Ever since Darwin: Why plants are important for evo-devo research

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Abstract

In this essay, I provide examples of: (i) the presence of fractal properties and a continuum of forms in living organisms; (ii) the potential contributions of plant evo-devo towards a general theory of development encompassing various multicellular organisms; (iii) the "arrival" of a wealth of forms in plants that cannot be explained by natural selection alone. As elucidated by evo-devo studies, evolutionary diversification is also due to, e.g., (epi)genetics, correlation, phenotypic integration, self-organization, and physical constraints. Four kinds of phyllotaxis patterns in vascular plants – from Fibonacci systems with divergence angles around 137.5° to spiral systems with divergence angles below 80° – are described and illustrated: *Cycas* (gymnosperm), *Huperzia* (clubmoss), *Pandanus* (screw palm), and *Costus* (corkscrew ginger). They serve as examples of morphogenetic variation in plants that call for evo-devo explanations beyond (or prior to) the "survival of the fittest". Charles Darwin was already convinced that natural selection had not been the only driving force in evolution.

Towards a theory of development encompassing various multicellular organisms

Vervoort (2014, pp. 209-210) proposed a theory of development comparing plant versus animal development, especially in respect to the independent origin of multicellularity. He stated that "most developmental biologists working on animals do not feel competent to address and discuss plant developmental data, and vice versa".

Minelli (2018) is clearly a glorious exception. His recently published book *Plant Evolutionary Developmental Biology* proves that he succeeded in doing "the metamorphosis of an evo-devoist trained in zoology to something like a plant evo-devoist" (Minelli, 2018, p. ix). With his comparison of lichens and galls

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(Minelli, 2017) he had already showed his flair for switching between various kingdoms of life, and for floating unconventional ideas.

Comparisons between animal and plant development were already made in the 18th century. Caspar Friedrich Wolff [1734-1794] and Johann Wolfgang von Goethe [1749-1832] belong to the pioneers capable of doing both (Arber, 1946; Aulie, 1961; Rutishauser and Moline, 2005; Abzhanov, 2018; Rutishauser, 2018). There is an old tradition to look first at plants to better understand the architecture and development of animals. Wolff had begun his inquiries with plant studies in order to get a heuristic Ariadne thread ("Richtschnur") before entering the supposedly much more complex bauplans of animals. Wolff (1759), who was cited several times by Goethe (1790, 1823), belonged to the epigeneticists (Wyder, 1998). Wolff understood the morphogenesis of organisms and their parts as a succession of developmental processes, including tissue differentiation. He first detected the existence of *shoot apical meristems* (*SAMs*) in the buds of vascular plants (Figs. 1-4).

In Darwin's view, plants and animals share a common ancestry and therefore have physiological properties in common. Darwin studied the circular motion (circumnutation) of searching tendrils and climbing shoots. According to him, the climbers belong to the most animal-like groups of plants: How do they find and get in contact with supporting objects? (Costa, 2018). Both animal-like plants and plant-like animals were of interest to Darwin. For example, the modified trichomes of sundews (*Drosera*) with their liquid droplet tips reminded him of the tentacles of marine invertebrates (Rutishauser, 2009).

Today, we are learning more and more about how plants perceive their environment and how they react accordingly. Neurotransmitters as known from animals are also active in plants (Baluška *et al.*, 2006; Baluška and Mancuso, 2007). Thus, we have to accept that there is something like intelligence and learning behaviour in plants. Now it is up to us as researchers to "think like a plant" (Holdrege, 2005), and to get a "feeling for the organism", as experienced by Nobel Prize winner Barbara McClintock [1902–1992] (Keller, 1983; Rutishauser, 2018).

Developmental aspects (including genetics and comparative morphology) of all kinds of multicellular organisms are needed in order to create a theory of development (Minelli and Pradeu, 2014). Thus, not only metazoans (multicellular animals) and land plants (including bryophytes and vascular plants) but also fungi, lichens and various algal clades belonging to other eukaryote lineages need to be studied for the identification of general principles of development. These principles comprise gene regulatory networks through which genes act not as soloists but in concert (Huang 2011; Benitez *et al.,* 2018).

Various multicellular organisms such as land plants as well as brown and red algae show polar growth that may last for a long period. Especially known for indeterminate apical growth are shoots of vascular plants with meristematic tips, the shoot apical meristems. They show a unique morphogenetic potential giving rise to leaves as lateral appendages (Figs. 1-4), and – by lateral branching – also to daughter shoots and flowers. Many biologists and mathematicians are attracted by the regular spiral (helical) leaf arrangement patterns in vascular plants, often coming close to Fibonacci systems with divergence angles between consecutive leaves of ca. 137.5° (Fig. 1a). Thus, plants (especially bryophytes and vascular plants) have distinctive morphogenetic modalities that are rare in, or absent from, other multicellular organisms such as metazoan animals lacking indeterminate apical growth (Benitez *et al.*, 2018).

Developmental geneticists, biophysicists and specialists in computer simulation have already started to better understand the various phyllotactic patterns, especially in model organisms such as *Arabidopsis*, linking molecular (e.g., auxin, cytokinin) drivers with biophysical processes (Cooke, 2006; Smith *et al.,* 2006; Bainbridge *et al.,* 2008; Newell *et al.,* 2008; Besnard *et al.,* 2014; Runions *et al.,* 2014; Rutishauser, 2016b; Minelli, 2018, p. 103]. Most spiral phyllotactic patterns follow Hofmeister's rule: A new leaf primordium tends to form at the shoot apical meristem as far away from the previously initiated leaves, resulting mainly in Fibonacci systems with divergence angles (d) around 137.5° (Fig. 1), and related Fibonacci-type patterns such as Lucas systems (with d = ca. 99.5°) and bijugate systems (with d = 180° + ca. 68.8°). However, phyllotaxis researchers will also have to explain spiral systems violating Hofmeister's rule, such as those found in clubmosses, screw palms and corkscrew gingers (Figs. 2-4).
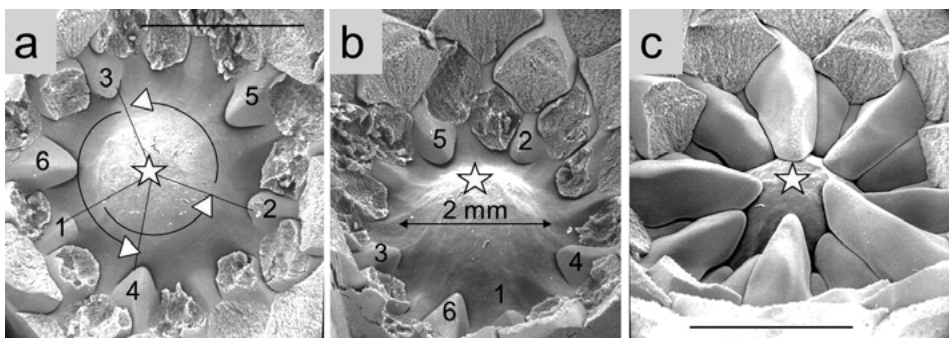

Figure 1. Shoot tip of the gymnosperm *Cycas circinalis*: (a) and (b) show a quite large shoot apical meristem (SAM, diameter 2 mm, stars indicate its centre), seen from above and from a slightly lateral position; (c) shows the same shoot tip prior to the removal of young tightly packed leaves surrounding the SAM. The youngest six leaf primordia reveal typical spiral phyllotaxis (Fibonacci system) with divergence angles between consecutive leaf primordia close to 137.5° (as indicated by crescents with arrowheads). Scale bars = 2 mm [SEM micrographs by RR, UZH]
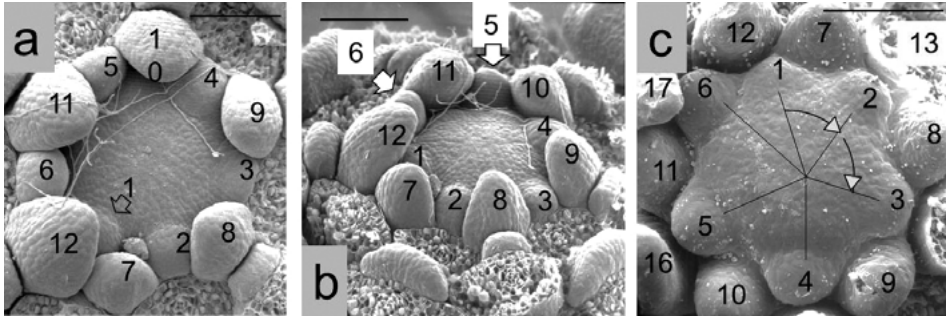
Figure 2. Shoot tips of the clubmoss *Huperzia squarrosa* (Lycopodiaceae): The youngest 12 leaf primordia reveal «Fibonacci-type» spiral phyllotaxis with divergence angles of consecutive leaf primordia close to 65.5°. This (1,5,6) spiral system has contacts between leaves that show age differences of 5, 6 and 11 plastochrones. This aberrant phyllotactic pattern is often found in lycophytes, but very rare in seed-plants including conifers (Fierz, 2014; Gola and Banasiak, 2016). See more on this and related «Fibonacci-type» phyllotaxes in Rutishauser (1998). Scale bars = 150 μm [SEM micrographs by RR, UZH]

The phyllotaxis patterns presented in Figures 1–4 allow some conclusions (for details see figure legends): (i) SAMs are usually 0.1–0.5 mm in diameter (Figs. 2-4). Larger SAMs are rare; they can be found in only a few vascular plants such as cycads (Fig. 1a, b). (ii) Highly regular phyllotaxes probably evolved as optimal solutions of package problems (Fig. 1c), answering the question: How can young leaves be arranged so that they are as compact as possible within a shoot bud? Thus, irregular (seemingly chaotic) phyllotaxis patterns in vascular plants seem to be much rarer than regular ones (Rutishauser, 2016b). (iii) Certain features, such as the shape of leaf primordia and relative frequencies of peculiar spiral patterns, may be genetically fixed as well as the result of developmental correlations because they are restricted to one group of vascular plants, being absent from other closely related taxa. For example, spiral patterns with divergence angles of exactly 120° are favoured in combination with leaf primordia showing triangular shapes, fitting into each other along the corners of an equilateral triangle, as found in screw palms (*Pandanus*) and Cyperaceae (sedge family) among monocots (Fig. 3). (iv) Regular spiral patterns with divergence angles as low as 50-80° are frequent in clubmosses (lycophytes, Fig. 2) and in a subgroup of monocots, the corkscrew gingers (Costaceae) of the banana–ginger alliance (Fig. 4). It seems best to accept that the spiral patterns with divergence angles below 80° resulted from convergent evolution in these two distinct groups of vascular plants that evolved leaves independently: microphylls in lycophytes,

megaphylls in seed plants (Pires and Dolan, 2012; Gola and Banasiak, 2016). The completely different shape of the leaf primordia, being tangentially elliptical in clubmosses and crescent-like in corkscrew gingers, may be another argument in favor of convergent evolution (see Minelli, 2018, pp. 313-327 for additional examples of convergence and parallelism in plants).
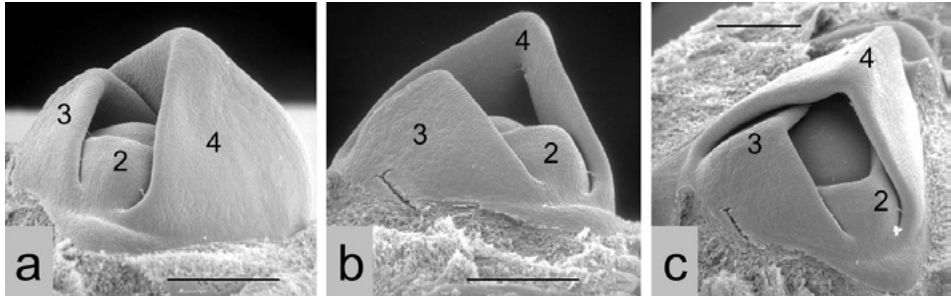

Figure 3. Shoot tip of the screw palm *Pandanus utilis* (Pandanaceae): Three different views of the same tip. The triangular shape of the leaf primordia 2–4 next to the shoot apical meristem is strongly correlated with orthotristichous phyllotaxis (divergence angle 120°). The youngest leaf primordium (1) is hidden. This variant of spiral phyllotaxis is also found in many Cyperaceae. In *Pandanus*, older leaf stages towards the rosette periphery start to twist their position by secondary stem torsion, leading to the leaf arrangement of typical «screw palms» with divergence angles clearly exceeding 120°. Scale bars = 300 µm [SEM micrographs by RR, UZH]
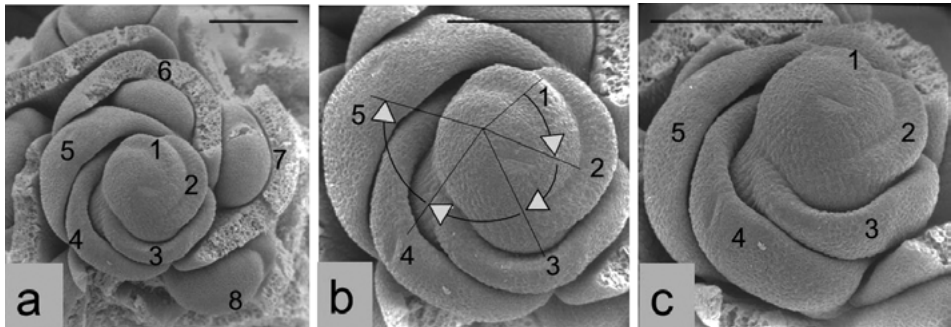

Figure 4. Centre of developing inflorescence in corkscrew ginger *Costus scaber* (Costaceae). Its spiromonostichous phyllotaxis resembles a spiral staircase (divergence angles ca. 60°). Note the crescent-shaped bract primordia 1–7, with floral buds in the older axils. In *C. scaber*, the bracts of the terminal spike-like inflorescence continue with divergence angles as low as ca. 60° (as shown here), whereas other corkscrew gingers such as *Chamaecostus cuspidatus* switch back to Fibonacci systems (with divergence angles of ca. 137.5°) when starting inflorescence development at the tip of aerial shoots (Kirchoff and Rutishauser, 1990). New aerial shoots (starting from the sympodial rhizome) of corkscrew gingers (Costaceae) first show Fibonacci angles (or nearly so), but gradually diminish their divergence angles below 90° along the leafy zone of the upright stems. Scale bars = 200 µm [SEM micrographs by RR, UZH]

Continuum and fractal patterns in plants as compared with animals

Goethe (1823) wrote: "Nature has no system; she has – she is – life and development from an unknown centre towards an unknowable periphery." Thus, Goethe believed that nature's patterns are not fixed – he detected and tried to explain all kinds of transitions both between and within organisms (Abzhanov, 2018; Sattler, 2018).

Furthermore, Goethe (1790) was aware that there are complementary perspectives on vascular plants. Some of the various architectural models designed to conceptually dismantle a growing shoot (e.g. leaves and stems as subunits) were already described by Goethe (1790: see Rutishauser and Sattler, 1985; Rutishauser, 2018; Sattler, 2019 this volume).

Various kinds of homology ("sameness") exist in metazoan animals as well as vascular plants. Comparing iterated parts (e.g., limbs, leaves) in organisms with modular (metameric) construction we tend to speak of "serial homology" (Darwin, 1872; Rutishauser and Moline, 2005; Minelli and Fusco, 2013). Serial homology in arthropods and vertebrates depends to some degree on genetic networks including *Hox* genes. Serial homology in seed plants depends on regulatory networks with e.g. MADS-box genes giving "identity" to the floral organs typically found in four kinds (Vervoort, 2014).

Serial homology may also exist between the whole body of a multicellular organism and its parts. Minelli (2003b, p. 574) provided evidence for fractal patterns in modular animals (arthropods, vertebrates): "It is possibly not by chance that segmented appendages are only present in animals whose main body is also segmented." In vertebrates (e.g., mice) the single limb shares some kind of homology ("sameness") with the main body axis that runs from head to tail. Therefore, Minelli (2003a, 2003b, p. 573) proposed the *paramorphism concept* for modular animals: "It may be justified, instead, to look for correspondences between the appendages and the main body axis of the same animal, as the latter might be the source of the growth and patterning mechanisms which gave rise to the former."

A similar kind of axis paramorphism is present in vascular plants with respect to the iteration of both shoots and leaves, as recently summarized by Minelli (2018, pp. 243–244): "[…] it is sensible to expect that paramorphism is a kind of 'modulated fractal pattern', where the iteration of a small set of rules over different body axes (the longitudinal axis of shoot and leaf) is to some extent constrained by the different context but nevertheless results in recognizable repetitions of a basic regularity." Thus, a single leaf of a vascular plant shares a kind of homology with the whole shoot, which includes both stem and leaves. This process of iteration that continues from the whole shoot with its

leaves to each leaf with its leaflets was observed by botanists well before the times of contemporary evo-devo. In particular, Agnes Arber (1950) and Rolf Sattler (1994, 1996) considered a single leaf of vascular plants (especially when compound) as a partial repetition of the whole shoot to which it belongs. Arber (1950) presented her ideas as the "partial-shoot theory" of the leaf (see Kirchoff, 2001; Rutishauser and Isler, 2001; Flannery, 2003), whereas Sattler used concepts such as homeosis, partial homology and the "continuum model" to explain developmental similarities between compound leaves and shoots with respect to growth modes, architectural complexity and symmetry (arguments further developed by Sattler, 2019 this volume).

Fractal patterns in plants and animals are attractive because growing organisms seem to be able to produce them in an elegant way using simple algorithms (Minelli, 2018, p. 238). Thus, fractal properties according to the holographic paradigm may help to explain modular construction in both metazoan animals and vascular plants: The whole is built up of the parts in such a way that each part bears something of the whole within it (Rutishauser and Isler, 2001; Rutishauser and Moline, 2005). Fractal properties are obvious in phyllotaxis patterns as shown in Figures 1-4: The patterns observable towards the periphery of a shoot bud are repeated by new leaf primordia at the shoot apical meristem (see more on phyllotaxis in Minelli, 2018, pp. 102-106).

Riverweeds (Podostemaceae) as well as bladderworts (Lentibulariaceae, especially genus *Utricularia*) serve to illustrate the continuum and fractal properties in vascular plants (Rutishauser *et al.*, 2008; Rutishauser, 2016a; Minelli, 2018, pp. 254-256). Both of these groups of flowering plants may be called "morphological misfits" because they do not fit the classical root-shoot model of typical seed plants. If, however, for ease of communication, we cling to structural categories such as 'leaf' and 'stem' and 'root' for the description of morphological misfits in vascular plants, we get into trouble with either/or homology ("sameness") of the various plant parts. Then we are forced to accept the existence of structural intermediates such as "stem-leaf mixed organs" in Podostemaceae, as found and genetically analyzed by Katayama *et al.* (2010).

Process philosophical approach in biology: 'leaf', 'stem' and 'root' are usually taken for granted as organs in vascular plants. However, when we realize that these structural categories are arbitrary concepts to some degree, each of them encompassing a certain set of developmental processes, then we are prepared to abandon structural concepts and instead refer to combinations of developmental (morphogenetic) processes that depend – to some degree – on gene regulatory networks. This radical view was proposed by Sattler (1992, 1994, 1996, 2018, 2019 this volume), Sattler and Rutishauser (1997) and Langdale (2008).

According to Sattler (see his "Beyond-Wilber" website): "A structure is not seen as having processes, a structure is seen *as* process(es)." Thus, there is no longer a structure-process dualism. This process philosophical approach was used by Nicholson and Dupré (2017) for all kind organisms: "The living world is a world of process rather than a world of things."

Somewhere between the structural approach and process philosophy are the concepts of dynamic patterning modules and biogeneric materials as proposed by Newman and Bhat (2009), Hernández-Hernández *et al.* (2012) and Benitez *et al.* (2018). They may prove to be heuristically quite fruitful concepts when we want to fully understand the mechanisms responsible for the major evolutionary transitions among eukaryotic lineages that became multicellular.

Natural selection is insufficient to explain the wealth of forms in vascular plants and other multicellular organisms

Minelli (2018) pointed to four aspects of evolutionary developmental biology, while focusing on plants (see also Langdale, 2008; Wagner, 2014; Harrison, 2017; Rutishauser, 2018): (i) During the last 20 years there was a rapid growth of evo-devo as a new approach to understanding the evolution and development of organismal form. (ii) To a considerable extent, evo-devo deals with developmental genes, their evolution and their expression. (iii) Evo-devo explains the *arrival* of the fittest whereas Darwinism explains the *survival* of the fittest. (iv) There is a strong need to focus on the phenotype which is at the same time the product of development and the direct target of selection. Accordingly, Minelli (2018) calls for a renaissance of comparative plant morphology in evo-devo. Such a discipline complementing developmental genetics may be labelled as "MorphoEvoDevo" (Wanninger, 2015).

Darwin (1872) showed in the 6th edition of "Origin of Species" that he was well aware that natural selection is not sufficient to explain the wealth of forms ('bauplans') in the various kingdoms of life. To make sure that the reader of his book received this key message, Darwin wrote not once but twice (in the Introduction as well as in Chapter VII) that "I am convinced that natural selection has been the main, but not the exclusive, means of modification." Darwin (1872, chapter VII) also admitted: "Many characters appear to be of no service whatever to their possessors, and therefore cannot have been influenced through natural selection." With respect to plants he pointed to "an admirable essay", written by the botanist Carl Wilhelm von Nägeli [1817-1891]: "He specifies the arrangement of the cells in the tissues, and of the leaves on the axis, as cases in which natural selection could not have acted." Darwin (1872, chapter VII) continued his objection to natural selection as exclusive means of morphological

change ("modification") in evolution: "It should always be borne in mind that when one part is modified, so will be other parts, through certain dimly seen causes, such as an increased or diminished flow of nutriment to a part, mutual pressure, an early developed part affecting one subsequently developed, and so forth, – as well as through other causes which lead to the many mysterious cases of correlation, which we do not in the least understand. These agencies may be all grouped together, for the sake of brevity, under the expression of the *laws of growth*."

The *'laws of growth'* as proposed by Darwin – and later articulated more formally by D'Arcy Thompson (1917, 1961) – may in a contemporary inter-pretation also encompass developmental genetics and all interacting ontoge-netic processes from the molecular to organismal level, including epigenetics, correlation, self-organization, phenotypic integration (i.e. interdependence of morphological traits, also termed synorganization), morphogenetic fields and gradients, physical constraints such as intrinsic material properties and tissue tension during development, and even neuronal aspects in plants (Baluška *et al.*, 2006; Newman, 2014; Vecchi and Hernández 2014; Wanninger, 2015; Abzhanov, 2017; Cabej, 2018; Bateman and Rudall, 2019 this volume).

Darwin's and Thompson's 'laws of growth' got a refreshing renewal in the 'law-of-form' approach by Newman *et al.* (2006). They are aware that the roots of their approach go back well before the rise of contemporary evo-de-vo, amalgamating ideas of Goethe, Geoffroy St-Hilaire, Owen, Bateson, D'Arcy Thompson, and also Brian Goodwin (Newman, 2014, p. 107). Newman *et al.* (2006) favour a kind of evolutionary saltationism when they suggest: "[…] once multicellularity had been achieved, the emergence of distinct body plans likely occurred with much less genetic change and at a faster pace than would be pre-dicted by gradualistic models of evolution by natural selection."

As already admitted by Darwin (1872, see underlined words in the quotation above) phyllotaxis patterns as observable in vascular plants (Figs. 1-4) appear as developmental patterns that are not under the control of natural selection. There are developmental constraints ('laws of growth') that force most spiral patterns to approach the famous Fibonacci angle, which is about 137.5° (Cooke, 2006; Mirabet *et al.*, 2012; Swinton *et al.*, 2016). Fierz (2014) examined the phyl-lotaxes of 6,000 cones of one single European black pine tree (*Pinus nigra*). She counted 5,838 cones (97%) exhibiting the main Fibonacci pattern with 8 and 13 parastichies. Additional nine aberrant spiral patterns with "Fibonacci-type" se-quences were quite rare and occurred with different frequencies. Interestingly, all of them have something to do with the golden ratio 0.618. With only one cone observed, the (1, 5, 6) spiral system was the rarest phyllotaxis observed

among the 6000 pine cones, showing divergence angles of d = ca. 65°! This is exactly the pattern that is much more frequent in clubmosses (Fig. 2). It seems that vascular plants with leaf primordia that are much smaller than their shoot apical meristem tend to deviate more easily from the typical Fibonacci phyllotaxis, escaping to other kinds of Fibonacci-type spiral systems or even to irregular ("chaotic") ones. Thus, we have to consider – besides mathematical rules – also physical constraints imposed by the shoot apical geometry (Rutishauser, 1998, 2016b; Cooke, 2006).

Fibonacci systems (with divergence angles approaching 137.5°) and related spiral patterns are – besides land plants such as lycophytes and seed-plants – also known from brown algae (Phaeophyceae, e.g. *Sargassum*) and red algae (Rhodophyceae). These multicellular eucaryotes gained indeterminate apical growth and repeated formation of lateral appendages as a result of convergent evolution. The lineages on the tree of life leading to brown algae, red algae and land plants (as part of *Chara*-like green algae) diverged from unicellular ancestors more than 1,000 millions of years ago (Pires and Dolan, 2012; Peaucelle and Couder, 2016). Fibonacci spirals were even obtained in physics experiments that had no relation to biology (Douady and Couder, 1998). Thus, there are strong arguments in favour of the view that self-organization processes beyond natural selection allowed the emergence of Fibonacci systems and related patterns in living organisms.

Conclusions

Not everything is possible in plant development. There are architectural constraints, favouring some body-plan features while excluding other imaginable patterns in living organisms. This short essay gives emphasis on evo-devo research of land plants. For example, the *paramorphism concept* as proposed for modular animals by Minelli (2003a, b) has its counterpart in land plants when compound leaves repeat the developmental pathways ("programs") of the shoots to which they belong. Thus, there are fractal properties common to both multicellular animals and multicellular plants. Unlike metazoan animals, plants (as well brown and red algae) may form multicellular bodies with indeterminate apical growth and iteration of lateral appendages (Minelli, 2018). The resulting regular Fibonacci-type patterns obey Hofmeister's rule with a new leaf primordium positioned in the least crowded spot around the shoot apical meristem (Fig. 1). Much rarer spiral patterns that violate (at least to some degree) Hofmeister's rule are also found in plants (Figs. 2–4). Thus, the various spiral patterns in plants and other multicellular organisms cannot be explained exclusively by natural selection. They follow 'laws of growth' (e.g. self-orga-

nization, gene regulatory networks, auxin gradients), as already foreseen by Charles Darwin. It is now time to switch in evolutionary biology from the Modern Synthesis to the Extended Synthesis by the inclusion of developmental and evolutionary processes that contribute to non-aptation (Bateman and Rudall, 2019 this volume), giving rise to a wealth of forms in living organisms beyond (or prior to) natural selection (Pigliucci and Müller, 2010; Huang, 2011; Horsthemke, 2012; Wagner, 2014). As concluded by Minelli and Baedke (2014), "Investigating evolvability means shifting the focus from the survival of the fittest to the arrival of the fittest".

Acknowledgements

References

Abzhanov, A. 2017. The old and new faces of morphology: the legacy of D'Arcy Thompson's 'theory of transformations' and 'laws of growth'. *Development*, 144: 4284–4297.

Arber, A. 1946. Goethe's botany: The Metamorphosis of Plants (1790) and Tobler's Ode to Nature (1782). *Chronica Botanica*, 10: 63–126.

Arber, A. 1950. *The Natural Philosophy of Plant Form.* Cambridge University Press, Cambridge.

Aulie, R.P. 1961. Caspar Friedrich Wolff and his 'Theoria Generationis' 1759. Journal of the History of Medicine and Allied Sciences, 16: 124–144.

Bainbridge, K., Guyomarc'h, S., Bayer, E., Swarup, R., Bennett, M., Mandel, T., Kuhlemeier, C. 2008. Auxin influx carriers stabilize phyllotactic patterning. *Genes & Development*, 22: 810–823.

Baluška, F., Mancuso, S. 2007. Plant neurobiology as a paradigm shift not only in the plant sciences. *Plant Signaling & Behavior*, 2: 205–207.

Baluška, F., Mancuso, S., Volkmann, D. (eds.) 2006. *Communication in plants. Neuronal aspects of plant life.* Springer, Berlin.

Bateman, R.M., Rudall, P.J. 2019. Hyper-epigyny is the ultimate constraint on orchid floral morphology and an ideal model for testing the Extended Synthesis. In: G. Fusco (ed.) *Perspectives on evolutionary and developmental biology.* Padova University Press, Padova, pp. 203-233.

Benitez, M., Hernández-Hernández, V., Newman, S.A., Niklas, K.J. 2018. Dynamical patterning modules, biogeneric materials, and the evolution of multicellular plants. *Frontiers in Plant Science*, 16: 871.

Besnard, F., Refahi, Y., Morin, V., Marteaux, B., Brunoud, G., Chambrier, P. *et al.* 2014. Cytokinin signalling inhibitory fields provide robustness to phyllotaxis. *Nature*, 505: 417–421.

Cabej, N.R. 2018. *Epigenetic Principles of Evolution.* 2nd edition. Academic Press, Cambridge, MA.

Cooke, T.J. 2006. Do Fibonacci numbers reveal the involvement of geometrical imperatives or biological interactions in phyllotaxis? Botanical Journal of the Linnean Society, 150: 3–24.

Costa, J.T. 2018. The impish side of evolution's icon. *American Scientist*, 106: 104–111.

Darwin, Ch. 1872. *The Origin of Species,* 6th edition. See Online Variorum of Darwin's Origin of Species. http://darwin-online.org.uk/Variorum/1872

Douady, S., Couder, Y. 1998. The phyllotactic patterns as resulting from self-organization in an iterative process. In: R.V. Jean, D. Barabé (eds.) *Symmetry in Plants.* World Scientific Press, Singapore, pp. 539–570.

Fierz, V. 2014. Aberrant phyllotactic patterns in cones of some conifers: a quantitative study. *Acta Societatis Botanicorum Poloniae*, 84: 261–265.

Flannery, M.C., 2003. Agnes Arber: form in the mind and the eye. *International Studies in the Philosophy of Science*, 17: 281–300.

Goethe, J.W. von 1790. *Versuch die Metamorphose der Pflanzen zu erklären.* Gotha. [English translation by Arber 1946]

Goethe, J.W. von 1823. *Scientific Studies*, ed. and trans. Douglas Miller, vol. 12. In V. Lange, E. Blackall, C. Hamlin (eds.) Goethe's Collected Works. Suhrkamp, New York (published 1995).

Gola, E.M., Banasiak, A. 2016. Diversity of phyllotaxis in land plants in reference to the shoot apical meristem structure. *Acta Societatis Botanicorum Poloniae*, 85: 3529.

Harrison, J.C. 2017. Development and genetics in the evolution of land plant body plans. *Philosophical Transactions of the Royal Society B*, 372: 20150490.

Hernández-Hernández, V., Niklas, K.J., Newman, S.A., Benitez, M. 2012. Dynamical patterning modules in plant development and evolution. *International Journal of Developmental Biology*, 56: 661–674.

Holdrege, C. 2005. *Thinking like a Plant. A Living Science for Life.* Lindisfarne Books, Great Barrington, MA.

Horsthemke, B. 2012. Waddington's epigenetic landscape and post-Darwinian biology. Bioessays, 34: 711–712.

Huang, S. 2012. The molecular and mathematical basis of Waddington's epigenetic landscape: a framework for post-Darwinian biology? Bioessays, 34: 149–57.

Katayama, N., Koi, S., Kato, M. 2010. Expression of *SHOOT MERISTEMLESS, WUSCHEL*, and *ASYMMETRIC LEAVES1* homologs in the shoots of Podostemaceae: implications for the evolution of novel shoot organogenesis. *The Plant Cell*, 22: 2131–2140.

Keller, E.F. 1983. *A Feeling for the Organism. The Life and Work of Barbara McClintock.* Freeman and Company, New York.

Kirchoff, B.K. 2001. Character description in phylogenetic analysis: Insights from Agnes Arber's concept of the plant. *Annals of Botany*, 88: 1203–1214.

Kirchoff, B.K., Rutishauser, R. 1990. The phyllotaxis of *Costus* (Costaceae). *Botanical Gazette*, 151: 88–105.

Langdale, J.A. 2008. Evolution of developmental mechanisms in plants. *Current Opinion in Genetics & Development*, 18: 368–373.

Minelli, A. 2003a. *The Development of Animal Form: Ontogeny, Morphology, and Evolution.* Cambridge University Press, Cambridge.

Minelli, A. 2003b. The origin and evolution of appendages. *International Journal of Developmental Biology*, 47: 573–581.

Minelli, A. 2017. Lichens and galls. Two families of chimeras in the space of form. *Azafea Revista de Filosofía*, 19: 91–105.

Minelli, A. 2018. *Plant Evolutionary Biology. The Evolvability of the Phenotype.* Cambridge University Press, New York.

Minelli, A., Baedke, J. 2014. Model organisms in evo-devo: promises and pitfalls of the comparative approach. *History and Philosophy of the Life Sciences,* 36: 42–59.

Minelli, A., Fusco, G. 2013. Homology. In: K. Kampourakis (ed.) *The Philosophy of Biology: A Companion for Educators, History, Philosophy and Theory of the Life Sciences.* Springer, Dordrecht, pp. 289–322.

Minelli, A., Pradeu, T. (eds.) 2014. *Towards a Theory of Development.* Oxford University Press, Oxford.

Mirabet, V., Besnard, F., Vernoux, T., Boudaoud, A., 2012. Noise and robustness in phyllotaxis. *PLoS Computational Biology*, 8: e1002389.

Newell, A.C., Shipman, P.D., Sun, Z. 2008. Phyllotaxis as an example of the symbiosis of mechanical forces and biochemical processes in living tissue. *Plant Signaling & Behavior*, 3: 586–589.

Newman, S.A. 2014. Physico-genetics of morphogenesis: the hybrid nature of developmental mechanisms. In: A. Minelli, T. Pradeu (eds.) *Towards a Theory of Development.* Oxford University Press, Oxford, pp. 95–113.

Newman, S.A., Bhat, R. 2009. Dynamical patterning modules: a 'pattern language' for development and evolution of multicellular form. *International Journal of Developmental Biology*, 53: 693–705.

Newman, S.A., Forgacs, G., Müller, G.B. 2006. Before programs: the physical origination of multicellular forms. *International Journal of Developmental Biology*, 50: 289–299.

Nicholson, D. J., Dupré, J. (eds.) 2018. *Everything flows: Towards a processual philosophy of biology.* Oxford University Press, Oxford.

Peaucelle, A., Couder, Y. 2016. Fibonacci spirals in a brown alga [*Sargassum muticum* (Yendo) Fensholt] and in a land plant [*Arabidopsis thaliana* (L.) Heynh.]: a case of morphogenetic convergence. *Acta Societatis Botanicorum Poloniae*, 85: 3526.

Pigliucci, M., Müller, G.B. (eds.) 2010. *Evolution: the Extended Synthesis.* MIT Press, Cambridge, MA.

Pires, N.D., Dolan, L. 2012. Morphological evolution in land plants: new designs with old genes. Philosophical Transactions of The Royal Society B, 367: 508–518.

Runions, A., Smith, R.S., Prusinkiewicz, P. 2014. Computational models of auxin-driven development. In: E. Zažímalová, J. Petrášek, E. Benková (eds.) *Auxin and Its Role in Plant Development.* Springer, Heidelberg, pp. 315–357.

Rutishauser, R. 1998. Plastochrone ratio and leaf arc as parameters of a quantitative phyllotaxis analysis in vascular plants. In: R.V. Jean, D. Barabé (eds.) *Symmetry in Plants.* World Scientific Press, Singapore, pp. 171–212.

Rutishauser, R. 2009. Vom Milch trinkenden Sonnentau (*Drosera*) zum schlafenden Wassersalat (*Pistia*): Charles Darwin als Botaniker. Vierteljahrsschrift der Naturforschenden Gesellschaft in Zürich, 154: 75–81.

Rutishauser, R. 2016a. Evolution of unusual morphologies in Lentibulariaceae (bladderworts and allies) and Podostemaceae (river-weeds). *Annals of Botany*, 117: 811–832.

Rutishauser, R. 2016b. *Acacia* (wattle) and *Cananga* (ylang-ylang): from spiral to whorled and irregular (chaotic) phyllotactic patterns – a pictorial report. *Acta Societatis Botanicorum Poloniae*, 85: 3531.

Rutishauser, R. 2018. Von Goethes dynamischer Pflanzenmorphologie zur evolutionären Entwicklungsbiologie ("EVO-DEVO"): Holismus and Reduktionismus ergänzen sich. *Elemente der Naturwissenschaften*, 108: 80–100.

Rutishauser, R., Grob, V., Pfeifer, E. 2008. Plants are used to having identity crises. In: A. Minelli, G. Fusco (eds.) *Evolving Pathways. Key Themes in Evolutionary Developmental Biology.* Cambridge University Press, Cambridge, pp. 194–213.

Rutishauser, R., Isler, B. 2001. Developmental genetics and morphological evolution of flowering plants, especially bladderworts (*Utricularia*): Fuzzy Arberian Morphology complements Classical Morphology. *Annals of Botany*, 88: 1173–1201.

Rutishauser, R., Moline, P. 2005. Evo-devo and the search for homology ('sameness') in biological systems. *Theory in Biosciences*, 124: 213–241.

Rutishauser, R., Sattler, R. 1985. Complementarity and heuristic value of contrasting models in structural botany. I. General considerations. *Botanische Jahrbücher für Systematik*, 107: 415–455.

Sattler, R. 1992. Process morphology: structural dynamics in development and evolution. *Canadian Journal of Botany*, 70: 708–714.

Sattler, R. 1994. Homology, homeosis, and process morphology in plants. In: B.K. Hall (ed.) *The Hierarchical Basis of Comparative Biology.* Academic Press, New York, pp. 423–475.

Sattler, R. 1996. Classical morphology and continuum morphology: opposition and continuum. *Annals of Botany*, 78: 577–581.

Sattler, R. 2018. Philosophy of plant morphology. *Elemente der Naturwissenschaft,* 108: 55–79 (for a more comprehensive version see http://www.beyondwilber.ca/about/plant-morphology/philosophy-of-plant-morphology.html)

Sattler, R. 2019. Structural and dynamic approaches to the development and evolution of plant form. In: G. Fusco (ed.) *Perspectives on Evolutionary and Developmental Biology.* Padova University Press, Padova, pp. 57-67.

Sattler, R. «Beyond Wilber» Internet-Website (visited September 2018) http://www.beyondwilber.ca/about/plantmorphology/plant_morphology.html

Sattler, R., Rutishauser, R., 1997. The fundamental relevance of morphology and morphogenesis to plant research. *Annals of Botany*, 80: 571–582.

Smith, R.S., Kuhlemeier, C., Prusinkiewicz, P., 2006. Inhibition fields for phyllotactic pattern formation: a simulation study. *Canadian Journal of Botany*, 84: 1635–1649.

Swinton, J., Ochu E, and The MSI Turing's Sunflower Consortium, 2016. Novel Fibonacci and non-Fibonacci structure in the sunflower: results of a citizen science experiment. *Royal Society Open Science*, 3: 160091.

Thompson, D.W. 1917. *On Growth and Form*, 1st edn. Cambridge University Press, Cambridge, UK.

Thompson, D.W. 1961. *On Growth and Form*, abridged edn. Cambridge University Press, Cambridge, UK.

Vecchi, D., Hernández, I. 2014. The epistemological resilience of the concept of morphogenetic field. In: A. Minelli, T. Pradeu (eds.) *Towards a Theory of Development.* Oxford University Press, Oxford, pp. 79–94.

Vervoort, M. 2014. Comparison of animal and plant development: a right track to establish a theory of development. In: A. Minelli, T. Pradeu (eds.) *Towards a Theory of Development.* Oxford University Press, Oxford, pp. 203–217.

Wagner, A. 2014. *Arrival of the Fittest: Solving Evolution's Greatest Puzzle.* Oneworld, London.

Wanninger, A. 2015. Morphology is dead – long live morphology! Integrating MorphoEvoDevo into molecular EvoDevo and phylogenomics. *Frontiers in Ecology and Evolution*, 3: 54.

Wolff, C.F. 1759. *Theoria Generationis.* Teil 1. Pflanzen. Teile 2/3. Tiere. Halle. [see essay by Aulie 1961]

Wyder, M. 1998. *Goethes Naturmodell. Die Scala Naturae und ihre Transformationen.* Köln, Weimar, Wien.