

Differentiation and specialization in the evolution of plants

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Summary: Differentiation (D) and specialization (S) are the key modes of structural evolution of plants. These changes occur on both the morphological and the anatomical level. The current article analyzes the occurrence of structures with various levels of D & S in different plant body organizations in certain taxa. The parallel nature of the main directions of D, which occurred independently on varying structural bases, is pointed out. The role of D processes in structural and taxonomic evolution was analyzed using bryophytes and angiosperms as examples. Dicotyledonous plants are clearly distinguishable from monocotyledonous plants by a wider distribution of specialized structures at the morphological and anatomical level. S of various structures in bryophyte species occurred in a less coordinated way. The level and specifics of structural D are important characteristics of taxon archetypes.

Keywords: evolution, plants, evolutionary morphology and anatomy, modes of structural evolution, differentiation, specialization, modular organization, archetype of taxon, algae, bryophytes, angiosperms

Differentiation (D) and specialization (S) are the main modes of structural evolution of living organisms (KHOKHRYAKOV 1974, 1975, 1981; AMADON 1943; ZMITROVICH 2006, 2010; TIMONIN 2007; IORDANSKY 2009; etc.). An extensive amount of literature is dedicated to studying these processes in plants. However, as a rule, most articles illustrate the directions of progressive transformations in separate structures or the anatomical and morphological structures of low-level ranks. An comprehensive analysis of D and S (D & S) in lower and higher plants is of immediate interest. It is vital for understanding how modular plant organization appeared and how its morphological and functional complexity increased (NOTOV 1999, 2011, 2016, 2017). A joint evaluation of process roles will help to gain a more detailed understanding of archetypes of systematic groups and evaluate the evolutionary specifics of taxa (LYUBARSKII 1996). This research will help implementation of S.V. MEYEN's (1975, 1990) ideas about a nomothetic theory of evolution and unconventional generalizations in biology. The goal of this article is to call attention to some approaches in analyzing D & S modes in plants.

Materials and methods

Most plants are modular organisms (NOTOV 1999, 2011). Establishment of this type of organization is connected with D of growth processes that ensure modular structure (NOTOV 2017). D & S of modules appeared multiple times in the course of progressive evolution (KHOKHRYAKOV 1974, 1975; NOTOV 2016). It led to a significant increase in the complexity of the external body structure and to the formation of a multi-level hierarchical system of structural units (GATSUK 2008). D & S of the internal structural elements were primarily aimed at connecting parts of the organism and increasing its integrity. When conducting a comprehensive analysis of D & S processes in plants it is important to understand the ways and means of progressive sophistication of the system of structural biological units in various structural body organization types. Consequently, this

article considers materials concerning the levels of morphological D of algae and higher plant bodies (GOLLERBAKH 1977; KAMNEV 1989; KHAYLOV et al. 1992; MASYUK 1993; DUMAIS & HARRISON 2000; BELYAKOVA et al. 2006; ZMITROVICH 2006; PRAZUKIN 2010; MATTIO & PAYRI 2011; LELIAERT et al. 2012; UMEN 2014; PEAUCELLE & COUDER 2016; AOUISSI et al. 2017; etc.). Special attention is given to variations of modular body organizations in different types of structural organization (siphonous, siphonocladous, filament, plectenhyous, parenchymatous, tissue thalli, telomes, shoots) (see Table 1).

Flowering plants have achieved the maximum level of structural D & S. To understand the evolutionary role of D processes, we investigated the distribution of structures with various levels of D & S in dicotyledons and monocotyledons – Magnoliopsida and Liliopsida species (KHOKHRYAKOV 1981; TAKHTAJAN 1997; etc.). Mosses and liverworts – the most substantial groups of bryophytes – were studied as an alternative model group and represent the gametophyte line of evolution (SHLYAKOV 1975; IGNATOV & IGNATOVA 2003; POTEKIN 2007; RYKOVSKY 2014). They are now considered as phyla – Bryophyta and Marchantiophyta (IGNATOV & IGNATOVA 2003; POTEKIN 2007; etc.). In bryophytes, we also analyzed groups that are distinguished by the specifics of archegonium placement. Among them, there are acrocarpous and pleurocarpous mosses (Bryopsida class, Acrocarpae and Pleurocarpae groups), acrogynous and anacrogynous liverworts (Jungermanniopsida class, Acrogynae and Anacrogynae groups) (Table 2). The prevalence of structures with different levels of D & S has been evaluated. The pattern of propagation of structures with the most complex structures and maximum level of D has been explored. All together, these characteristics permit the evaluation of the fullness of realization of D & S modes in the structural evolution of the investigated groups.

Results & Discussion

Main directions of structural D & S in plants

When analyzing the main directions of D & S, it is necessary to take into account the specifics of modular organization of plants. All morphologically separate ‘organs’ of plants are ‘external’ (TIMONIN 2007). They are fundamentally different from the internal organs of animals, and to some extent tissue systems that permeate the whole body in plants correspond with them (SHAFRANOVA 1990). The paths of morphological and anatomical D of plants are strategically multidirectional and to some extent independent. Morphology ‘provides’ the functional activity and efficiency of interaction with the environment, while anatomy provides the integrity of the plant organism. There are two main directions of morphological D. The first direction is associated with the separation of two subsystems (body parts) that interact with various components of the external environment (solid and gaseous or liquid media). D into axial and appendicular elements was achieved within the second direction. At the anatomical level, the formation and progressive complication of the transport and shaping subsystems was of key importance. Secondary meristems along with the ability for secondary thickening and intercalary growth appeared because of D of the shaping subsystem (SHAFRANOVA 1981; TIMONIN 2007).

The main directions of D of the external structure of the body happened independently in different taxa on different structural bases (Table 1). Specialization of axial and appendicular structures, as well as the structures that interact with the substrate, happened on the basis of siphon cells of plectenhyous and parenchymatous thalli, tissue thalli, telomes and shoots in

Table 1. Levels of D of modular structures in plants with different structural organization. Main structural and functional subsystems of the organism: St – interacting with solid substrate (rhizoids, fixation holdfast, roots); Fs – connected to photosynthesis. Their level of D is marked numerically: 0 – morphological D is non-existent; 1 – elements are equal or there is a tendency for D; 2 – elements are different, Fs is differentiated into axial structures (axis, stems) and appendicular structures (assimilating lamina and blades, leaves, specialized (often phyllo-morphic) systems of axes (branches)); 3 – complicated hierarchical D of elements and their combinations. – D with pseudocyclic integration ('assembly' of complex structures, which are outwardly similar to the original morphological units (see NOTOV 2016)). The table represents the most widely occurring types of St and Fs combinations.

Type of structural organization	Level of structural differentiation									
	St ₀ Fs ₀	St ₀ Fs ₁	St ₁ Fs ₁	St ₁ Fs ₂	St ₁ Fs ₃	St ₁₋₂ Fs' ₃	St ₂ Fs ₂	St ₂ Fs ₃	St ₃ Fs ₃	St ₃ Fs' ₃
Thalli siphonous	+	+	+	+	+	+	+	+		
• siphonocladous	+	+	+	+	+	+	+	+		
• filamentous	+	+	+	+	+	+	+	+		
• parenchymatous	+	+	+	+	+		+	+	+	
• pseudoparenchymatous	+	+	+	+	+	+	+	+		
• tissue		+	+	+	+	+				
Telomes		+	+	+	+	+				
Shoots				+	+	+	+	+	+	+

different groups of cladophytes and telophytes (GOLLERBAKH 1977; MASYUK 1993; ZMITROVICH 2006; NOTOV 2016; etc.). The tendency for D of the apical meristem appeared in all these series (SHAFRANOVA 1981). However, only higher plants achieved the main stages of complication in tissue organization, especially in the transport subsystem (TIMONIN 2007).

In different types of morphological and anatomical organization (including the siphonous, parenchymatous, and pseudoparenchymatous types), D in axial and appendicular elements led to the emergence of shoot-like structures as well as hierarchically differentiated and elaborately branched systems. Shoot-like structures can be found in various classes and phyla of algae (HAECKEL 1904; GOLLERBAKH 1977; KAMNEV 1989; MASYUK 1993; MATTIO & PAYRI 2011; PEAUCELLE & COUDER 2016; AOUISSI et al. 2017; etc.). They look quite similar to shoots of higher plants on the outside and can be found in some species of *Caulerpa* Lamour., *Cystoseira* Ag., *Delesseria* Lamour., *Tokidadendron* M.J. Wynne, *Macrocystis* C. Agardh, *Sargassum* Ag., etc.). Quite often, these structures are called 'branches', 'leaves', 'leaf' (TIMONIN 2007; MATTIO & PAYRI 2011; PEAUCELLE & COUDER 2016; AOUISSI et al. 2017). In brown and red algae, these 'leaves' may have veins and multiple layers. Some *Sargassum* species have spiral patterning in the shoot apex and phyllotaxis similar to that of higher plants (PEAUCELLE & COUDER 2016; LINARDIC & BRAYBROOK 2017).

Functional organization of complexly differentiated thallomes (KHAYLOV et al. 1992; PRAZUKIN 2010; etc.) and specifics of branching (SHAFRANOVA 1981; PEAUCELLE & COUDER 2016; LINARDIC & BRAYBROOK 2017) of some algae has been studied. Unfortunately, the diversity of architectural models has not yet been researched. The available illustrative material allows us to assume that there are algorithms of D in axial structures similar to those of architectural models of trees (HALLE et al. 1978). Such analogies of models have been found in corals (DAUGET 1991).

Due to the wide parallelism, a detailed analysis of the evolution of morphological and functional subsystems in algae and higher plants using the described approach can help assessment of the conjugation of the key morphological and anatomical transformations.

Such an analysis is also important for understanding the mechanisms of how multicellular structures are formed in plants. It appears that multicellularity in plants developed several times and in different ways (NIKLAS et al. 2013; NIKLAS 2014, 2016; NOTOV 2017).

Structural D & S in some taxa of higher plants

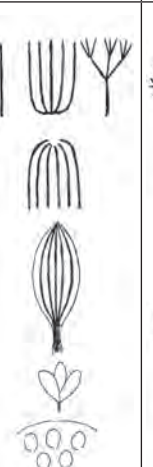
Flowering plants. In dicotyledonous and monocotyledonous plants the differences in the relative roles of D & S modes became quite evident at the morphological and anatomical levels. Various versions of higher D & S in dicotyledons are found in body architecture, in the structure of the main organs and elements and in anatomical organization (Table 2).

Dicotyledons have clear hierarchical D of roots in root systems and S of veins in the vascular systems of leaves. Leaves with stipules and flowers with double perianths are common. Secondary meristems (cambium and phellogen) are present. Arboraceous dicotyledonous plants are characterized by the significant diversity of architectural models with complicated hierarchical D of axes in the canopy. For example, it is typical for models of Rauh, Attims, Stone, Aubrevill and Scarrone (see HALLE et al. 1978). Inflorescences with floral elements of high level pseudocyclic aggregation are noted specifically among dicotyledonous plants. For example, inflorescences that are consistent with the third and fourth level of pseudocyclic rank have been described in some umbellates, legumes and composites (KUZNETSOVA 1986; NOTOV 2016; KUZNETZOVA & TIMONIN 2017).

Morphogenetic programs of monocotyledonous flowering plants do not allow a complicated hierarchical D of structures and elements of various levels. Roots in root systems and leaf veins are equivalent and equal. As a rule, stipules are inconspicuous; flowers with a double perianth are rare (Table 2). A relatively lower level of anatomical differentiation of axial organs can be noted as well as the lack of specialized lateral secondary meristems. Single-axis architectural models (Holttum) and models with equivalent axes (Tomlinson, Chamberlain, less often Leeuwenberg, Schoute) are typical of arboraceous monocotyledons (HALLE et al. 1978). Models with heterogenic skeletal axes are very rare (for example, in Pandanaceae). At the same time, the amount of superordinate ranks of axes is insignificant. Isomodular construction prevails in annual monocotyledons, and it also doesn't allow axis differentiation (MARKOV 1990).

Bryophytes. Structures with higher levels of D & S are less consistently distributed in large taxa of bryophytes than in flowering plants classes. Different types of D & S of structures in mosses (Bryophyta) are more full-fledged than in liverworts (Marchantiophyta) (Table 2). Bryophyta are more specialized on many levels than Marchantiophyta. Moss bodies always have a shoot-like structure and multicellular rhizoids are typical (SHLYAKOV 1975; POTEKIN 2007; RYKOVSKY 2014). Only mosses have conductive tissue with hydroids and leptoids as well as mechanical tissue from stereides. Some groups have been noted for having gametophytes with conductive tissues in the stem and leaves, which make up an integrated conductive system. The capsule of the sporogonium in mosses often has a rather complex anatomy. Stomata may be found in the epidermis. As a rule, a columella evolves inside the capsule. For green mosses (Bryopsida), a structurally complex peristome is typical. Their protonemata are usually well-developed. Filamentous protonemata are widely distributed (SHLYAKOV 1975; POTEKIN 2007).

Table 2. Distribution pattern of structures with various levels of D & S in some groups of higher plants: * – indicates D, S and hierarchy of structural elements that are in opposition to their equivalence and equality (see text for explanation).

MAGNOLIOPHYTA		BRYOPHYTA		MARCHANTIOPHYTA		
Magnoliopsida	Liliopsida	Bryopsida		Jungermanniopsida		Marchantiopsida
		Pleurocarpae	Acrocarpae	Acrogynae	Anacrogynae	
						

Liverworts (Marchantiophyta) have forms with thalloid and shoot-like structures. In some groups, there are only thalloid forms. There are no exemplars with conductive or mechanical tissues. Rhizoids are always unicellular. Sporogonia have a simpler structure. Tissue in the walls of the capsule are not differentiated, there is no columella (SHLYAKOV 1975; POTEKIN 2007; RYKOVSKY 2014). There are no structures within the capsule that ensure that spores are distributed in batches.

Groups differing by the location of archegonia are often distinguished in Bryopsida and Jungermanniopsida. The archegonia in Bryopsida may be located on the top of the main or equal to the main axis (Acrocarpae) or at the apex of specialized branches of the second, third or higher branching rank (Pleurocarpae). These locations are connected to D of axes in the shoot system. In Jungermanniopsida, the archegonia in some cases also do not prohibit the further growth of the axis (Anacrogynae) and in other cases the axis ceases to grow (Acrogynae). These qualities are also connected to various levels of D of body axes and correlated to the distribution of structures with different levels of D & S. Clear D of shoots in terms of growth and functions is typical for Pleurocarpae (Table 2). Leaves on axis of various rank are often different in size and structure. Complexly branched shoot systems are often formed. Architectural models of Pleurocarpae may be similar to some models of arboraceous plants (NOTOV 2011). Perichaetial leaves of Pleurocarpae are often specialized more than in Acrocarpae. D & S in shoots of Pleurocarpae are usually connected to the formation of S of lateral structures (paraphyllia, pseudoparaphyllia) and the ability to form rhizoids at leaf bases (Table 2) (IGNATOV & IGNATOVA 2003). However, features of many Pleurocarpae go together with a relatively low level of anatomical D.

There is no D of shoots and leaves in Acrocarpae D (Table 2). However, anatomy is more diverse in this group. There are different types of D & S of stem and leaf cells. Many Acrocarpae have prosenchymatous leaf cells and the midrib is developed better (IGNATOV & IGNATOVA 2003). Clear

D & S of conductive tissue is noted only in Acrocarpae. Polytrichaceae have assimilatory lamina in leaves and midribs with hydroids, leptoids and stereides. Leaves with assimilatory lamina are found in Pottiaceae. Leaves in Fissidentaceae have a rather complex morphological structure.

Some similar tendencies occur in Jungermanniopsida. 'Acrogynaety' is connected to functional D of axes. Acrogynae have a higher level of morphological D of the body in general. Shoot structure with a clear D of axes is typical of them, as well as the diversity in type of branching, leaves and structures that protect gametangia (SHLYAKOV 1975; POTEKIN 2007; RYKOVSKY 2014). S of leaves resulted in the appearance of perianthium with various structures. Due to S of one of the leaf's lobes, structures that maintain moisture were formed. There are dissected leaves (Table 2). 'Anacrogynaety' assumes the lack of functional D of axes and is connected to a lower level of morphological S. The body has a thalloid structure. Protective structures are less diverse.

Different levels of gametophyte D & S are typical of Anacrogynae and Marchantiopsida, which also have thalloid structure. They have differentiated gametophores of various morphological nature. In some cases, the gametophore has developed assimilative, main and protective tissues (SHLYAKOV 1975; POTEKIN 2007; RYKOVSKY 2014). Assimilative tissues may have a complicated structure. D of rhizoids into simple and ligulate is typical. Protective structures are diverse. Compared to Marchantiopsida, the thallomes of Jungermanniopsida have simpler morphological and anatomical structure: there are no gametophores or assimilative tissues; only simple rhizoids are formed (Table 2).

The evaluation of the role of D & S processes in the evolution of flowering and bryophytic plants allow to uncover certain conjoined tendencies in the development and structure of elements of various levels. In some cases, they correlate with the general algorithm of the development program and level of complexity of the body structure. This includes the hierarchy level of D of shoot systems and thallome axes. These connections between features make a significant addition to the archetypes of investigated taxa. A similar analysis in taxa of lower and higher plants of high rank is of current interest.

Conclusion

D & S were the main modes of structural evolution of plants. They played a key part in the formation and progressive development of modular organization and in the sophistication of external and internal structure. Significant parallels in the main directions of D in lower and higher plants have been revealed. Similar processes of S and hierarchical sophistication of structural elements were carried out on the basis of siphonous cells as well as filamentous, parenchymatous, plectenchymatous and tissue thalli, telomes and shoots. A special investigation of the main alternatives of growth processes in different groups of algae is of current interest. An analysis of their structural diversity from the point of view of the architectural model framework would be appropriate.

The role of D in structural and taxonomical evolution has been analyzed using bryophytes and flowering plants as examples. Dicotyledonous plants are clearly distinguished from monocotyledonous plants by a wider distribution of specialized structures at the morphological and anatomical level. In classes of bryophytes, D & S of various structures occurred in a less organized way. For a number of reasons, Bryophyta are characterized by a higher relative level of specialization than Marchantiophyta. Thallomes in Marchantiopsida are morphologically

and anatomically more differentiated than in Jungermanniopsida (Anacrogynae). Bryophytes have been observed to have structural particularities of various levels, which are connected to the characteristics of growth processes and the level of D of the external body structure. The analysis of modes of D & S allows to construct archetypes of systematic groups and evaluate the evolutionary specifics of taxa. When studying other plant taxa it is reasonable to search for structure particularities that correlate to the complexity level and hierarchy of shoot systems or thalloid axes.

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