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Mirror Symmetry of Life

Beata Zagórska-Marek

Abstract

Functioning in the Earth gravity field imposes on living organisms a necessity to read directions. The characteristic feature of their bodies, regardless unicellular or multicellular, is axial symmetry. The development of body plan orchestrated by spatiotemporal changes in gene expression patterns is based on formation of the vertical and radial axes. Especially for immobile plants, anchored to the substrate, vertical axis is primary and most important. But also in animals the primary is the axis, which defines the anterior and posterior pole of the embryo. There are many little known chiral processes and structures that are left- or right oriented with respect to this axis. Recent developments indicate the role of intrinsic cell chirality that determines the direction of developmental chiral processes in living organisms. The still enigmatic events in cambia of trees and handedness of phyllotaxis as well as plant living crystals are in focus of the chapter.

Keywords: intrinsic cell chirality, charophytes, cambium, morphogenesis, figured wood, plant development, phyllotaxis, shoot apical meristem, snail shells, handedness, dislocations

> *I see the mirror fairy tale of infinite reflections spinning out to weave no end....*
> *Bolesław Leśmian "Prolog"*

1. Introduction

Polarized environment, from the beginning of life on our planet, imposes on living organisms a necessity to read directions. Light and gravity are the two most important oriented signals that come from well-defined sources. The response to these primary polar signals allowed for development of the secondary, more sophisticated reactions to the network of other polar signals like gradients of chemical molecules or mechanical stresses. The signals of chemical and physical nature provide the extrinsic but also an intrinsic information for biological systems.

One of the basic features of the organism developing in polar environment is its axiality. This brings in consequence following possibilities: 1) multiplication of repetitive units of the body and their special alignment along the axis (segmentation, metamerism) and 2) deviations of structures from the axis to the left or to the right (development of L/R symmetry).

The main axis in the motionless plants, fastened to the ground, is mostly vertical, extending between the apical and basal poles. The animal main axis, regardless its position in the gravity field, connects the anterior and posterior poles. The axis

formation starts at the very early stages of development. The identity of segments formed iteratively along the axis in both plants and animals is genetically controlled and their evolutionary multiplication creates a great potential for morphological and functional diversity through many useful modifications. This process is in a sense similar to the effects of gene duplication on the molecular level.

Subsequent emergence of L/R symmetry may be observed on all, hierarchically different levels of body organization. Some general principles, like minimum energy rule, are universal in nature leading to the identical solutions on all these levels. Good example represent spherical geodesic shapes. The structure of carbon allotrope - C_{60} closed fullerene, is also present in coated endocytic vesicles reinforced by the clathrin cage [1], in regularly sculptured surface of pollen grains [2] and in a cellular pattern on the surface of the plant paraboloid apical meristem [3].

Other universal basic forms are chiral helices and spirals commonly observed on molecular, cellular and organismal levels. They are of particular interest here because of distinct mirror symmetry they have, which is the main focus of this chapter. Chirality of many macromolecules: nucleic acids, proteins or cellulose fibers [4], coiled coils of collagen, or such structures as tubulin cytoskeleton, thickenings of plant cell wall, plant tendrils, spiral snail shells or narwhal tusks are but a few examples. Not only structures but also some developmental processes may be chiral. The apical cell divisions in moss gametophores [5], cell cleavage in the embryos of snails [6, 7] or lateral organ initiation on plant shoot apical meristem (SAM) proceed clockwise (CW) or counterclockwise (CCW). Two interesting problems may be addressed while considering chiral structures in biological systems – mechanism of their formation and proportion between the two chiral configurations.

The aim of this chapter is to provide the readers with the overview of some examples of bio-chirality discovered over the years both in animals and plants. The stronger accent will be placed on the latter because they are less known and because they have always been in a focus of the author's research. The mechanisms of many cases of mirror-symmetry presence in plants are yet to be elucidated.

2. Mirror symmetry on cellular level

Cell chirality or handedness is a newly discovered phenomenon, which nowadays is intensely studied, mostly in animal cells [7–10]. It is manifested in the presence of chiral structures within the cells but also in the cell behavior that may lead to directional movements or assuming L or R orientation of cell alignment. In animals it affects organs laterality [10], in plants results in development of spiral, helical or wavy patterns [3, 11–15].

During primary axis formation on the cellular level the polarity of the cell is manifested in an uneven distribution of receptors, ion channels and hormone carriers on plasma membrane, and internally in the ion currents and cytoskeletal fibers parallel to the developing axis but also in the polar distribution of ultrastructural components like cell organelles or nutrients. All these sophisticated processes have been investigated mainly in plant egg cells or fucoid zygotes [16–18] and animal oocytes [19, 20]. However, even in the integrated system of multicellular organism, singular cell polarity is often a case. In animal body the epithelial cells of intestines constituting a planar 2D barrier, have their polarity unified. It is manifested in nonrandom distribution of glucose transporters which facilitates the oriented transepithelial sugar transport [21]. In plants the polar distribution of the auxin influx (AUX) and efflux (PIN) carriers in plasma membrane results in polar transport of the hormone between the cells [22]. In L1 layer of SAM auxin is transported

acropetally, whereas inside of the plant body, in the provascular tissues and later in cambium, the hormone transport is basipetal. Change in the distribution of carriers and thus of the cell polarity redirects the transport, often affecting the directions of plant organ growth [23]. This, for instance, has been noted in gravitropic response of the roots [24].

Many elements of the cell ultrastructure are spectacularly chiral. In some green algae exemplified by multicellular filamentous *Spirogyra* or unicellular *Spirotaenia* and *Chlamydomonas spirogyroides* the chloroplasts are of considerable length, flat and ribbon-like. They assume helical course in the cortical cytoplasm of the cell. Not much is known about the chiral configurations of their coiling. Images available in various data bases suggest that in *Spirogyra* both configurations may be present in different filaments [25], in different cells of the same filament or even within the same cell [26]. However, the error resulting from improper focusing during microscopic observations cannot be excluded. The sample taken for analysis from the aquarium of the Botanical Garden of Wrocław showed under light microscope hundreds of cells of the same S configuration of chloroplasts coiling from the right to the left (**Figure 1**). Mechanisms by which the configuration is regulated remain undiscovered.

Another clearly chiral component of the cell is basal body. In eukaryotic, plant and animal cells some identical structures bear different names although they look the same. Two centrioles of the centrosome, basal bodies or kinetosomes in the motile or ciliary epithelial cells have the same architecture. Composed of 9 triplets of microtubules (MT), overlapping on all available images either CW or CCW, they resemble a pinwheel toy. It is unclear, however, whether both configurations, being a mirror-image of one another, are indeed present in all different types of the cells. Transmission electron micrographs (TEM) of tangentially sectioned cell surface show that in a particular cell all basal bodies underlying cilia are of the same chirality [27]. However, unless it is clearly stated like in [28], it is not known whether
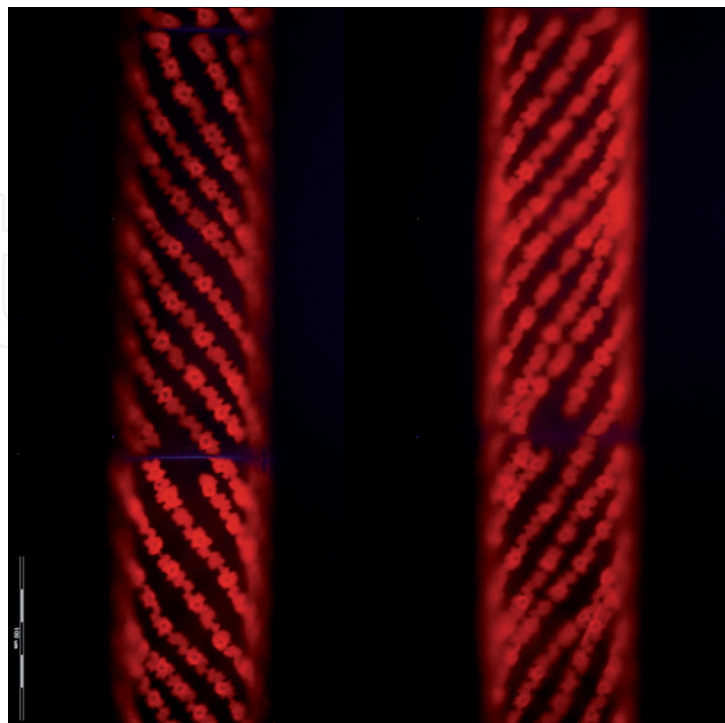

Figure 1.
The same filament of Spirogyra *photographed under fluorescent microscope at different optical levels: at its upper surface (left) and well below, close to its opposite side (right). S helix of the chloroplast, visualized here by the red autofuorescence of chlorophyll, may be falsely interpreted as Z, when due to the changing focus is watched from the inside of the cell.*

basal body is seen on TEM from the surface of the cell or from its inside. This is the reason for chiral configurations of basal bodies being uncertain. The image of *Paramaecium micronucleatum* by Dennis Kunkel [27] shows CCW overlapping triplets, whereas in *Paramecium tetraurelia* [29] the triplets overlap CW.

In flagellar apparatus of *Chlamydomonas* or *Acrosiphonia* gamete both chiral configurations of basal bodies are present on the same electron micrograph [30, 31] but in these cases it is certainly an effect of opposite orientation of flagella and their two basal bodies facing each other horizontally. The bodies are in fact of the same chirality. This case shows again how careful one must be analyzing and interpreting the examples of mirror-symmetry of the chiral ultrastructural components of the cell on TEM images, that can be easily flipped and show the same structure either from above or from the bottom side. There is one additional aspect of mirror symmetry presence in the locomotion apparatus of green algae. The flagellar roots of the two basal bodies are slightly rotated one with respect to the other – CW in representatives of Chlorophyceae and CCW in Ulvophyceae [30, 32, 33]. This finding, among the others, was the foundation of the profound revision of green algae taxonomy [30, 33].

The process of cilia beating is chiral. Both ciliates, motile spermatozoids and stationary epithelial cells readily change the direction of cilia movement either to navigate or alter the current of surrounding fluids [34]. Interestingly, the latter has been employed by unicellular *Stentor rosei*, to avoid, in quite deliberate and calculated manner, the irritating particles experimentally added to the medium [35]. The cell, however, is not always in full control over the cilia beating. The doublets of some ciliates, having notably the same chirality of basal bodies, show that in the form being a mirror image of the typical one, food particles are expelled from the oral apparatus instead of being directed towards it [28]. Typical chiral form of *Paramecium* swims forward employing leftward rotation. Stressful conditions like low temperature or heavy metals force the ciliate to spin in opposite direction [36].

Among fibrillar elements constituting cytoskeleton, a tensegral structure of eukaryotic cytoplasm it is actin microfilament (MF) that is chiral. Mammalian cells exhibit specific, actin dependent L/R asymmetry which is different in normal and cancerous cells and changes when inhibitors of actin function are applied [37]. In bacteria changeable chirality of actin homologs MreB has impact on their growth and cell shape [38]. Actin is also responsible for directional, chiral movement of cytoplasm in the cells of charophytes [39]. Another important component of cytoskeleton, MTs. *per se* are not chiral. However, their arrangement in the cortical cytoplasm, beneath plasma membrane, is often oriented in plant cells (**Figure 2**). The elongating cells in the axial organs of the model plant *Arabidopsis thaliana* apparently have the chirality of their cortical cytoskeleton genetically controlled. In *spiral 1* and *spiral 2* mutants the cortical MTs, watched from the cell surface, form an ascending S helix, whereas in *lefty* mutant the helix is Z. The mutations lead to abnormal growth of the plant axial organs which, strangely enough, become twisted oppositely to the configuration of MT helix in their cells – Z in the *spiral*, S in the *lefty* mutants [40–42].

Configuration of cortical cytoskeleton, below plasma membrane, in some differentiating plant cells may change with time causing the development of interlocked pattern of the cellulose microfibrils deposited in the secondary wall [43]. Both chiral systems: intracellular and extracellular, parallel each other in consecutive stages of the secondary cell wall formation. The cycle of changes in microfibrils orientation always starts from the ascending S helix in S1 layer of the secondary wall (watched from the outside of the cell), it alters to Z in the S2 layer and returns to S helix in the S3 layer. No exception from this rule has been found
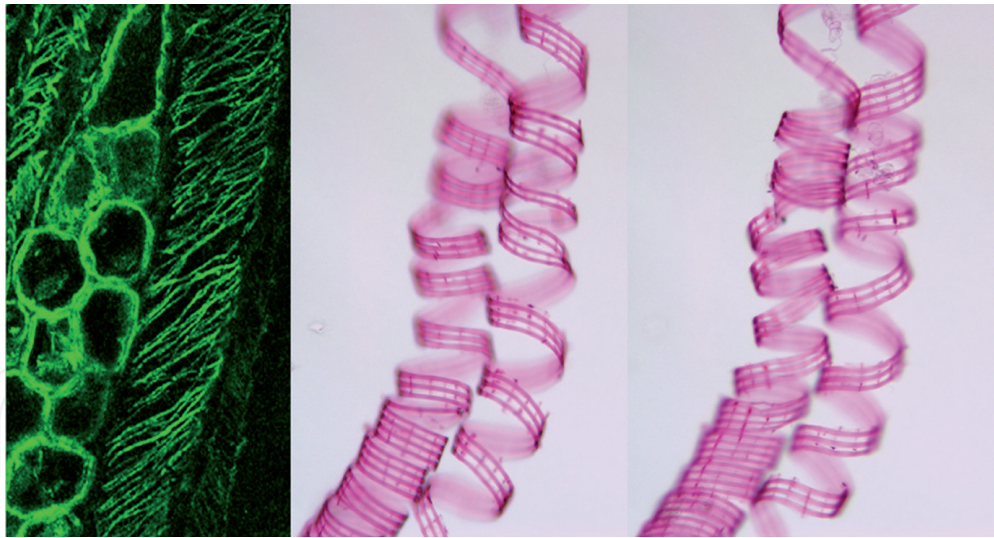
Figure 2.
Immunofluorescent visualization of Z helical cortical cytoskeleton in the elongated cambial cell of Cinnamomum camphora *(left) and two S helices of the secondary cell wall thickenings isolated from the protoxylem cells of* Scindapsus *sp. photographed at two different optical levels. The middle photo shows the surface of the thickenings seen from their outside.*

even though, at least theoretically, the opposite sequence of changes in microfibrils orientation is possible. Moreover, the cycle of changes in the chirality of microfibrillar helix appears to be independent of the overall orientation of the differentiating cell within figured wood, which also exhibits L/R symmetry [44]. This astounding regularity points to existence of yet undiscovered mechanism that must precisely regulate the phases sequence in the full cycle of changes in the cortical MTs orientation. Must be also independent of the other, hypothetical one, which controls L/R symmetry of cambial cellular events such as oriented anticlinal divisions and intrusive growth. This assumption is supported even further by the S helix of the secondary wall thickenings in differentiating protoxylem. The first, S1 deposit of this wall, not yet completely covering the primary wall surface prevents the cells, exposed to mechanical stress caused by longitudinal expansion of growing shoot, from breaking (**Figure 2**).

The discovery of cell intrinsic chirality resulted from the fundamental question how the laterality of organs within the animal body is accomplished. Over the years much attention has been paid to this phenomenon and its connection with the development of L/R symmetry of the whole multicellular organism. It was found that blood neutrophiles polarity, defined by position of centrosomes with regard to the cell nucleus, makes them capable of directional movements in absence of polar external signals. This property disappears after application of drugs affecting MT function [45].

The model invertebrate organism *Drosophila melanogaster* provided evidence that myosin encoding gene mutation switches cell chirality and results in the development of *situs inversus* phenotype of the hindguts or genitalia [7, 8, 10, 46]. In vertebrates the development of typical L/R asymmetry from anteceding state of embryo bilateral symmetry is generated by various mechanisms. One of them is based on function Ɩ of axonemal dynein. This motor-protein is responsible for appropriate beating of cilia in nodal epithelial cells, causing the directed ion current. Defects in the gene structure encoding for the dynein results in random selection of heart position in mouse embryo [47]. The involvement of C kinase signaling pathway in the reversal of cells chirality leading to mirrored position of heart was recently shown in chicken embryos [48].

All the above studies show how intrinsic cell polarity may be translated onto the higher level of multicellular organism organization in animals. Very little though is known about L/R symmetry regulation in multicellular plant organisms.

3. Chiral processes and structures in multicellular organisms

The axiality of multicellular organism is similar to the polarity of a single cell but on hierarchically higher level of organization. The first evolutionarily step towards axiality of the integrated biological system composed of many cells represent 1D filaments of cyanobacteria, eukaryotic algae and fungi or moss protonemata. Higher plants maintain this ancestral condition as a kind of atavistic trait at the embryonic stage of their development - linear suspensor, which originates from the basal cell of already polarized and divided zygote, transports nutrients to the 3D globular embryo, developing from the apical cell [18]. Many forms of animals with such model organisms as tiny worm *Coenorhabditis elegans* [49] or fruit fly *Drosophila melanogaster* and finally ourselves, exhibit axiality, metamerism and L/R symmetry.

In this section the short survey of the most interesting cases of mirror symmetry in multicellular plants and animals will be made and the mechanisms that stay behind them will be discussed.

3.1 Changing chirality in the thalli of charophytes

Architecture of these green algae resembles that of the horsetails. The thallus of *Chara* is composed of the giant internodal cells typically enveloped by the sheet of cortical cells, which take an origin from the adjacent nodal cells. From the nodes the 1-st order branchlets grow out horizontally, on which the reproductive structures are positioned: ovaloid oogonia and spherical antheridia. They may be treated as the 2-nd order axial outgrowths of the branching thallus. The peculiar, to date unexplained transition takes place from the Z orientation of enveloping cortical cells in the main axis of the thallus, through their mostly parallel alignment in the branchlets, to the S orientation in oogonia (**Figure 3**). The developmental sequence of these changes in the chiral structure of extant *Chara* species is always the same, although gyrogonites (fossilized oogonia) of charophytes show that in the late Devonian period the right-handed (Z) oogonia were also present. They belonged to the charophyte family Trochiliscaceae and got extinct with the onset of Mesozoic
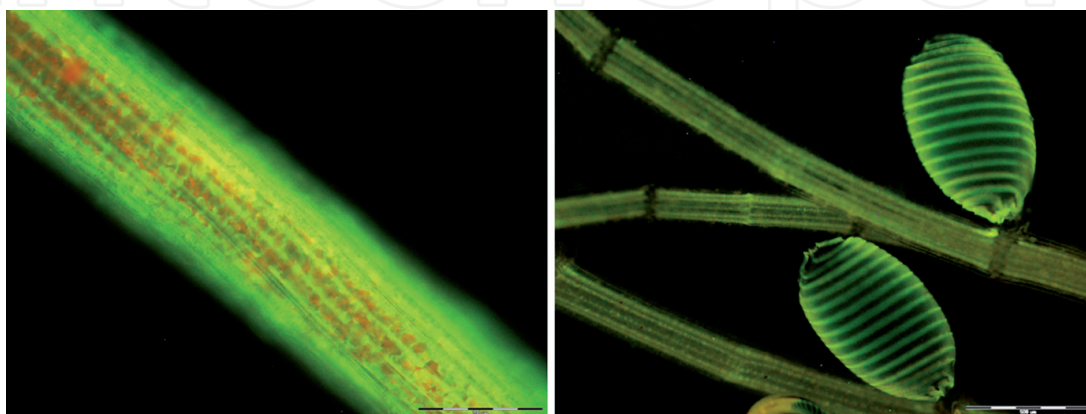

Figure 3.
Details of Chara *sp. thallus architecture. Left photo shows the main axis covered by Z oriented cortical cells; on the right photo two S chiral oogonia sit on the branchlets enveloped by the cortical cells, which run parallel to their axes.*

era [50–52]. We will probably never know if they had the same sequence of chiral changes, but *in reverso*, like the extant *Chara* branching thalli.

The cortical cells of *Chara* parallel orientation of the cytoplasmic streaming in the central internodal cell they envelop. How do they read this direction? How is this information translated from the interface between ecto- and endoplasm, where the cellular engine of cyclosis is located [39, 53, 54], to the surface of the cell wall, on which the enveloping cells slide? Finally, how and why does it change in the *Chara* branching system, from the right in the main axis to the left in oogonia? Is actin – motor protein involved? Actin microfilaments must then have orientation of their alignment determined by the position of the cell in branching thallus. How? These problems remain unresolved.

3.2 Oriented cell divisions in apical cells of mosses and ferns

The control over orientation of the cell division plane is of particular importance in plant tissues. Plant protoplasts are "imprisoned" within the boxes of their cell walls. They cannot migrate as freely as do the animal cells during embryonic stages of ontogenetic development. Morphogenesis of plants relies entirely on the properly oriented cell divisions.

In the simple multicellular filaments of green algae we encounter for the first time the manifestation of L/R symmetry. The plane of cell divisions may be inclined relative to the filament axis either to the left or to the right as exemplified by the filamentous green alga *Coleochaete nitellarum* [55]. Also in planar (2D) gameto-phytes of ferns the pyramidal apical cell (AC) with rectangular base divides alter-nately to the left and to the right in a regular sequence (**Figure 4**).

Precision in controlling chiral configuration of cell divisions is even more striking in 3D leafy gametophores of mosses. Their tetrahedral AC, watched from its triangular base, divides either CW or CCW and this direction is randomly established in the development of the gametophore main axis. However, it is not so in the case of its lateral branches – the chirality of their AC is always opposite to that of the supporting axis [5]. It is possible that this antidromic correlation trig-gers the horizontal gradient of some putative signals vertically transported from the neighboring leaves of gametophore (**Figure 5**). Two genes of the model moss *Physcomitrella patens* were identified to be engaged in a process of cell divisions in leafy gametophore: *PpTONE1* controlling intracellular organization of MT cyto-skeleton and *PpNOG1* assuring proper development of AC [56, 57].
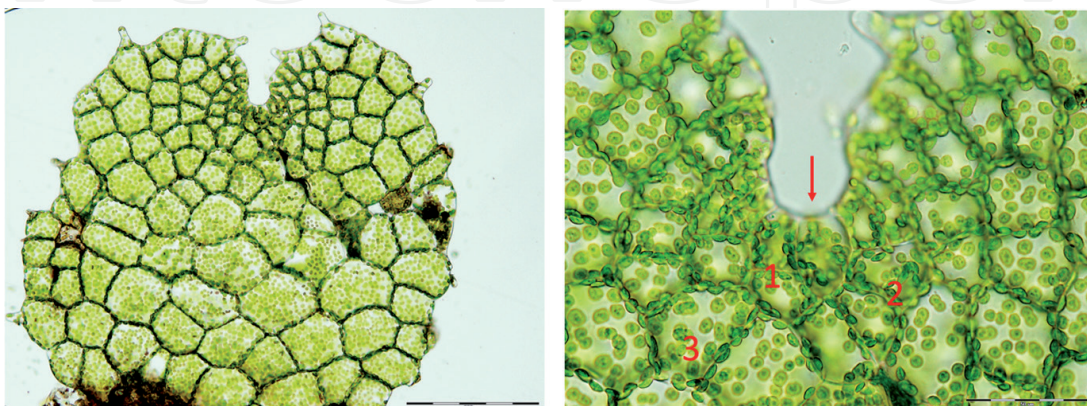

Figure 4.
Typically heart shaped fern gametophyte. This planar structure develops due to activity of AC (red arrow) located atop of its symmetry axis and cleaving derivatives alternately to the left and to the right. On the right photo they are numbered decreasingly.
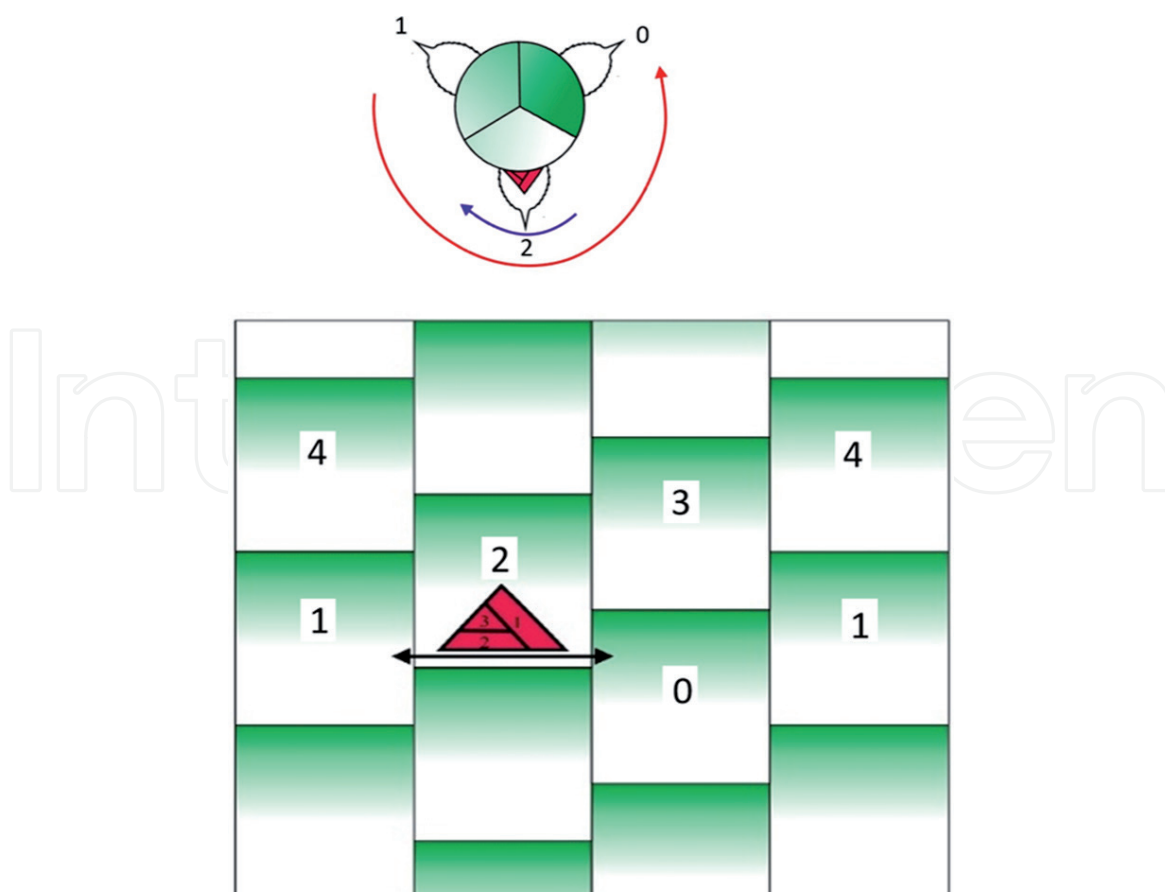
Figure 5.
Scheme of the split open surface of cylindrical moss leafy gametophore. It explains horizontal gradient of the hypothetical signal (green) originating from the leaf segments cleaved CCW (upper red arrow) by the tetrahedral AC of the main axis. The lateral branch AC (red), reading the gradient, starts cleaving its segments CW (upper blue arrow). Main axis segments are numbered increasingly.

3.3 "Music of trees"

Anticlinal, pseudotransverse divisions of elongated stem cells in cambium, cylindrical meristem located in trees between the outer bark and the inner secondary xylem, are chiral. Their partitions, while watched from outside of the tree, are inclined to the right (Z divisions) or to the left (S divisions). Cambium therefore is a plant tissue that exhibits clear L/R symmetry. Also subsequent growth of the cells shortened by the divisions is oriented. Cambial cellular events are not randomly distributed over the surface of the meristem but orderly segregated into domains of opposite chirality. The S and Z domains alternate along the vertical axis of the cambial cylinder [58, 59]. This leads to emergence of structural waviness within which the cells assume alternately the opposite S and Z orientation. Because cambial structure is replicated every year in the annual wood increment, the history of all these developmental changes is recorded in the wood and may be extracted for the periods equaling the age of a tree. The domain pattern and resulting structural waviness are propagated vertically in cambium thus the cells in a particular location undergo the cycle of inclination change (**Figure 6**). This barely known biological rhythm is the longest in nature. Its period approximates 20 years although in some cases may be shorter. Theoretical model predicts that propagation of cell oscillations associated with the domain pattern motion may lead to development of the spiral grain in a tree trunk [14]. Handedness of the spiral grain should depend, according to the model, on the nature of the wave front i.e. the direction of the first change in stem cells inclination during the initial period (**Figure 7**).

Neither the molecular mechanisms, nor the nature of domain positional information for dividing and growing cells have been elucidated so far. The first suspect

Figure 6.
Scheme of the relationship between hypothetical cambial morphogenetic wave and the domain pattern composed of S (blue) and Z (red) domains. They lead to development of wavy cambium and subsequently to wavy wood. (A) Tangential face of the beech wood, (B) radial split face of the oak wood showing dynamics of the wavy pattern: inclined ripples indicate upward movement of the structural waviness in cambium - bark is on the right side of the photo.
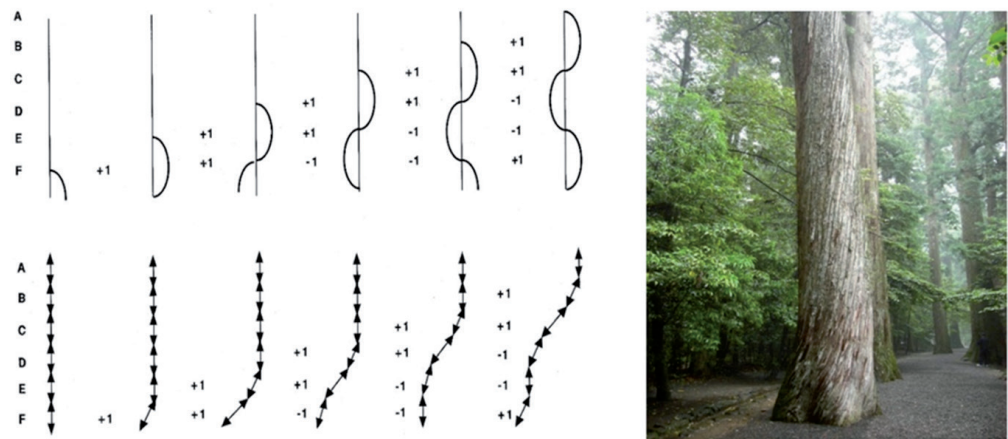

Figure 7.
Scheme explaining how morphogenetic wave propagated upward and exciting oscillations of cambial cells may lead to development of spiral grain in such trees as majestic sugi tree (Cryptomeria japonica) *on the right photo.*

is the polar auxin transport changing directions due to redistribution of the hormone carriers in plasma membrane of cambial stem cells. The intrinsic cell chirality resulting from unknown nature of the intracellular oscillator cannot be excluded. In one tree more than one domain pattern may be present – they usually differ in the domain size and propagation velocity. According to the hypothesis put forward by their discoverer, the domain patterns result from morphogenetic waves traveling in the tissue and capable of superposition [59]. This means that the trees play silent music, the beauty of which is mostly unknown even to the scientists.

3.4 Twinning vines

The helical growth of plant organs is not uncommon [15]. Some plants developed quite effective strategy to grow quickly towards the light source relying on the support, provided sometimes even by another plant. This way they do not have to spend too much energy for building sturdy skeleton composed of mechanical tissues. Finding support is possible thanks to circumnutation of the shoot tip, caused by differential growth along the circumference [60]. Some vines are heterochiral, i.e. capable of twinning CW and CCW. Around 90% of the homochiral species twirl CCW [61, 62] but in some genera the direction of twinning is a

species specific trait. *Wisteria sinensis* and Japanese *Wisteria floribunda,* both the attractive ornamental vines, are opposite in this respect. Darwin, who was very interested in twinning plants and made observations on *W. sinensis* stated: "*I have seen no instance of two species of the same genus twinning in opposite directions, and such cases must be rare*" [61]. He could say so because in his times Japanese *Wisteria* has not yet been introduced to England.

The confusing descriptions of *Wisteria* in botanical literature [63] show clearly that there is a certain problem with definition of a chiral configuration of structures or processes with mirror symmetry in biological systems. *W. sinensis* ascending shoot twins CW when looked at from its base and CCW when looked at from above. The same configuration of this plant twining, in some sources is claimed to be CCW [64] in others CW [65]. In Darwin's words the plant "*moves against the sun*" [61]. Compton and Lack [63] claim that *W. floribunda:*" ... has climbing woody stems twining from left to right...", which should not be if it is truly opposite to *W. sinensis*. It all shows the importance of clear convention how the chiral configuration is determined. Moving along the S helix upward is a CW motion whereas descending along the same line we move CCW. While looked at from outside the *W. sinensis* twins from the left to right (Z configuration). It is opposite (S configuration) when looked at from the inside of the growing shoot's helical structure. The same necessity of defining chiral configuration according to specific convention applies to the cellulose microfibrils rotated in the layers of the plant cell secondary wall, to the spiral grain in a tree trunk or to the cells enveloping charophyte oogonia. It seems that definition of the helix chiral configuration, looked at from its outside, as being S or Z is the most reasonable and unequivocal.

Molecular mechanism responsible for the direction of plant climbers twinning is not known. The results of the studies on the *lefty* and *spiral* mutants of the model plant *Arabidopsis thaliana* [40–42] suggest the involvement of the genetic factor. It is possible that the species specific behavior depends on distinct and constitutive gene expression patterns established differently for each species.

3.5 Aestivation

The petal folding in a flower bud, in most of the flowering plants, is clearly chiral. Petals overlap either CCW or CW and this chiral configuration is often later maintained in fully developed flower (**Figure 8**). The direction of petals

Figure 8.
The chiral CW folding (aestivation) of petals in Hawaiian plumeria's flower bud (left) is maintained in a pinwheel-like corolla of an open flower (right).

folding may be, like in the case of circumnutation, the species specific trait. For instance, *Anagallis arvensis* petals always twist CCW, whereas in Hawaiian plumerias they do it otherwise. Common European weed *Malva neglecta* in turn is heterochiral, capable of producing CW and CCW buds on the same individual plant.

3.6 Phyllotaxis

Among best known chiral phenomena and investigated since the ancient times [66] is helical phyllotaxis – the regular distribution of lateral organs such as leaves or flowers on a plant shoot. Their consecutive primordia, circumferentially equidistant, emerge on the vertically growing shoot apex in the regular intervals. The primordia may be connected with an imaginary line called ontogenetic helix. The helix S or Z configuration depends on whether the process of primordia initiation proceeds CW or CCW. The plantlets growing from seeds have this configuration established at random in the main axis. It is not so, however, in the axes of lateral branches. Their ontogenetic helix may be either concordant (a homodromy case) or discordant (an antidromy case) with that of the supporting axis. It has been found, that even when both phyllotactic correlations occur with the same frequency [67] the supporting axis and the laterals may have the same chirality of vascular sympodia - elements of the internal transport system strongly related to phyllotaxis (**Figure 9**).

The sympodia follow the course of one set of superficial secondary helices - phyllotactic prastichies. Two sets of parastichies running in opposite directions constitute a phyllotactic lattice. This is why even when ontogenetic helices in two axes making up one branching unit are discordant, the axes still may be concordant on the level of their vasculature. The numbers of parastichies in the sets of opposite chiral configuration belong to the mathematical series, the quality of which is associated with the size of circumferential distance between successive primordia. This distance, usually given in an angular measure, is known as divergence angle. The most common is the main Fibonacci series (1,1,2,3,5,8,13...) present in the system with the divergence angle approximating 137,5 degrees or Lucas series (1,3,4,7,11 ...) with the angle close to 99,5 degrees. There are also many other divergencies and phyllotactic patterns [68].
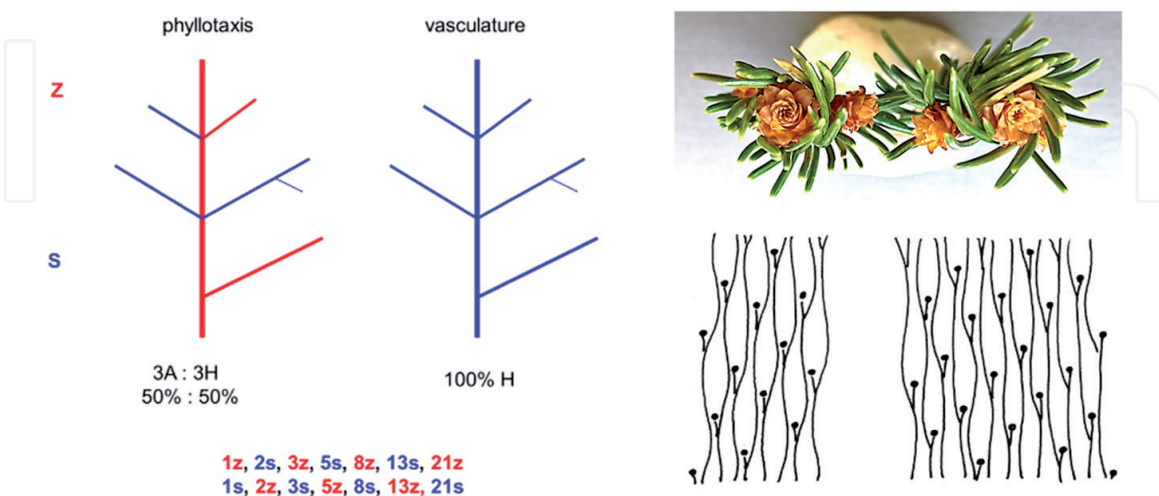

phyllotaxis vasculature

Z

S

3A : 3H   100% H
50% : 50%

1z, 2s, 3z, 5s, 8z, 13s, 21z
1s, 2z, 3s, 5z, 8s, 13z, 21s

Figure 9.
Scheme on the left shows how, in the laterals of one coniferous branching shoot, ontogenetic helix may be either S (blue) or Z (red) but orientation of vascular sympodia the same in the whole system. The sympodia chiral configuration depends on their number, which is one of the mathematical series shown below the scheme. H- homodromic, A - antidromic correlations of chiral configurations. Upper right photo shows the righthanded and lefthanded whirls of needles in two coniferous shoots with the same S Fibonacci phyllotaxis. Their opposite chiral configurations, resulting likely from growing shoot rotation, are caused by the different sympodia numbers and orientations shown below.
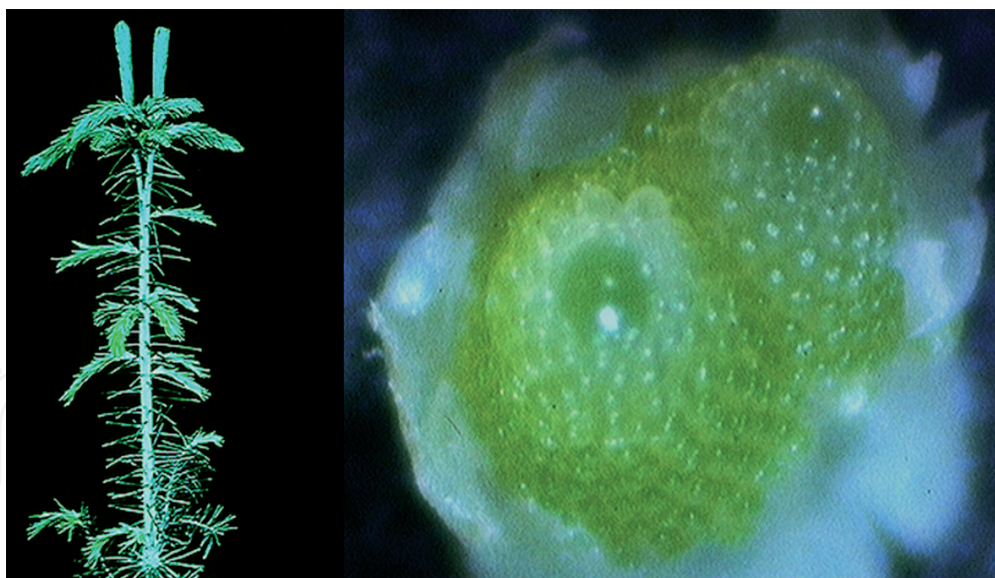
Figure 10.
*Shoot apical meristems isolated from winter buds of balsam fir (*Abies balsamea*) are truly green living crystals. The needle primordia are tightly packed on their lateral surface resembling crystal lattice. The unique case shown here illustrates the atavistic trait of dichotomy, rare in otherwise strictly monopodial conifer.*

Asymmetry of phyllotactic lattice with regard to the shoot axis is most probably responsible for the peculiar twirling of needles frequently seen on the top of coniferous shoot (**Figure 9**). The chirality of these twirls results likely from the growing shoot torsion and is rather related to the orientation of vascular sympodia than to the chiral configuration of ontogenetic helix.

Regularity of primordia initiation resembles crystal growth. The plant apical meristem where the primordia are tightly packed may be called by *licentia poetica*, a living crystal [69] (**Figure 10**). The similarity has been strengthened by the discovery that in phyllotactic lattices dislocations occur [68–70]. Single dislocation often changes not only a quality of the pattern but, most importantly, the chirality of ontogenetic helix (**Figure 11**).

3.7 Snail shell, narwhal tooth and ourselves

Chirality of spiral snail shells has intrigued the scientists for centuries not less than the regularity of phyllotaxis. One of the memorable episodes from the Jules Verne's
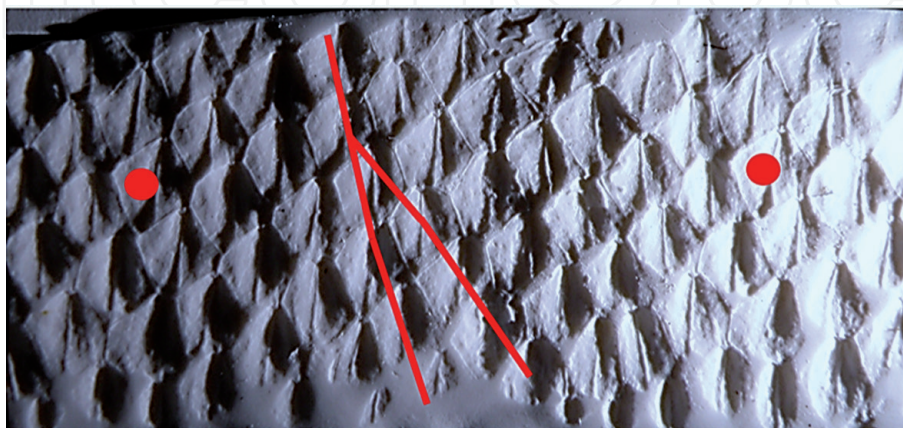

Figure 11.
Modeling clay replica of magnolia's reproductive shoot shows single dislocation (red lines) in the phyllotactic lattice. This developmental event changes here not only the phyllotactic pattern but also the chiral configuration of ontogenetic helix. Red dots label the same pattern element replicated twice on both sides of the unrolled surface of the shoot; it enables counting the numbers of parastichies in two opposite sets; the numbers change from 5:9 to 5:8.

famous novel *Twenty Thousand Leagues Under the Seas* tells the story of Professor Aronnaux finding the extreme rarity – lefthanded shell of the olive snail. It is known to malacologists that approximately 90% of all gastropods have their shells righthanded – of Z type. However, there are snails like *Amhidromus inversus* that have dextral and sinistral shells equally frequent, or like *Neptunea angulata* where the shells are exclusively sinistral. Notably the Z shell grows as the descending spiral, coiling from the top downward. Therefore moving downward the dextral spiral of the shell we execute CW motion not CCW as it would be in the case of ascending helices of plant structures.

The direction of the shell coiling is initiated in the embryo by the spiral cell cleavage typical for lower Metazoa including snails. At this stage there is a possibility of altering the normal pattern and forcing experimentally the development of opposite chirality. The genetic mechanisms determining the chirality patterning in snails are slowly being unraveled through studying specific gene expression patterns in wild type organisms and mutants [71, 72].

However, the reason for a change in a frequency of shell chiral configuration among individuals within a population sometimes can be truly surprising. It was found that among small, properly righthanded *Satsuma* snails the opposite, lefthanded individuals started growing in number. Thorough studies revealed that it was due to activity of predators [73]. The snakes *(Pareas iwasakii)* with their asymmetric jaws, preferably eating the righthanded snails, decimated their population. Through the selective elimination of these snails from the initial population, the snakes contributed to the prevalence of rare lefthanded snails. The divergence of the initial population led to development of a new species. What a wonderful example of Darwinian selection!

In contrast to the snails equipped with molecular mechanism allowing for development of S or Z shells another famous chiral structure in animal kingdom, the narwhal tusk exhibits always a lefthanded spiral (S). It is so even in a case of both tusks being fully developed in one individual, which is rare. The opposite spiral is perhaps also possible as shows the walking stick used by Darwin displayed in the collections of Science Museum, UK [74]. Either the material it is made of is not a narwhal tusk or Darwin, who was very interested in cases of mirror-symmetry in nature [61], consciously adopted and used this particular object being aware of its uniqueness. The third, least probable possibility is that the artist carved the right spiral from the polished left spiral of the narwhal tusk. The reason for the prevalence of one chiral configuration in spiraling of the narwhal tusks is unknown.

L/R symmetry of our body is best illustrated by asymmetry of the internal organ positions like heart or liver. It is our hands, however, that are most frequently presented as an example of mirror symmetry. Less known aspect of the symmetry in a human body is the hair whorl resembling, with all due proportion, the twirling needles in coniferous shoot (**Figure 9**). There is a dispute over significance of the observation that the righthanded people have more frequently their hair twirling CW on the top of their heads. Half of the lefthanded people have in turn the CCW hair whorls. Until now the search for possible common, genetic etiology of these chiral phenomena has been unsuccessful [75]. There is also unknown whether the scalp hair whorl chirality is concordant or discordant with the smaller whorls of minute hair covering our whole body. These become visible, especially in children, when their skin is suntanned.

4. Conclusion

There is no one universal mechanism that stays behind the mirror symmetry of life. The frequency of both chiral configurations is not the same in different biological systems. However, as it has been discussed here, it was not always assessed

carefully enough by investigators. *Spirogyra* case is uncertain. The narwhal tusks are probably always S-helical. On the contrary the shell coiling in most of the snails is of Z type. In many systems the chiral configuration of structures or processes is strictly controlled, in many others the control is loose or absent, which results in equal frequency of both S and Z forms.

In light of the newly discovered intrinsic cell chirality in animal cells we have now a great perspective of disentangling the ultracellular and molecular basis for the dynamic wavy and spiral patterns developing in cambia of trees - one of the most intriguing and least known biological rhythms. Discovered and thoroughly characterized by Hejnowicz and his followers in the last decades of past century it still remains a great mystery. Neither the nature of specific positional signals coming from the dynamic morphogenetic field to the cambial stem cells nor the mechanism of their response i.e. S or Z oriented cell divisions on the cylindrical surface of this embryonic tissue, have been elucidated. The tissue is also intriguing because of its structure. It may be compared to that of the liquid crystals – the elongated cambial stem cells may be aligned in the regular horizontal tiers, like the molecules in the smectic phase of the liquid crystal, or irregularly but parallel to the vertical axis, like in the nematic phase. The oscillating cambial cells taken together with their derivatives, continuously rotated in the successive wood layers, resemble the third, cholesteric phase of the liquid crystal [76].

Biomechanics of structures based on the possibility of changing chiral configurations, clearly the adaptive trait, cannot be underestimated. The resulting interlocked systems provide high resistance to mechanical stress. Interlocked are the cellulose microfibrils in the successive layers of the secondary cell wall in a single cell and, on the macroscale, the oppositely oriented wood fibers in the packets of consecutive wood increments of such giants as mahogany or camphor trees. Also the system of cortical resin canals in the young coniferous shoots, which runs oppositely to oriented vascular sympodia strengthens the axis mechanically.

These examples together with the crystalline character of phyllotactic patterns and cambial cells arrangements bring us back to already mentioned, at the beginning of this chapter, universality of some solutions based last but not least on the presence of mirror symmetry of life.

Acknowledgements

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