The International Journal of Plant Reproductive Biology 8(1) Jan., 2016, pp.14-23

DOI 10.14787/ijprb.2016 8.1.14-23

Phenomenon of embryoidogeny as a basis for interdisciplinary synthesis of knowledge in developmental biology

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Received : 02.03.2015; Accepted and published on line: 01.11.2015

ABSTRACT

Nontraditional ideas on plant reproduction examined in this work are considered to be the result of the discovery of the embryoidogeny phenomenon, a new category of vegetative propagation. In light of data on flowering plants reproduction in situ, in vivo and in vitro, we firstly revealed that vegetative propagation is represented by two types: embryoidogenous and gemmorhizogenous, but not just one gemmorhizogenous, as previously considered. In the formation of a new individual there are not two pathways of morphogenesis, but three ones: embryogenesis, embryoidogenesis and organogenesis. These pathways and modes are universal both in nature and in the experimental conditions. This allowed us to distinguish the embryoidogeny phenomenon and to consider its role in the reproduction system of flowering plants. This phenomenon, which we first considered from the position of the theory and principles of reproduction, somatic and stem cells, has a great biological significance, importance to scientific progress and practical value. Its detailed analysis can become a basis for further integration and synthesis of knowledge leading us to understanding the internal mechanisms of functioning of the living systems at all levels of structural organization.

Keywords : embryoidogenesis, embryoid, gemmorhizogeny, stem cells, integrity, reliability system, primal phenomenon.

INTRODUCTION

Development of the plant organism and knowledge of the mechanisms of morphogenetic processes occurring in its course is one of the most important problems of modern biology. Plant embryology, considered as a purely theoretical science, is currently experiencing a peak due to the general progress of natural science and is demanded both for the fundamental elaborations and the solution of biotechnological questions.

Koltsov (1935) predicted that the combination of sciences – genetics and embryology, as well as cytology and biochemistry, will create a united science – the developmental biology, which will allow solving general biological problems.

Modern embryology has integrative nature, which is emphasized by its new name: developmental biology.

At the current stage of development of this discipline the problem of arrangement of ideas on reproduction gets especial importance that defines the necessity of systemic analysis of the embryoidogeny phenomenon and revealing its role in elaboration of general biological problematics.

In this connection it is worth to consider in more details the notion of propagation and related definitions characterizing its various types in plants (Batygina 1999b, 2010a, 2011, Batygina & Vasilyeva 2002).

Types and modes of reproduction and propagation— The phenomenon of propagation is one of the main

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properties of the living matter and, as *Charles Darwin* proposed, the premise to natural selection inevitably realizing on our planet. Science on it must become the general scientific paradigm and will serve as a basis for the new ideology in terms of integration and consolidation of traditional and non-traditional trends of the study of biosystems (Batygina 2010b, 2011, 2014).

All processes resulting in the increase of biological units are referred to as propagation. According to traditional classification, plants have three types of propagation: sexual, asexual, and vegetative.

The issue is disputable on the scope of terms “sexual process” and “sexual propagation”, which require some refinement. From our viewpoint the sexual process includes meiosis and fusion of gametes (from different meioses), which results in arising of a zygote, i.e., a new individual. At that the increasing number of individuals does not occur, since a single new organism forms, as a rule, from the single zygote. The increasing of sexual progeny is provided just by the multiplicity of generative structures (ovules, pollen grains, gametes, zygotes) and so by the multiplicity of sexual processes. That is why, when only one sexual process takes place, one should talk about sexual reproduction. The term “sexual process” is often replaced in literature by the notion “sexual propagation”, which is not correct, and these terms could not be considered as synonyms (Batygina & Vasylieva 2002).

On our opinion, instead of terms “sexual” and “asexual propagation” as applied to the flowering plants one should use the notions “seminal” and “vegetative propagation”.

The seed, which is one of the units of propagation and dissemination, contains *the initial of new organism – the sexual embryo* – and specialized storage tissue (endosperm, perisperm, etc.) enclosed into the seed coat (testa, spermoderm).

One should note that in the same seed two processes of new individual producing can proceed simultaneously: sexual (formation of embryo) and asexual (formation of embryoid). Owing to this, the seed can contain several embryos of different origin (polyembryony) and give the seedlings of different genetics: matroclinous posterity (2n=2n) – from nucellus and integuments (etc.) or the individuals with new genetics (n + n – from zygote).

Vegetative propagation in the classical meaning is the increasing of species individuals in number as the result of separation of the viable parts of the plant vegetative body (buds, shoots, roots, etc.); in many cases this process is accompanied by regeneration of missing organs in separated plant parts. This is essentially distinguished the vegetative propagation from the seminal one, in the course of which during seed germination the individual of full value “is being born” from the embryo at once.

Posterity, arising as a result of vegetative propagation, independently on the place of its formation (vegetative or generative structures), produces clones – totality of the genetically homogenous individuals, identical by genotype to the maternal organism[1].

In view of the aforesaid we consider it possible to state the non-traditional view on types and modes of seminal and vegetative propagation, their relations in the system of reproduction of flowering plants, morphogenesis pathways and the mechanisms underlying them, which define the switching over the developmental programs in onto- and phylogeny. As it was established for the first time by T.B. Batygina (1999a, b) the new individuals can form upon the vegetative propagation in flowering plants not only by mean of bud, but embryoids as well.

Mechanisms of morphogenesis and stem cells—The progress of developmental biology is impossible without knowledge of essence and mechanisms of morphogenesis, the complicated and multi-facetted morphogenetic processes at all ontogenetic stages from the zygote and seedling up to entire adult plant.

We propose the system of non-traditional notions on the nature and role of somatic and stem cells in organization of embryo’s body and its architecture, in reproduction, and particularly in switching over developmental programs in life cycle. Probably, the somatic cell and nature of its division (asymmetric division – Batygina 1974, 2005) are the corner stone for morphogenesis, ontogenesis and evolution. In this

1. According to new data, the clone sometimes is supposed to consist of not rather uniform individuals as a result of mutational, etc., processes (Batygina 1993).

connection, probably, the principle of determining role of somatic evolution proposed earlier by us (Batygina 2010a, 2011, 2014) requires especial attention and extensive discussion.

Since the 70ties of 20th century in the laboratory of embryology of BIN RAS for the first time the cells of "dormant meristem" began to be studied with an attempt to reveal their role in the morphogenesis of embryonic structures and study the mechanism of their formation *de novo* in ovule in different species of flowering plants (Batygina & Freiberg 1979, Batygina 1991).

From the embryological viewpoint for the first time we had considered the traditional and non-traditional conceptions on reproduction and elaborated some theoretical aspects of the science on stem cells and their main properties, which demonstrated the integrity of morphogenous and reproductive processes at all stages of plant life cycle. For the first time in terms of embryogeny laws (laws of origin, numbers, disposition, destination, parsimony and critical mass), taking into account developmental biology of various species, the conception is elaborated on the zygote as a stem cell of the first order, the ancestress of all stem cells of a plant (Batygina *et al.* 2004, Batygina & Rudskiy 2006).

It is not only the zygote, that is the stem cell, but also the initial cells of embryoids (somatic embryos) of various origins are (Batygina *et al.* 1978, 2004, Batygina 1989, 1993, 1997, 2000, 2005, 2009, 2010a, b, 2011). It is proved, that the stem cells represent not the part of apical meristem (Clark1997, Weigel & Jürgens 2002, Ivanov 2003, 2007, Bosch 2008, Lohmann 2008, Stahl & Simon 2010 etc.), but its source (Batygina *et al.* 2004, Batygina & Rudskiy 2006, Batygina 2010a, 2011). Thus, the formation of stem cells derived from zygote is typical for all organs (flower, stem, leaf, root) and all stages of life cycle (sporophyte, *gametophyte), moreover their functioning firstly depend on their localization and purpose*.

In this connection the notion of stem cells was for the first time broadened, their properties were formulated and their role in plant morphogenesis was shown (Batygina *et al.* 2004, Batygina & Rudskiy 2006). The data were generalized on genetic control of stem cells maintenance in shoot apical meristem (system of genes WUS-CLV) and role of phytohormones in this process.

Our non-traditional conception on stem cells, and, particularly, the reasonability of broadening this notion (Batygina *et al*. 2004, Batygina & Rudskiy 2006, Batygina 2010a, 2011) was recently supported with molecular-biological methods (Albert & Ezhova 2013). All cells capable to form zygotic embryos, embryoids and buds must be considered as stem ones, including the zygote.

History of notions on embryoidogeny—Origins and the "birth" of a new direction in developmental biology– the study of the phenomenon of embryoidogeny and the discovery of its general biological significance is probably connected with the unique theoretical elaborations of outstanding scientists, introducing new approaches and experimental methods, which determined the 20th century as the "golden age of biology".

Blossoming of natural science in the XIXth century was also reflected in the solution of problems related with the sexual plant reproduction. In 1878 Strasburger first described the formation of numerous structures in nucellus *in vivo* – "adventive embryos" (Adventivkeime or Adventivembryon in German) in the ovules of *Funkia ovata* and *Nothoscordum fragrans*. In 1934 Winkler considered this phenomenon as a special case of vegetative propagation, however, Gustafsson (1946) did not agree with such interpretation.

Starting from the end of the XIXth century experimental methods of research of plant morphogenesis *in vitro* were used. Thus, the era of plant tissue culture commenced (Vöchting 1892). Haberlandt (1902) predicted the obtaining of somatic embryos from plant cells, and in the 6th decade Steward *et al.* (1958) and Reinert (1963) were the first in obtaining embryo-like structures in callus culture *in vitro*. The term "embryoid" was proposed by B.P.Tokin yet in 1959 for invertebrate animals. Subsequently in 1966 Vasil & Hildebrandt proposed the term for the definition of embryo-like structures, while noting the applicability of this term to "adventive" embryos developing *in vivo* in ovule from the somatic cells of nucellus or integuments.

These findings have caused "an explosion of discussion". Swamy & Krishnamurty (1981) entered into this discussion. They rejected the idea of "somatic embryo": they considered this structure as a bud, since the latter do not form epiphysis and hypophysis. At the same time, the works of Haccius (1965) and Batygina (1974, 1996) have revealed the absence of epiphysis or hypophysis or both of these structures in embryoids, as well as in sexual embryos of several groups of monocots and dicots. At present there is no clarity on this question.

In the 1970s, contradictory opinions concerning morphogenesis pathways in the *in vitro* culture existed. According to the generally accepted view, the formation of new individual in flowering plants realizes either by sexual mode – the sexual process precedes embryogenesis (heterophasic reproduction) or by asexual (vegetative) mode – the formation of buds and roots (homophasic reproduction), i.e., regeneration occurs (Battaglia 1963, Batygina 1999a). However it is appeared that upon the homophasic reproduction new individual can form not only by regeneration (organogenesis – gemmorhizogenesis), but also by means of embryoids formation – *embryoidogenesis*[2].

In light of data on flowering plants reproduction in situ, in vivo and in vitro, we firstly revealed that vegetative propagation is represented by two types: embryoidogenous (embryoids) and gemmorhizogenous (bud plus roots), but not just one gemmorhizogenous, as previously considered. In the formation of a new individual there are no two pathways of morphogenesis (embryogenesis and organogenesis, as previously considered), but three ones: embryogenesis, embryoidogenesis and organogenesis. These pathways and modes of formation of new individual are universal both in nature and in the experimental conditions (Batygina, 1984) (Fig. 1, 3). This allowed us to distinguish the phenomenon of embryoidogeny as a new category of vegetative propagation and to consider its role in the reproduction system of flowering plants. Long standing elaboration of theoretical basics of plant reproduction permits to establish the status and interaction of different types, modes and forms of seed and vegetative propagation, realization of each in a rather extent determines the reproductive strategy of the species (Fig. 1). The creation of new classification of types and modes of flowering plants reproduction and propagation considers being a result of this elaboration (Batygina 1987, 1989, 1990, 1991, 1992, 1993, 1994, 1996, 1997, 2000, 2005, 2006, 2009, Batygina & Vasilyeva 2002, Batygina *et al*. 1978).

Phenomenon of embryoidogeny and its role in integration of knowledge—Phenomenon of embryoidogeny, considered by us from viewpoint of theory and principles of reproduction, somatic and stem cells, is of a great biological significance, importance for scientific progress and applied implication (Batygina 1977–2014). This notion spans the diversity of mechanisms underlying various manifestations of asexual reproduction by mean of embryoids. It interferes with a lot of aspects of biology, and its detailed analysis can become a basis for further integration and synthesis of knowledge.

Embryoidogeny (Greek *embryon* – embryo, *oidos* – species, *genus* – origin) – a new phenomenon of vegetative propagation of flowering plants *in situ, in vivo* and *in vitro*, elementary structural unit of which is the embryoid.

Embryoid –an incipient organism asexually formed *in situ, in vivo* and *in vitro*. Embryoids develop exogenously or endogenously, usually from a somatic cell, rarely from an embryonic cell complex. The tendency to embryoid formation was observed in flowering plants of different taxa and ecological zones, at all stages of ontogenesis, starting with the zygote. They can arise in natural conditions on various structures and organs of plants.

The formation of a new own axis (relative to the maternal organism), connecting the shoot and root apices developing at opposite poles, is typical for the embryoid. As a rule, it has no common vascular system with the maternal plant, only a short-term relationship with it was noted. Genesis, the shape and size of the embryoid are taxon-specific. Embryoid inherits the main features established for sexual embryos: polarity, symmetry, cellular and histogenous differentiation, autonomy, etc. Both types of embryos are bipolar structures, the incipient new individuals (but not parts of individual, as in the case of bud). Their role in

2. **Creating of unified terminology** is a serious problem. The term "***embryogenesis***" has always been used to describe the process of formation of a sexual embryo as the result of *fertilization – heterophasic reproduction*. At the same time, the term "***somatic***" refers to the origin of the embryo *from somatic cells of different origins – homophasic reproduction*. Hence, using the term ***"somatic embryogenesis"*** in our view is not entirely correct. One must use the more correct term "***embryoidogenesis***", meaning **the process of formation of embryoid**, which is a structural unit of ***embryoidogeny*** *phenomenon,* a new category of vegetative propagation discovered by us in 1977.

reproduction system is also similar: they are the basic structural units of propagation.

The main difference between sexual embryo and embryoid is in their origin – biparental (with the participation of sexual process) and uniparental inheritance respectively. For a complete characterization of embryoids a comparison of their development with bud formation is also important. The similarity between the two is first of all in the asexual mode of formation (uniparental inheritance). In addition, both of them are the elementary structural units of vegetative propagation. The main difference is that the bud is a part of a whole organism, unipolar structure (it has only shoot apex and does not form cotyledons) which becomes bipolar during the process of development, when the root is formed.

Table 1—Comparative characteristics of embryo, embryoid and bud

Characteristics	Embryo	Embryoid	Bud
Presence of own axis and vascular system	Yes	Yes	No
Polarity	Bipolar	Bipolar	Unipolar
Degree of individuality	Incipient new organism	Incipient new organism	Part of maternal organism
Type of inheritance (origin)	Biparental	Uniparental	Uniparental

The notion "embryoidogeny" as a new category of vegetative propagation was proposed for the first time by T.B. Batygina (1977). The main thesis of the concept on embryoidogeny is in universality of morphogenesis of embryoids and sexual embryos produced in both natural and experimental conditions, i.e. in *in vitro* culture. While distinguishing it into a special type of reproduction, we used two criteria: ontogenetic (homophasic reproduction, uniparental inheritance) and morphological (bipolar organization of the structure with shoot and root apices and a polar axis).

Forms of embryoidogeny—Depending on the origin and position of embryoids on the maternal plant two main forms of embryoidogeny could be distinguished: floral (reproductive) – the formation of embryoids in the flower and seed, and vegetative organs.

The floral embryoidogeny includes, in turn, embryonic (monozygotic) produced by zygotic or somatic cells of the embryo, *ovular* – from cells of ovule integument and nucellus, and gametophytic – from cells of micro- and megaspores, male and female gametophyte.

Vegetative embryoidogeny includes foliar (on the leaf), cauligenous (on the stem) and rhizogenous (on the root).

Embryoidogeny plays an important role in the formation of a wide range of modes and types of reproduction and propagation of plants (Batygina 1999 a, b–2014).

Variety of reproduction modes based on different potencies of somatic cells, including those associated with formation of embryoids, weaves many threads into a symphony of real life.

The initial cells of embryoids in natural conditions and in *in vitro* culture—In different species of angiosperms the initial cells of monozygotic, nucellar, integumentary, foliar, cauligenous and rhizogenous embryoids are relatively uniform in morphology and structure. They have a number of features in common with rapidly dividing meristematic cells: small sizes, dense cytoplasm, large nucleus with a significantly increased nucleolus and many small vacuoles, and are characterized by high metabolic activity, intensive synthesis of RNA. Before the first division they usually acquire polarity (a vacuole forms, the nucleus is often located eccentrically).

In embryoids as in the sexual embryo initial cells are genetically determined, conform to the general laws of cell division, and their further development takes place in the system of the whole individual. This is likely provided normal formation of the embryoid, germs and plants in nature.

Embryoid formation in *in vitro* culture may follow the pathway of direct or indirect embryoidogenesis. The former is characteristic for the cells that have been determined before they were explanted; a trigger only needs, stimulating the process. The latter occurs in culture of cells capable for proliferation and callus formation.

Probably, the mature totipotent zygote (or, in case of parthenogenesis, forming egg cell), which passed the complicated pathway of morphogenetic transformations and able to proliferation, can be considered as homologue of initial cell of embryoid in natural condition and in *in vitro* culture. Zygote upon sexual reproduction functions as an initial cell of sexual embryo.

The repeatedly mentioned similarity of initial cells of embryoids at different forms of embryoidogeny with the zygote, which is the initial of sexual embryo, probably, allows to speak about the *homology of initial cells* in the different systems of reproduction in natural conditions and in *in vitro* culture.

Embryoidogeny and its biological significance— Theoretical data allowed to reveal the significance of embryoidogeny as the basis of such phenomena as cloning (being one of the mechanisms of reliability in plant organism), the phenomenon of polyembryony and genetic heterogeneity of seeds, the system of reliability (reserves, failures, apoptosis), embryoidogenous viviparity, the phenomenon of switching over morphogenetic developmental programs, species-specificity and possible repeat in their changes in ontophylogeny, the key mechanism of which is the somatic and stem cells. Short, energetically favourable pathway of the formation of numerous individuals with uniparental or biparental heredity, which increases the range of the species, is referred to the adaptive advantage of embryoidogeny.

Embryoidogeny and ecology—The capacity of the plant organism to form embryoids at all stages of development on different organs (vegetative and generative), at the same time maintaining the capacity for sexual reproduction, increases the flexibility and tolerance of reproductive systems. This extends the adaptive abilities of the organism, and also creates the preconditions for forming heterogeneous (age and genetic aspect) populations.

The ratio of types and modes of reproduction in a single life cycle is largely determined by environmental conditions. Diversity of modes, flexibility and tolerance of reproduction in one life cycle of flowering plants, of course, has an adaptive significance, ensuring survival of the species under normal conditions and stress.

Embryoidogeny and its applied aspects—Obtaining of seedlings free of viruses (e.g. citrus), haploids and genetically identical forms using embryoids (e.g. cereals).

Embryoidogeny and scientific progress—Disparate phenomena of reproduction: embryonic monozygotic, nucellar, integumentary and gametophytic embryoidogeny are combined by us for the first time into a united integrated system underlain by the common mechanisms (Fig. 1). Mechanisms of the most important

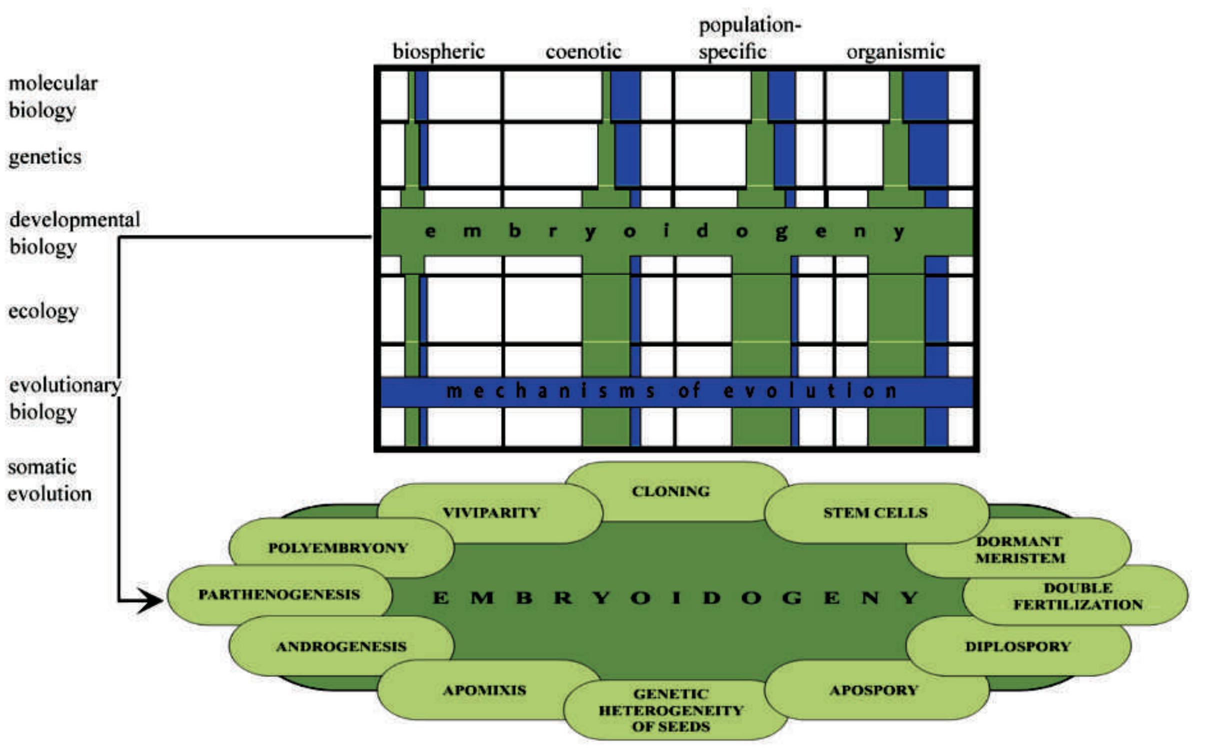

Fig.1— Embryoidogeny phenomenon defines various mechanisms of many associated phenomena (shown inside the ovals) and serves as a basis for cross-disciplinary synthesis of knowledge in the biology (Batygina & Notov orig.).

problem of developmental biology – the problem of organism integrity, the systems of reliability, reserves, failures and apoptosis were revealed; they occur at the basis of the following categories: the center of origin of the species, ethology, ecology, genetics (phenotype and genotype), epigenetics, duplicate structures (embryoids, sexual embryos, twins, brood buds, etc) (Batygina 2011, 2012, 2014, Batygina & Osadtchiy 2013).

In connection with considered significance of the embryoidogeny phenomenon for scientific progress we would like to discuss one extremely interesting problem, in which solving this phenomenon could play an important role, as we suppose.

Currently there are numerous evidences about wide distribution and diversity of manifestations of embryoidogeny phenomenon in plant kingdom (Batygina 1977-2014), and occurrence of similar phenomena in some taxa of animal organisms (Tokin 1959, Bryan 1968, Isaeva 2010). It is possible, that one should look for the prerequisites for manifestation of this phenomenon among some kind of fundamental properties of multicellular organisms' morphogenesis, which primary causes lie beyond the framework of biology and are determined by some physical processes underlying them.

In this connection it will be interesting to mention the work, where such relationship is considered in the aspect of views of the great litterateur and scientist of the 18th century Johann Wolfgang von Goethe (Barlow 2012). According to his opinion, in nature there exist some key, basic phenomena to which all other associated effects can be traced. Goethe proposed to refer them to as "Urphänomen", or "Primal Phenomenon", accrediting especial status to them. The Primal Phenomena are underlain by physico-chemical processes affecting non-organic matter, and they must be distinguished from class of secondary phenomena, which in case of biology embraces the events accompanying development and behaviour of living forms. The Primal Phenomena create conditions whereby the derived phenomena come into being (Don 1996).

Primal Phenomena are deeply embedded within morphogenetic processes which cause development of organic form. Processes such as free diffusion, reactiondiffusion systems, oscillations, gradients, and other purely physico-chemical features, are fundamental to morphogenesis of multicellular organisms. They are examples of Goethe's Primal Phenomena; because they are rely upon interactions between chemical molecules and local physical and geophysical forces. Further they "set in train" derived phenomena, such as polarity and positional information (Barlow 2012).

Into the sphere of Primal Phenomena the events could be placed that underlie and support the autoreproductive origination of cellular patterns. Auto-generative cellular patterning underlies the generation of new organs as well as the branching pattern of the whole plant body (Barlow & Lück 2007). A derived system of internal, hormonally-mediated correlations joins to the latter as the inevitable response from the organs in which branching and its derivative physiological systems have created.

We suppose that the embryoidogeny phenomenon in plants and similar phenomena in other multicellular organisms are also conditioned by morphogenous processes, which are derived from some basic physical phenomena or regularities falling within the scope of Primary Phenomenon notion and making determinative influence to the morphogenesis. It can become very interesting subject for further investigations of embryoidogeny phenomenon and its role in evolution of plant kingdom.

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