PHYLLOTACTIC SPECTRA IN CACTI: *MAMMILLARIA* SPECIES AND SOME GENERA FROM *REBUTIA* GROUP

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ABSTRACT

Phyllotaxis of globular or hemispheric cacti from *Mammillaria* genus and from *Rebutia* group shows the significant differences between the two groups. An extremely wide spectrum of phyllotaxis with many infrequent patterns has been found in *Rebutia* group while in *Mammillaria* genus it appears to be quite narrow with the main Fibonacci pattern dominant. Therefore one of possible factors responsible for these differences might be a genetic one. Ontogenetic transformations of phyllotaxis both continuous (quantitative) and discontinuous (qualitative) have been found in studied cacti. These developmental events together with dichotomy frequently occurring in some taxa increase the level of phyllotaxis diversity. As more than one expression of the pattern occurred due to continuous transformations in many studied cacti – the numbers of opposite spirals can no longer be treated as a feature of the diagnostic value in cactus taxonomy. Because of intense developmental changes significant is rather a range of phyllotaxis diversity (phyllotactic spectrum) than a single pattern or its expression in a given taxon.

KEY WORDS: *Mammillaria*, *Rebutia*, cacti, phyllotactic patterns.

INTRODUCTION

A regularity in the arrangement of areoles and tubercles has frequently been observed in family *Cactaceae*. Distribution of these structures on a cactus body is a consequence of their developmental connections with initiated leaves. Leaves originate in a spiral sequence, then leaf bases (or podaria) are modified to form tubercles and what remains of the leaf is only a rudimental scale or a vestige at the end of the tubercle. Areoles develop in the axils of leaf primordia (Boke 1944, 1952, 1953, 1961) and dependently on their meristematic activity after initiation can be treated either as axillary buds or modified dwarf shoots (Boke 1944; Freeman 1970). In general they are arranged in regular vertical lines forming ribs in the cereoid species such as *Echinocereus*, *Echinocactus*, *Echinopsis*, *Helianthocereus* etc., or in spirals in globular cacti. In both cases their arrangement is strongly dependent upon phyllotaxis. In some globular genera, especially where tubercles are so distinct as in *Dolichothele*, *Parodia*, *Coryphantha* and particularly in *Mammillaria*, the spirals have often been mentioned in morphological descriptions: either as a set of lines winding only in one direction (Engelmann 1858) or as two oppositely oriented, crossing sets (Krainz 1956-60). In the majority of globular cacti (as *Mammillaria*) the numbers of oppositely winding spirals, reported in literature, belong to the main Fibonacci series: 1,2,3,5,8,13,... (Craig 1945; Backeberg 1961, 1979; Haage 1986). On the other hand, in rib-forming cacti, the number of ribs is rarely a member of this series. It is also known that in these genera spiral phyllotaxis different than the main Fibonacci may occur. Church (1904)

reported for some species of *Echinopsis* either true whorls or typical spiral patterns, usually with the numbers in a contact parastichy pair (for definition see Adler 1974) only slightly differing: 5:6, 6:6, 6:7, 6:8, 7:7 etc. Such parastichy numbers seemed to this author the most typical for cereoid cacti (for instance 5:6 for *Cereus candicans* and *Echinopsis tubiflora*). In rib-forming genera phyllotactic patterns quite often change ontogenetically. This is manifested either as a reduction or an addition of one or more ridges (Church 1904). A change in a rib number is also well described for tribe *Hylocereae* (Rauh 1979).

In light of these data it becomes particularly interesting to find out more about phyllotaxis in morphologically different cactus genera. Is the Fibonacci phyllotaxis typical for other globular cacti as according to literature in *Mammillaria* and in the majority of Dicotyledones? Does the expression of phyllotaxis have a value of diagnostic feature in taxonomy of cacti?

MATERIALS AND METHODS

Cacti selected for the present study were morphologically diverse, although they all represented the group morphologically defined as globular or hemispheric cacti. They belonged to genus *Mammillaria* Haw. and to some genera of *Rebutia* group: *Aylostera* Speg., *Mediolobivia* Backeb., *Sulcorebutia* Backeb. and *Rebutia* K. Sch. These genera in *Rebutia* group are closely related and by some authors are treated as subgenera of *Rebutia* (Krainz 1956-60; Willis 1973; Rauh 1979;

Weber 1988). Representatives of *Mammillaria* species may attain quite notable size (Craig 1945; personal observations) and grow either as a single axis or as a densely branched multi-axial system. Plants of *Rebutia* and other cacti from this group are usually much smaller, and have often numerous lateral branches. In both cases areoles are located at the end of tubercles, they are especially well developed in *Mammillaria*. For this genus the numbers of crossing spirals (contact parastichy pairs) are reported in literature as mainly belonging to the main Fibonacci pattern. Moreover, some pair numbers have been used as a diagnostic feature in determining particular species within the genus (Craig 1945; Backeberg 1961, 1979; Rauh 1979). Number, colour, size and type of spines are variable and especially in *Rebutia* their diversity contributes to many forms of the plants (Backeberg 1959). In spite of differences in shape and dimension representatives of both groups may look alike because of regular distribution of phyllotactic pattern elements.

All examined plants belonged to the collection of the Botanical Garden of Wrocław University and to the private collection of Ms. Zofia Pyjek (Wrocław, Psie Pole). The majority of species was represented only by a few specimens, rarely by more than 20 plants. This was limited by the number of plants available for analysis in both collections. Some of specimens, especially in *Rebutia* group, were probably vegetatively propagated and, in fact, they might be a clone derived from one plant.

All studied species of cacti are listed in Table 1 (*Mammillaria* genus) and in Table 2 (*Rebutia* group). The nomenclature of investigated cactus species was adopted from Backeberg (1979).

Phyllotaxis was identified in each plant on the basis of a pair of contact parastichies visible on its surface. The pair of contact parastichies (an expression of the pattern – for defini-

tion see Zagórska-Marek 1994) sufficiently defines phyllotaxis as there are no two identical consecutive numbers representing two different phyllotactic patterns. Depending on the size of the shoot with respect to the size of the sector occupied by the leaf each phyllotactic pattern can be expressed by many pairs of contact parastichies (expressions of the pattern).

After selecting arbitrarily one areole as a marker, the numbers of oppositely winding spirals were counted from this marker on each specimen. In these cactus species, which densely branch and form compact clumps, a pattern of the main axis and patterns of the lateral branches (cuttings) were counted and scored as independent cases. Phyllotactic pattern was identified twice: in a lower and in an upper part of the axis in order to record possible ontogenetic transformations. The orientation of ascending clockwise parastichies was determined as S and counterclockwise as Z and given as S and Z indexes in the opposed parastichy pair formula. Because in most of the cases only a few specimens of each species were examined, both S and Z configurations of ontogenetic helix was in such sample insufficiently represented. Therefore the chirality of phyllotaxis in this paper was not considered.

RESULTS

Genus *Mammillaria* was represented by 181 species and 19 forms. A complete list of investigated plants (Tab. 1) shows all phyllotactic patterns and expressions encountered in studied material and also patterns reported in literature for each species.

Phyllotaxis, determined in 1446 examined axes, was classified on the basis of the numbers of contact parastichy pair into 14 different phyllotactic patterns (Fig. 1). Usually only one pattern occurred in all representatives of a given species but

Fig. 1. A comparison of phyllotactic patterns in *Mammillaria* and in some genera representing *Rebutia* group. Less frequent patterns are not shown: in *Mammillaria* below 0.1% frequency; in *Rebutia* group patterns equalling or below 0.3-0.2% frequency. All these patterns are listed in the text.

TABLE 1. A list of all examined plants belonging to *Mammillaria* genus with observed patterns and expressions occurring in investigated material and reported in literature.

Abbreviations used in table: Trf. – continuous transformation of phyllotactic pattern; Phyllotactic patterns: Fib. – the main Fibonacci pattern (1,2,3,5,8,...), Bij. – bijugy of the main Fibonacci (2,4,6,10,...), Trj. – trijugy of the main Fibonacci (3,6,9,15,...), Tetr. – tetrajugy of the main Fibonacci (4,8,12,20,...), Luc. – Lucas phyllotaxis (1,3,4,7,11,...), A – (1),3,7,10,... pattern, B – 1,4,5,9,14,... pattern, C – (1), 2,5,7,12,... pattern, D – 1,6,7,13,20,... pattern, E – bijugy of the 1,7,8,15,... pattern (2,14,16,...), F – (1),2,7,9,16,... pattern. An asterisk (*) indicates patterns in which only one pair of parastichies was distinguished (without distinct conspicuous parastichies).

Literature: Bg – Backeberg 1979; Cr – Craig 1945.

<i>Mammillaria species</i>	Number of cases	Contact parastichies pairs in studied material	Phyllotactic pattern	Pairs of contact parastichies reported in literature
<i>M. albicoma</i> Boed.	2	8:13	Fib.	8:13 Bg, Cr
<i>M. armillata</i> Brand.	2 1	5:8 8:13	Fib. Fib.	5:8 Bg, Cr
<i>M. aurihamata</i> Boed.	9	5:8	Fib.	8:13 Bg, Cr
<i>M. bachmannii</i> Boed.	1	8:13	Fib.	8:13 Bg, Cr
<i>M. backebergiana</i> Buchenau	1 1	8:13 10:16	Fib. Bij.	8:13 Bg
<i>M. baxteriana</i> (Gat.) Boed.	1 1	5:8 at the apex 8:13	Fib. Fib.	13:21 Bg, Cr
<i>M. bella</i> Backbg.	2	8:13	Fib.	– Bg
<i>M. bocasana</i> Pos.	7 8 1 1 1	5:8 8:13 13:21 7:10 10:13	Fib. Fib. Fib. A *	8:13 Bg, Cr
<i>M. bocensis</i> Craig	1	8:13	Fib.	8:13, 13:21 Bg, Cr
<i>M. boedekeriana</i> Quehl	3	8:13	Fib.	8:13 Bg, Cr
<i>M. bombycina</i> Quehl	3 2 2 1	5:8 at the apex 8:13 6:10 7:10	Fib. Fib. Bij. A	11:18 Bg, Cr
<i>M. boolii</i> Linds.	15 1	3:5 5:8	Fib. Fib.	5:8 Bg
<i>M. brauneana</i> Boed. and var.	2	8:13	Fib.	21:34 in f. typica Bg, Cr
<i>M. bravoae</i> Craig	2 3	8:13 13:21 and 21:34 Trf.	Fib. Fib.	13:21 Bg, Cr
<i>M. bucareliensis</i> Craig	1	8:13	Fib.	8:13, 13:21 Bg, Cr
<i>M. cadereytensis</i> Craig	3	8:13	Fib.	13:21 Bg, Cr
<i>M. calacantha</i> Tieg.	1	8:13 and 13:21 Trf.	Fib.	13:21 Bg, Cr
<i>M. candida</i> Scheidw.	3 1	8:13 13:21	Fib. Fib.	13:21 Bg, Cr
<i>M. canelensis</i> Craig	1 1 1	8:13 13:21 7:11	Fib. Fib. Luc.	13:21 Bg, Cr
<i>M. capensis</i> (Gat.) Craig	1	8:13	Fib.	5:8 Bg, Cr
<i>M. carmenae</i> Cast. & Nun. de Cac.	1	5:8	Fib.	? in Bg
<i>M. carnea</i> Zucc.	6 6 4 1	5:8 lateral branch 8:13 13:21 10:16	Fib. Fib. Fib. Bij.	8:13 Bg, Cr

TABLE 1. – cont.

<i>M. celsiana</i> Lem.	1	5:8	Fib.	13:21 Bg, Cr
	2	8:13	Fib.	
	4	13:21	Fib.	
<i>M. centraliplumosa</i> Fittk.	14	8:13	Fib.	– Bg
	1	6:10	Bij.	
	1	11:18	Luc.	
<i>M. centricirrha</i> Lem. var. <i>neumanniana</i> (Lem.) Schelle	17	5:8	Fib.	5:8 in f. typica Bg
	10	8:13	Fib.	
	1	8:13 and 13:21 Trf.	Fib.	
<i>M. chionocephala</i> Purp.	2	5:8	Fib.	13:21 Bg, Cr
	2	8:13	Fib.	
	1	13:21	Fib.	
<i>M. collinsii</i> (Br. & R.) Orc. x <i>tenampensis</i> (Br. & R.) Berg.	1	5:8	Fib.	8:13 in both species Bg, Cr
	1	8:13	Fib.	
<i>M. columbiana</i> SD. and var. <i>bogotensis</i> (Werd.) Dugand	8	8:13	Fib.	? in Bg; 13:21 Cr for f. typica
	1	13:21	Fib.	
	1	6:10	Bij.	
<i>M. compressa</i> DC.	13	5:8	Fib.	8:13 Bg
	5	8:13	Fib.	
<i>M. confusa</i> (Br. & R.) Orc.	1	3:5	Fib.	8:13 Bg, Cr
	4	5:8 lateral branch	Fib.	
	5	8:13	Fib.	
	1	13:21	Fib.	
	1	4:6 lateral branch	Bij.	
	1	5:9 lateral branch	B	
	1	7:12	C	
	1	7:11 dichotomy	Luc.	
	1	10:11 dichotomy	*	
<i>M. cowperae</i> Shurly	3	5:8 young plants	Fib.	13:21 Bg
<i>M. crocidata</i> Lem.	2	8:13	Fib.	13:21 Bg, Cr
<i>M. crucigera</i> Mart.	5	8:13	Fib.	– Bg; 8:13 Cr
	2	8:13 and 13:21 Trf.	Fib.	
	3	13:21	Fib.	
	1	10:16	Bij.	
<i>M. densispina</i> (Coult.) Vpl.	3	5:8	Fib.	8:13 Bg, Cr
	2	8:13	Fib.	
	1	6:10	Bij.	
<i>M. diacentra</i> Jac.	5	13:21	Fib.	13 spirals Bg
<i>M. discolor</i> Haw.	3	8:13	Fib.	8:13 Bg and Cr
	1	13:21	Fib.	
<i>M. dioxanthocentron</i> Backbg.	7	8:13	Fib.	13:21 Bg
	2	13:21	Fib.	
<i>M. donatii</i> Berge	1	8:13	Fib.	13:21 Bg, Cr
<i>M. droegeana</i> (Reb.) Hildm.	1	12:19	C	8:13 Bg, Cr
<i>M. duoformis</i> Craig & Daws.	7	8:13 and 13:21 Trf.	Fib.	13:21 Bg
<i>M. durispina</i> Boed.	2	5:8	Fib.	8:13 and 21:34 Bg, Cr
	8	8:13	Fib.	
	1	4:7	Luc.	
	1	6:10	Bij.	
<i>M. elegans</i> DC.	22	8:13	Fib.	? in Bg; 13:21 Cr
	4	13:21	Fib.	
	1	11:18	Luc.	
	1	10:16	Bij.	
	1	20:33	D	

TABLE 1. – cont.

<i>M. elongata</i> DC. and var. <i>rufocrocea</i> (SD.) K. Sch. and var. <i>subcrocea</i> (DC.) SD.	8 40 1	3:5 5:8 6:10	Fib. Fib. Bij.	3:5 and 5:8 for typical forms Bg, Cr
<i>M. ernestii</i> Fittk.	6 8 1 1	5:8 8:13 10:16 7:11	Fib. Fib. Bij. Luc.	–
<i>M. erythrocalix</i> Buchenau	2 2 3 1 1 1	3:5 lateral branch 5:8 8:13 4:6 lateral branch 6:10 6:9 lateral branch	Fib. Fib. Fib. Bij. Bij. Trj.	5:8 and 8:13 Bg
<i>M. esseriana</i> Boed.	4	8:13	Fib.	13:21 Bg, Cr
<i>M. evermanniana</i> (Br. & R.) Orc.	1 1 1	3:5 5:8 8:13	Fib. Fib. Fib.	13:21 Bg, Cr
<i>M. fasciculata</i> Eng.	1	6:10	Bij.	5:8 Bg, Cr
<i>M. fischeri</i> Pfeiff.	1 2	8:13 13:21	Fib. Fib.	? in Bg
<i>M. flavescens</i> (DC.) Haw. var. <i>nivosa</i> (Lk.) Backbg.	1 4	5:8 8:13	Fib. Fib.	8:13, 13:21 in Bg; Cr: 11:17 for <i>M. nivosa</i> Lk.
<i>M. flavovirens</i> SD.	2 1 1 1	8:13 13:21 6:10 7:12	Fib. Fib. Bij. C	8:13 Bg, Cr
<i>M. floresii</i> Backbg.	5 2	5:8 8:13	Fib. Fib.	8:13 Bg
<i>M. formosa</i> Gal.	2	13:21	Fib.	13:21 Bg, Cr
<i>M. fuauxiana</i> Backbg.	1	13:21	Fib.	? in Bg
<i>M. fuliginosa</i> SD.	6 3 1	5:8 8:13 13:21	Fib. Fib. Fib.	21:34 Bg, Cr
<i>M. fuscata</i> Pfeiff. and var. <i>sulphurea</i> (Sencke) Backbg.	14 5 16	5:8 at the apex 8:13 and 13:21 Trf. 13:21	Fib. Fib. Fib.	13:21 (?) Bg
<i>M. geminispina</i> Haw. and var. <i>nobilis</i> (Pfeiff.) Backbg.	19 7 1 2	8:13 13:21 7:11 11:18	Fib. Fib. Luc. Luc.	13:21 for f. typica Bg and Cr
<i>M. glareosa</i> Boed.	1	8:13	Fib.	– Bg; 5:8 Cr
<i>M. glochidiata</i> Mart.	5 1	5:8 10:16	Fib. Bij.	5:8 Bg, Cr
<i>M. goldii</i> Foster & Glass	1	8:13	Fib.	– Bg
<i>M. gracilis</i> Pfeiff.	8 9 9	3:5 5:8 8:13	Fib. Fib. Fib.	5:8 Cr and 8:13 by K. Schumann (according to Bg)
<i>M. graessneriana</i> Boed.	1 1	8:13 6:10	Fib. Bij.	21:34 Bg and Cr
<i>M. grusonii</i> Rge.	2	5:8	Fib.	? in Bg
<i>M. gueldemanniana</i> Backbg. var. <i>guirocobensis</i> (Craig) Backbg.	2	8:13 and 13:21 Trf.	Fib.	8:13 Bg for f. typica

TABLE 1. – cont.

<i>M. guerreronis</i> (H. Bravo) Backbg.	2	8:13 and 13:21 Trf.	Fib.	8:13 Bg
<i>M. gummifera</i> Eng.	1	13:21	Fib.	13:21 Bg, Cr
<i>M. haageana</i> Pfeiff.	3	5:8	Fib.	13:21 Bg, Cr
	4	8:13	Fib.	
<i>M. haehneliana</i> Boed.	2	8:13	Fib.	8:13 Bg, Cr
<i>M. hahniana</i> Werd. and var. <i>werdermaniana</i> Schmoll	5	8:13	Fib.	13:21 for f. typica Bg, Cr
	5	13:21	Fib.	
	1	7:11	Luc.	
	1	9:15	Trj.	
<i>M. halbingeri</i> Boed.	1	8:13	Fib.	13:21 Bg, Cr
	1	13:21	Fib.	
<i>M. hamata</i> Lehm.	1	8:13	Fib.	? in Bg
<i>M. hemisphaerica</i> Eng.	10	8:13	Fib.	8:13 and 13:21 Bg and Cr
	1	6:10	Bij.	
<i>M. herrerae</i> Werd.	3	5:8	Fib.	13:21 Bg; 8:13 Cr
	3	8:13	Fib.	
	5	13:21	Fib.	
<i>M. heyderi</i> Muehlpf.	3	5:8	Fib.	13:21 Bg, Cr
	1	4:6	Bij.	
<i>M. hidalgensis</i> Purp.	4	5:8	Fib.	8:13 Bg, Cr
	5	8:13	Fib.	
	1	4:6	Bij.	
	1	6:10	Bij.	
	1	5:7	C	
	1	9:14	B	
<i>M. hirsuta</i> Boed.	6	5:8	Fib.	8:13 Bg, Cr
	3	8:13	Fib.	
	1	5:7	C	
	1	7:12	C	
	1	9:14	B	
<i>M. hoffmanniana</i> (Tieg.) H. Bravo	5	8:13	Fib.	13:21 Bg, Cr
<i>M. hutchinsoniana</i> (Gat.) Boed.	8	5:8 lateral branch	Fib.	8:13 Bg, Cr
	5	8:13 in main axis	Fib.	
<i>M. ingens</i> Backbg.	2	8:13	Fib.	13:21 Bg
<i>M. insularis</i> Gat.	10	5:8	Fib.	5:8 Bg, Cr
<i>M. johnstonii</i> (Br. & R.) Orc. var. <i>guayamensis</i> Craig	5	5:8	Fib.	13:21 f. typica Bg, Cr
	5	8:13	Fib.	
	1	13:21	Fib.	
<i>M. kelleriana</i> Schmoll	1	8:13	Fib.	13:21 Bg, Cr
	1	13:21	Fib.	
	1	9:14	B	
	1	14:16 dichotomy	E	
<i>M. kewensis</i> SD. and var. <i>craigiana</i> Schmoll	6	3:5	Fib.	8:13 for f. typica Bg, Cr
	2	5:8	Fib.	
	2	8:13	Fib.	
	2	13:21	Fib.	
<i>M. klissingiana</i> Boed.	1	5:8	Fib.	13:21 Bg, Cr
	5	8:13	Fib.	
	1	6:10	Bij.	
<i>M. knebeliana</i> Boed.	2	8:13	Fib.	13:21 Bg, Cr
<i>M. kunzeana</i> Boed. & Quehl	9	8:13	Fib.	8:13 Bg, Cr

TABLE 1. – cont.

<i>M. lanata</i> (Br. & R.) Orc.	3 1	5:8 13:21	Fib. Fib.	13:21, 21:34 Bg and Cr
<i>M. lenta</i> Brand.	1	8:13	Fib.	13:21 Bg, Cr
<i>M. leona</i> Pos.	1 1	5:8 7:11	Fib. Luc.	8:13 Bg
<i>M. longicoma</i> (Br. & R.) Berg.	2	8:13	Fib.	13:21 Bg, Cr
<i>M. louisae</i> Linds.	2	5:8	Fib.	– Bg
<i>M. macracantha</i> DC.	3	8:13	Fib.	13:21 (?) Bg
<i>M. magnimamma</i> Haw.	2 26 5 1	3:5 5:8 8:13 6:10	Fib. Fib. Fib. Bij.	8:13 Bg, Cr
<i>M. mainae</i> Brand.	11	5:8	Fib.	8:13 Bg, Cr
<i>M. marnierana</i> Backbg.	2 4	5:8 8:13	Fib. Fib.	13:21 Bg
<i>M. martinezii</i> Backbg.	1	8:13	Fib.	? in Bg
<i>M. matudae</i> H. Bravo and var. <i>duocentralis</i> Fittk. and var. <i>serpentiformis</i> Fittk.	2 18 32 5 1 1	3:5 1-yr. seedling 5:8 1-yr. seedling 8:13 13:21 10:16 9:14	Fib. Fib. Fib. Fib. Bij. B	13:21 Bg
<i>M. mazatlanensis</i> (Reb.) Sch. & Guerke var. <i>monocentra</i> Craig	7	5:8	Fib.	5:8 for f. <i>typica</i> Bg, Cr
<i>M. meiacantha</i> Eng.	4 15 1	5:8 lateral branch 8:13 and 13:21 Trf. 9:15	Fib. Fib. Trj.	8:13 Bg
<i>M. melanocentra</i> Pos.	3	8:13 and 13:21 Trf.	Fib.	8:13 Bg, Cr
<i>M. mendeliana</i> (H. Bravo) Werd.	2 1 1	8:13 13:21 12:20	Fib. Fib. Tetr.	13:21 Bg, Cr
<i>M. mexicensis</i> Craig	2	8:13 and 13:21 Trf.	Fib.	8:13 Bg, Cr
<i>M. microcarpa</i> Eng.	8 2	5:8 8:13	Fib. Fib.	13:21 Bg, Cr
<i>M. microhelix</i> Werd.	11 5 1	5:8 1-yr. seedling and lateral branch 8:13 13:21	Fib. Fib. Fib.	8:13 (?) Bg; 8:13 Cr
<i>M. microthele</i> Muehlpf.	1 2 1	8:13 13:21 10:16	Fib. Fib. Bij.	? in Bg
<i>M. mollendorffiana</i> Shurly	34 16	5:8 1-yr. seedling 8:13	Fib. Fib.	13:21 Bg
<i>M. mollihamata</i> Shurly	7 1	5:8 8:13	Fib. Fib.	21:34 and 19:30 Bg
<i>M. morganiana</i> Tieg.	6 1	8:13 13:21	Fib. Fib.	8:13, 13:21 and 21:34 Bg; 13:21 Cr
<i>M. muehlenpfordtii</i> Foerst.	2 1	8:13 at the apex 18:29	Fib. Luc.	13:21 Bg
<i>M. multidigitata</i> Linds.	1	7:9	F	13:21 Bg

TABLE 1. – cont.

<i>M. mystax</i> Mart.	2	8:13	Fib.	13:21 Bg, Cr
<i>M. nana</i> Backbg.	1	5:8	Fib.	5:8 Bg
<i>M. nejapensis</i> Craig & Daws.	1 1 1	5:8 8:13 13:21	Fib. Fib. Fib.	
<i>M. neocoronaria</i> Knuth	1 5	5:8 8:13	Fib. Fib.	8:13 Bg, Cr
<i>M. neopalmeri</i> Craig	2	5:8	Fib.	8:13 Bg, Cr
<i>M. nunezii</i> (Br. & R.) Orc. and var. <i>solisii</i> (Br. & R.) Backbg.	5 19 1 1	5:8 8:13 13:21 10:16	Fib. Fib. Fib. Bij.	13:21 for f. <i>typica</i> Bg, Cr
<i>M. obconella</i> Scheidw.	1	13:21	Fib.	13:21 Bg
<i>M. ochoterenae</i> (H. Bravo) Werd.	3 1	8:13 16:26	Fib. Bij.	13:21 Bg, Cr
<i>M. oliviae</i> Orc. (form of <i>M. microcarpa</i> Eng.)	2 1	5:8 8:13	Fib. Fib.	– Bg 13:21 Cr
<i>M. orcuttii</i> Boed.	3 3 1	5:8 8:13 13:21 and 21:34 Trf.	Fib. Fib. Fib.	13:21 Bg, Cr
<i>M. pachycylindrica</i> Backbg.	4 1 1	8:13 and 13:21 Trf. 7:11 at the apex 11:18	Fib. Luc. Luc.	13:21 Bg
<i>M. pacifica</i> (Gat.) Boed.	1	5:8	Fib.	? in Bg
<i>M. painterii</i> Rose	1	8:13	Fib.	8:13 Bg, Cr
<i>M. parensis</i> Craig	11	8:13	Fib.	8:13 Bg, Cr
<i>M. parkinsonii</i> Ehrenbg., var. <i>brevispina</i> Craig and var. <i>dietrichae</i> (Tieg.) Backbg.	1 17 1 1 2 2 1	5:8 8:13 one after dichotomy 13:21 6:10 10:16 11:18 7:12 dichotomy	Fib. Fib. Fib. Bij. Bij. Luc. C	8:13, 13:21 Bg 8:13 in Cr
<i>M. patonii</i> (H. Bravo) Werd.	1 2	5:8 8:13	Fib. Fib.	5:8 (?) Bg
<i>M. pentacantha</i> Pfeiff.	3 1	8:13 13:21	Fib. Fib.	5:8 and 8:13 (?) Bg
<i>M. perbella</i> Hildm.	1	16:26	Bij.	13:21 Bg, Cr
<i>M. petterssonii</i> Hildm.	11 1 2	5:8 1-yr. seedling 8:13 1-yr. seedling 6:10 1-yr. seedling	Fib. Fib. Bij.	13:21 Bg, Cr
<i>M. phaeacantha</i> Lem.	1 1	13:21 21:34	Fib. Fib.	8:13 Bg, Cr
<i>M. phymatothele</i> Berg	1	8:13	Fib.	8:13 Bg, Cr
<i>M. pilensis</i> Shurly	1 3	8:13 13:21 and 21:34 Trf.	Fib. Fib.	13:21 Bg
<i>M. pitcayensis</i> H. Bravo	4 3	8:13 13:21	Fib. Fib.	13:21 ? Bg
<i>M. polyedra</i> Mart.	1 1	5:8 young plant 6:10 young plant	Fib. Bij.	13:21 Bg, Cr

TABLE 1. – cont.

<i>M. praelii</i> Muehlpf. and var. <i>viridis</i> (SD.) Craig	3 3	5:8 8:13 at the apex	Fib. Fib.	13:21 in typical form Bg and Cr
<i>M. pringlei</i> (Coult.) Brand. and var. <i>longicentra</i> Backbg.	13 1 1	8:13 13:21 13:20 dichotomy	Fib. Fib. D	13:21 in f. typica Bg, Cr
<i>M. prolifera</i> (Mill.) Haw. var. <i>haitiensis</i> (K. Sch.) Borg	4 1 1	5:8 8:13 4:6	Fib. Fib. Bij.	5:8 Bg and Cr for f. typica
<i>M. pseudorekoi</i> Boed.	4 5	5:8 and 8:13 Trf. 8:13	Fib. Fib.	8:13 Bg
<i>M. pseudoscrippsiana</i> Backbg.	1 1	13:21 19:31	Fib. C	8:13 (?) Bg
<i>M. pyrrhocephala</i> Scheidw.	19 18 6 1 1	5:8 8:13 13:21 4:7 lateral branch 8:12 dichotomy	Fib. Fib. Fib. Luc. Tetr.	13:21 Bg
<i>M. queretarica</i> Craig	5 5	5:8 8:13	Fib. Fib.	13:21 Bg, Cr
<i>M. rekoi</i> (Br. & R.) Vpl.	2	5:8	Fib.	8:13 Bg, Cr
<i>M. rhodantha</i> Lk. & O. and var. <i>sulphurea</i> K. Sch.	18 5	8:13 13:21	Fib. Fib.	13:21 Bg, Cr in f. typica
<i>M. rosensis</i> Craig	2 4	5:8 8:13	Fib. Fib.	13:21 Bg, Cr
<i>M. roseoalba</i> Boed.	17 2 1	5:8 lateral branch 8:13 7:11	Fib. Fib. Luc.	8:13 Bg, Cr
<i>M. rossiana</i> Heinr.	2 10	5:8 8:13	Fib. Fib.	8:13 Bg
<i>M. ruestii</i> Quehl	3 6 1	5:8 8:13 13:21	Fib. Fib. Fib.	13:21 Bg, Cr
<i>M. sanluisensis</i> Shurly	1 4	5:8 8:13	Fib. Fib.	8:13 Bg
<i>M. sartorii</i> Purp.	1	8:13	Fib.	8:13 Bg, Cr
<i>M. schiedeana</i> Ehrenbg.	11 6	5:8 8:13	Fib. Fib.	13:21 Bg, Cr
<i>M. schwarzii</i> Shurly	3	8:13	Fib.	8:13 Bg
<i>M. scrippsiana</i> (Br. & R.) Orc. var. <i>rookshyana</i> Backbg.	4 1	5:8 8:13	Fib. Fib.	13:21 Bg, Cr and 26 spirals by Cr
<i>M. seideliana</i> Quehl	7 2	8:13 13:21	Fib. Fib.	8:13 Bg, Cr
<i>M. seitziana</i> Mart.	1	10:16	Bij.	8:13 Bg, Cr
<i>M. sempervivi</i> DC.	1 4 2	5:8 and 8:13 2-yr. seedling, Trf. 8:13 13:21	Fib. Fib. Fib.	13:21 Bg, Cr
<i>M. sheldonii</i> (Br. & R.) Boed.	9 1	5:8 8:13	Fib. Fib.	8:13 Bg, Cr
<i>M. simplex</i> Haw.	2 1	5:8 8:13	Fib. Fib.	8:13 Bg

TABLE 1. – cont.

<i>M. sinistrohamata</i> Boed.	2	5:8	Fib.	13:21 Bg, Cr
<i>M. soehlemannii</i> Haage & Backbg.	5	5:8	Fib.	– Bg
	2	8:13	Fib.	
<i>M. solisoides</i> Backbg.	2	8:13	Fib.	8:13 Bg
	3	13:21	Fib.	
<i>M. sonorensis</i> Craig	1	5:8 seedling	Fib.	5:8, 8:13 Bg, Cr; and 10:16 Cr
<i>M. spinosissima</i> Lem.	1	3:5 1-yr. seedling	Fib.	13:21 Bg, Cr
	2	5:8 1-yr. seedling	Fib.	
	18	8:13	Fib.	
	1	6:10	Bij.	
<i>M. standleyi</i> (Br. & R.) Orc.	1	13:21	Fib.	13:21 Bg, Cr
<i>M. subdurispina</i> Backbg.	4	8:13	Fib.	13:21 Bg
<i>M. supertexta</i> Mart.	4	8:13	Fib.	? in Bg
<i>M. swinglei</i> (Br. & R.) Boed.	2	8:13	Fib.	8:13 Bg, Cr
	1	6:10	Bij.	
	1	7:11	Luc.	
<i>M. tetracantha</i> SD.	2	8:13	Fib.	? Bg; 13:21 Cr
	2	13:21	Fib.	
<i>M. theresae</i> Cutak	1	3:5 seedling	Fib.	– Bg
	4	5:8 seedling	Fib.	
<i>M. tolimensis</i> Craig	1	8:13	Fib.	8:13 and 13:21 Bg and Cr
	1	6:10	Bij.	
	1	7:11	Luc.	
	1	9:14	B	
<i>M. umbrina</i> Ehrenbg.	11	8:13	Fib.	8:13 Cr
<i>M. uncinata</i> Zucc.	4	8:13 and 13:21 Trf.	Fib.	8:13 Bg, Cr
	1	10:16	Bij.	
<i>M. vagaspina</i> Craig	1	8:13	Fib.	8:13 Bg, Cr
	1	13:21	Fib.	
<i>M. vaupelii</i> Tieg.	1	5:8 young plant	Fib.	13:21 Bg and Cr
	4	8:13	Fib.	
	1	13:21	Fib.	
<i>M. wiesingeri</i> Boed.	1	5:8	Fib.	16:26 Bg, Cr
	4	8:13	Fib.	
	1	13:21	Fib.	
<i>M. wildii</i> Dietr.	12	8:13	Fib.	few at the beginning Bg; 13:21 Bg, Cr
	1	6:10	Bij.	
<i>M. winteriae</i> Boed.	2	5:8 seedling	Fib.	8:13 Bg, Cr
	2	8:13	Fib.	
	1	9:16	F	
<i>M. woodsii</i> Craig	2	13:21	Fib.	13:21 Bg, Cr
<i>M. wrightii</i> Eng.	1	5:8	Fib.	8:13 Bg, Cr
<i>M. yucatanensis</i> (Br. & R.) Orc.	2	5:8	Fib.	13:21 Bg, Cr
	3	8:13	Fib.	
	1	10:16	Bij.	
<i>M. zeilmanniana</i> Boed.	10	5:8	Fib.	13:21 Cr
	3	8:13	Fib.	
<i>M. zucchariniana</i> Mart.	1	8:13	Fib.	16:26 Bg, Cr

TABLE 1. – cont.

<i>Mammillaria</i> sp.	70	1,2,3,5,8,...	Fib.
	2	2,4,6,10,...	Bij.
	3	1,3,4,7,...	Luc.
	1	1,4,5,9,...	B
	1	13:16	*

for some species two or three patterns were found in different genets or ramets (for definition see White 1979). In one species (*Mammillaria confusa*), with multiple dichotomies of ramets, six different phyllotactic patterns occurred (Fig. 2). In the majority of plants (94.1%) contact parastichy numbers belonged to the main Fibonacci pattern, usually with one (70 species) or two expressions (76 species) for each species. Three expressions occurred in 25 species and four in 5 species of *Mammillaria* (Tab. 1). Patterns different than the main Fibonacci were represented mainly by primary bijugy (3.0% of all cases) and Lucas phyllotaxis (1.5% – Fig. 1). Other patterns such as 1,4,5,9,..., (1),2,5,7,... and trijugy of the main Fibonacci were less frequent (up to 0.5%). Some patterns were found only in one or two plants. These were: pairs 13:20 and 20:33 (1,6,7,...), 7:9 and 9:16 [(1),2,7,9,...], 7:10 [(1),3,7,10,...], 8:12 and 12:20 [4(1,2)], and pairs of parastichies: 10:11, 10:13, 13:16 and 14:16 [2 (1,7)]. Their frequency was about 0.1%.

For some species of *Mammillaria* represented by higher number of examined individuals, spectra of phyllotaxis were constructed. They well illustrate the diversity and the most common expressions of patterns within the genus (Fig. 3).

***Rebutia* group** was represented mainly by *Rebutia* (27 species and 9 forms) but also by genera: *Aylosteria* (11 species), *Mediobolivia* (2), *Lobivia* (1) and *Sulcorebutia* (3 species).

Representatives of investigated species with their phyllotaxis are listed in Table 2. Phyllotaxis was identified for 606 plants and represented by 35 different phyllotactic arrangements (Fig. 1). Several patterns, usually from 6 to 9 occurred in each species; more patterns (up to 13) were encountered only in a few species (Fig. 4). Species with only one or two patterns were also infrequent. These results are undoubtedly strongly affected by insufficient number of plants in each species. In *Rebutia* group primary bijugy (26.1%) and Fibonacci pattern (24.3%) dominated. Quite common was also Lucas phyllotaxis (12.4%). Trijugy of the main Fibonacci pattern (3, 6, 9,...) and patterns: 1,4,5,9,..., 1,5,6,11,... and (1),2,5,7,... occurred in ca. 5-6% of all cases. Less frequent was pattern (1), 3,7,10,... which occurred in 3.8% of all cases. Other patterns were infrequent and found only in few instances (1 to 6 plants – equalling or below 1% frequency). Among them there were: (1),2,7,9,..., (1),3,8,11,..., (1),4,11,15,..., 1,6,7,13,..., 1,7,8,15,..., true whorls (with number of elements in a whorl $k = 5...8$), multijugies of several phyllotactic patterns [expressed as pairs: 6:8 – 2(1,3); 8:10 – 2(1,4); 10:12 – 2(1,5); 14:18 – 2(1,7); 10:14 and 14:24 – 2(2,5); 14:20 – 2(3,7); 8:12 – 4(1,2); 16:28 – 4(1,3); 10:15 – 5(1,2); 12:18 – 6(1,2) and a pair 14:21 – 7(1,2)].

Such pairs of contact parastichies as 9:13; 11:13; 11:14; 13:14; 13:16; 13:17 and 15:17 were also present and they

Fig. 2. Diversity of patterns in *Mammillaria* genus. In the majority of plants only one pattern was observed but a such result was probably affected by insufficient number of representatives of particular species.

Fig. 3. Spectra of phyllotaxis in selected species of *Mammillaria*.

usually appeared in slightly deformed plants (e.g. in slightly oval lateral branches) or after transformations (Fig. 7). For some species represented by more numerous sample of individual plants, spectra of phyllotaxis in Fig. 5 were constructed the same way as in *Mammillaria*.

Some uncommon patterns found in studied cacti from *Mammillaria* and from *Rebutia* group were documented in photographs (Figs 6 and 7).

Ontogenetic transformations of phyllotactic patterns were observed in both groups of plants. In *Mammillaria* genus all cases of transformations (60 cases – 4.0%) were continuous in a sense proposed by Zagórska-Marek (1987). They were changing an expression of the main Fibonacci pattern (Tab. 1). In *Rebutia* group transformations were less numerous than in *Mammillaria* (6 cases – 1%) and resulted in a qualitative change of phyllotaxis. They usually occurred in hybrids. An addition of one Z-oriented parastichy caused transformation 10z:17s → 11z:17s in *Aylosteria kupperiana* and of one S-parastichy – transformation 11z:13s → 11z:14s in *Rebutia kranziana* (hybr.) (Fig. 7 D). At the top of this latter plant the sets of conspicuous parastichies 11z:14s:25z are quite distinct. Reduction of parastichies occurred during transformations: 16z:26s → 16z:25s in *R. hyalacantha* and 10z:14s → 9z:14s in *R. chrysacantha*. More complicated situation was observed in *Rebutia cajasensis* where phyllotaxis changed twice in a following manner: 13s:21z → 14s:22z → 14s:21z.

DISCUSSION

In spite of similarities in distribution of areoles positioned at the end of more or less distinct tubercles, diversity of phyllotaxis in both investigated groups of plants was differently manifested.

In the majority of *Mammillaria* species contact parastichies, reported in literature and encountered during the study, belonged to the main Fibonacci pattern. Other patterns described in literature such as: Lucas phyllotaxis in *Mammillaria bombycina* Quehl (Craig 1945; Backeberg 1961, 1979), *M. vetula* Mart. (Craig 1945) and the primary bijugy in three species: *M. sonoriensis* Craig, *M. zuccariniana* Mart. (Craig 1945; Backeberg 1961; 1979), *M. wiesingeri* Boed. (Krainz 1956-60) and also pattern 1,5,6,11,... expressed as 11:17 parastichies in *M. nivosa* Lk. (Craig 1945), were not confirmed for these particular species but occurred in others (Tab. 1).

Some unusual pairs of parastichies as 10:11 (*M. confusa*) and 14:16 (*M. kelleriana*) were sometimes found in newly formed apices after dichotomous branching of ramets. Disturbances and little irregularities in an areole arrangement usually occurred just after splitting of the apex, then the patterns became more regular. Dichotomy increases a chance of some infrequent patterns appearance such as (1),2,5,7,... or tetrajugy of the main Fibonacci (Tab. 1), however more common patterns like Lucas or Fibonacci may also be generated. Bo-

Fig. 4. Diversity of patterns in *Rebutia* group.

Fig. 5. Spectra of phyllotaxis in more numerous representatives of *Rebutia* group.

TABLE 2. A list of studied cacti in *Rebutia* group including, similarly as in Table 1, all observed patterns. Abbreviations used in table: Trf. – a transformation of phyllotactic pattern; Literature: Kr – Krainz 1956-60; Bg – Backeberg 1979, H – Haage 1986; Rh – Rauh 1979. An asterisk marks these patterns which until now have not been reported in literature.

Species	Number of cases	Phyllotactic series	Contact parastichies pairs	Number of spirals (ribs) reported in literature
<i>Aylostera albiflora</i> (Ritt. & Buin.) Backbg.	6 6	1,2,3,5,... 2,4,6,10,...	5:8 6:10	
<i>Aylostera albipilosa</i> (Ritt.) Backbg.	1	3,6,9,15,...	9:15	
<i>Aylostera deminuta</i> (Web.) Backbg.	2 1	1,2,3,5,... 2,4,6,10,...	8:13 6:10	Tubercles in 11-13 ribs (H)
<i>Aylostera fiebrigii</i> (Guerke) Backbg	3 3 5 1	1,2,3,5,... 2,4,6,10,... 1,3,4,7,... (1),3,7,10,...	8:13 10:16 11:18 10:17	
<i>Aylostera kupperiana</i> Backbg.	2 1 1 1 1 1 1	2,4,6,10,... 1,3,4,7,... 1,4,5,9,... (1),3,7,10,... 1,5,6,11,... (1),3,8,11... *	6:10 7:11 9:14 10z:17s Trf. → → 11z:17s 11:19 9:13	ca.15 ribs; (Bg, H)
<i>Aylostera muscula</i> (Ritt. & Thiele) Backbg.	4 1 1 1 1	1,2,3,5,... 1,5,6,11,... (1),3,7,10,... 5(1,2) 4(1,3)	8:13 17:28 10:17 10:15 16:28	
<i>Aylostera narvaecense</i> Card.	1	1,3,4,7,...	7:11	ca.18 ribs (Bg)
<i>Aylostera pseudodeminuta</i> Backbg.	14 12 3 3 2 9 8 1 1 4 2 2 1	1,2,3,5,... 2,4,6,10,... 1,3,4,7,... 1,4,5,9,... 1,5,6,11,... (1),2,5,7,... (1),3,7,10,... 1,6,7,13,... 3,6,9,15,... 2,6,8,14,... 5:5 7:7 5 (1,2)	5:8 and 8:13 4:6, 6:10 and 10:16 4:7 and 7:11 4:5 and 5:9 5:6 5:7 7:10 6:7 6:9 and 9:15 6:8 5:5 7:7 5:10	
<i>Aylostera pseudominuscula</i> (Speg.) Speg.	1 1	1,2,3,5,8,... 3,6,9,15,...	5:8 9:15	13 ribs (H)
<i>Aylostera spegazziniana</i> (Backbg.) Backbg.	1	1,3,4,7,...	7:11	15-20 spiral ribs (Kr, H)
<i>Aylostera spinosissima</i> Backbg.	2 3	1,2,3,5,... 2,4,6,10,...	5:8 and 13:21 6:10 and 10:16	
<i>Aylostera</i> sp.	7 10 1 4 1	1,2,3,5,... 2,4,6,10,... 1,3,4,7,... 3,6,9,15,... 4,8,12,...		
<i>Lobivia peclardiana</i> Krainz var. <i>winteriae</i> Krainz	4 1 1	2,4,6,10,... 1,3,4,7,... (1),4,11,...*	6:10 and 10:16 11:18 15:26	Hybr.? (Bg); 13-19 ribs (H)
<i>Mediolobivia eucaliptana</i> Krainz	7 6 2	1,2,3,5,... 2,4,6,10,... 1,3,4,7,...	3:5 and 5:8 4:6, 6:10 and 10:16 7:11 and 11:18	

TABLE 2. — cont.

<i>Mediolobivia eucaliptana</i> Krainz	1 1 1	1,5,6,11,... (1),2,5,7,... 3,6,9,15,...	5:6 5:7 6:9	
<i>Mediolobivia haefneriana</i> Cullm.	2 1 6 19 5 2 2	1,2,3,5,... 2,4,6,10,... 1,4,5,9,... 1,5,6,11,... (1),2,5,7,... 5:5 6:6	5:8 4:6 4:5 and 5:9 5:6 5:7 5:5 6:6	ca. 11 ribs (Bg)
<i>Rebutia arenacea</i> Card.	1 1 1	1,2,3,5,... 2,4,6,10,... *	8:13 10:16 13:16	Tubercles in ca. 30 spirals (Bg)
<i>Rebutia buiningiana</i> Rausch	1	2,4,6,10,...	10:16	20 spiral ribs (H)
<i>Rebutia cajasensis</i>	1 1 1	1,2,3,5,... 2,6,8,14,... 7(1,2)	13s:21z Trf. → → 14s:22z Trf. → → 14s:21z	
<i>Rebutia calliantha</i> Bewg.	10 1 2 2	1,2,3,5,... 2,4,6,10,... 1,3,4,7,... 3,6,9,15,...	8:13 6:10 7:11 9:15	Tubercles in ca.27 spirals (H)
<i>Rebutia chrysacantha</i> Backbg.	4 1 2 1	1,4,5,9,... 1,5,6,11,... (1),2,5,7,... 2 (2,5)*	9:14 and 14:23 11:17 5:7 14:24, at the apex: 10z:14s Trf. → 9z:14s	
<i>Rebutia fulviseta</i> (= <i>Aylosteria fulviseta</i> Rausch)	2 2 3	1,2,3,5,... 2,4,6,10,... 1,3,4,7,...	5:8 6:10 4:7 and 7:11	16 spiral ribs (H)
<i>Rebutia glomeriseta</i> Card.	2 3 2 1 1	1,2,3,5,... 2,4,6,10,... 1,3,4,7,... (1),2,5,7,... 3,6,9,15,...	8:13 6:10 and 10:16 7:11 7:12 9:15	± 20 ribs (H)
<i>Rebutia graessneriana</i>	1	3,6,9,15,...	9:15	
<i>Rebutia grandiflora</i> Backbg.	4 7 1 1	1,2,3,5,... 2,4,6,10,... 1,3,4,7,... 2,6,8,14,...	5:8 6:10 and 10:16 11:18 6:8	± 26 spiral ribs (H)
<i>Rebutia hyalacantha</i> (Backbg.) Backbg.	7 12 1 3 2 1	1,2,3,5,... 2,4,6,10,... (1),2,7,9,... 1,3,4,7,... 1,5,6,11,... (1),2,5,7,...	5:8, 8:13 and 13:21 6:10, 10:16 and 16z:26s Trf. → → 16z:25s 7:11 and 11:18 6:11 and 11:17 7:12	
<i>Rebutia kariusiana</i> Wessn.	1 3 1 1 1	1,2,3,5,... 2,4,6,10,... 1,5,6,11,... 2 (1,5)* *	8:13 10:16 and 16:26 17:28 10:12 11:13	
<i>Rebutia krainziana</i> Kesseln.	2 1 2 1 1 1	2,4,6,10,... 1,3,4,7,... 1,4,5,9,... 1,5,6,11,... 1,7,8,15,... (1),2,7,9,...	6:10 and 10:16 11:18 9:14 and 14:25 11:17 7:8 7:9	Tubercles in spirals (Bg)

TABLE 2. – cont.

<i>Rebutia krainziana</i> Kessl.	2 1 2 2 1 1	3,6,9,15,... 2 (1,4) * * * *	6:9 and 9:15 8:10 13:17 9:13 11z:14s Trf. → → 11z:13s	
<i>Rebutia marsoneri</i> Werd. and var. <i>spathulata</i> Don.	8 9 2 1 1 2 2 1 4	1,2,3,5,... 2,4,6,10,... 1,3,4,7,... 1,5,6,11,... 1,6,7,13,... (1),2,5,7,... (1),2,7,9,... (1),3,7,10,... 3,6,9,15,...	5:8 and 8:13 6:10 and 10:16 7:11 and 11:18 6:11 6:7 5:7 and 7:12 7:9 and 16:25 10:17 6:9 and 9:15	
<i>Rebutia minuscula</i> K. Sch.	7 5 2 2 2 1 1 1 1	2,4,6,10,... 1,3,4,7,... 1,4,5,9,... 1,5,6,11,... (1),3,7,10,... 3,6,9,15,... 2,6,8,14,... 2 (1,7)* *	6:10, 10:16 and 16:26 7:11 and 11:18 9:14 and 14:23 5:6 and 6:11 7:10 and 10:17 6:9 6:8 14:18 13:14	ribs in 16-20 spirals (H)
<i>Rebutia multicolor</i>	1 1 1	1,2,3,5,... (1),2,5,7,... *	13:21 12:19 15:17	
<i>Rebutia nitida</i> (= <i>Aylosteria nitida</i> Ritt.)	20 13 8 3 4 5 4 4	1,2,3,5,... 2,4,6,10,... 1,3,4,7,... 1,4,5,9,... 1,5,6,11,... (1),2,5,7,... (1),3,7,10,... 3,6,9,15,...	3:5, 5:8 and 8:13 4:6, 6:10 and 10:16 7:11 4:5 and 5:9 5:6 5:7 and 7:12 7:10 6:9	ca. 16 ribs (H)
<i>Rebutia patericalyx</i>	1 2 1 5	1,2,3,5,... 2,4,6,10,... 1,3,4,7,... 3,6,9,15,...	5:8 10:16 11:18 6:9	
<i>Rebutia permutata</i> W.Heinr.	1 1 2 1 2 1	1,3,4,7,... 1,5,6,11,... 3,6,9,15,... (1),2,5,7,... (1),2,7,9,... (1),3,7,10,...	11:18 11:17 6:9 12:19 7:9 7:10	
<i>Rebutia petersonii</i>	1	1,3,4,7,...	11:18	
<i>Rebutia pulvinata</i>	1	1,3,4,7,...	7:11	
<i>Rebutia robustispina</i>	1 1	1,2,3,5,... (1),2,5,7,...	5:8 5:7	
<i>Rebutia schiedeana</i>	1 1 2 1 1	1,2,3,5,... 2,4,6,10,... 3,6,9,15,... 2 (3,7)* 7(1,2)	5:8 6:10 6:9 14:20 14:21	
<i>Rebutia senilis</i> Backbg., var. <i>breviseta</i> Backbg., var. <i>iseliniana</i> Krainz, var. <i>kesselringiana</i> Bewg., var. <i>schieliana</i> Bewg., var. <i>sieperdaiana</i> (Buin.) Backbg. and var. <i>stuemeri</i> Backbg.	17 19 12 6 3 3	1,2,3,5,... 2,4,6,10,... 1,3,4,7,... 1,4,5,9,... 1,5,6,11,... 1,6,7,13,...	5:8, 8:13 and 13:21 6:10, 10:16 and 16:26 4:7, 7:11 and 11:18 5:9, 9:14 and 14:23 5:6, 11:17 and 17:28 6:7 and 7:13	

TABLE 2. – cont.

	7	(1),2,5,7,...	5:7, 7:12 and 12:19	
	4	(1),3,7,10,...	7:10 and 10:17	
	7	3,6,9,15,...	6:9, 9:15 and 15:24	
	1	8:8	8:8	
	1	5 (1,2)	10:15	
	1	6 (1,2)	12:18	
	1	2 (1,5)*	10:12	
	1	2 (2,5)*	10:14	
<i>Rebutia sordida</i>	2	1,2,3,5,...	8:13	
	1	2,4,6,10,...	10:16	
	1	1,3,4,7,...	11:18	
<i>Rebutia tamboensis</i>	1	1,2,3,5,...	8:13	
	3	2,4,6,10,...	6:10 and 10:16	
<i>Rebutia violaciflora</i> Backbg. and var. <i>knuthiana</i> (Backbg.) Don.	3	1,2,3,5,...	8:13	
	6	2,4,6,10,...	6:10, 10:16 and 16:26	
	1	1,5,6,11,...	11:16	
	3	1,3,4,7,...	7:11 and 11:18	
	1	1,4,5,9,...	14:23	
<i>Rebutia xanthocarpa</i> Backbg. and var. <i>luteirosea</i> Backbg.	7	1,2,3,5,...	3:5, 5:8, 8:13 and 13:21	
	10	2,4,6,10,...	4:6, 6:10 and 10:16	
	2	1,3,4,7,...	4:7 and 7:11	
	1	1,4,5,9,...	4:5	
	1	1,6,7,13,...	6:7	
	1	2,6,8,14,...	6:8	
<i>Rebutia</i> sp.	5	1,2,3,5,...	8:13 and 13:21	
	9	2,4,6,10,...	6:10, 10:16 and 16:26	
	3	1,3,4,7,...	7:11 and 11:18	
	1	1,4,5,9,...	9:14	
	1	(1),2,5,7,...	7:12	
	6	3,6,9,15,...	6:9 and 9:15	
	1	(1),4,11,...*	11:15	
<i>Sulcorebutia canigueralii</i> (Card.) Backbg.	1	1,2,3,5,...	8:13	ribs in ca. 13 spiral rows (Bg)
<i>Sulcorebutia kruegeri</i> (Card.) Ritt.	4	1,2,3,5,...	5:8 lateral branch	
	1	2,4,6,10,...	10:16	
<i>Sulcorebutia rauschii</i> Frank	1	1,2,3,5,...	8:13	ribs to 16, in spirals (Bg, Rh)
	1	2,4,6,10,...	6:10	

ke's study on dichotomizing plants of *Mammillaria perbella* and *M. parkinsonii* (1976) showed that in both daughter apices phyllotaxis could be expressed only by the numbers of the main Fibonacci series. It is possible to hypothesise that in these species in which so called cruciate-dichotomy regularly occurs (*Mammillaria parkinsonii*, *M. perbella*, *M. pseudoperbella*, *M. crucigera*, *M. geminispina*) phyllotactic patterns emerging in twin apices represent the most common phyllotaxis. On the contrary, in these species in which dichotomy happens more occasionally and not in a cruciate manner (e.g. as in *Mammillaria kelleriana*), patterns should be unusual, irregular and even impossible to identify. Nevertheless, in both cases the dichotomy should be regarded as one of the factors increasing the extent of phyllotactic spectrum of the particular *Mammillaria* species.

Intraspecific variability of phyllotactic patterns in *Mammillaria* was mainly expressed by different pairs of contact parastichies (an expression of patterns – Fig. 3, Tab. 1). As was mentioned before, some authors pointed out an expression of the main Fibonacci pattern as an important taxonomic feature of the particular species (Craig 1945; Backeberg 1961, 1979; Rauh 1979). However in the majority of studied representatives of *Mammillaria* more than one expression occurred

(Fig. 3, Tab. 1). Phyllotaxis in the seedlings and young plants was represented by lower numbers of parastichies than in the mature cacti, regardless the phyllotactic pattern. Moreover, in many cases an expression of the pattern changed during the further growth of a mature plant. At first, an initial radial expansion of the apex surface is accompanied by simultaneous increasing of the leaf (tubercle) primordium size. This process of cortical thickening of the stem, typical for cacti (Hejniewicz 1985), usually does not introduce changes in an expression of a pattern. Then, mainly in more cylindrical species, changes of the growth parameters occur: further radial expansion of the surface, beginning of the stem elongation, and slower than at the beginning growth of tubercles. Potentially, it could effect in an alteration of contacts between the neighbouring leaf (tubercle) primordia and contribute to continuous transformations of phyllotactic patterns, especially in the intermediate zone between apical and lateral part of the plant. Similar changes of phyllotaxis expressions, originated as consequences of the apex growth, occur in development of seedlings. For example, in ontogeny of *Opuntia polyacantha* the change in the main Fibonacci pattern expression followed the increase of plant size and of the number of vascular sympodia (Gibson 1976).

Fig. 6. The examples of phyllotactic patterns in *Mammillaria* genus.

A. *Mammillaria pseudoscrippsiana* – conspicuous parastichies 12z:19s:31z from the phyllotactic series (1),2,5,7,12,... .

B. *M. droegeana* – a contact parastichy pair 12z:19s from the same series. A pair 8:13 was reported as a typical pattern for A and B species (Backeberg 1961, 1979).

C. *M. centricirra* var. *neumaniana* – the main Fibonacci pattern in expression 13s:21z. Typical expression given in literature is 5:8 (Backeberg 1961, 1979).

D. *M. canelensis* – the Lucas pattern expressed as 7z:11s.

E. *M. lanata* – the main Fibonacci pattern 13s:21z.

F. *M. elegans* – series 1,6,7,13,... expressed by contact parastichies 13z:20s.

● – an areole selected as the marker of the surface.

Fig. 7. The unusual and interesting patterns in *Rebutia* group.

A. *Aylosteria kupperiana* – a pair of contact parastichies 8z:11s which identifies an unusual pattern (1),3,8,11,19,... . The set of 19th parastichies is also conspicuous.

B. *A. kupperiana* – pentajugy of the main Fibonacci pattern expressed by contact parastichies 10z:15s.

C. *Rebutia permutata* – phyllotaxis characterized by a pair of parastichies 10s:17z (at the top).

D. *R. krainziana* (hybrid) – a transformation of the phyllotactic pattern from 11z:13s in the lower part of the plant to 11z:14s. At the top of the plant the sets of parastichies 11z, 14s and 25z are present.

E. *R. krainziana* – a parastichy pair 13z:17s visible in an apical part of the cactus. The course of parastichies is not very regular.

● – an areole selected as the marker of the surface.

Generally, genus *Mammillaria* was characterized by quite narrow range of phyllotaxis diversity, especially within the particular species (Figs 2 and 3). The main Fibonacci pattern, apparently prevailing in studied *Mammillaria*, and only a small percentage of other patterns (mainly Lucas phyllotaxis and bijugy of the main Fibonacci – Fig. 1) generated a phyllotactic spectrum similar to those, which are well known in some gymnosperms (Crafts 1943; Gregory, Romberger 1972; Zagórska-Marek 1985, 1987; Lisiecka 1993) and in some Dicotyledones (Battjes and al. 1993; Jean 1994; Szymanowska-Pulka 1994; Zagórska-Marek 1994). It is important that the expression of the main Fibonacci pattern is dependent on the proportions of the apex and tubercle primordia and can be different even within one specimen.

Results of the present study showed that both: a number of possible expressions within each species of *Mammillaria* and occurring developmental changes of phyllotaxis indicate an insignificance of a pattern expression as a taxonomic feature.

Different from that in *Mammillaria* phyllotactic spectrum occurred in *Rebutia* group (Figs 1 and 5). Enormous diversity, especially in *Aylosteria*, *Mediolobivia* and *Rebutia senilis* (Fig. 4, Tab. 2) and dominance of patterns different from the main Fibonacci was characteristic for many species in this group of plants. It is interesting that all categories of phyllotactic patterns were observed: spiral (in the majority of cases) including multijugies of several patterns and whorled (found only in *Rebutia*). Among the most infrequent and interesting patterns in *Rebutia* group were (1),3,7,10,... and (1),3,8,11,19,..., the existence of which in nature has recently been discussed in literature (Zagórska-Marek 1987, 1994; Jean 1994). The first pattern was quite common in some species of *Rebutia* group (Figs 5 and 7 C, Tab. 2). The second occurred only in one plant of *Aylosteria kupperiana* in an expression 8:11, although the set of 19th parastichies, nearly vertical, was also well seen (Fig. 7 A). Occurrence of this peculiar pattern in other cacti has been earlier reported for *Mammillaria mollihamata* Shurly, where the arrangement of tubercles in 19 and 30 spirals was found (Backeberg 1961, 1979). Other unusual pairs of parastichies appeared mostly in slightly oval apices. Such phyllotaxis might be regarded as aberrant.

Enormous diversity of phyllotaxis in *Rebutia* group (35 different pattern) is most probably genetically determined. Representatives of this group of cacti characterize considerable plasticity in morphological form that possibly expresses genetic variability. Numerous variable forms of *Rebutia krainziana*, often described even as subspecies, probably result from mutational variations (Haude 1988). In another genus of cacti – *Copiapoa*, the high level of genetic variability is proposed to be one of the reasons for rich morphological diversity of spines in mature plants and in seedlings (Kapitany 1996). Some cacti of *Rebutia* group, especially *Mediolobivia* and some species of *Rebutia*, are known as potentially capable to produce hybrids, even between not very closely related forms (Haun 1989). It increases genetic instability of particular species.

In natural populations of cacti in which diversity of morphological traits results from hybridization, plants are enormously variable, especially at the beginning of the hybrid population development. A hybrid combination of features is maintained by vegetative propagation of specimens (Grant, Grant 1980). Polymorphism and geographic distribution of such populations are the basis for differentiating the clonal microspecies from the complex species or within the groups of cacti such as *Opuntia* (Grant, Grant 1980) and *Echinocereus* (Cota, Philbrick 1994). Certainly, these studies refer to different populations of cacti in their natural environment but

they indicate a potential source of variability also in other cactus species. In light of this suggestion it becomes particularly interesting the stability of phyllotaxis in *Mammillaria*. The mechanism responsible for it remains unknown.

The fundamental differences in phyllotaxis between *Mammillaria* genus and *Rebutia* group resemble those found by Zagórska-Marek (1994) for different *Magnolia* species. *Magnolia soulangeana* for instance has stable phyllotaxis whereas in *Magnolia acuminata* phyllotactic patterns vary to extreme. We still know very little about how this different behaviour is determined.

In both groups of investigated cacti diversity of phyllotaxis was independent of the age of plants as shown in Tab. 1. Occurrence of various patterns in seedlings and in young plants, similarly as in mature specimens, suggested that the pattern was directly determined in the early stage of ontogeny and then could be changed only due to transformations. Only genetic predisposition, specific for each species, seems to affect to phyllotactic pattern formation just after germination of the seeds. The mechanism of this process, from the initial stage of cotyledons, is currently investigated by the author of this work. On the other hand it is not unlikely that for cuttings (which in fact often were rooted lateral branches) the phyllotactic pattern and its expression could be affected by phyllotaxis of the main axis as in some conifers such as *Picea* and *Abies* (Lisiecka 1993). The architecture of the vascular system was not investigated during the present study, therefore the question whether a such correlation between the number of vascular sympodia and their distribution in both the main and lateral axes exists will be answered in the future.

Despite the limited number of available specimens representing analysed species, regularities that have been found are beyond any doubt. In the future the other collections and genera of cacti will be studied.

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SPEKTRA FILOTAKSJ KAKTUSÓW: RODZAJ *MAMMILLARIA* I NIEKTÓRE GATUNKI GRUPY *REBUTIA*

STRESZCZENIE

Zbadano wzory filotaktyczne, występujące u kaktusów z rodzaju *Mammillaria* oraz u przedstawicieli rodzajów: *Aylostera*, *Lobivia*, *Mediobolivia*, *Rebutia* i *Sulcorebutia*. Zakres występujących wzorów filotaktycznych był odmienny dla obu grup kaktusów.

W rodzaju *Mammillaria* stwierdzono 14 wzorów, wśród których dominowała filotaksja Fibonacciego (94% wszystkich wzorów). Dla większości gatunków stwierdzono występowanie tylko jednego lub dwóch wzorów. Więcej wzorów (do 6) pojawiało się u tych gatunków, u których często występuje dychotomiczne rozgałęzianie pędów, co oznacza, że dychotomia może być czynnikiem zwiększającym różnorodność filotaksji. Wewnątrzgatunkowe zróżnicowanie wyrażone było pojawianiem się różnych ekspresji wzorów. Dla poszczególnych gatunków *Mammillaria* stwierdzono występowanie kilku ekspresji wzoru Fibonacciego, a także dość częste zmiany ontogenetyczne filotaksji (transformacje ciągłe). Wyniki te wskazują, że pary parastych kontaktowych, podawane w literaturze jako „diagnostyczne” dla gatunków *Mammillaria*, nie mają znaczenia taksonomicznego. Wydaje się, że dla poszczególnych gatunków charakterystyczne jest raczej spektrum filotaksji.

Grupę *Rebutia* charakteryzowała znaczna różnorodność filotaksji (35 różnych wzorów). Dla większości gatunków występowało od 6 do 9 różnych wzorów, wśród których najczęstszymi były bijugia i wzór Fibonacciego. Rzadziej w obrębie gatunku dominowała trijugia, wzór Lucasa lub wzory 1,5,6,... i (1),2,5,7,... Stwierdzono występowanie rzadko spotykanych wzorów filotaktycznych. Do najciekawszych należy kwestionowany przez Jeana (1994) wzór o liczbach parastych 8:11 tworzących ciąg (1),3,8,11,..., znaleziony u *Aylostera kupperiana*. Różnorodność filotaksji charakteryzująca gatunki z grupy *Rebutia* może mieć genetyczne podstawy. Wobec znacznej zmienności wzorów w grupie *Rebutia* ciekawym staje się poznanie mechanizmów decydujących o różnorodności lub względnej stałości (jak u *Mammillaria*) wzorów filotaksji.

SŁOWA KLUCZOWE: *Mammillaria*, *Rebutia*, kaktusy, wzory filotaktyczne.