodium* microphyllous phyllotaxis is extremely diverse. 24 various patterns were found in anisotomous *L. clavatum* and "only" 11 in isotomous *L. annotinum*. Spiral patterns expressed by $k:(k+1)$ parastichy numbers were present together with typically whorled $k:k$ patterns. In both species k number was higher in plagiotropic shoots than in orthotropic. It was also higher in *L. clavatum* than in *L. annotinum*. In the first species phyllotactic spectrum was wider with many patterns almost equally frequent, whereas narrow spectrum of *L. annotinum* showed clear dominance of only one pattern. The patterns, which are the most frequent in other plants, such as Fibonacci or Lucas, were uncommon in studied *Lycopodium* species. Discontinuous phyllotactic transitions occurred typically in two locations on the shoot: just below the dichotomic branching or above the borders, that separate the annual increments of the axis. Transitions were moderately frequent occurring in more than 7% of developmentally independent shoot segments. Dichotomous branching, resulting in variable shoot diameter, seasonal fluctuations of growth as well as a small size of microphylls relative to the shoot circumference are proposed to be the main factors contributing to the high phyllotactic diversity in studied species.

KEY WORDS: *Lycopodium*, phyllotaxis, phyllotactic transformation, dichotomy.

INTRODUCTION

The phenomenon of phyllotaxis in *Lycopodium* has been studied rather occasionally, in addition to a taxonomic description of the species, without however sufficient quantitative and qualitative data on its diversity (Church 1904). Phyllotaxis seems to be particularly fascinating in this genus because of specific, different than in higher plants origin of leaves (microphylls). A great possibility of exploring the distribution of different types of phyllotaxis appears.

During past few years our knowledge on the diversity of phyllotactic patterns has been steadily increasing. Spectra of phyllotaxis are well known for some conifers such as *Abies*, *Pinus* or *Picea* where the main Fibonacci pattern prevails and other spiral patterns represent only about 6% of the cases. Among the latter the Lucas pattern and primary bijugy are most frequent (Crafts 1943; Namboodiri, Beck 1968; Gregory, Romberger 1972; Zagórska-Marek 1985, 1987; Lisiecka 1993). A similar range of phyllotaxis diversity characterizes some pteridophytes: *Dryopteris* (Cutter, Voeller 1959; Cutter 1964), *Osmunda cinnamomea* and *O. regalis* (Steeves 1963). In a majority of Dicotyledones with spiral phyllotaxis, the spectra of different patterns follow again the same principle of the main Fibonacci pattern prevalence, both in vegetative and in generative shoots (Girolami 1953; Battjes and al. 1993; Jean 1994; Szymanowska-Pułka 1994). An interesting exception is the case of *Magnolia acuminata* gynoeceia, where more than ten different types of phyllotactic series can be encountered even in one tree. Among them some unique patterns are present (Zagórska-Marek 1987, 1993, 1994). In

Magnolia acuminata not the main Fibonacci phyllotaxis but other patterns such as primary bijugy, the Lucas pattern or even trijugy prevail in flowers born on the same tree. Moreover, such tendency is maintained in consecutive seasons (Zagórska-Marek 1994). Other exceptions from the Fibonacci pattern prevalence represent vegetative shoots of some gymnosperms such as *Torreya* or *Cephalotaxus* (Tomlinson, Wheat 1979) and inflorescences of *Dipsacus* (Church 1904; Cutter 1964) where bijugy dominates.

Phyllotactic pattern often changes during ontogeny of the shoot. New parastichies may become conspicuous within the same type of phyllotactic series (the series of possible parastichy numbers in a particular pattern), which means that only the expression of the pattern changes. Such transformations are called continuous (Zagórska-Marek 1987) and occur in different stages of plant development: in growing seedlings, during transition to flowering and in capitulum formation in *Asteraceae* (Sinnott 1960; Larson 1977, 1980; Meichenheimer 1979; Battjes and al. 1993; Szymanowska-Pułka 1994). They can also be induced by gibberellic acid (Maksymowych and al. 1976; Erickson and Meichenheimer 1977).

An entirely different type of transformations (called discontinuous) results in a qualitative change of phyllotaxis. These transformations proceed from one spiral pattern to another (Zagórska-Marek 1985, 1987, 1994) or from a spiral to a whorled pattern (Kwiatkowska 1993, 1994). Such transformations are most probably due to the changes in geometry of the apical meristem dome, associated with the shift of the meristem axis and are usually in compliance with the rule of the minimal circumferential change (Zagórska-Marek 1987, 1994;

Nakielski, Zagórska-Marek 1995). The question about the possibility of discontinuous transitions in vascular cryptogames has already been answered by conclusions from Cutter and Voeller (1959) observations on experimentally defoliated fern sporophytes. Meristems of *Dryopteris* usually generate bijugy as the first initial pattern. Due to defoliation this phyllotaxis changes either into another spiral pattern (Fibonacci or Lucas) or to whorls. A natural, not induced experimentally, discontinuous transition from 3+3 to 4+4 contact parastichy pair is demonstrated in Church's (1904) book for *Lycopodium selago*. However, nothing is said there whether such transformations are common in other species of pteridophytes or how frequently they occur in nature. The main question to be answered then is, which phyllotactic patterns and possible transformations occur in plants with microphylls – leaves having different phylogenetic origin than the megaphylls of ferns. This was the major reason for selecting *Lycopodium* for this study. The second reason was that this plant branches dichotomously which in fact introduces circumferential discontinuity in an apex development. It is then easy to accept the hypothesis that dichotomy, affecting in a special way organogenesis of the apex, may result in frequent discontinuous phyllotactic transformations.

MATERIALS AND METHODS

For the present study whole, dead plants of *L. clavatum* and *L. annotinum* that dried out naturally, were collected from several populations in different locations in Poland (Izerskie Mountains, Ostrzeszowskie Hills and from Beskid Niski) for quantitative analysis. As all species of *Lycopodium* are protected in Poland – special permissions of the Nature Conservation Offices in Kalisz and in Jelenia Góra were granted to collect some living shoots. Up to 15 shoot tips from each population were fixed in FAA for anatomical sectioning. Series of sections were prepared by standard paraffin method and stained by Ehrlich's hematoxylin or safranin and fast green (Johansen 1940).

In this paper most of the patterns are shown as flat projections of the lateral stem surface. Stem segments were rolled over the surface of clay and diagrams of leaf arrangement were made on the basis of such prints. Some patterns were satisfactorily identified on microphotographs of anatomical sections from the apical part of shoot where microphylls are tightly clustered. Sporophytic phyllotaxis was also determined directly on elongated shoots. In all the cases, contact parastichies were identified and recorded in the formula of contact parastichy pair has been used. The pair of contact parastichies demonstrates an expression of the pattern, identifies a phyllotactic series and indirectly the chirality of ontogenetic spiral. On each segment of the stem one leaf was marked and starting from this point, the parastichies were counted in two sets. The parastichies winding upward counterclockwise were assumed to have Z configuration, clockwise – S configuration. Their S or Z orientation in each set was given as an index in a formula: $A_s : B_z$ in which A and B were contact parastichy numbers. Each number in the phyllotactic series is the sum of two preceding numbers and parastichies in successive sets have opposite orientation. Therefore, the chirality of ontogenetic spiral, which becomes an ontogenetic helix on elongated stems, was established in each case by extrapolating $A_s : B_z$ formula to the first number in a particular phyllotactic series.

The distinction between whorled and spiral (helical) patterns with whorls (multijugies) was made on the basis of ver-

tical and circumferential distribution of leaves. Whorled k:k patterns from k:k multijugate patterns have been distinguished on the basis of the orientation of the third, i.e. k+k number of phyllotactic series – in multijugate patterns k+k parastichies are inclined, whereas in whorled, their course is vertical (for example $4_s:4_z:8_s$ – spiral tetrajugy; $4_s:4_z:8_o$ – whorled pattern). Pseudowhorls were distinguished from true whorls on the basis of contact parastichies $[k:(k+1)]$ and circumferential spacing of leaves (uneven in pseudowhorls).

Phyllotaxis was scored on each independent developmentally segment of the stem i.e. on a stem before dichotomy and on both new axes after the split of the shoot. If transitions occurred on the same segment, phyllotactic patterns were counted as two separate cases.

RESULTS

Two species of *Lycopodium* have been selected, both branching dichotomously but differing in a type of dichotomy in orthotropic shoots. These were: *Lycopodium clavatum* L. and *L. annotinum* L. They are plants with creeping, unlimited in growth, plagiotropic stems and short perpendicular or bow ascending orthotropic branches. Growth of the latter ends when strobila is formed at the stem tip (*L. annotinum*) or on a special stalk (*L. clavatum*). On all the axes annual borders occur (Fig. 1). They result from seasonal activity of the

Fig. 1. *Lycopodium clavatum* – dry stem, anisotomously branched, with dissected leaves. One parastichy splits just before dichotomy. An arrow head marks an annual border where a change of the shoot growth rate is expressed by a different course of parastichies. Some parastichies existing before dichotomy climb up the surface of both shoots, continuing their course. Some others on the inner surface of branching shoots are formed anew. x 16.

Fig. 2 A and B. Successive transverse sections of the apical region of plagiotropic shoot, splitting anisotomously. Twin shoots are in the same developmental stage but the difference in their size is obvious. The shoot which is thicker will continue plagiotropic growth, the smaller will become an orthotropic axis. Phyllotaxis on this particular shoot before dichotomy was expressed by $10_2:11_s$ contact parastichy pair. The same phyllotactic pattern was formed on the main axis after the split.

shoot apex. When the parental meristem of the orthotropic shoot splits into two new apices, twin daughter shoots have often different size, destination and function (Nolan 1976). The division can be equal, resulting in two shoots of a similar diameter (isodichotomy, isotomy) and this is a typical feature of *L. annotinum*. When both newly formed apices are of different diameters (Troll 1937; Øllgaard 1979) and the larger stem overgrows the weaker, the branching is called anisotomous, also referred to as anisodichotomous (Fig. 2). It is characteristic of shoots of *L. clavatum*. In anisotomy growth of some diminutive shoots is halted and they become the bulbils (gemmae) (Wigglesworth 1907; Stevenson 1976). In both species, however, the plagiotropic shoots always dichotomize anisotomously.

On 78 shoots of *Lycopodium annotinum*, 971 segments showed 11 different phyllotactic series. In *Lycopodium clavatum*, on 89 shoots made of 1187 segments, 24 phyllotactic series were found. Phyllotaxis of one shoot of *Lycopodium clavatum* was so irregular that it could not be classified. In *Lycopodium annotinum* the opposed parastichy pair numbers most often belonged to the 1,4,5,9... series (nearly 39% of all cases) and to the Lucas series 1,3,4,7... (21.5%). True 4-leaved whorls (Fig. 3), expressed by 4:4 parastichy pair (14%), as well as 1,5,6,11... series (nearly 12%), were also frequent. Other patterns appeared in less than 10% of all the cases. In this species pseudowhorls were often formed with 5 leaves in one pseudowhorl. They originated either from 1,4,5... (more often) or from 1,5,6... series. In *Lycopodium clavatum* three patterns: two spiral and one whorled, expressed by 5:6, 6:6 and 6:7 parastichy numbers, exceeded each 10% of all the cases. Three other patterns (7:7, 7:8 and 8:9) occurred each in almost 10% of all the cases. Other series were found in less than 5% of the cases.

One of the most unusual patterns was found in *Lycopodium clavatum* – it was the bijugy of the 1,4,5,9... series, expressed by 8:10 parastichy numbers. To the author's knowledge the pattern has not been reported before. In this particular case, 2 parastichies representing the first member of the phyllotactic series could also be seen. Some patterns dominating in the explored material are demonstrated on maps made of the modelling clay records (Figs 3, 4). Only one expression of each series was typically present with few exceptions. For instance three expressions of primary bijugy were found: 4:6 – dominant, 2:4 and 6:10 less frequently. Similarly, Fibonacci phyllotaxis expressed usually by 3:5 numbers for *L. clavatum* and 2:3 for *L. annotinum* was also represented in both species, although seldom, by 5:8 parastichy numbers. In *L. annotinum* an expression of the most frequent pattern was 4:5. The 5:9 expression was found only in two cases. For some series represented by higher numbers of contact parastichies (7:10, 7:9 and 5:7) also the preceding elements of the series could clearly be seen on modelling clay prints. The frequency of all identified patterns is shown in Fig. 5.

All of the patterns, either spiral or whorled, can be described by the common module, which is the phyllotactic triangular unit (PTU). Some attributes of the PTU such as the triangle base inclination to the shoot axis, thus the position of the upper leaf in a triad and the ratio in which its projection divides the base of the triangle are fixed for particular pattern. The change of these parameters can lead in consequence to discontinuous transformation of the pattern (Zagórska-Marek 1987).

When phyllotaxis of *Lycopodium* is placed on a phyllotactic grid, which is the lattice of phyllotactic triangular units (PTU), presenting all possible contact parastichies on the stem surface (Zagórska-Marek 1987, 1994), phyllotactic do-

Fig. 3. *Lycopodium annotinum*. 4-leafed true whorl (4s:4z). Orientation of the third set of eight parastichies (not shown) is vertical. Bar = 1 mm. **A**. The record of elongated stem segment rolled over the surface of modelling clay. **B**. A map of leaf arrangement on the same stem segment, reconstructed from the record. Dots show the position of microphylls, lines – the course of oppositely oriented parastichies. The marker leaves are indicated by the small dashes on the map and black dots on the photograph.

mains emerge and it appears that they are different for both investigated species (Fig. 6). The most frequent phyllotactic patterns are expressed by $k:k$ or $k:(k+1)$ contact parastichy pair and are located on the diagonal of the grid. The shift of the phyllotactic domain to the left or to the right depends on k value: for *Lycopodium annotinum* $k=(2),3,4,5$ and for *Lycopodium clavatum* $k=(3,4),5,6,...11$ (the numbers given in brackets are these of the less frequent patterns).

A comparison of phyllotaxis on plagiotropic and orthotropic shoots showed significant differences. In plagiotropic shoots the numbers of parastichies were higher (Fig. 7). In addition, as analysed on the series of anatomical sections the diameter of plagiotropic shoots was clearly larger than of orthotropic shoots (Fig. 2). The frequency of pattern appearance could however be affected to some extent by the fact, that only a few plagiotropic shoots were examined – 12 in *L. annotinum* and 11 in *L. clavatum*.

The chirality of ontogenetic helix was determined for all helical patterns. The two chiral configurations were almost equally frequent (Fig. 8). S helix orientation slightly prevailed in 1,4,5,9... pattern present in shoots of *L. annotinum*. For *L. clavatum* the same chirality was more frequent in 1,5,6,11... and 1,6,7... patterns. Z-direction of the genetic helix was more frequent in 1,7,8... and 1,8,9... patterns.

Phyllotaxis in the shoot before splitting and in newly formed branches was compared in all dichotomic shoots (Fig. 9). In both species contact parastichy pairs were usually different in the parental and both daughter segments. Less frequently one of the daughter branches had the same phyllotaxis as the parental segment. In anisotomous *Lycopodium clavatum* contact parastichy pairs were usually 7:8, 8:9 on the greater axis and 5:6, 6:7 on the smaller one. In isotomous shoots of *L. annotinum* the same 4:4 phyllotaxis sometimes occurred before and after dichotomy.

TABLE 1. Transformations involving at least one whorled pattern in stems of *Lycopodium annotinum* and *L. clavatum*. On the right the numbers of these transitions are shown, in which the parastichies are added; on the left the numbers of those, in which parastichy numbers decrease

<i>Lycopodium clavatum</i>	<i>Lycopodium annotinum</i>	Transformations	<i>Lycopodium annotinum</i>	<i>Lycopodium clavatum</i>
0	0	3:3 ↔ 3:4	1	0
0	0	3:3 ↔ 4:4	1	0
0	5	3:4 ↔ 4:4	15	0
0	0	3:5 ↔ 5:5	1	0
2	20	4:4 ↔ 4:5	13	0
0	6	4:4 ↔ 5:5	0	0
2	10	4:5 ↔ 5:5	13	1
1	3	5:5 ↔ 5:6	6	5
0	0	5:5 ↔ 5:7	0	1
2	0	5:5 ↔ 6:6	0	1
3	1	5:6 ↔ 6:6	5	8
0	0	5:6 ↔ 7:7	0	2
6	0	6:6 ↔ 6:7	1	3
2	0	6:6 ↔ 7:7	0	1
0	0	6:6 ↔ 7:8	0	1
1	0	6:6 ↔ 7:9	0	0
3	0	6:7 ↔ 7:7	0	7
0	0	6:7 ↔ 8:8	0	1
3	0	7:7 ↔ 7:8	0	5
1	0	7:7 ↔ 8:8	0	0
0	0	7:7 ↔ 8:9	0	1
1	0	7:8 ↔ 8:8	0	2
2	0	8:8 ↔ 8:9	0	1
0	0	8:9 ↔ 10:10	0	1
1	0	9:9 ↔ 9:10	0	2
1	0	9:10 ↔ 10:10	0	0

Fig. 4. Maps of leaf distribution on the elongated stem, made from modelling clay records as shown in Fig. 3.

A, B. – *Lycopodium annotinum*. **A.** Primary bijugy expressed by $2s:4z$ contact parastichy pair. Set of six S-oriented parastichies could also be easily drawn. Two ontogenetic helices have S chirality. Bar = 1 mm.; **B.** $4z:5s$ parastichy pattern. The chirality of ontogenetic helix is S. Bar = 1 mm. **C, D.** – *Lycopodium clavatum*. **C.** $5z:6s$ parastichy pattern with S chirality of ontogenetic helix. Bar = 1 mm.; **D.** $6z:7s$ parastichy pattern with S-ontogenetic helix. Bar = 1 mm.

In both species transformations of phyllotaxis occurred. There were two typical locations of these changes: one above the annual border separating two successive growth increments of the shoot (almost a half of all transformations in *L. annotinum* and nearly 3/4 in *L. clavatum*), the second at the end of the stem segment just before dichotomous branching, i.e. below the furrow between two new shoots (Fig. 10). In *L. clavatum* patterns changed qualitatively 88 times (7.4%) and the transitions occurred mainly between two helical patterns. In *L. annotinum* phyllotaxis was modified qualitatively in 110 cases (11.3%). The most frequent transitions occurred between whorled and helical patterns (Fig. 11 A) and also be-

tween two helical patterns only. Less frequently two purely whorled patterns were involved in a transition (Fig. 11 B). The type and the number of particular transformations and also the minimal circumferential change required were calculated according to Zagórska-Marek (1987) and are presented in Table 1 and 2.

DISCUSSION

It is intriguing that the patterns which are the most frequent in other plants, such as Fibonacci and Lucas, are uncommon

TABLE 2. Transformations involving only helical patterns. A change of a pattern chirality during transformation is marked in B column as (+), whereas opposite situation is represented by (-) mark. Some values of circumferential change, required to modification of phyllotactic pattern, are cited after Zagórska-Marek (1987) and marked with asterisk (*), the others have been calculated the same way as hers.

Transformations	Ontogenetic helix change	Circumferential change (in °)	Number of cases for:	
			<i>Lycopodium annotinum</i>	<i>Lycopodium clavatum</i>
A	B	C	D	E
3s:5z → 4s:5z	+	+ 32.5 *	2	0
3s:5z → 4z:5s	-	+ 275.0 *	1	0
5z:8s → 7z:8s	-	+ 40.0	0	1
3z:4s → 4z:5s	-	+ 99.5 *	3	0
4z:5s → 3s:5z	-	- 155.7	1	0
4z:5s → 3z:5s	+	- 30.0 *	1	0
4z:5s → 3z:4s	-	- 77.9 *	1	0
4z:5s → 3s:4z	+	+ 96.3 *	1	1
4z:5s → 5z:6s	-	+ 77.9 *	3	1
4z:5s → 5s:6z	+	- 89.3 *	3	0
4z:5s → 4s:5z	+	- 137.5 *	2	0
4z:6s → 4z:5s	-	- 42.5 *	2	0
5z:6s → 4z:5s	-	- 64.1 *	4	0
5z:6s → 4s:5z	+	+ 118.8 *	0	1
5z:6s → 4z:6s	-	- 24.5 *	1	0
5z:6s → 5z:7s	+	+ 39.6 *	2	0
5z:6s → 6z:7s	-	+ 64.2	0	4
5z:6s → 6s:7z	+	- 98.0	0	3
5z:6s → 6z:8s	-	- 73.4 *	0	1
5z:7s → 5z:6s	+	- 35.6	0	1
5z:7s → 6z:7s	+	+ 27.5	0	1
6z:7s → 6s:8z	+	- 116.8	0	1
6z:7s → 7z:8s	-	+ 54.3	0	2
6z:7s → 7s:8z	+	- 104.0	0	1
6z:8s → 5s:6z	+	+ 92.2 *	0	1
6z:8s → 7z:8s	-	+ 18.9	0	1
6z:8s → 7s:8z	+	- 125.5	0	1
7z:8s → 6z:7s	-	- 47.3	0	3
7z:8s → 6s:7z	+	+ 145.9	0	3
7z:8s → 6z:8s	-	- 18.2	0	1
7z:8s → 8z:9s	-	+ 47.6	0	1
7z:9s → 7z:8s	+	- 27.5	0	1
8z:9s → 7z:8s	-	- 41.8	0	2
8z:9s → 7s:8z	+	+ 154.2	0	1
8z:9s → 8z:10s	-	+ 25.7	0	1
8z:9s → 9s:10z	+	- 111.3	0	1
8z:10s → 8s:9z	+	- 152.1	0	1
9z:10s → 8z:10s	-	- 14.2	0	2

Fig. 5. Diagram of pattern frequency in both investigated species of *Lycopodium*. Contact parastichy pairs are arranged according to gradually increasing number of parastichies. Patterns different from formula $k:k$ and $k:(k+1)$ are located at the left side of the horizontal axis. Two spectra of phyllotaxis overlap but they culminate differently. For *L. annotinum* one high peak is characteristic and relatively narrow spectrum of phyllotactic patterns, whereas in *L. clavatum* it is more expanded with several patterns reaching similar frequency.

A

B

Fig. 6. Domains of the phyllotactic patterns in *Lycopodium annotinum* (A) and *Lycopodium clavatum* (B) shown on the PTU grid. Lines refer to contact parastichies, at the points of their crossing microphylls are located. An arrow shows the marker leaf, a black triangle – a PTU unit. Borders of the domains are drawn with heavy lines. An area of the most frequent patterns is dotted. If several expressions of pattern are present the dominant pair of contact parastichies is placed in a domain, the others are pointed by the circles elsewhere in the lattice.

Fig. 7. Phyllotaxis of plagiotropic and orthotropic shoots of *Lycopodium annotinum* (A) and *Lycopodium clavatum* (B). Patterns in plagiotropic shoots are expressed by higher numbers of parastichies than in orthotropic.

in *Lycopodium*. The earlier observations of phyllotaxis on *Lycopodium selago* shoots also showed that both of these patterns were infrequent (Church 1904). As typical for this species Church reported 1,4,5..., 1,5,6... patterns, true 3,4 – or 5-leaved whorls and primary bijugy in diminutive shoots. Vindt-Balguerie’s results (1982) showed that in bulbils of *L. selago* low expressions of Fibonacci series (2:3) may also occur. The spectrum of phyllotactic patterns, obtained in this study for *L. annotinum*, is very similar to that reported by Church for *Lycopodium selago*. Thus, in phyllotaxis these two species are closer one to another than *L. annotinum* to *L. cla-*

vatum, where in the latter the contact parastichy numbers are much higher.

In the lattice of PTU units phyllotaxis of *Lycopodium* forms a domain in which two leaf arrangements prevail: $k:k$ and $k:(k+1)$, where $k=3...11$. Such contact parastichy pattern seems to be the most typical for both *Lycopodium* species. Patterns distinct from these arrangements are very rare (Fig.6). Expressions of phyllotaxis common in other plants (2:3, 3:5, 5:8; 3:4; 2:4, 4:6 and 6:10) are in the minimum of a frequency curve and they hardly ever appear.

It is important to stress that the formula of $k:k$ contact parastichy pair is possible only when true whorls are present. True whorls are formed in spiral (multijugy) and whorled phyllotaxis, when leaf primordia are equally spaced along the circumference. Slight vertical displacements of leaves do not affect the whorled nature of their spacing. In multijugy, every successive whorl is rotated by the angle smaller than the half of the angle between two circumferentially consecutive members of the preceding whorl. In whorled phyllotaxis leaves are initiated precisely between the two leaves of the preceding whorl. In simple spiral phyllotaxis, with one ontogenetic helix thus only one leaf initiated at the particular level, the $k:k$ formula cannot be used, even if due to uneven elongation of internodes, the groups of leaves are gathered at almost the same level, forming pseudowhorls (Schoute 1936; Kwiatkowska 1993, 1994). In *Lycopodium annotinum* and *L. clavatum* true whorls are composed of a different number of microphylls. If there are few of microphylls in one whorl, they are regularly ordered, the higher number of leaves usually disturbs their arrangement (Fig. 11 A).

Fig. 8. Chirality of helical patterns in *Lycopodium annotinum* (A) and *L. clavatum* (B).

$^aY_a^a$	$^bY_a^b$	$^aY_a^b$	$^bY_a^c$		
number of branches				total	species
26	20	151	200	397 branches	<i>L. annotinum</i>
6.6%	5.0%	38.0%	50.4%		
1	6	108	288	403 branches	<i>L. clavatum</i>
0.3%	1.5%	26.7%	71.5%		

Fig. 9. Possible combinations of patterns in dichotomizing shoots. Letters a, b and c refer to different patterns. The same letters on different axes symbolize the same phyllotactic pattern.

Fig. 10. *Lycopodium clavatum* – dislocation, i.e. bifurcation of one parastichy, in the phyllotactic pattern preceding before dichotomy. Due to an increase in Z-parastichy number phyllotaxis changes from $7_s:8_z$ to $7_s:9_z$ which means that initially Z-chirality of the ontogenetic helix alters. $\times 16$.

Pseudowhorl formation, observed in *L. annotinum*, has been recently described in *Anagallis*, where besides typical true whorls and helical patterns, 3- and 4-leaved pseudowhorls occur. Interestingly, they are made of leaves located on one revolution of ontogenetic helix: three in Fibonacci and four in Lucas pattern (Kwiatkowska 1993, 1994). Other examples of such leaf arrangement were reported for *Peperomia* and *Lilium martagon* and all observed pseudowhorls with different numbers of leaves in fact derived from the main Fibonacci phyllotaxis due to uneven elongation of internodes (Schoute 1936). 5-leaved pseudowhorls in *L. annotinum* are probably formed similarly, with microphylls clustering on one revolution of ontogenetic helix.

A

7:7 → 6z:7s

B

5:5 → 6:6

Fig. 11. Phyllotactic transformations in *Lycopodium clavatum*. **A.** A transition from whorled to a helical pattern ($7:7 \rightarrow 6z:7s$). In the lower part of the stem leaves are grouped on a similar level in whorls of 7. 14 orthostichies can also be drawn here. The arrangement of microphylls upward becomes less regular and ultimately one parastichy is reduced, which is marked by an asterisk. **B.** Direct transition between two whorled patterns ($5:5 \rightarrow 6:6$). Transformation occurs when one Z-oriented parastichy and then, almost at the same level, the next S-parastichy are added to their sets. Both of them are marked with asterisks. At a site of dislocations the course of neighbouring parastichies is slightly disturbed. Bar = 1 mm.

Phyllotaxis of other species of *Lycopodium*, known from the literature, has a similar character as in analysed species. Typical spiral patterns, true whorls as well as pseudowhorls are present. The first two categories were reported for *Lycopodium selago* by Church (1904). In *L. obscurum* s.l. pseudowhorls are present consisting of three leaves (Hickey 1977). It can be speculated that they derive from Fibonacci series, similarly as in *Anagallis arvensis* (Kwiatkowska 1994). In *L. appressum* 9-leaved pseudowhorls are common (Pipoly, Stevenson 1983). More complicated phyllotaxis according to Stevenson (1976) occurs in *L. lucidulum*. There are two categories of patterns in this species: simple spiral and k:k patterns referred by the author to as pseudowhorls due to spiral initiation and uneven size of leaf primordia. The latter could be reinterpreted as true whorls, appearing either in low expressions of the multijugate patterns, then 2k parastichies should be inclined, or in truly whorled phyllotaxis – then 2k parastichies should be vertical. It is known that an initiation of whorled elements in a spiral sequence can occur in vegetative shoots, as in *Rauwolfia* (Mia 1960) and in generative ones, as in *Lychnis*, where different whorls of floral segments are initiated spirally (Lyndon 1990). What is decisive for their recognition as true whorls is not the order of initiation but their circumferential spacing. It seems that some "pseudowhorls" are in fact disputable and they should be revised from this point of view.

An increase of the k value, in *L. clavatum* manifested by the displacement of the most frequent patterns to the right in PTU grid, is probably due to different proportions between microphyll primordia and the meristem circumference in both analyzed species. In the left corner of the lattice leaf primordia are large relative to the small apex circumference. Such proportions are probably typical for the shoot apex of *Lycopodium annotinum*. When the meristem circumference is relatively big in comparison to primordia size, possibly as in *L. clavatum*, higher orders of phyllotaxis appear (Lyndon 1990). It is clear in cacti (Church 1904, personal observations), Aracean spadices (Davis and Bose 1971) and capitula of *Asteraceae*.

The diversity of phyllotactic patterns in *Lycopodium* can be compared only with that occurring in gynoecia of *Magnolia acuminata* (Zagórska-Marek 1987, 1994). The reasons of such behavior in *Magnolia* are unknown. Charlton's studies on vegetative phyllotaxis (mixed spiral and distichous) suggest genetic instability of this genus (1994). In *Lycopodium* wide range of the phyllotactic spectrum is mainly caused by three factors: small leaf primordia, dichotomy and variable sizes of shoots. After dichotomy the patterns forming on twin daughter shoots are distinct from parental at least in a half of all the branches (Fig. 9). Variations in shoot diameter are mainly dependent on the type of shoots: plagiotropic, with $k > 8$, are larger than orthotropic (Fig. 2 and 7) but also on a type of dichotomy – in anisotomously branching *Lycopodium clavatum* diameters of twin shoots are always different. Generally small dimension of microphyll primordia relative to the apex in *Lycopodium* cannot be alone held responsible for pattern diversity. Similar relation of the primordia size to the apex circumference, as in *Lycopodium*, are typical for the vegetative shoots of gymnosperms (Gregory, Romberger 1972) and for the large capitula of the majority of *Asteraceae* (Sinnott 1960), where the main Fibonacci pattern dominates. Thus yet another factor, maybe the genetic control of the meristem stability, is probably involved in a process of pattern formation in *Lycopodium*. This problem however needs some further studies.

Helical patterns in examined *Lycopodium* species demonstrate equal contribution of S and Z chirality of ontogenetic helix which is typical for plants with an undetermined helix inclination (Fig. 8). One of the exceptions: domination of the Z oriented helix in 1,7,8... series occurred in some orthotropic axes of *L. clavatum*. 7:8 expression of the parental pattern was often repeated after dichotomy in one of the daughter shoots (Fig. 9). Because at the same time in the second (weaker) daughter shoot a 5:6 parastichy pair (or sometimes 6:7) had the chirality opposed to that of the larger axis, S-chirality automatically prevail in these shoots. Tendency to form such antidromous branches seemed to be especially clear in one population of *L. clavatum* but the problem has not been investigated thoroughly. A possibility of antidromy of phyllotactic patterns was suggested by Church (1904) for *L. selago*.

During ontogeny of both species of *Lycopodium* phyllotaxis transformed rather frequently but the process proceeded in different ways. In *L. clavatum* mainly two helical patterns were involved, in *L. annotinum* several consecutive changes usually occurred, resulting in a gradual increase or reduction in parastichy number. Helical patterns usually transformed this way into whorled from which again the helical phyllotaxis was formed. Direct transitions between two whorled pattern were very rare (Fig. 11 B). The majority of transitions either between two helical or the helical and whorled patterns complied with the rule of the minimal circumferential change of the meristem surface and were in agreement with the hypothesis of the discontinuous transformations by Zagórska-Marek (1987, 1994).

The very similar sequence of gradual alternations of phyllotaxis has been recently described in shoots of *Anagallis arvensis*, where transformation of decussate (2:2) into tricussate (3:3) pattern is accomplished through intermediate of Fibonacci (2:3) phyllotaxis (Kwiatkowska 1993, 1994). Everyone of consecutive changes theoretically requires minimal sectorial change in a meristem circumference and may be explained as resulting from ontogenetic drift of the geometric proportions within the apex: either the meristem circumference ontogenetically increasing or the leaf primordia decreasing in size.

In *Lycopodium* a specific rare type of transformations was noted in which the chirality of the pattern changed but the series and its expression was the same. According to Zagórska-Marek (1985, 1987) who found the same rare transformations in *Abies balsamea*, such alternations require a drastic reconstruction of the meristem surface: reducing it by the sector of angular size of 137.5° or increasing by 222.5° sector). In few cases transformations of patterns, observed in *Lycopodium*, were such that they theoretically required quite a large sectorial change (Table 2). A drastic uneven increase of a meristem circumference associated with a change of a meristem shape into oval, common for dichotomizing shoots of *Lycopodium* (Haertel 1937; personal observations) and higher plants (Fischer 1974; Tomlinson, Posluszny 1977), possibly could facilitate such transformations. They often occurred through dislocations in parastichy pattern appearing in sectors where the shoot was visibly enlarged before dichotomy (Fig. 10).

In *Lycopodium* discontinuous transformations can be interpreted as the consequences of the changes in the apex symmetry caused by seasonal fluctuations of growth rate or by uneven expansion of the apex circumference before dichotomy. A meristem genetic instability and a shift of the shoot axis, postulated to be the reasons of discontinuous pattern

transformation (Zagórska-Marek 1994), may be true for *Lycopodium* species, especially regarding the fact that during dichotomous division of the apical meristem, a number of initials and their location must change. Frequent dichotomic branching of shoots probably multiplies ontogenetic variability of phyllotaxis, which is higher in *Lycopodium* than in most of investigated seed plants. The significance of microphylls for phyllotaxis diversity can be expressed only by expansion of the phyllotactic spectrum, due to proportion within the apex (microphyllous primordia are small in comparison to a meristem circumference).

ACKNOWLEDGMENTS

The author wishes to thank Prof. Beata Zagórska-Marek for all the discussions and the help in preparing this manuscript; and to Dr. Dorota Kwiatkowska and Dr. Johannes Battjes for helpful suggestions. This research project has been supported by grant No 6 P204 046 06 from KBN (Polish Committee for Scientific Research).

LITERATURE CITED

- BATTJES J., VISCHER N.O.E. and BACHMANN K., 1993. Capitulum phyllotaxis and numerical canalization in *Microseris pygmaea* (Asteraceae: Lactuceae). *American Journal of Botany* 80: 419-428.
- CHURCH A.H., 1904. On the relation of phyllotaxis to mechanical laws. Williams and Norgate, London, pp. 1-333.
- CRAFTS A.S., 1943. Vascular differentiation in the shoot apices of ten coniferous species. *American Journal of Botany* 30:382-392.
- CUTTER E.G., 1964. Phyllotaxis and apical growth. *New Phytologist* 63: 39-46.
- CUTTER E.G., VOELLER B.R., 1959. Changes in leaf arrangement in individual fern apices. *The Journal of the Linnean Society of London, Botany*, 56, No. 366: 225-236.
- DAVIS T.A., BOSE T.K., 1971. Fibonacci systems in aroids. *Fibonacci Quarterly* 9: 253-263.
- ERICKSON R.O., MEICENHEIMER R.D., 1977. Photoperiod induced change in phyllotaxis in *Xanthium*. *American Journal of Botany* 64: 981-988.
- FISHER J.B., 1974. Axillary and dichotomous branching in the palm *Chamaedorea*. *American Journal of Botany* 61: 1046-1056.
- GIROLAMI, G., 1953. Relation between phyllotaxis and primary vascular organization in *Linum*. *American Journal of Botany* 40: 618-625.
- GÓMEZ-CAMPO C., 1974. Phyllotactic patterns in *Bryophyllum tubiflorum*. *Harv. Bot. Gaz.* 135: 49-58.
- GREGORY R.A., ROMBERGER J.A., 1972. The shoot apical ontogeny of the *Picea abies* seedling. I. Anatomy, apical dome diameter, and plastochron duration. II. Growth rates. *American Journal of Botany* 59: 587-597, 598-606.
- HAERTEL K., 1937. Studien an Vegetationspunkten einheimischer Lycopodien. *Beitraege zur Biologie der Pflanzen*, 25, part 2, pp. 124-169.
- HICKEY R.J., 1977. The *Lycopodium obscurum* complex in North America. *American Fern Journal* 67: 45-48.
- JEAN R.V., 1994. Phyllotaxis. A systemic study in plants morphogenesis. Cambridge University Press, Cambridge, New York, Melbourne.
- JOHANSEN D.A., 1940. Plant microtechnique. McGraw-Hill Book Company, Inc., New York and London, pp. 1-523.
- KWIATKOWSKA D., 1993. Ontogenetic changes of phyllotaxis and primary vasculature in *Anagallis arvensis*. In: Abstracts of The XV International Botanical Congress, Yokohama, Japan.
- KWIATKOWSKA D., 1994. Zmiany rozwojowe wzoru filotaksji i pierwotnego systemu waskularnego pędów *Anagallis arvensis*. PhD Thesis. Wrocław University.
- LARSON P.R., 1977. Phyllotactic transitions in the vascular system of *Populus deltoides* Bartr. as determined by ^{14}C labeling. *Planta* 134: 241-249.
- LARSON P.R., 1980. Interrelations between phyllotaxis, leaf development and the primary-secondary vascular transition in *Populus deltoides*. *Annals of Botany* 46: 757-769.
- LISIECKA A., 1993. Chiralność filotaksji w rozgałęziających się pędach jodły i świerka. M Thesis, Wrocław University.
- LYNDON R.F., 1990. Plant development. The cellular basis. Topics in plant physiology. 3. Eds. Black M. and J. Chapman, Unwin Hyman London, Boston, Sydney, Wellington, pp. 1-320.
- MEICENHEIMER R.D., 1979. Relationships between shoot growth and changing phyllotaxy of *Ranunculus repens* var. *glabratus*. *American Journal of Botany* 66: 557-569.
- MAKSYMOWYCH R., CORDERO R.E. and ERICKSON R.O., 1976. Long-term developmental changes in *Xanthium* induced by gibberellic acid. *American Journal of Botany* 63: 1047-1053.
- MIA A.J., 1960. Structure of the shoot apex of *Rauwolfia vomitoria*. *Botanical Gazette* 122: 121-124.
- NAKIELSKI J., ZAGÓRSKA-MAREK B., 1995. Czynniki geometrii w modelowaniu wzrostu organu roślinnego. In: Systemy, symetrie, ewolucja. T. VI, pp. 109-124, Wrocław University (in Polish).
- NAMBOODIRI K.K., BECK C.B., 1968. A comparative study of the primary vascular system of conifers. I. Genera with helical phyllotaxis. *American Journal of Botany* 55: 447-457.
- NOLAN J.R., 1969. Bifurcation of the stem apex in *Asclepias syriaca*. *American Journal of Botany* 56: 603-609.
- ØLLGAARD B., 1979. Studies in *Lycopodiaceae*, II. The branching patterns and infrageneric groups of *Lycopodium* sensu lato. *American Fern Journal* 69: 49-61.
- PIPOLY J.J., STEVENSON D.W., 1983. Phyllotaxis, stellar morphology and shoot apical organization of *Lycopodium appressum* (Lycopodiaceae). *American Journal of Botany* 70(5 part 2), 29.
- SCHOUTE J.C., 1936. On whorled phyllotaxis. III. True and false whorls. *Recueil des Travaux Botaniques Neerlandais* 33: 670-687.
- SINNOTT E.W., 1960. Plant morphogenesis. McGraw-Hill Book Company, inc., New York-Toronto-London, pp. 148-169.
- STEEVES T.A., 1963. Morphogenetic studies on *Osmunda cinnamomea* L. the shoot apex. *Journal of the Indian Botanical Society* 42A: 225-236.
- STEVENSON D.W., 1976. Observations on phyllotaxis, stellar morphology, the shoot apex and gemmae of *Lycopodium lucidulum* Michx. (Lycopodiaceae). *Botanical Journal of the Linnean Society* 72: 81-100.
- SZYMANOWSKA-PUŁKA J., 1994. Phyllotactic patterns in capitula of *Carlina acaulis* L. *Acta Societatis Botanicorum Poloniae* 63: 229-245.
- TOMLINSON P.B., POSLUSZNY U., 1977. Features of the dichotomizing apices in *Flagellaria indica* (Monocotyledones). *American Journal of Botany* 64: 1057-1065.
- TOMLINSON P.B., WHEAT D.W., 1979. Bijugate phyllotaxis in *Rhizophoreae* (Rhizophoraceae). *Botanical Journal of the Linnean Society* 78: 317-321.
- TROLL W., 1937. Vergleichende Morphologie der höheren Pflanzen. I., Berlin.
- VINDT-BALGUERIE E., 1982. Étude au microscope électronique à balayage de la bulbille de *Huperzia selago* (L.) Bernh. (Lycopodium): méristème apical, initiation foliaire et phyllotaxie. *Canadian Journal of Botany* 60: 667-673.
- WIGGLESWORTH G., 1907. The young sporophytes of *Lycopodium complanatum* and *Lycopodium clavatum*. *Annals of Botany* 21, No. 82: 211-234.
- ZAGÓRSKA-MAREK B., 1985. Phyllotactic patterns and transitions in *Abies balsamea*. *Canadian Journal of Botany* 63: 1844-1854.
- ZAGÓRSKA-MAREK B., 1987. Phyllotaxis triangular unit; phyllotactic transitions as the consequences of the apical wedge disclinations in a crystal-like pattern of the units. *Acta Soc. Bot. Poloniae* 56(2): 229-255.
- ZAGÓRSKA-MAREK B., 1994. Phyllotactic diversity in *Magnolia* flowers. *Acta Societatis Botanicorum Poloniae* 63: 117-137.

ZMIENNOŚĆ FILOTAKSJ I NA PĘDACH
LYCOPodium CLAVATUM L. I *LYCOPodium ANNOTINUM* L.

STRESZCZENIE

Zbadano wzory ulistnienia plagio- i ortotropowych pędów *Lycopodium annotinum* L. i *L. clavatum* L. Filotaksję określano za pomocą formuły par parastych kontaktowych. Na pędach *L. annotinum* stwierdzono występowanie 11, a u *L. clavatum* 24 różnych wzorów filotaktycznych, zarówno helikalnych jak i okółkowych. Przyczynami różnorodności filotaksji u obu badanych gatunków są najprawdopodobniej: stosunkowo małe zawiązki liści w porównaniu do obwodu merystemu, zmienność średnicy pędu oraz dychotomia. Filotaksja obu pędów potomnych, po rozgałęzieniu dychotomicznym, jest odmienna od wzoru rodzicielskiego przynajmniej w połowie wszystkich zbadanych rozgałęzień. Wielkość łodygi zależna jest od typu pędu: pędy plagiotropowe mają większą średnicę niż ortotropowe oraz od sposobu rozgałęziania: w wyniku izotomii powstają pędy o zbliżonej średnicy (*L. annotinum*), przy anizotomii (*L. clavatum*) są one różne.

U obu gatunków występowały transformacje wzoru, zlokalizowane najczęściej powyżej granicy wzrostu rocznego lub na odcinku pędu bezpośrednio przed dychotomią. U *Lycopodium* nieciągłe transformacje wzoru mogą być następstwem zmian wielkości i kształtu wierzchołka podczas sezonowych wahań szybkości wzrostu oraz sektorialnego zwiększania obwodu łodygi przed dychotomią. Dychotomia prowadzi również najprawdopodobniej do zmiany liczby i położenia inicjałów w merystemie, potencjalnie może więc ułatwiać transformację wzoru filotaktycznego.

Pochodzenie liści nie wpływało bezpośrednio na filotaksję. Stosunkowo niewielkie rozmiary mikrofilii w porównaniu do obwodu pędu zwiększają jedynie możliwość występowania wzorów o wysokiej liczbie parastych.

SŁOWA KLUCZOWE: *Lycopodium*, filotaksja, transformacja filotaksji, dychotomia.